

THE DEPTH DISTRIBUTION OF SOIL ORGANIC CARBON IN RELATION TO
LAND USE AND MANAGEMENT AND THE POTENTIAL OF CARBON
SEQUESTRATION IN SUBSOIL HORIZONS

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Abstract

Routine soil surveys for estimating the soil organic carbon (SOC) pool account for a soil depth of about 1 m. Deeper soil horizons, however, may have a high capacity to sequester significant amounts of SOC as the turnover time and chemical recalcitrance of soil organic matter (SOM) increases with depth. The subsoil carbon (C) sequestration may be achieved by higher inputs of fairly stable organic matter to deeper soil horizons. This can be achieved directly by selecting plants/cultivars with deeper and thicker root systems that are high in chemical recalcitrant compounds like suberin. Furthermore recalcitrant compounds could be a target for plant breeding/biotechnology to promote C sequestration. A high surface input of organic matter favors the production of dissolved organic carbon that can be transported to deeper soil horizons and thus contribute to the subsoil C storage. By promoting the activity of the soil fauna organic matter can be transferred to deeper soil layers and stabilized (*e.g.*, in earthworm casts). Manipulating the subsoil microorganisms may result in higher amounts of fairly stable aliphatic compounds. The subsoil below 1-m depth may have the potential to sequester between 760 and 1520 Pg C. These estimates are, however, highly uncertain and more studies on C storage in subsoil horizons and the assessment of the chemical nature of subsoil organic C are needed.

I. INTRODUCTION

Soils are the largest terrestrial pool for organic carbon in the biosphere. Large-scale changes in land use like deforestation and agricultural activities, including biomass burning, plowing, drainage, and low-input farming have resulted in significant changes in soil organic carbon (SOC) pools (Lal, 2003). By mineralization, leaching, erosion, or change in land use, 50 to 70% of the antecedent SOC is lost as CO₂. Thus, world soils historically have been a major source of atmospheric enrichment of CO₂, although uncertainties in the statistics exist. About 20% of the global emissions presently come from land use change (IPCC, 2001).

Information on global and regional SOC pool is available (*e.g.*, Eswaran *et al.*, 1993; Batjes, 1996). However, data on vertical distribution of the SOC pool in relation to vegetation and land use is scanty (Jobbágy and Jackson, 2000). It is widely accepted that soil organic matter (SOM) is largely concentrated in the top 30 cm of the soil, but there is a growing evidence that deeper soil horizons have the capacity to sequester high amounts of SOC despite the concentrations in the subsoil (Liski and Westman, 1995; Richter and Markewitz, 1995; Jobbágy and Jackson, 2000; Swift, 2001). One reason for the uncertainty is that the usual fixed depth of about 1 m is generally considered adequate in routine soil surveys. That being the case, the magnitude of underestimation of the global SOC budget remains to be speculative.

Land use changes, however, may affect the SOC storage in deeper soil horizons. For example, by comparing data from 74 publications, Guo and Gifford (2002) observed that conversions of forest land to pasture or crop land had no effect on SOC stocks below 1

and 0.6-m depth, respectively. In contrast, conversion of crop land to pasture caused substantial C accumulation below 1-m depth. However, conclusions on the effects of land use changes on soil C stocks are hampered by the small global database. For example, among 78 studies on the effects of conversion from forest to agricultural land only 2 studies reported stores below 1-m soil depth (Murty *et al.*, 2002).

Information is also scanty about the contribution of above-ground vs. below-ground residues to the amount of C sequestered in the subsoil (Follett, 2001). The knowledge of SOC distributions and the controls on C sequestration within soil profiles are used to predict the effects of land use changes on the C emission (Jobbágy and Jackson, 2000). The importance of SOC sequestration in subsoils mitigating the greenhouse effect is related to the increase in turnover time of SOM with increases in depth, and to the fact that subsoil SOC occurs in fairly stable and most probably highly recalcitrant forms to biodegradation (Batjes, 1996; Kögel-Knabner, 2000; Nierop and Verstraten, 2003).

This review article collates and synthesizes the available literature on the vertical distribution of SOC in relation to principal C sources, describes changes in quality and quantity of C with soil depth, and discusses differences in SOC pool in relation to land use. The focus is not on collecting the information on the stabilization of SOC in subsoil horizons by physical protection through aggregate formation (Six *et al.*, 2004) but to review the literature on the chemical recalcitrance as the only mechanism by which SOC can be protected over long periods of time (Krull *et al.*, 2003). Potential strategies to enhance the subsoil C sequestration by management practices are also discussed.

II. SOURCES AND DYNAMICS OF SOIL ORGANIC CARBON WITHIN SOIL PROFILES

A. PLANT LITTER AS THE PRINCIPAL SOURCE OF SOIL ORGANIC MATTER FORMATION

Plant litter is the primary source of SOC formation while microbial residues are secondary sources (Kögel-Knabner, 2002; Krull *et al.*, 2003). The relative contribution of animal residues as precursor of humus in soil is rather small (Wolters, 2000). Plant litter consists of intracellular and storage materials and cell wall components. Refractory plant derived biomacromolecules that are relatively resistant to biodegradation and selectively concentrated in SOM are extremely important to the potential of C sequestration by management (Figure I; Derenne and Largeau, 2001). In general, leafy plants decompose faster than woody, and leaves faster than roots (Wang *et al.*, 2004).

(Figure I)

Proteins are abundant in plant cells and probably less stable in the soil, but peptide type compounds are stabilized in SOM over long periods (Knicker *et al.*, 1993). The most abundant plant biopolymer is cellulose which decomposes slowly aerobically but is relatively enriched under anaerobic conditions (Martin and Haider, 1986; De Leeuw and Largeau, 1993). In contrast, higher decomposition rates are observed for the non-cellulosic polysaccharides, hemicelluloses and pectin (Swift *et al.*, 1979). The second

most abundant biopolymers are lignins which are largely contributing to terrestrial biomass residues. These compounds exhibit a higher resistance to microbial degradation compared to celluloses, and are virtually resistant under anaerobic conditions (Haider, 1992). Tannins are also abundant constituents of terrestrial plants, and the proanthocyanidins are important potential sources of refractory material in soils and contribute to the formation of humic substances (Derenne and Largeau, 2001). Important components of soil lipids which represent a relatively stable C pool are already found in plant lipids (Kögel-Knabner, 2002). The fate of decomposition products from chlorophyll and other pigments and their relevance to humus formation is largely unknown. The non-hydrolyzable cutans and suberans are also common components of higher plants (Bernards, 2002; Heredia, 2003). Their preservation in soils and contribution to the recalcitrant aliphatic fraction of SOM is, however, debatable (Augris *et al.*, 1998). Suberin is mostly found in root tissues but also in aboveground parts of woody tissues and is a major contributor to the SOM (Bull *et al.*, 2000; Nierop *et al.*, 2003). Data on the contribution of recalcitrant biomacromolecules to plant residues are highly variable as conventional methods are generally not specific enough (Rahn *et al.*, 1999; Kögel-Knabner, 2002). In general, forest litter is higher in lignin due to woody tissues while crop residues are higher in polysaccharides (cellulose and hemicellulose; Table I). Only 50-60% of the total organic C in plant litter is accounted for by chemical degradative techniques.

