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Plant Chemistry and Morphological Considerations for Efficient Carbon Sequestration

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Abstract: Carbon sequestration to soils counteracts increasing CO_2 levels in the atmosphere, and increases soil fertility. Efforts to increase soil carbon storage have produced mixed results, due to the multifactorial nature of this process, and the lack of knowledge of molecular details on the interplay of plants, microbes, and soil physiochemical properties. This review discusses the carbon flow from the atmosphere into soils, and factors resulting in elevated or decreased carbon sequestration. Carbon partitioning within plants defines how much fixed carbon is allocated belowground, and plant and microbial respiration accounts for a significant amount of carbon lost. Carbon enters the soil in form of soluble and polymeric rhizodeposits, and as shoot and root litter. These different carbon sources are immobilized in soils with varying efficiency as mineral-bound or particulate organic matter. Plant-derived carbon is further turned over by microbes in different soil layers. Microbial activity and substrate use is influenced by the molecular weight and chemical class of the plant-derived carbon. Further, soil carbon formation is altered by root depth, plant growth strategy (perennial versus annual), and C/N ratio of rhizodeposits. Current gaps of knowledge and future directions are highlighted.

Keywords: Carbon partitioning · Rhizodeposits · Root exudation · Soil organic carbon

Joelle Sasse Schläpfer is an Assistant Professor at the University of Zurich, heading the Plant-Soil Interactions group. Her research focuses on elucidating the molecular mechanisms of root-microbe crosstalk, specifically by studying the effects of plant-derived compounds on various microbes. Thus, focusing on the dynamics of root exudation is central, as it changes with plant species, developmental stage, and even diurnally. Further, experimental conditions as well as abiotic and biotic stresses impact exudation. In her work, analytical techniques are applied to assess metabolic changes of plant tissues and the rhizosphere.

1. Introduction

Soils play a crucial role as both sources and sinks for greenhouse gases. They emit CO_2,[1] while photosynthetically active organisms actively remove CO_2 from the atmosphere, storing a part of fixed carbon in soils. Land plants account for 50% of global photosynthesis.[2] Thus, they are one means to bind atmospheric carbon and to deposit it belowground, mediating climate change and increasing soil fertility.[3] For efficient belowground carbon stabilization, compounds have to be protected from microbial degradation.[4] An efficient way for this is to chemically bond low-molecular weight compounds to mineral surfaces to form mineral-associated organic matter (MAOM, see Fig. 1).[5] The amount of carbon immobilized in MAOM is defined by the amount of minerals present. If minerals are limited, soils can become carbon saturated.[6] Climate conditions or soil management practices can result in an effective C saturation level below the theoretical level.[7] The second soil organic matter (SOM) fraction has no saturation level: particulate organic matter (POM) consists of high-molecular weight, mostly plant-derived polymers, which can be water-soluble or occluded in aggregates. The stability of this fraction depends on microbial activity, and on a set of specialized enzymes for polymer degradation. In addition, edaphic factors such as temperature and pH are central to POM stability, as they regulate microbial activity.[8] POM carbon can quickly be degraded when environmental factors or land use changes.[5] At present, it is still unclear how MAOM and POM fractions are formed, stabilized, and how much carbon flows between the fractions.

Carbon sequestration is a multifaceted process. Thus, to efficiently increase carbon levels in soils, multiple factors and their interplay need to be understood. This review focuses on carbon flow from the atmosphere into soils through plants and microbes. Aspects regulating carbon sequestration efficiency in a positive or negative manner are discussed: i) maximization of belowground carbon partitioning within plants, ii) minimization of carbon loss due to plant and microbial respiration, iii) efficiency of rhizodeposit incorporation into SOM fractions, and iv) effects of root depth, C/N ratio of rhizodeposits, and plant species on carbon sequestration. Other crucial aspects for carbon sequestration, such as different ecosystems behaviour, the role of arbuscular and ectomycorrhizal symbionts, and the effects of physiochemical properties on exudation are discussed elsewhere.[6,9–12]

2. Plant Carbon Partitioning

2.1 *A Significant Amount of Carbon is Partitioned Belowground*

Fixed carbon is partitioned between growth, reproduction, storage, and respiration. For efficient carbon sequestration, carbon fluxes should be directed belowground, and respiration should be minimized. In CO_2 labeling experiments, 20–40% of labeled carbon typically remains in the labeled leaf[13,14] and a similar fraction is allocated to growing leaves (Fig. 2). Depending on plant species, developmental stage and experimental setup,

