Plant roots and carbon sequestration

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Carbon management is a serious concern confronting the world today. A number of summits have been organized on this subject ranging from the Stockholm to Kyoto protocol. The current level of carbon in the atmosphere is about 375 ppm. It is estimated that if the carbon increases in the atmosphere at the present rate and no positive efforts are pursued, the level of carbon in the atmosphere would go up to 800–1000 ppm by the end of current century, which may create havoc for all living creatures on earth. Soil may be an important sink for the carbon storage in the form of soil organic carbon. This form of carbon is also a matter of serious concern for agricultural scientists across the globe because various researches reveal that the soil under intensive cultivation results in declining potential productivity due to reduction in soil organic carbon, thereby proving an obstacle for sustainable agriculture. Plants are the main source of the soil organic carbon, either from the decomposition of aerial plant parts or underground plant parts, e.g. roots in the form of root death, root exudates and root respiration. About 40% of the photosynthates synthesized in the plant parts is lost through the root system into the rhizosphere within an hour and the rate of loss is influenced by several factors, e.g. plant age, different biotic and abiotic stresses, etc. The rhizospheric environment of the plant is different compared to bulk soil with respect to physical, chemical and biological properties. Thus the aim of this article is to provide an insight on the contribution of plant roots for transfer of carbon from atmosphere to rhizosphere and further their significance in sustainable agriculture.

Keywords: Carbon, roots, sequestration, soil, sustainable agriculture.

SINCE the beginning of the industrial revolution, carbon dioxide concentration in the atmosphere has been rising alarmingly. Prior to the industrial revolution carbon concentration was around 270 ppm, but today it is around 372 ppm[1]. If the pace of increase in carbon concentration remains constant and efforts are not made to reduce it, carbon concentration in the atmosphere would go up to 800–1000 ppm by the turn of the current century[2]. Carbon sequestration refers to taking carbon dioxide from the atmosphere through crops and storing the carbon in soil in the form of soil organic matter. An effort has been made in this article to understand how plant roots play a significant role in carbon transfer from the atmosphere into the soil.

Soil carbon sequestration

Soils are the largest carbon reservoirs of the terrestrial carbon cycle. Soils contain about three times more C than vegetation and twice as much as that present in the atmosphere[3]. Soils contain much more C (1500 Pg of C to 1 m depth and 2500 Pg of C to 2 m; 1 Pg = 1×10^{15} g) than is contained in vegetation (650 Pg of C) and twice as much C as the atmosphere (750 Pg of C)[4]. Carbon in the form of organic matter is a key element to healthy soil. It is estimated that each tonne of soil organic matter releases 3.667 tonnes of CO_2, which is lost into the atmosphere. Similarly, the build-up of each tonne of soil organic matter removes 3.667 tonnes of CO_2 from the atmosphere[5]. The conversion of natural habitats to cropland and pasture, and unsustainable land practices such as excessive tillage frees carbon from organic matter, releasing it to the atmosphere as CO_2. Depleted of organic carbon, soils develop a carbon deficit. Soils can regain lost carbon by reabsorbing it from the atmosphere. This process is called carbon sequestration.

Through photosynthesis, plants convert CO_2 into organic forms of carbon, viz. sugars, starch and cellulose, also known as carbohydrates. In natural habitats, carbon from plants is deposited in the soil through roots and plant residues, such as fallen leaves.

Plant roots

Plant roots have ability to synthesize, accumulate and secrete a diverse array of compounds. More than 200 carbon

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compounds released from plant roots in the form of exudates are reported, which is termed as rhizodeposition[6]. These exudates contain simple water-soluble compounds such as amino acids, organic acids, sugar and various plant secondary metabolites to complex polymeric compounds such as polysaccharides, polypeptides and enzymes. On the basis of molecular weight, they can be grouped into high molecular-weight compounds such as mucilage, gelatinous material, covering root surfaces, ectoenzymes and low molecular-weight compounds such as organic acids, sugars, phenolics, amino acids, phytosiderophores, flavonoids and vitamins. Secretion of compounds into the rhizosphere is one of the most remarkable metabolic features of plant roots[7]. Cereals transfer 20–30% of total assimilated carbon into the soil, and half of this amount is subsequently found in the roots and about one-third is lost in the form of CO_2 by root respiration and microbial utilization of root-borne organic substances[8]. The remaining part of underground translocated carbon is incorporated into the soil microorganisms and soil organic matter. Pasture plants transfer about 30–50% of assimilate below the ground and their translocation patterns are similar to cereals. Researchers argue that photosynthetically fixed carbon in cereals and grasses is transported rapidly towards the root and can reach the external environment of the root within an hour[9]. On an average, the total amount of carbon translocated into the soil by cereal and pasture plants is approximately the same (1500 kg C/ha), if we consider the same growth period. However, during one vegetative period, cereals and grasses allocated below the ground are about 1500 and 2200 kg C/ha respectively[5]. This accounted for nearly 5 to 21% of all photosynthetically fixed carbon transferred to the rhizosphere through root exudates and ranged from 20 to 50% of plant biomass.