(Table I)

The composition of plant materials can be deduced from solid-state ^{13}C NMR spectra and molecular level information from analytical pyrolysis or (thermo)chemolysis (Kögel-Knabner, 2002). The solid-state ^{13}C NMR spectra of aboveground beech (*Fagus sylvatica* L.) litter is dominated by signals from polysaccharides (cellulose and hemicelluloses) and lignin, and alkyl C from lipids and cutins. The ^{13}C NMR spectra of straw from wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.) and rye (*Secale cereale* L.) as well as hay are all dominated by polysaccharides while aromatic C, essentially lignin, and alkyl-C (lipids, cutins, peptides) are lower than in forest litter (Fründ and Lüdemann, 1989; Rowell *et al.*, 2001). The main components of corn (*Zea mays* L.) leaves are polysaccharides, lignin, lipids and alkyl-aromatics (Gregorich *et al.*, 1996; Poirer *et al.*, 2003).

Carbon-13 CP/MAS NMR spectroscopy indicates that oilseed rape (*Brassica napus* L.) shoots and roots contain comparable high amounts of cellulose and hemicellulose C (Trinsoutrot *et al.*, 2001). Signals from lipids and cutin, and essentially from peptides are prominent in the spectrum of ryegrass (*Lolium perenne*) leaves (Kögel-Knabner, 2002). The ^{13}C NMR spectra indicate that polysaccharides and aromatic components dominate in the roots of beech (Table I). Corn roots contain a wide range of fatty acids beside carbohydrates, lignin, lipids and alkyl-aromatics (Gregorich *et al.*, 1996). Oilseed rape roots are higher in aromatic and phenolic C compared to shoots (Trinsoutrot *et al.*, 2001). Wheat roots are higher in aryl and O-aryl C (mainly from lignin and polyphenols) but lower in alkyl C than wheat straw (Wang *et al.*, 2004). The NMR spectra indicate that the roots of grasses are high in polysaccharides and low in lignin and suberins. Little information exists on the composition of aliphatic biopolymers like cutin and suberin

from agricultural crops. Furthermore the composition of the components of different plant parts may be variable (Nierop *et al.*, 2001)

B. DIFFERENCES BETWEEN ABOVE- AND BELOW-GROUND PLANT RESIDUES

The composition of the above-ground C input may be substantially different to the below-ground input (Kögel-Knabner, 2002; Rasse *et al.*, 2004). The above-ground input in forests consists mainly of leaf and needle litter but branches, bark and fruits also contribute to the litterfall. In addition, woody debris is an important component of the OM input in natural forests whereas herbaceous litterfall is of minor importance in forests. There is relatively less information available on the above-ground C input for arable and grassland ecosystems. However, C inputs depend on the amount and type of crop residues and fertilizer application, and are much higher if the crop residues are returned to the soil.

The below-ground C input as root litter and rhizodeposition considerably contributes to SOM (Fernandes *et al.*, 1997). Roots contribute more C to SOM than aboveground residue (Wilhelm *et al.*, 2004). Annual C inputs from fine roots frequently equal or exceed those from leaves (Jackson *et al.*, 1997). This can occur to great depths and transfers C deep into subsoil horizons with a global average maximum rooting depth of 4.6 m (Nepstadt *et al.*, 1994; Trumbore *et al.*, 1995; Canadell *et al.*, 1996). While tundra, boreal forests, and temperate grasslands have 80-90% of their roots in the upper 30 cm,

deserts and temperate coniferous forests have only 50% of their roots up to this depth (Jackson *et al.*, 1996).

The organic C released by living roots (i.e., the rhizodeposition) accounts for a substantial input of OM in soils. Rhizodeposition can lead to C accumulation or consumption by altering the decomposition rate of SOM (Kuzyakov *et al.*, 2000; Kuzyakov, 2002). Pastures have a higher below-ground allocation compared to wheat due to a longer vegetation period (Kuzyakov and Domanski, 2000). Rhizodeposition by corn is reportedly 3 times greater than suggested previously (Allmaras *et al.*, 2004). For the amount of rhizodeposition under forests, only limited data are available and no generalization can be made.

With respect to C sequestration in the subsoil the lower biodegradability of plant roots and the root-to-shoot ratios of different vegetation types are highly relevant. The lower degradability of roots can be attributed to their higher lignin content compared to shoots as lignin is supposed to be chemically recalcitrant (Tegelaar *et al.*, 1989; Table II).

Beside lignin, higher tannin contents and less readily decomposable compounds in roots compared to shoots probably contribute to the lower decomposition rate of roots (Waid, 1974; Beuch *et al.*, 2000; Kraus *et al.*, 2003). However, these data may not be reliable due to analytical uncertainties (*e.g.*, Preston *et al.*, 1997). Furthermore the relative decomposition rates between the above- and below-ground parts may differ with the plant species (Wang *et al.*, 2004). More than half of all SOM still remains uncharacterized at the molecular level (Hedges *et al.*, 2000). The available data on root:shoot ratios of different vegetation types and plant species are also highly variable (Table III). Under

similar climatic conditions, grassland and steppe soils generally receive a higher proportion of total C input as root litter compared to forest and cropland.

(Table II)

(Table III)

C. SPECIFIC MICROBIAL PRECURSORS OF SOIL ORGANIC MATTER

Major recalcitrant biomacromolecules as precursors of SOM formation may also be derived from the microbial biomass (Hedges *et al.*, 2000). The fungal cell wall contains the highly crystalline, non-water soluble polysaccharides chitin and β -glucan (Kögel-Knabner, 2002). Fungi also synthesize lipids and melanins although to a minor extent. The non-hydrolyzable melanins protect fungal cells against microbial attack and are possible precursors of humic substances (Saiz-Jimenez, 1996; Butler and Day, 1998). The arbuscular mycorrhiza occurs in about 80% of plant species (Strack *et al.*, 2003).

Arbuscular mycorrhizal hyphae contain significant amounts of the iron-containing glycoproteinaceous substance glomalin that may contribute to the recalcitrant soil C fraction (Treseder and Allen, 2000; Rillig *et al.*, 2003). The ectomycorrhiza in woody trees receive most of the C allocated to the belowground biomass whereas the roots mainly serve as a transport tissue for carbohydrates (Steinmann *et al.*, 2004).

Bacterial cell wall polysaccharides are relatively easily decomposed but their basic units glucosamine, galactosamine or muramic acid are found in hydrolysis residues of soils and

accumulate during litter decomposition (Stevenson, 1994; Coelho *et al.*, 1997). Bacterans are insoluble, non-hydrolyzable aliphatic biomacromolecules present in substantial amounts in bacteria. They have a high potential to accumulate in soils and are potential precursors for aliphatic components of SOM (Augris *et al.*, 1998). The few published analyses of the microbial biomass using ^{13}C NMR spectroscopy indicate that bacterial biomass differs distinctly from fungal biomass as fungi are higher in O-alkyl and lower in alkyl C (Baldock *et al.*, 1990).