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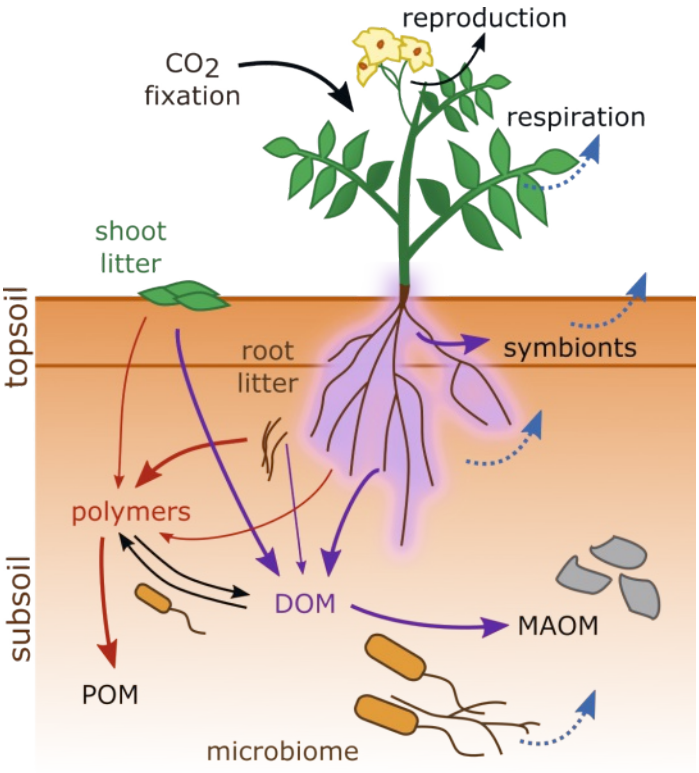

Fig. 1. Major carbon fluxes from plants into soils. Fixed carbon is partitioned between above- and belowground plant tissues. Major carbon sinks are tissue biomass, reproductive organs, symbionts (*e.g.* mycorrhizal fungi, rhizobia). Carbon is lost as respiration at multiple levels (blue arrows). Plant-derived carbon enters soils as litter or rhizodeposits, as water-soluble, low-molecular weight compounds as part of the dissolved organic matter (DOM) fraction (purple), or as insoluble, high-molecular weight polymers (red). Gram – bacteria turn over labile carbon, whereas gram + bacteria and saprotrophic fungi break down polymers, mostly in lower soil layers. Polymers are integrated into particulate organic matter (POM). Plant- and microbe-derived soluble compounds can interact with mineral surfaces, generating mineral-associated organic matter (MAOM). Arrow thickness indicates relative amounts of carbon.

about 50% of the label is transported belowground.[13–17] Up to 20% of fixed carbon can be allocated to microbial symbionts, such as mycorrhiza.[18]

2.2 *Low Amounts of Plant-derived Carbon in Soils*

Of the 50% fixed carbon allocated belowground, half stays within the root for growth and storage.[19,20] Of the remaining 25%, more than half is lost by plant and microbial respiration, and the remaining 5–15% is detected in soils (Fig. 2).[17] However, these numbers vary widely between studies, with 40–90% of root carbon recovered from soil.[21] Some of this variation is explained by plant species, developmental stage, and experimental parameters. Ecosystems typically have narrow carbon rhizodeposition rates with 30–50% in pastures, and 20–30% for cereals.[20] An additional reason for the variation in rhizodeposition reported by different studies is the definition of rhizodeposition as either all carbon entering the soil, including respiration, or as a specific fraction, *e.g.* water-soluble compounds. Although it is clear that carbon enters the soil in a variety of different forms, from litter to polymers or volatile compounds (see also Section 3), it is at present unclear how these contribute quantitatively to SOM formation and respiration. In most studies, the focus is on the soluble fraction, as this is straightforward to quantify. In agar microcosms with ryegrass seedlings, 30% of labeled carbon translocated to roots. Whereas 1% carbon was detected in exudates in sterile conditions, this value increased to 3–34% in association with a variety of microbes.[22,23] In nonsterile, hydroponically grown wheat seedlings, 3% of the label was detected cumulatively in exudates.[13] Similarly, 0.7–2.5% of fixed carbon was found in the root wash solution for 12 soil-grown plants,[15] and 0.3% in soluble maize rhizodeposits.[24] Importantly, maximum exudation of labeled carbon correlated with leaf export rates, indicating a direct coupling of carbon fixation with exudation.[13]