Plant roots and soil carbon

All the organic carbon found in the soil is primarily plant-derived. The two main sources of carbon in the soil are: (1) accumulation of soil organic matter due to the humification after plant death and (2) root exudates and other root-borne organic substances released into the rhizosphere during plant growth as well as sloughing of root hairs and fine roots by root elongation. The first mode of carbon sequestration is well documented, but carbon sequestration by plant roots is still under investigation. CO_2 fixed by crop plants and its translocation into the roots is a simultaneous process. Figure 1 reveals the pathway of carbon transfer from biosphere towards the rhizosphere[10]. Carbon is added in the soil system by plant roots through root death, root exudates and root respiration. It is difficult to quantify the contribution of these three separately. Metabolically active respiring roots are responsible for exudation and respired CO_2. However, non-metabolically active roots release carbon in its soluble form, which is termed as lysis. The mechanism of root death provides a greater insight into the understanding of carbon sequestration into the soil[11]. There are three states of root death:

(1) Non-apoptotic death, where metabolic activity immediately ceases and all the carbon and nutrients from the roots enter into the soil (e.g. in mechanically damaged roots).
(2) Non-apoptotic death, where the root become excised, remains metabolically active and slowly depletes and exhausts internal soluble C reserves (e.g. sewerage of the main roots).
(3) Apoptotic death, where re-translocation of both carbon and nutrients occurs to the other growing areas of the plants.

Theoretically, almost all soluble components present inside the root can be lost into the rhizosphere, but exudation is dominated by low molecular-weight solutes present in the cytoplasm in high concentration[12]. The continual release of carbon compounds from the roots into the soil falls into two categories: exudates that are lost simply as a result of passive diffusion and over which the plant exerts little control (basal exudation), and exudates which are released for a specific purpose and over which the plant exerts a close degree of control. Photosynthates transfer towards root vicinity via roots is in the form of organic molecules by the process of root lysis, root exudation and root death.

Plant roots and rhizospheric carbon

The compounds released by plant roots which deposit in the root sphere are many and complex (Table 1)[10], often ranging from mucilage, root border cells, extracellular enzymes, simple and complex sugars, phenolics, amino acids, vitamins, organic acids, nitrogenous macromolecules as purine and nucleosides to inorganic or gaseous molecules such as HCO_3, OH^-, etc.[12].

Transfer of carbon from the atmosphere to the soil through the plant system is largely dependent on a gradient which

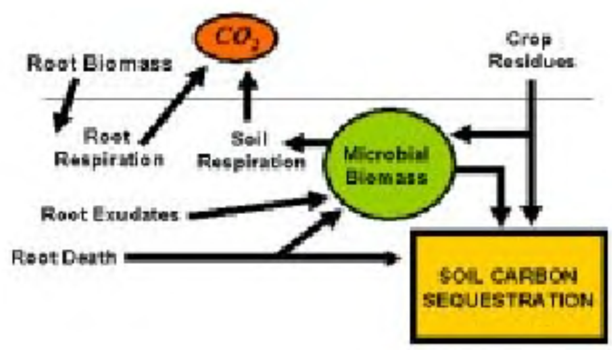

Figure 1. Carbon sequestration in soil via plant roots[18].

Table 1. Carbon compounds released by roots into rhizosphere[10]

Amino acids	Organic acids	Sugars	Vitamins	Purines/nucleosides	Enzymes	Inorganic ions/ gaseous molecules
α-Alanine	Citric	Glucose	Biotin	Adenine	Acid/alkaline phosphatase	HCO_3^-
α-Alanine	Oxalic	Fructose	Thiamin	Guanine	Invertase	OH^-
Asparagine	Malic	Galactose	Niacin	Cytidine	Amylase	H
Aspartate	Fumaric	Maltose	Pantothenate	Uridine		CO_2
Cystine	Acetic	Xylose				
Glutamate	Butyric	Rhamnose				
Glycine	Valeric	Arabinose				
Leucine	Piscidic	Deoxyribose				
Lysine	Formic	Oligosaccharides				
Methionine	Aconitic					
Serine	Lactic					
Threonine	Pyruvic					
Proline	Glutaric					
Valine	Malonic					
Tryptophan	Aldonic					
Ornithine	Erythronic					
Histidine	Tetronic					
Arginine						
Homoserine						
Phenylalanine						
Aminobutyric acid						
Aminoadipic acid						

is maintained continuously as a result of constant removal of exudated carbon from the soil solution either by biotic (e.g. soil microbial uptake) or abiotic process, such as sorption. Soil provides formidable technical barriers in measuring the flux of individual carbon compounds, but in a study on maize crop it was found that 0.5–10% of fixed carbon is transferred into the soil[6].