D. THE STABILIZATION OF PLANT DERIVED COMPOUNDS AND SOIL ORGANIC MATTER

Several stabilization mechanisms are responsible for protection of plant residues and their decomposition products in the soil against microbial attack, and facilitate accumulation of humic substances (Sollins *et al.*, 1996). Biochemical stabilization is promoted by the complex chemical composition of the organic matter (Cadisch and Giller, 1997). The chemical recalcitrance can either be an inherent property of the plant litter (e.g., due to recalcitrant compounds like lignin, tannin, cutin, suberin) or can be attained through condensation and complexation reactions during decomposition resulting in the accumulation of stable aromatic and long chain aliphatic compounds (Paul *et al.*, 1997). The physicochemical stabilization is the result of chemical or physicochemical binding between plant litter compounds and SOM, and soil minerals such as clay and silt particles (Six *et al.*, 2002). The glycoprotein glomalin produced mainly by hyphae of arbuscular mycorrhizal fungi might also be involved in stabilization of aggregates (Wright and

Upadhyaya, 1998; Rillig *et al.*, 1999). The type of clay probably also plays an important role as for example 1:1 and 2:1 clays have substantial differences in CEC and specific surface tentatively resulting in different adsorption capacities for organic materials. The Fe- and Al-oxides have contrasting effects on the physicochemical stabilization as they can reduce the available soil mineral surface for adsorption of SOM but also co-flocculate SOM and consequently stabilize it (Wiseman and Püttmann, 2005). The availability of organic C for microbial decomposition is reduced by inclusion of OM within soil aggregates (Golchin *et al.*, 1994). Physical protection by aggregates is a consequence of the separation between microbes and enzymes and their substrates (*i.e.*, organic matter) as is indicated by the positive influence of aggregation on SOM accumulation (Six *et al.*, 2002).

E. TRANSLOCATION OF ORGANIC MATTER TO SUBSOIL HORIZONS

In the course of the decomposition of plant material watersoluble intermediates are released into the soil solution where they present a major portion of the dissolved organic matter (DOM) beside compounds released by microorganisms (Guggenberger *et al.*, 1994). Another major source of water-soluble C is humus (Gregorich *et al.*, 2003). Contradictory to the widespread assumption, Kalbitz *et al.* (2003) found no evidence that DOM represents the most biodegradable pool of SOM. The DOM is transported in soil profiles and with increasing depth strongly adsorbed to mineral surfaces resulting in reduced decomposition of organic C (Baldock and Smernik, 2000; Kaiser and Guggenberger, 2000; Kalbitz *et al.*, 2000). Sorption to the mineral phase in subsoils may

be more effective than in topsoils because mineral surfaces are not yet saturated with OM (Rasse *et al.*, 2004). In forest mineral soils DOM can contribute to stable C due to high DOM fluxes and a mean residence time up to 12.5 years (Kalbitz *et al.*, 2003).

The soil fauna (*i.e.*, earthworms, ants and termites) are capable to dig burrows several meters deep into the soil (Benckiser, 1997; Wolters, 2000). While the importance of earthworms in soil systems has long been recognized, little quantitative information is available about the role of termites (Lee and Foster, 1991). Qualitatively polysaccharides are lost preferentially and lignin accumulated in wood-feeding termites, and some evidence for polysaccharide loss in soil-feeding termites is indicated (Hopkins *et al.*, 1998). Within earthworm burrows formed by anecic species significant amounts of OM are translocated to the subsoil by covering the inner surface of the burrows with middens which are accumulations of raw and decomposed plant residues, casts and soil (Nielsen and Hole, 1964). The casts are a product of the digestion of organic substrates with soil minerals in their gut (Shipitalo *et al.*, 1994; Shuster *et al.*, 2001). The organic C in these casts is mainly physically stabilized and earthworms may alter the size and dynamics of the microaggregate-protected SOM pool (Lavelle, 1988; Guggenberger *et al.*, 1996; Binet and LeBayon, 1999; Whalen *et al.*, 2004). The stability of earthworm casts is high especially in the subsoil (Ge *et al.*, 2001). In regions of high animal activity recalcitrant SOM is enriched, at least temporarily (Wolters, 2000). Earthworms produce a more even distribution of OM in the soil profile. However, what proportion of earthworm casts are deposited in the soil profile under field conditions is not known (Whalen *et al.*, 2004). Endogeic earthworm species which live in mineral soil horizons are considered major agents of aggregation and SOM stabilization (Lavelle and Spain, 2001). Earthworm

activity may be of great significance for the long-term stabilization of SOM (Bossuyt *et al.*, 2004).

III. DEPTH DISTRIBUTION OF SOIL ORGANIC CARBON AND ROOTS

The storage of SOC in the soil depends on the balance between additions and losses of C (Sollins *et al.*, 1996). Biotic controls like the abundance of faunal, microbial and plant species, and environmental controls like temperature, moisture and soil texture influence stabilization and destabilization processes of SOC. The C storage varies mainly as a result of climatic, geological and soil-forming factors in the long-term, whereas vegetation and changes in land use patterns affect storage in the short-term (Batjes, 1996). Global estimates of the SOC pool to 2-m soil depth in tropical regions were lower than for soils from all other regions. The highest SOC concentrations were observed in the upper soil layers but large amounts are also stored between 1 and 2-m depth (Batjes, 1996). Any disturbance and relocation of SOC is, therefore, fundamental to the global C balance (Moiser, 1998). The knowledge of the key factors determining long term SOC storage, however, is still limited (Neff *et al.*, 2002).

The SOC pool and its dynamics with regards to climate and texture with soil depth are not understood (Jobbágy and Jackson, 2000). Without additions of external C, the radiocarbon age of the OM reflects the mean residence time and thus the radiocarbon age is a measure of stability (Rumpel *et al.*, 2002). Consequently, the stability of SOM significantly increases with depth along with the radiocarbon age (Paul *et al.*, 1997). At depth, chemical interactions are probably more important than physical processes in

stabilization of SOC while aggregation has its strongest effects in the surface horizons (Paul *et al.*, 2001).