A small fraction of labeled carbon is further detected in soil microbial biomass, accounting for 5% of labeled carbon in ryegrass,[16] 7% in maize,[24] and 4–13% in soil of 12 different plant species.[15] Values in microbial biomass range from 0.1–6.7% of fixed carbon.[17] The timing of measurement is crucial, as for soil-grown wheat, 16% of the signal was detected in soil after 1 d, but this value dropped to 9% after one week.[14] On an ecosystem level, 3–5% of total carbon is incorporated into SOM of pastures or cropland.[20]

For increased carbon sequestration, several aspects of carbon partitioning should be investigated more closely. First, plant species with high belowground carbon allocation should be identified, also considering the ratio of root carbon vs sequestered carbon. Second, experimental factors resulting in high variation between studies should be determined in comparative studies.

2.3 *Carbon Loss by Respiration*

Plant and microbial respiration account for most of the carbon losses from plant ecosystems. Typically, 30% fixed carbon is lost by aboveground, and 15% by belowground respiration, accounting for almost half of the photosynthetic activity.[17,24,25] For wheat and barley, root respiration was determined at 7–15% of total carbon.[19] A large fraction of rhizodeposited carbon is respired, as shown for the 62% respiration of rhizodeposited carbon in maize 16 d after labeling.[24]

For belowground respiration, plant and microbial contributions are often not distinguished. Estimates place root respiration at half of total soil respiration.[15,26,27] However, these numbers vary widely. In a pot experiment, maize roots accounted for 78% of respiration, and microbes for only 22%.[25] It is indeed challenging to distinguish the two types of respiration, as roots in soils are colonized densely by microbes. Thus, even when roots are removed from soil and washed, the respiration detected still contains carbon from residual microbes, resulting in an overrep-

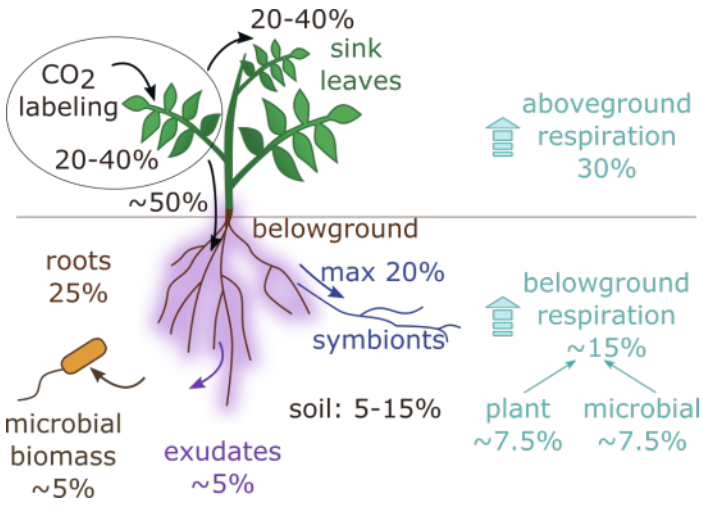

Fig. 2. Plant carbon partitioning. Carbon partitioning in a vegetatively growing plant. Labeled CO_2 is administered to a mature leaf, and is partitioned from there. Bold numbers indicate carbon remaining in the labeled leaf, and general partitioning to above -and belowground tissues. Colored numbers indicate belowground carbon partitioning. Numbers are averages across many studies, and vary widely depending on plant species, developmental stage, ecosystem, and experimental setup.[13–15,17–21]

resentation of root vs microbial respiration. As plant and microbial respiration are affected differently by environmental factors, it is crucial to determine both contributions individually in future studies.

Root respiration is likely proportional to belowground allocated carbon, as determined in ryegrass.[26] Further, respiration and rhizodeposition are lower at night than during the day,[25,28] indicating a tight coupling of photosynthesis with carbon sequestration and loss. Interestingly, for 12 plant species, soil respiration was similarly coupled to photosynthetic activity and plant growth rates, but SOC (soil organic carbon) formation was independent.[28] Thus, for efficient carbon sequestration to soils, it will be relevant to determine the ratio of fixed carbon used for biomass, rhizodeposition, and respiration for various plant species to determine efficient strategies for increasing sequestration. In principle, maximally efficient sequestration could be envisioned for plants with different strategies: on the one hand, slow-growing species with low photosynthetic activity and moderate sequestration could support limited respiration and thus, high carbon immobilization in soils. On the other hand, fast-growing species with high photosynthesis rate and sequestration might induce high respiration, but equally high carbon sequestration and moblization. These two strategies remain to be compared.