Role of rhizodeposits

Rhizodeposits play a significant role in improving soil health and quality. Carbon is lost from the roots leading to a proliferation of microbial population within the endo-rhizosphere, surface rhizosphere and outside the roots (ecto-rhizosphere). Specific compounds released by plant roots are involved in chemotaxis, hormonal activity and chemical defence against competitive plant species and detrimental microorganisms[13]. It solubilizes certain nutrients from the soil, such as Fe, Mn and P (Table 2)[10]. Root exudates could enhance microbial activity by providing substrates for co-metabolism and may also have enzymatic properties that can breakdown contaminants, e.g. increased degradation of phenanthrene by oat exudates, pyrene by corn exudates, atrazine by poplar exudates and 2-chlorobenzoic acid by wild rye exudates. Individual chemical components such as flavonoids, aromatic acids, amino acids and dicarboxylic acids function as specific chemo-attractants for microorganisms. Once the carbon is released in the rhizosphere, many bacteria may multiply rapidly in response to growth stimulation by quercetin or other flavonoid molecules released by plants and in turn promote further exudation of new or existing flavonoids into the rhizosphere. Organic acid does lower rhizosphere pH, making P and micronutrients such as Mn, Fe and Zn readily available in calcareous soils. However, the relationship between organic acid and rhizosphere acidification is not that simple[14]. Extrusion of H^+ from roots depends on the amount of anions absorbed by roots relative to cations gaseous molecules (e.g. CO_2, H_2), which play an important role in mineral nutrition of plants. Roots release CO_2 into the soil environment from carbohydrate respiration and stimulation by lumichrome, a plant and bacterial exudate molecule. These accumulations are up to 17.5% in the root zone and increased levels of CO_2 can enhance the dissolution of soil $CaCO_3$ to produce Ca^{2+} for plant uptake[12]. Similarly, HCO_3^- excreted directly by plant roots into the soil can aid the dissolution of calcite to yield soluble supplies of Ca^{2+} for plant nutrition. CO_2 released by roots can also have indirect effects on N and P nutrition. Phenolic compounds solubilize Fe, P and other nutrients from unavailable sources for uptake by plants. Dicots release phenolic molecules that influence Fe and P mobility due to formation of stable chelates of Fe and Al present in insoluble Fe- and Al-phosphates, thereby increasing the solubility of Fe and P for plant uptake. Other changes in exudate composition could change the rhizosphere pH, thereby immobilizing or mobilizing contaminants in the soil[15].

Root exudates are thought to be a major source of substrate of microbial activity in the rhizosphere. Rhizodeposits act as chemical attractants and repellants, and may regulate the soil microbial community in their immediate

Table 2. Possible functional role of root exudate components in the rhizosphere[10]

Component	Rhizosphere function
Phenolics	Nutrient source
	Chemo-attractant signals to microbes
	Microbial growth promoters
	Nod gene inducers in *rhizobia*
	Nod gene inhibiters in *rhizobia*
	Resistance inducers against phytoalexins
	Act as chelaters
	Phytoalexin against soil pathogens
Organic acids	Nutrient source
	Chemo-attractant signals to microbes
	Chelaters of poorly soluble mineral nutrients
	Acidifiers of soils
	Detoxifiers of Al
	Nod gene inducers
Amino acids and phytosiderophores	Nutrient source
	Chemo-attractant signals to microbes
	Chelaters of poorly soluble mineral nutrients
Vitamins	Promoters of plant and microbial growth
	Nutrient source
Purines	Nutrient source
Enzymes	Catalysts for phosphorus release from organic molecules
	Biocatalyst for organic matter transformation in soil
Root border cells	Produce signals that control mitosis
	Produce signals controlling gene expression
	Stimulate microbial growth
	Release chemo-attractants
	Synthesize defence molecules for the rhizosphere
	Act as decoys that keep root cap infection-free
	Release mucilage and proteins
Sugars	Nutrient source
	Promoters of microbial growth

vicinity, cope with herbivores, encourage beneficial symbiosis, change the chemical and physical properties of the soil, and inhibit the growth of competing plant species[16]. The enhanced microbial population may be either beneficial or detrimental to plant growth.