A. DEPTH DISTRIBUTION OF ROOTS

On a regional scale, plant allocation above- and below-ground is probably the major determinant of the relative distribution of SOC with depth (Jobbágy and Jackson, 2000). Above-ground OM has probably only limited effects on SOM levels compared to below-ground OM as has been demonstrated by longterm residue management studies (Campbell *et al.*, 1991; Clapp *et al.*, 2000; Reicosky *et al.*, 2002). The dominant role of root C in soil is also indicated by higher relative contributions of root vs. shoot tissues to the SOC pool estimated by Rasse *et al.* (2004) based on datasets from a variety of *in situ* and incubation experiments. Vegetation types differ in their vertical root distribution leaving distinct imprints on the depth distribution of SOC. The depth to which 95% of root biomass occurs is the lowest for grasses, highest for shrubs, and intermediate for trees (Table IV; Jackson *et al.*, 1996; 1997). The average maximum rooting depth for trees and shrubs is considerably deeper than for grasses and herbs (Canadell *et al.*, 1996). Root depths up to 40 m have been reported for *Eucalyptus marginata* in southern Australia, 18 m for woody plants in the Brazilian cerrado and 25 m for *Quercus fusiformis* at the Edwards Plateau, central Texas (Jackson *et al.*, 1999; 2000). Forests may have shallower SOC profiles compared to grasslands as indicated by differences in root-to-shoot ratios (Table III). The remaining roots at greater depth, however, may be important for SOC stocks in subsoil horizons. For example, Gill and

Burke (2002) observed that the decomposition rate of *Bouteloua gracilis* roots at 1-m depth was 50% slower than at 0.1-m depth, with estimated residence times of 36 and 19 years, respectively. The C loss rates from roots decreased linearly with depth. Based on the global biogeography of roots, Schenk and Jackson (2002) estimated that most profiles had 95% of all roots in the upper 2 m but the remaining 5% may reach much greater depths. By comparing 14 profiles containing both woody and grass roots, six profiles had equal depths for 95% of the roots from woody plants and grass, in three profiles woody plants rooted deeper, and in five profiles grasses rooted deeper than woody plants. Further rooting depths varied greatly among sites. The models developed by Schenk and Jackson (2002) for estimating rooting depth accounted for at most 50% of the observed variance. Cairns *et al.* (1997) reported that 65% of global root biomass inventories in forest ecosystems did not include the sampling depth, and only 15% sampled below 1 m. Yet, it was assumed that investigators captured practically all roots.

(Table IV)

B. DEPTH DISTRIBUTION OF SOIL ORGANIC CARBON BASED ON ESTIMATES

The amount of C stored in Histosols below 1-m depth is probably significant as the actual depth of these organic soils is much greater than 1 m (Eswaran *et al.*, 1993). Batjes (1996) estimated that Histosols contain 65% of their SOC to 2 m between 1 and 2-m depth. Large amounts of SOC lie also below 1 m in both mineral and organic soils

including Acrisols, Gleyic and Humic Cambisols, Ferralsols, Humic Gleysols, Thionic Fluvisols, Nitosols, Humic Podzols, Mollic Andosols and Vertisols. For Histosols and Podzols, however, discrepancy in SOC stocks exist for the second meter in estimates reported by Batjes (1996) and Jobbágy and Jackson (2000). Such discrepancies contribute to uncertainty in estimates of C storage in deep soil layers of the boreal regions for which there are almost no SOC data below 1-m depth.

The amount and vertical distribution of OM in boreal, temperate, tropical and subtropical soils probably vary distinctively with depth (Batjes, 1998). Batjes (1996) estimated that in peat soils reserves of C stored globally between 1 and 2 m are more than the reserve stored up to 1-m depth. Most soils store 37 to 39% of their total SOC to 2 m between 1 and 2-m depth. The SOC is more deeply distributed in arid shrublands than in arid grasslands, and subhumid forests have shallower SOC distribution than subhumid grasslands (Jackson *et al.*, 2000). Forty-three percent of SOC in the top meter of shrublands was found between 40 and 100 cm, but only 34% of SOC in grasslands was found within this depth.

For the first time, estimates of SOC pool to 3 m-depth in soil profiles associated with natural vegetation have been reported by Jobbágy and Jackson (2000). All profiles with potential effects on the vertical distribution of SOC were, however, excluded from the analysis (*e.g.*, agricultural soils disturbed by plowing). Shrublands and forests store more SOC in the second and third meters than grasslands relative to the SOC storage until 1-m depth (Table IV). Separated by biomes, deserts, tropical deciduous forests, tropical grasslands/savannas, sclerophyllous shrubs, temperate grasslands and crops had more than 50% of the amount of SOC until 1 m in the second and third meters. Globally more

C than that contained in the atmosphere is stored between 1 and 3 m below the soil surface. Global totals for the second and third meters indicated that tropical evergreen forests and tropical grasslands/savannas store most SOC between at 1 and 3-m depth.

C. DEPTH DISTRIBUTION OF SOIL ORGANIC CARBON BASED ON SOIL DATA

The world database for a meta analysis on soil C stocks is quite small (Guo and Gifford, 2002). Furthermore, measurements of SOC at depths > 1 m are rare. In temperate climates, large amounts of SOC are probably stored in B and C horizons. In a Dystric Cambisol under spruce (*Picea abies* (L.) Karst.), however, the soil between 1 and 1.4 m accounted only for 1.8% of the SOC contained in the mineral soil, with increasing contribution of ancient, stabilized C with depth (Rumpel *et al.*, 2002). The SOC pool between 1 and 1.1-m depth contributed 5.9% of the total SOC pool until 1.1 m in an abandoned grazed mixed grass prairie in Canada whereas the same increment contributed only 4.4% in the adjacent native mixed grass prairie (Henderson *et al.*, 2004). However, considerable vertical variations in SOC were observed in this study. In a clayey soil from an agricultural field in Iowa, the SOM contents between 1 and 1.3 m were reduced by 85% compared to the top 0.3 m, and further reduced by 9% between 2.7 and 3 m (Taylor *et al.*, 2002). However, in a sandy soil from Michigan no difference in SOM contents between 1-1.3 m and 3.9-4.2 m were observed. Mikhailov *et al.* (2000) studied effects of cultivation on SOC stocks in chernozem soils in Russia. In the native grassland, 13% of the total SOC to 1.3-m depth was stored between 1 and 1.3 m. In the soil profile of the

annually cut hay field, 8% of the total SOC was stored between 1 and 1.25 m whereas 8% was stored between 1 and 1.18 m at the continuously cropped field, and between 1 and 1.2 m of the 50-yr continuous-fallow field. The SOC concentrations below 1-1.2 m up to 2.3-m depth at the grassland, hay and cropped fields were higher compared to the fallow field. The SOC contents in B horizons (0.9-1.7 m) of four Ferralsols in Brazil accounted for 13 to 44% of the C content in A horizons (0-33 cm; Gonçalves *et al.*, 2003). In soils of eastern Amazônia, SOC contents in the upper meter dropped off steeply, however, the large volume of deep soil (1-8 m) contained 60% of the total C inventory of forest, degraded pasture and managed pasture soils to 8-m depth (Trumbore *et al.*, 1995). Three profiles in primary forests of Amazônia stored 28-30 % of their total SOC to 2.1 m between 1 and 2.1-m depth (Telles *et al.*, 2003). In a sandy soil in north-eastern Australia, Bird *et al.* (2003) found appreciable SOC densities below 1 m and up to 2.5-m depth. Urban soils in Germany contain considerable amounts of SOC below 1-m depth (Wu *et al.*, 1999; Beyer *et al.*, 2001; Lorenz and Kandeler, 2005). Pouyat *et al.* (2002) reported relatively high C amounts in urban soils to 1-m depth due to increase in below-ground productivity. The SOC storage at depth in urban ecosystems, however, is highly variable and affected by physical disturbances, burial of soil by fill and carbonaceous parent materials like debris, ash, slag, garbage and sewage sludge, also partially from the deposition of airborne particles, and soil management inputs (Pouyat *et al.*, 2002). These materials frequently contain elemental C which is usually considered highly resistant (Derenne and Largeau, 2001; Currie *et al.*, 2002). The SOM in industrialized urban areas may, therefore, consist of a mixture of natural humic substances and anthropogenic organic particles (Kögel-Knabner, 2000). Although urban land-use conversion represents

only a small proportion of the land base, changes occurring in SOC storage may probably be more persistent than in other land-use conversions. Compared to their natural counterparts, the urban soils probably show a substantially different behavior against environmental hazardous compounds and microbial activity (Beyer *et al.*, 2001).