Microbial respiration is a consequence of microbial activity and is shaped strongly by edaphic factors. Low temperature and pH decrease microbial activity and thus, respiration.[29,30] Soil warming in contrast often increases microbial activity, soil respiration and SOM loss.[29] SOM storage is largely defined by microbial carbon use efficiency, a measure describing how much carbon is respired by microbes vs potentially immobilized in soils.[31] Further, microbial respiration is shaped by plant-derived compounds. Multiple studies have demonstrated that addition of fresh carbon can lead to the stimulation of microbial activity, and enhanced SOM decomposition, a phenomenon termed positive priming. SOM decomposition can be increased more than half, and depends on different factors such as plant species, chemical classes of exuded compounds and soil texture.[32] Single compounds such as glucose or oxalic acids have distinct effects on microbial respiration.[33] Generally, exuded sugars and benzoids increase microbial respiration, whereas phenols and multiple secondary metabolites inhibit respiration. For some chemical classes such as flavonoids, contrasting effects are observed depending on the compound tested.[34] Thus, microbial respiration is shaped by soil edaphic factors, by carbon use efficiency, but also by presence of specific compounds.

For efficient carbon sequestration, plant respiration should be at a minimum for efficient carbon release into soils. Further, rhizodeposits ideally bind to mineral surfaces without microbial turnover and respiratory loss. For microbial turnover, carbon use efficiency should be maximized, and priming effects minimized to prevent losses of existing SOM, and to allow formation of new SOM.

3. Sources of Plant-derived Carbon in Soils

Plant-derived carbon is deposited into soils in different forms: aboveground and belowground plant litter are substrates for microbial decomposition, root caps slough off border cells, surviving in soils for extended periods of time and disintegrating afterwards. Roots and border cells release water-soluble compounds (exudates), volatile compounds, and polymeric substances such as mucilage (Fig. 3). Specialized proteins and enzymes, DNA, and vesicles are released from root cells into soil. All these forms of rhizodeposition add carbon to the soil, but there are crucial differences between the aforementioned groups in regards to how accessible the compounds are to microbial breakdown, how efficiently they can be integrated into microbial biomass, how easily they interact with mineral surfaces, and how stable they are in the soil environment. Rhizodeposition is also termed the 'hidden half of the hidden half', as the process is challenging to investigate in native conditions.[17] Adding to the complexity is that SOM is chemically complex, with over 4000 compounds being detected.[35] Interestingly however, the chemical composition of SOM in different soils seems to be similar: A survey across 42 North American soils found SOM to be composed of 20% or more O-alkyl, alkyl, and aromatic C compounds, 10% or more amide or carboxyl moieties, and 10% or less phenolic, N-alkyl/methoxyl and di-O-alkyl compounds.[36] In a modeling approach, the authors translated these findings into on average 15–20% of lignin, proteins, carbohydrates, char-like molecules, and lipids, with a smaller amount of carbonyl compounds.[36] Thus, although rhizodeposits and SOM are both chemically complex, general patterns are likely to emerge when dynamics of carbon input are better researched. In the following sections, the contribution of soluble and polymeric rhizodeposits and of plant litter to SOM formation is discussed, as these are the major and best-researched fractions of carbon input into soils.

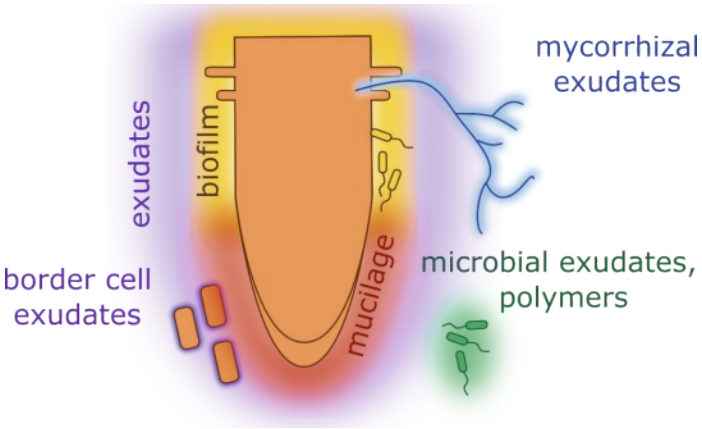

Fig. 3. Rhizodeposition. Plant-derived rhizodeposits include soluble compounds (purple: exudates), and polymers (red: mucilage). Border cells are sloughed off by the root cap, and produce specialized exudates involved in defense. Roots are densely colonized by microbes, which form a biofilm (yellow) and turn over some plant compounds. Mycorrhiza import plant-derived compounds, and produce exudates (blue). Microbes in the rhizosphere metabolize plant-derived compounds, and produce low- and high-molecular weight compounds (green).

3.1 *Soluble Rhizodeposits*

Root exudates are water-soluble, chemically diverse compounds of low and high molecular weight. They comprise primary compounds such as sugars, organic acids, and nucleotides, and secondary metabolites.[37] Exudation is dynamic, changing with plant species and developmental stage, abiotic and biotic stress, environmental factors, and experimental conditions. Major compounds found in exudates are sugars (mostly glucose, but also galactose, mannose, arabinose, xylose), organic acids (lactate, acetate, oxalate, succinate, fumarate, malate, citrate), and amino acids (alanine, glutamate among most abundant, but high species diversity).[38–40] Sugars dominate early in development, whereas amino acids and phenolics predominate in later stages.[41–43] Organic acid exudation is heavily influenced by abiotic stresses such as nutrient deficiencies, as they can release nutrients from mineral surfaces.[37,40] Interestingly, specific organic acids such as oxalate might also make other mineral-bound, organic compounds accessible for microbial degradation, resulting in respiration increase.[44] The relative abundance of different chemical classes results in different soil stabilization behavior. Maize exudates rich in sugars, fatty acids, and urea stabilized sand better than barley exudates rich in organic acids and amino acids.[45] Also, organic

acids and amino acids are easily sorbed to minerals due to their charge, whereas sugar monomers or polymers aggregate more easily.[38]

Exudates are not only released in a temporal, but also in a spatial pattern from roots. Imaging of maize roots revealed distinct gradients for sucrose, coumaric acid, vanillic acid, and caffeic acid.[46] Radial gradients around roots were further measured for ions (nitrate, ammonium, water, CO_2, O_2, nutrients), metabolites (hexoses, adenine), and various enzymes.[47] Lateral root gradients were detected for sucrose and tryptophan, with sucrose being abundant at tips, and tryptophan around older root parts.[48] Interestingly, these spatiotemporal exudation patterns correlate with quantitative and qualitative differences in microbiome composition.[49–51] Generally, exudates are nutrients and signaling molecules for root-associated microbiomes.[37] Sugars and organic acids are carbon sources, whereas amino acids also serve as nitrogen source for plants and microbes, especially in soils with low inorganic nitrogen content.[40] Amino acids can account for 10–40% of soluble nitrogen.[40] Absolute concentrations of sugars, organic acids, and amino acids in soils are low, due to fast microbial turnover rates.[38,52,53] Specific compounds such as malate and glutamate can increase litter decomposition rates, usually without corresponding increases in DOM (dissolved organic matter) or microbial biomass.[54]

A large microbial community is associated with roots, also producing exudates and polymers, the latter as extracellular matrix or biofilm. Due to the tight spatial association of microbes and roots and the fast metabolite turnover time, it is at present not possible to discriminate clearly between plant- and microbe-derived compounds in native environments, and it is unclear how much and which exudates are turned over in which timeframe by root-associated microbes and free-living microbes. It is estimated however that 20% of sugars in soils are plant-derived, and 80% are present in microbial biomass or SOM, adding up to a total of 7–15% sugars in SOM depending on soil type.[38]

All plant-derived, water-soluble carbon contributes to the dissolved organic carbon (DOC) pool in soils. With pulse-labeled tillering ryegrass, 1% of labeled carbon was recovered from the DOC fraction, and 5% from the microbial biomass.[16] Historically, DOM was thought of as recalcitrant molecules with high stability, a concept that was later revised.[35] DOM compounds can either interact with mineral surfaces, becoming MAOM, or are turned over by microbes depending on accessibility, concentration, bioavailability, and biodegradability.[35] Further, DOM components are mobile as they are dissolved in water, and they are the major source of carbon movement from top to lower soil levels, being an energy source for microbes in the different layers (see also Section 4.1). The balance between DOM-mineral and DOM-microbial interactions is at present unclear. For increased MAOM production, a tilt towards DOM-mineral interactions would be desirable. Indeed, plant carbon from the DOM fraction is incorporated rather efficiently into MAOM: rhizodeposits contributed 46%, whereas belowground- and aboveground litter only contributed 9% and 7%, respectively.[55] Overall, the historic perception as MAOM originating from microbial compounds is changing, with newer studies suggesting that plant compounds account more than half of MAOM.[56–58]