D. CHANGES IN THE CHEMICAL COMPOSITION OF SOIL ORGANIC CARBON WITH DEPTH

For below-ground organic C inputs only a few studies are available on the contribution of plant litter residues to the chemical composition of SOC (Kögel-Knabner, 2002). As revealed by CPMAS ¹³C NMR spectroscopy, the composition of the below-ground C input may be substantially different to the above-ground input. Decomposition of plant litter is mostly associated with a relative increase in the content of alkyl C and a decrease in the content of O/N-alkyl C (mainly polysaccharides and proteins) while the content of aromatic C remains almost unchanged (Baldock *et al.*, 1997; Scheffer, 2002). Plant litter is mainly deposited in the surface soil, thereby strongly contributing to SOM in the upper soil horizons. The extent of decomposition tend to increase with soil depth. However root litter and the translocation of particulate OM and DOM may also affect the composition of the subsoil C (Kaiser and Guggenberger, 2000).

Within forest and arable soils litter compounds detectable by wet chemical analysis decreased with depth whereas humic compounds increased, and fulvic acids were translocated to deeper soil horizons (Beyer *et al.*, 1992; 1993). Based on molecular-level analysis, the proportion of root-derived suberin compared to cutin increased with increase

in depth in a forest soil (Nierop, 1998). Lignin could not be detected in the mineral horizon of a peaty gley soil whereas lignocellulosic material was only weakly decomposed in the overlying fermentation horizon (Huang *et al.*, 1998). Lignin-derived phenols were also not detected between 0.3 and 1.7-m depth in a Luvisol (Schmid *et al.*, 2001). In contrast, low amounts of lignin with a similarly low degree of decomposition were found between 0 and 0.3-m depth. The changes in the distributions of phenols and hydroxyalkanoic acids with depth in a Dystric Cambisol indicated that C derived from suberin/cutin is preferentially preserved at depth compared to C derived from lignin (Rumpel *et al.*, 2004). These results were confirmed by ^{13}C CPMAS NMR spectroscopy. Furthermore, lignin was not stabilized in the mineral soil horizons. In contrast, Schmidt and Kögel-Knabner (2002) reported that in 0-14 cm and in 46-91 cm depth in a Haplic Alisol under deciduous forest most of the OM was present in O-alkyl (mainly polysaccharides) beside methylene structures, each contributing one-third to the bulk OM.

The black carbon (BC) originating from incomplete combustion of OM is generally enriched with soil depth (Glaser *et al.*, 2000). Furthermore, char may be recalcitrant in soils (Baldock and Smernik, 2002; Skjemstad *et al.*, 2002). Lignite-derived material was estimated to contribute significantly to SOC in forest and agricultural soils (Schmidt *et al.*, 1996; Rumpel *et al.*, 1998). In soil profiles under natural vegetation in Brazil, charcoal was found from surface horizons to 2.1-m depth (Pessenda *et al.*, 2001). In a chernozemic soil profile, BC remained at a high level to 1-m depth while in the reference soil no BC was detected below 0.4 m (Kleber *et al.*, 2003). The NMR spectroscopy revealed that in 40-50 cm depth of the reference soil the intensity in the alkyl region was

slightly increased compared to 0-10 cm with a concomitant small increase in the aromatic C region. In contrast, the SOC in the deeper horizon of the chernozemic soil was dominated by aromatic C from the selective preservation of lignin residues but also from amendments of charred OM. By comparing a variety of German chernozemic soils, Schmidt *et al.* (1999) observed that charred OC contributed more to bulk soil C in subsurface (maximum depth 0.6 m) than in surface horizons. Furthermore, contributions from O-alkyl C decreased with depth indicating lower contributions of plant litter derived polysaccharides at depth. In the refractory (non-hydrolyzable) SOC fraction of a soil sample from 3-3.1 m depth in a ferralic tropical soil, ligneous and aliphatic materials (cutans, suberans) were absent whereas melanoidins (condensation products of amino acids and sugars) and BC particles were present (Poirier *et al.*, 2002).

The soil types investigated by modern analytical techniques are rather limited (Kögel-Knabner, 2000). The qualitative changes of SOC with depth can, therefore, not be generalized and some results of studies based on modern analytical techniques are discussed below. In the soil profile of a Vertisol in Australia, aryl C (mainly charcoal) increased from 0 to 1.2-m depth while alkyl and O-alkyl C (polysaccharides) concomitantly decreased (Skjemstad *et al.*, 2001). In contrast, in another Vertisol smaller changes in the chemical composition of SOC between 0 and 0.3-m depth were observed but OM between 0.9 and 1.2 m was dominated by alkyl C, and SOC was more decomposed in the subsoil. In a Luvisol, the changes in the relative contributions of alkyl and aromatic C to SOC were highly variable to 1.7-m depth whereas O/N-alkyl C decreased with depth (Schmid *et al.*, 2001). Carboxylic and aliphatic compounds increased with soil depth in forest and arable soils whereas polysaccharides decreased

(Beyer *et al.*, 1992). In soil profiles at the Hubbard Brook Experimental Forest alkyl C increased slightly from the surface to 82-cm depth whereas O-alkyl C and signals from lignin decreased (Dai *et al.*, 2001). This indicated that the degree of SOC decomposition increased with depth.

The C-13 NMR spectra for humic acids indicate that aromatic C undergoes structural changes with depth resulting in higher proportions of mostly C-substituted aromatic structures and/or higher proportions of non-lignin-derived aromatic structures (Kögel-Knabner, 2000). With increasing soil depth at three forest sites, Kögel-Knabner *et al.* (1991) observed a degradation of lignin structural units in humic acids.