3.2 *Polymeric Rhizodeposits*

Roots produce mucilage, which consists of 78% polysaccharides, but also of proteins, minerals, and lipids.[59] The composition depends on the plant species, but the polymers usually comprise of glucose, galactose, and uronic acids.[59] In a pulse labeling study, 40% of wheat root-derived carbon was present as polymeric glucose, likely in the form of mucilage. At earlier timepoints, soluble sugars were also detected, but these disappeared a few days after labeling.[14] Together with microbial polymers, mucilage creates a niche maintaining stable environmental conditions for soil life by binding water, and forming soil aggregates.[60]

Mucilage also serves as energy source for microbes. Plant beneficials such as free-living nitrogen fixing bacteria and other microbes degrade mucilage.[59] Some plant roots further produce hydrolases degrading mucilage.[59] The effect of these hydrolases on other carbon sources in soil remains to be studied, as well as the quantitative contribution of mucilage to overall rhizodeposition. In addition, the spatiotemporal dynamics of mucilage production and breakdown are still mostly unresolved. Novel imaging techniques such as infrared spectroscopy[61] will allow to better assess mucilage dynamics in native soils.

3.3 *Plant Litter*

Plant litter comprises low molecular weight compounds that are readily degraded by microbes and high molecular weight compounds requiring specialized enzymes for breakdown. Typical plant polymers are cellulose, hemicellulose, lignin, and tannins. Cellulose is a glucose polymer, and is degraded within months in soil.[38,62] Leaves consist of 15–35% cellulose, and roots contain 2–3x higher levels.[38] Hemicellulose is a polymer of multiple hexoses and pentoses, with faster degradation rates compared to cellulose.[38,61] Lignins are water-insoluble, aromatic polymers and quite recalcitrant to degradation, often detected in soils for extended periods of time.[63,64] Tannins are water-soluble, aromatic polymers, readily moving to lower soil layers as DOM. They are degraded by depolymerization and chemical transformation. Their degradation products are also part of DOM, and are important MAOM precursors.[63] Estimates of aromatic polymer turnover time differ widely, and the involvement of different microbes in the process is still unclear.[63,64] Generally, gram – bacteria are associated with turnover of easily accessible, low molecular weight compounds, and gram + bacteria as well as saprotrophic fungi with degradation of complex molecules.[65] Saprotrophic fungi incorporate more plant carbon into biomass compared to bacteria (>75% vs 13-60%[65,66]). A likely cause is the higher mobility of fungi in soils due to directed growth compared to bacteria.

Shoot litter has a 2.5–3x lower soil residence time compared to root litter, as shoots contain less complex molecules.[65,67] Shoot carbon is incorporated rather quickly into fungal metabolites (30–78% of labeled carbon), whereas lower amounts were found in the labile extractable organic carbon fraction (24%), and only 17% in SOC after five years.[65] Interestingly, the presence of both root and shoot litter had an additive effect on carbon incorporation into SOC.[65]

Plant litter is a main ingredient of POM, but microbial compounds can also be detected. The chemical composition of POM is still quite unclear. To make matters more complicated, large soil aggregates are often a mix of POM, MAOM, and smaller aggregates at different stages of decomposition. MAOM can also contain polymers or compounds with POM-type chemistry, increasing POM stability.[56] In the past, plant litter is seen as one of the main substrates for SOM formation,[68] but newer studies indicate that soluble and polymeric rhizodeposits are more efficiently integrated into POM and MAOM.[69] The absolute contribution of litter and rhizodeposits to different SOM pools remains to be determined. Further, it should be investigated whether plant species and developmental stage impact the efficiency of litter and rhizodeposit integration into SOM fractions.

In summary, carbon rhizodeposition by plants is complex. The contribution of plant litter, soluble and polymeric rhizodeposits to DOM, POM, and MAOM is unclear, as well as the influence of environmental factors, soil type, plant species and developmental stage on this balance. The form of plant-derived carbon that is most directly immobilized in MAOM should be identified for efficient carbon immobilization in soils. In addition, the formation of POM from different plant sources and its stability should be

determined, as well as the exchange between POM and MAOM to determine whether POM carbon storage is an additional viable option to store carbon long-term in some soils.

4. Plant Factors Contributing to SOM Stabilization

4.1 *Root and Soil Depth*

The topsoil or A horizon contains a major fraction of soil carbon.[70] Shoot litter contributes most to topsoil SOC, whereas root litter also contributes to subsoil SOC.[65] SOC distribution in soil layers reflects root distribution: in the top 10 cm of soil, 50% of maize roots and rhizodeposits are found. This number decreased to 30% at 10–20 cm, to 15% at 20–30 cm, and to 5% at 40–50 cm, where the longest roots reached.[24] To lower levels, plant-derived compounds are transported as DOM by rainwater and are often only detected after years.[65] Whereas carbon concentration decreases with soil depth, nitrogen concentration remains rather stable, which results in a lower C/N ratio with increased soil depth, impacting the efficiency of microbial biomass formation (see also Section 4.2,[35,71]).

Of the thousands of compounds detected in soils, most are present in all soil depths, but with differing abundances.[35] Hydrophilic compounds, lignin and other aromatic carbon compounds decrease in abundance with soil depth, and polymers are degraded.[35,71] These compounds are partially respired, and partially turned into microbial biomass and polymers. Extracellular microbial polymers, among them N-acetylgalactosamine and mannosamine, are present in significant amounts in soils,[57] and increase in abundance with soil depth. Overall, gram – bacteria are abundant in topsoil degrading readily available carbon, whereas gram + bacteria and fungi reside in subsoil, turning over more complex carbon sources with specialized enzymes.[57]

Regarding efficient carbon sequestration to soils, deep root systems are desirable. Due to lower temperatures and potentially low pH, microbial activities decrease in lower soil layers, and carbon is more readily incorporated into polymers. Also, because lower soil layers are generally less saturated with carbon, new carbon is more readily bound to minerals. Additional knowledge on the longitudinal and radial gradients of compounds around roots and differences between root types would enhance our spatiotemporal understanding of rhizodeposition, and make carbon sequestration efforts more efficient.

4.2 *C/N Ratio of Rhizodeposits*

Plant matter differs widely in its C/N ratio, whereas microbes require a relatively low C/N ratio for optimal growth:[8] Bacteria require a low C/N ratio of 3–5, and fungi a C/N ratio of 4.5–15.[72] Thus, quality of plant litter is defined as high when its C/N ratio is low. For high quality litter, an increase of MAOM is observed when minerals are not saturated.[7] For lower quality litter, POM and microbial respiration increase.[62] Thus, the determination of the C/N ratio of rhizodeposits and litter of major plant species, and the impact of these sources on microbial biomass and respiration and SOM formation is crucial. Further, the impact of abiotic and biotic stresses on C/N ratios warrants investigation.

Recognizing the low C/N ratio requirements of microbes, efforts were aimed at increasing the C/N ratio and thus SOM with nitrogen fertilizer applications. However, effects on SOM levels vary widely.[73,74] Nitrogen fertilization impacts the C/N ratio of rhizodeposits, but also changes the microbial community composition, soil pH, plant nutrient status and exudation, which may result in SOM degradation rather than increase. Mostly, fertilizer application results in higher aboveground carbon allocation. This can be coupled with unchanged root mass and rhizodeposition,[75] an increase in root mass and deposition,[17] or a reduction in rhizodeposition.[74,76] Similarly, effects of nitrogen fertilization on soil respiration are complex, with respiration either decreasing[77,78] or increasing.[15,79] To disentangle the effects of N fertilization on SOM and respiration, multiple aspects require consideration. First, the nutrient status of the plant: plants with low nitrogen levels cannot grow optimally and might thus release large amounts of carbon as rhizodeposits, fostering respiration and possibly direct MAOM formation. Nitrogen fertilization would thus result in elevated plant growth, lowering rhizodeposition and respiration. Second, presence and saturation of minerals define how many rhizodeposits are sorbed directly, making them inaccessible for microbial metabolism. Third, the C/N ratio of rhizodeposits and litter together with the C/N requirements of the microbiota define the substrate use efficiency, and thus, soil respiration.