In a soil profile (0-45 cm) under continuous corn thermochemistry using tetramethylammonium hydroxide (TMAH) indicated that lignin-derived syringyl units were preferentially degraded at depth (Chefetz *et al.*, 2000). Both the ¹³C-NMR spectra and TMAH chromatograms indicated that plant components decrease with depth as a result of mineralization, decomposition, and repolymerization processes. In 30–50 cm depth of both a corn and a forest soil, Gregorich *et al.* (1996) observed relatively fewer long-chain C compounds, including fatty acids, lipids, and sterols compared to 0-5 cm depth using pyrolysis-field ionization mass spectrometry (Py-FIMS). The subsoil also contained fewer monomeric and dimeric lignins and alkyl-aromatics. In a Humic Folisol, contributions of alkyl C at 64-82 cm depth were twofold higher compared to the overlying horizons indicating higher contents of more resistant organic compounds like long-chain aliphatics (Fox *et al.*, 1994). In contrast, in a Histic Folisol the contributions of alkyl C between 82 and 151-cm depth were lower than in the overlying horizons but total aromatic C was higher suggesting probably increasing lignin content. In the mineral

horizons in a forest soil, the leaching and decomposition of lignin components with increasing depth was observed as revealed by NMR and Py-FIMS (Preston *et al.*, 1994). In Typic Haplorthods under forest, alkyl C increased to 60-cm depth while O-alkyl C decreased for bulk soils, humic acids, and humin (Ussiri and Johnson, 2003). It was hypothesized that carbohydrates were preferentially degraded at depth whereas recalcitrant alkyl C (cutin, suberin, waxes) was selectively preserved but may also have been synthesized by microorganisms. Lignin decomposition in deeper soil horizons was probably slowed down as the aromatic C fraction increased with depth. In a mixed-conifer forest soil litter decomposition from the surface to 40-cm depth was characterized by increases in aromatic C and plant-derived alkyl C without the buildup of humified alkyl C which generally occurs in other ecosystems (Gressel *et al.*, 1996). The B horizons (91–169 cm depth) in Ferralsols showed higher intensities in the aromatic C region and lower proportions of alkyl C than the A horizons (0–33 cm depth; Gonçalves *et al.*, 2003).

IV. POTENTIAL OF SUBSOIL ORGANIC CARBON SEQUESTRATION

The sequestration of SOC can be achieved by increasing C stocks through sustainable land use and recommended management practices, by improving the depth distribution of SOC and by stabilizing SOC as recalcitrant C with long turnover time (Lal, 2004a; 2004b; Post *et al.*, 2004). One strategy for sequestration in subsoil horizons is to increase C inputs into the zones of the soil profile that have slower decomposition rates (Post and Kwon, 2000; Lal, 2004b; Table V). Based on estimates for the SOC pool between 1 and

3-m depth by Jobbágy and Jackson (2000) and the estimates for maximum rooting depths by Canadell *et al.* (1996), the subsoil below 1-m depth has probably the potential to store between 760 and 1520 Pg C. These estimates are, however, highly tentative as the database is very small and estimates were restricted to soil profiles with natural vegetation excluding *e.g.* agricultural soils with an altered vertical distribution of SOC. Since as much as 33% of global annual net primary production is solely used for the production of fine roots (Norby and Jackson, 2000), promoting the growth of the root biomass and management of the vertical root distribution is, therefore, one option. Another strategy to sequester SOC in subsoil horizons is to select plants and cultivars with a belowground biomass that is higher in biochemical recalcitrant compounds. Recalcitrance results in the stabilization of SOC due to the inherent chemical structure of the biomolecule (Gleixner *et al.*, 2001). Chemical recalcitrance appears to be the only mechanism for protection of SOC for long periods of time while adsorption and aggregation of OM in the soil only slows down the decomposition processes (Krull *et al.*, 2003).

(Table V)

Management practices must be aimed to optimize CO₂-utilization in photosynthesis to increase in particular the belowground productivity (Batjes, 1998). A concomitant high surface litter input may also result in high concentrations of dissolved organic carbon (DOC). The DOC transported with the percolating water has the potential to be sequestered on mineral surfaces in deeper soil layers (Baldock and Smernik, 2000; Telles

et al., 2003). The availability of adequate water levels and nutrient supply for root growth promotes the accumulation of sustainable OC levels in soils by high root residue production (Swift, 2001). Growing leguminous cover crops tends to preserve SOC due to residue inputs from root biomass (Gregorich *et al.*, 2001). To provide a permanent input of OM into deep soil layers, maintaining a vegetation cover with a deep root system is important (Sommer *et al.*, 2000). The introduction of relatively deeply rooted vegetation into shallow-rooted systems (*e.g.*, shrubs into grassland or afforestation of croplands) might store C deep in soil (Jobbágy and Jackson, 2000; Gill and Burke, 2002). The relative belowground translocation of assimilated C by pasture can reach up to 80% but only 60% by trees (Kuzyakov and Domanski, 2000). Long rotation would favor C sequestration in tree stands (Liski *et al.*, 2001).

Manipulating the quality and quantity of subsoil OM inputs from roots is another option to sequester C (Fernandes *et al.*, 1997). This can be achieved by selection of plant species and cultivars (Batjes, 1998; Mann *et al.*, 2002). Raising the proportion of plants with higher root-to-shoot ratios (*e.g.*, wheat instead of corn) will probably result in higher SOC stocks in deeper soil horizons. Selecting species and cultivars higher in lignin contents in the root biomass contribute also to C sequestration although globally lower root Ca concentrations and higher C:N ratios have a stronger impact on slowing down root decomposition (Silver and Miya, 2001). Slower decay rates were observed for roots > 5 mm in diameter compared to fine and intermediate-diameter roots (2-5 mm), probably due to higher proportions of resistant organic substances in thicker roots. Plants/cultivars with higher relative contribution of thicker roots may, therefore, be suitable for fostering C sequestration. The long-term stability of biomacromolecules can

be assessed from geological samples (de Leeuw and Largeau, 1993). During sedimentation and diagenesis lignins, tannins and suberans show the highest preservation potential. Selecting plants/cultivars with high contents of these compounds in the below-ground biomass may therefore promote SOC sequestration in soil profiles. New technologies may be used to modify chemical recalcitrant compounds in plants/cultivars for C sequestration (Ralph *et al.*, 1998; Pilate *et al.*, 2002; Chen *et al.*, 2004). Plant/cultivars may also differ as a source for SOC accumulation in the subsoil by differences in rhizodeposition but the contribution of rhizodeposits to SOC has not yet been directly measured in the field (Allmaras *et al.*, 2004).

The transfer of SOC to deeper soil layers and increase in SOM stability may also be promoted by manipulating the soil fauna (Wolters, 2000). Invertebrates like earthworms and many other taxa (*e.g.*, ants, termites) transport OM and mineral soil by bioturbation. Potentially manageable soil fauna include earthworms and termites which modify the soil environment through bioturbation (Fernandes *et al.*, 1997; Lavelle and Spain, 2001). Reducing disturbance by adaptation of crop cultivation practices (*e.g.* reduced or no-tillage), and providing favorable soil chemical and physical properties indirectly promotes soil faunal activities (Mitchell and Nakas, 1986). Soil invertebrates exhibit different feeding preferences, and attractiveness of litter to many invertebrates is positively correlated with Ca, N, moisture and carbohydrate contents, and negatively with the polyphenol and tannin concentrations (Wolters, 2000). Selecting plants/cultivars with favorable litter qualities for invertebrates may, therefore, directly promote SOC stabilization, and the horizontal transfer within the soil profile. However, knowledge gaps include the faunal food selection and associated changes in C pools as well as differential

effects on SOM turnover (Wolters, 2000). For example, fungi are a primary food source for many invertebrates, including earthworms.

The largest fraction of OC entering the soil is that contributed by plant residues (Paul and Clark, 1996). Managing microorganisms that carry out the decomposition of plant litter in the subsoil may promote C sequestration as the contribution of microbial products to SOC vs. plant inputs increase with soil depth (Rumpel *et al.*, 2002; Martens *et al.*, 2003). Microorganisms produce hydrolysis-resistant aliphatic biomacromolecules containing alkyl C (Hedges and Oades, 1997). These microbial-derived aliphatic materials may represent a relatively stable C pool and accumulate at depth (Lichtfouse *et al.*, 1995; Golchin *et al.*, 1996). An important fraction of the hyphal biomass in mycorrhizal tissues are recalcitrant compounds like chitin and glomalin that may account for a significant pool of SOM (Treseder and Allen, 2000). Ectomycorrhizal hyphae and exudates are probably more recalcitrant than arbuscular mycorrhizal ones (Langley and Hungate, 2003). Managing subsoil microorganisms to enhance C stabilization may be achieved by promoting C release from roots, retaining crop residues at the fields, reducing tillage and feeding microbes (Post *et al.*, 2004; Welbaum *et al.*, 2004). However, the knowledge on soil microbial communities including mycorrhiza and their possible role in subsoil C sequestration is limited.

V. CONCLUSIONS

To date, studies on the potential for long-term C storage in soils have been restricted to the upper soil section mainly to the plow layer or up to 1-m depth. However, many soil

profiles are deeper and especially the occurrence of roots at greater depths raise the question about the role of subsoil horizons to C storage. Furthermore, the mean residence time of SOC increases and the proportion of recalcitrant plant litter compounds tends to increase with depth. The paucity of available studies, however, hampers the knowledge of the potential for C sequestration in subsoil horizons. Subsoil SOC storage may be promoted by translocation of OM into deeper soil layers as DOC with the percolating water and due to bioturbation by soil animals. The most promising approach, however, may be to increase the contribution of the belowground biomass (i.e., roots, mycorrhiza, microorganisms). Plant roots contain higher amounts of chemical recalcitrant compounds (e.g., lignins, tannins, suberin) than shoots and root-derived C accumulates with soil depth. Uncertainty exists if compounds like glomalin found in mycorrhizal tissues accumulate in the soil. The soil microorganisms may contribute highly aliphatic biopolymers to the SOC fraction in the subsoil that is protected for long periods of time. Agricultural and forest land-use are mainly aimed at maximizing the above-ground growth. The focus must be to raise the proportion of chemical recalcitrant SOC, especially in the subsoil as recalcitrant compounds in the subsoil have the highest potential for C sequestration. Studies are needed to develop techniques for managing the above- and belowground parts of ecosystems/land uses including the plants with their above- and below-ground litter input, the soil fauna and soil microorganisms for SOC sequestration.

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Table I
Main Biomacromolecules in Plant Litter

Species	Source	Cellulose (%)	Lignin (%)	Reference
Alfalfa (<i>Medicago sativa</i> L.)	Stem	13-33	6-16	Scheffer (2002)
Beech (<i>Fagus sylvatica</i> L.)	Wood	32	24	Scheffer (2002)
	Bark	38	39	Scheffer (2002)
	Leaves	20	11-16	Scheffer (2002)
	Roots	33	22	Scheffer (2002)
	Fine roots	19	33	Scheffer (2002)
Brussels sprouts (<i>Brassica oleracea</i> var. <i>gemmifera</i> Zenker)	Crop residue	21	7	Rahn <i>et al.</i> (1999)
Corn (<i>Zea mays</i> L.)	Leaves	35	3	Fernandez <i>et al.</i> (2003)
	Stems	41	6	Fernandez <i>et al.</i> (2003)
	Coarse roots	45	10	Fernandez <i>et al.</i> (2003)
	Fine roots	49	12	Fernandez <i>et al.</i> (2003)
Millet (<i>Pennisetum americanum</i> L.)	Plants	29-37	9-13	Bilbro <i>et al.</i> (1991)
Potato (<i>Solanum tuberosum</i> L.)	Crop residue	23	9	Rahn <i>et al.</i> (1999)
Red beet (<i>Beta vulgaris</i> var. <i>vulgaris</i> L.)	Crop residue	13	3	Rahn <i>et al.</i> (1999)
Rice (<i>Oryza sativa</i> L. (Cult.))	Straw	35-37	11-13	Devèvre and Horwáth (2000)
Ryegrass (<i>Lolium perenne</i> L.)	Shoots	19-26	4-6	Scheffer (2002)
	Leaves	22	2	Fernandez <i>et al.</i> (2003)
	Roots	30	9	Fernandez <i>et al.</i> (2003)
Sorghum (<i>Sorghum bicolor</i> (L.) Moench)	Green manure	30-31	3-4	Clément <i>et al.</i> (1998)
Soybean (<i>Glycine max</i> (L.) Merr.)	Green manure	24-27	7-8	Clément <i>et al.</i> (1998)
Spruce (<i>Picea abies</i> L.)	Wood	40	28	Scheffer (2002)
	Bark	48	38	Scheffer (2002)
	Needles	15	14-20	Scheffer (2002)
	Straw	27-33	18-21	Scheffer (2002)
Wheat (<i>Triticum aestivum</i> L.)	Crop residue	39	12	Rahn <i>et al.</i> (1999)

Table II
Lignin in Root and Shoot Tissues

Plant	Lignin (%)		Reference
	roots	shoots	
Wheat	9-12	7-9	Dignac <i>et al.</i> (2005); Wang <i>et al.</i> (2004)
Corn	10	7	Dignac <i>et al.</i> (2005)
Hairy vetch (<i>Vicia villosa</i> Roth subsp. <i>Villosa</i>)	17	5	Puget and Drinkwater (2001)
Ryegrass	15	6	De Neergard <i>et al.</i> (2002)
Clover	19	8	De Neergard <i>et al.</i> (2002)

Table III
Root-to-Shoot Ratio in Different Vegetation Types and Crops

Source	Root-to-shoot ratio	Reference
Steppe	6-13	Kögel-Knabner (2002)
Tundra	6.6	Kögel-Knabner (2002)
Grassland	0.3-6	Kögel-Knabner (2002)
Forests	0.2-4	Kögel-Knabner (2002)
Corn	0.21-0.25 (0.35 – 0.38 incl. rhizodeposits)	Allmaras <i>et al.</i> (2004)
Wheat	0.28 (0.48 incl. rhizodeposits)	Allmaras <i>et al.</i> (2004)
Soybean	0.23 (0.38 incl. rhizodeposits)	Allmaras <i>et al.</i> (2004)
Oats	0.4	Bolinder <i>et al.</i> (1997)
Barley	0.5	Bolinder <i>et al.</i> (1997)

Table IV
Global Root Biomass Distribution, Rooting Depths, and SOC Storage

	Grasslands/Grasses	Shrublands/Shrubs	Forests/Trees	Reference
95% of the root biomass	top 0.6 m	top 1.35 m	top 1.0 m	Jackson <i>et al.</i> (1996, 1997)
Maximum rooting depth	2-2.5 m _a	7 m	5 m	Canadell <i>et al.</i> (1996)
SOC storage between 1-3 m relative to the amount stored in the top 1 m	43%	77%	56%	Jobbágy and Jackson (2000)