4.3 *Plant Species Considerations*

The ratio of carbon partitioning between roots, exudates, and root respiration remains quite constant for specific plant species[19] but differs between species, which results in distinct rhizodeposition between ecosystems. Perennials (*e.g.* many grassland species) have elevated root carbon partitioning as they store carbon in belowground organs for later outgrowth. They also have elevated rhizodeposition levels compared to annuals or crops.[19,74] Crop belowground carbon peaks in the first 1–2 months, likely establishing a large root system for efficient nutrient uptake and microbial interactions. It decreases significantly afterwards.[17] In contrast, grass belowground carbon peaks at 2–4 months, and rhizodeposition remains higher throughout development.[17] In addition, plant species with high photosynthesis rate have elevated capacity for carbon sequestration.[15] However, high carbon fixation does not necessarily result in elevated SOM formation.[15]

Interestingly, high plant diversity supports higher SOM levels across soil layers. SOM levels generally correlate with high carbon sequestration as well as with high above- and belowground biomass.[80–82] DOM quantity and transport through soil levels also correlate with plant diversity.[83] A potential explanation for the observed SOM increase by diverse communities was formulated recently:[84] highest SOM levels were detected for plant communities generating soil pore sizes of 30–150 μm. These pores contained fine roots and root hairs with high exudation. Further, oxygen and water levels were balanced optimally, supporting high microbial activity to immobilize exuded carbon.[84]

Specifically the presence of legumes is a good indicator for elevated carbon deposition.[82,84] Compared to other plants, legumes feature high rhizodeposition rates and low C/N levels, resulting in high microbial carbon use efficiency and efficient SOM increase. Comparing annual and perennial legumes with wheat, legumes generally and especially perennials exhibited high C and N rhizodeposition rates in vegetative and reproductive stages.[85] Deep root systems also increase rhizodeposition, as shown for perennial lucerne. For this species, roots grown in topsoil sustained a high microbial biomass whereas roots in deeper soil layers were associated with fewer bacteria. Nitrogen fixation was abundant in topsoil, with elevated amino acid exudation by lucerne, supporting a distinct microbial community, and efficient rhizodeposition turnover by microbes.[57] Deeper roots were associated with fewer microbes with lower activity, and exudates were more efficiently incorporated into SOM.[57] Whereas topsoil roots interacted with symbiotic bacteria, deeper roots were likely instrumental in water and nutrient uptake, creating a functional differentiation within the root system.

Legume rhizodeposits are distinct from nonlegumes: the legume Acacia produced more high-molecular weight and aromatic compounds, more protein-like and carboxyl-rich alicyclic molecules found in the DOM fraction compared to the nonlegume Eucalyptus.[71] Interestingly, the dissolved nitrogen levels were similar between the species, which might reflect plant nutrient requirements. Mixed cultures of legumes and other plants may feature lower respiration levels compared to monocultures, as

shown for the legume *Lotus corniculatus* and ryegrass.[86] Thus, a mixture of (perennial) grasses and legumes with deep root systems might be a good starting point for developing systems for efficient C sequestration and immobilization.

5. Conclusions

Increasing soil organic carbon to lower atmospheric CO_2 levels and to increase soil fertility is challenging due to its multifactorial nature. When designing strategies to increase carbon sequestration, plants are a first central factor, as they fix CO_2 at different rates, partition carbon to belowground structures with varying efficiency, and release carbon into soils as soluble, gaseous, and polymeric rhizodeposits, and as root and shoot litter. Importantly, almost half of the fixed carbon is lost again as respiration. The remaining carbon is either bound directly to minerals and immobilized, turned over by microbes, or moving into lower soil layers. How efficiently new soil organic carbon is formed depends on many factors. From the plant perspective, a high belowground carbon allocation as observed in perennials versus annuals is desirable. Deep root systems and low C/N ratios usually elevate SOM, as does a high plant biodiversity.

To be able to increase carbon sequestration in a targeted manner, it is key to quantify different types of rhizodeposits and litter in various plant species, and how efficiently these fractions increase SOM. Further, the partitioning of plant carbon into DOM, POM, and MAOM needs to become clear, as well as the exchange of carbon between the different fractions. An interesting aspect is the spatiotempral release of compounds from roots throughout plant development, and the likely functional specialization of roots in topsoil versus subsoil. Differential exudation shapes distinct microbial communities associated with roots that perform different functions. These patterns need to be better understood so that it becomes clear what type of carbon is released in the distinct layers, how efficiently this carbon is turned over by microbes, and how that affects microbes residing further away from roots, and finally SOM formation. As exuded compounds can have contrasting effects on microbial activity and SOM formation, a better understanding of spatiotemporal exudation is needed as well as systematic studies on the effects of different chemical classes on microbial communities of different soil layers. After these effects are more clear in controlled conditions, this work needs to be expanded to entire ecosystems, taking into account specific plant communities, soils with distinct microbiomes and physiochemical properties, and environmental factors.

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