_agrasses and herbs

Table V
Potential of Carbon Sequestration in Subsoil Horizons

Level	Strategy	Effects	Examples	Knowledge gaps
Ecosystem	Increase in proportion of land-uses with higher subsoil C stocks		Shrublands have deeper SOC distribution than grasslands Grasslands have deeper SOC distribution than forests	Insufficient database for agricultural soils
Plant/cultivar	Selecting plants/cultivar that raise the subsoil C stocks	Releasing more DOC during decomposition Slower decomposing roots	Conifer roots decompose slower than roots from broadleaf species Roots from broadleaf species decompose slower than roots from graminoid species	Differences between plant species/cultivars DOC dynamics i.e. DOC retention in the subsoil Insufficient database root decomposition in agricultural soils
		Higher root-to-shoot ratios	Wheat has a higher root-to-shoot ratio than corn	Insufficient database
		Deeper root systems	Shrublands have deeper rooting depths than grasslands Woody plants are more deeply rooted than herbaceous species Fine-root mean age increases with depth	Insufficient database on plant root systems Maximum rooting depth of most root profiles Effect of high variability of rooting depths among sites
		Higher relative contribution of thicker roots	Slower decay of roots > 5 mm diameter Roots > 2 mm diameter are older	Proportions of fine to coarse roots Standard method to quantify root production and loss
		Higher contribution of recalcitrant root litter compounds	Lignin concentration negatively correlated with root decay rate Root-derived suberin is a major	Definition of root size classes Definition and determination of root litter quality in terms of decomposability Standard method for the determination of lignin Quantification of the lifespan of

			contributor to SOM in forest soils and grasslands	root-derived molecular structures
			Lignins, tannins and suberans have a high preservation potential	Quantification of the lifespan of root-derived molecular structures
		Higher rhizodeposition		Direct contribution of rhizodeposits to SOC on the field level
		Higher proportion of plants associated with ectomycorrhiza than associated with arbuscular mycorrhiza	Mycorrhizal status probably affects root decomposition Ectomycorrhizal hyphae may be more recalcitrant than hyphae from arbuscular mycorrhiza	Mycorrhizal influence on belowground litter quality C sequestration by accumulation of mycorrhizal detritus
Soil fauna	Manipulating of soil fauna i.e. the invertebrates		C mineralization in earthworm casts is reduced – especially in the subsoil	Translocation and sequestration of carbon in the subsoil
		Directly by feeding with attractive food	Plant litter rich in Ca, N, moisture, carbohydrates attract invertebrates Invertebrate feeding leads to an enrichment of recalcitrant SOM	Prediction of invertebrate effects on ecosystem-level fluxes of C
		Indirectly by providing favourable soil chemical and physical properties for faunal activity		
Soil microorganisms	Managing of soil microorganisms		Old and recalcitrant alkyl C originates partially from microorganisms Alkyl C increases in the subsoil	SOM quality and microbial communities in the subsoil Contribution of microorganisms to alkyl C in relation to plants Studies on subsoil C sequestration by soil microorganisms
		Promoting C release in the subsoil “Primer plants” with deep, thick and fast decomposing roots providing channels for the establishment of subsoil microbial communities		

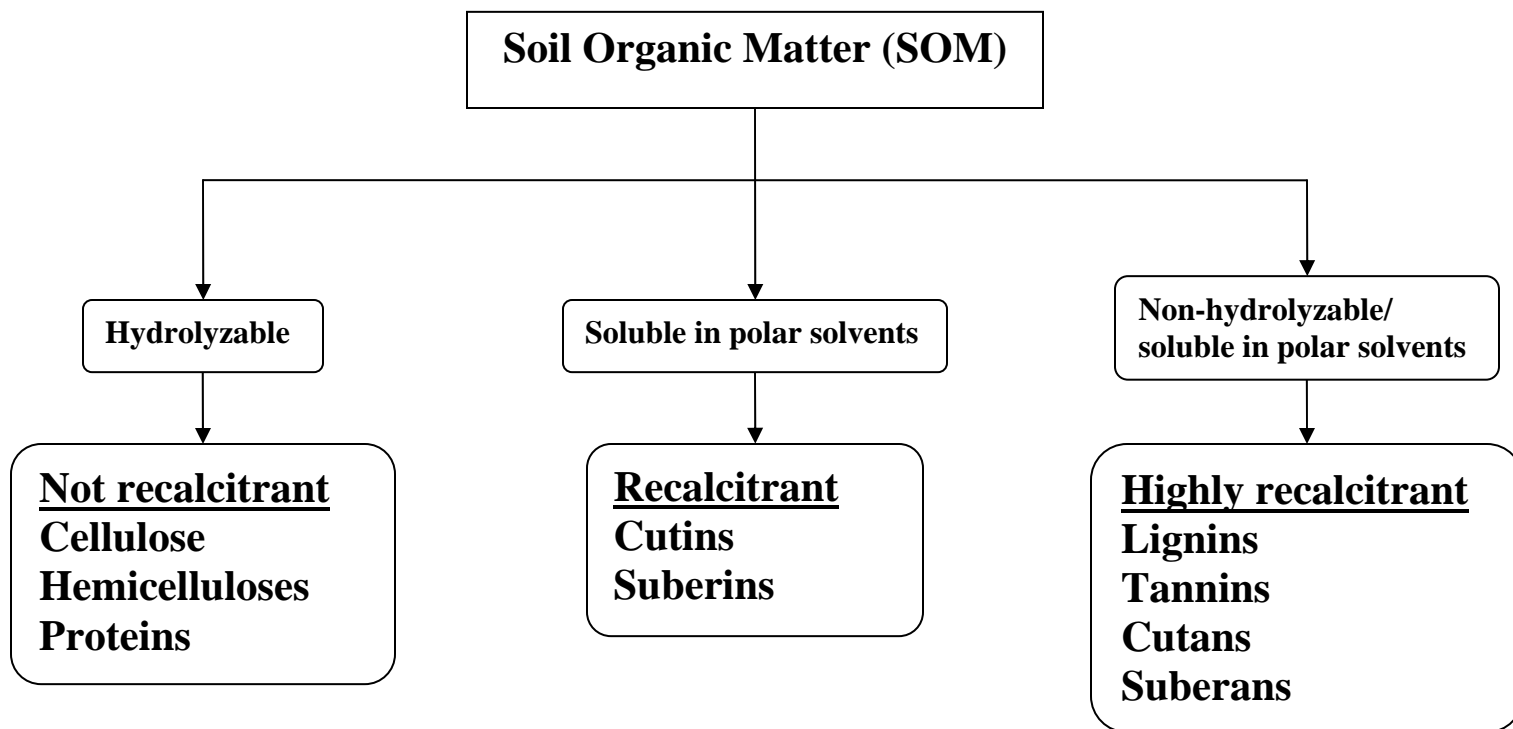


Figure I

Plant litter biomacromolecules as precursors of soil organic matter