Beneficial effect of microbial colonies may include mobilization of nutrients, phytohormone production and vesicular arbuscular micorrhizal infection. Detrimental effect may include nutrient immobilization, competition for substrate and plant pathogenesis. Root exudates also attract pathogenic microbes and promote the growth of plants, mutualistic fungi and rhizobacteria. Intense colonization of the rhizosphere can itself lead to stiff competition between microbes and the plant for nutrient resources. Chemical molecules of root exudates govern the development of plant–fungal symbiosis and provide powerful signals that alert the mycorrhizal fungi of the presence of a host plant. Root-derived phenolic compounds are thought to be involved in the genetic triggering of legume–*Rhizobium* interaction and infection by pathogenic microorganisms such as *Agrobacterium* may stimulate germination of propagules of pathogenic fungi-induced chemotaxis in various microorganisms, and participate in the microorganism recognition process. They are a major localized source of nutritional organic carbon and nitrogen for rhizosphere microorganisms and plant growth[17].

Plant roots, carbon sequestration and sustainability

The sequestration of carbon in soils used for agriculture, forestry and land reclamation has been recognized as a potential option to mitigate global change. Organic matter constitutes 1 to 8% of the weight of most soils. Because of the weight of soils to the plant rooting depth at which carbon accumulates, soils of the world store about 1600 Pg of carbon[18]. This represents a carbon storage capacity of the soil that is twice compared to the atmospheric carbon. The annual global rate of photosynthesis is generally balanced by decomposition and represents one-tenth of the carbon in the atmosphere or one-twentieth of the carbon in soils[19].

Archaeological evidence indicates that CO_2 content in the atmosphere had a great influence on agriculture. Successful plant breeding, fertilization and better pest control would not have been as effective if the major plant nutrient, i.e. carbon had not been increasing. Carbon, nitrogen, oxygen and hydrogen are the building blocks of life on earth. They also are the most important constituents of soil organic matter. The earth's carbon cycles have the ability to restore and even increase the soil organic matter content, improve fertility, increase the water-holding capacity, and improve tilth if properly established scientific principles are applied to good soil management and sustainable agriculture.

Soil organic carbon is composed of a wide range of compounds that decompose at different rates depending on their chemistry, soil temperature and moisture, organisms present, association with soil minerals and the extent of aggregation[20]. Excess exploitation results in loss of soil fertility and can be attributed to the misuse of the soil and its organic matter. Man's success in responding to the latest challenge of global climate change will depend on how we manage this vital resource. A proportion of the soil organic carbon present in undisturbed soils has been burned, lost through agriculture practices. This has contributed to the global rise of CO_2 in the atmosphere. However, soil organic carbon is not a non-renewable resource; unlike coal, gas and oil, it is a renewable resource. We can put it back through proper management practices[21] which help reduce the overall greenhouse gases. Plant roots increase soil organic matter, which will store more atmospheric carbon and result in greater soil fertility, better soil tilth, greater water-holding capacity, and reduced erosion. It also will make plants more stress-resistant and thus be able to better withstand the predicted climatic fluctuations[22]. Control of water levels during periods of non-plant growth could result in C sequestration, improved water quality, flood control and better wildlife habitat. Carbon deposits in soil result in the building of soil organic matter, which will reduce soil erosion, nutrient loss, environmental pollution and improve nutrient mobilization, water-retention capacity and microflora. Thus this could play an important role in sustainable agriculture[23].

Agricultural practices for carbon sequestration

The carbon content of most agricultural soils is now about one-third less than that in its native condition as either forest or grassland. Fortunately, modern agriculture has stopped this net loss to the atmosphere[24]. This has come about through higher levels of biomass production, the return of greater proportions of crop residue to the land, use of cover crops and conservation tillage such as reduced and no till[25]. Simultaneously, better fertility management through soil testing, precision farming and proper nutrient application can also lead to lowering of greenhouse gas emissions. Irrigation waters trap some CO_2 because irrigated soils produce high crop residues which sequester carbon at a rate of 0.16 to 0.27 Pg per year[22]. Precision farming holds promise for better nutrient control and pesticide application, which further improves organic matter in the soil[26]. The improved soil organic matter levels will sequester CO_2, enhance sustainability and reduce soil erosion. Plant residues in agricultural soils do not represent a large storage pool. However, their management influences water penetration, wind and water erosion and the extent of formation of soil organic matter, thus affecting long-term soil fertility and carbon storage[26].

Conclusion

Plant root acts as a medium for transfer of atmospheric carbon into the soil in the form of carbon-containing compounds, viz. organic acid, phenolic acid, amino acid, etc. Root lysis and root exudates contribute significant quantities of carbon deposited in sub-surface soil. These deposits have the potential for a greater contribution to long-term soil carbon sequestration due to slow oxidation than surface soil. Carbon components affect agriculture by reducing pH, nutrient mobilization and microbial growth. The exact amount of sequestration depends on land-management practices, edaphic factors, climate, and the amount and quality of plant and microbial inputs. Studies on carbon transfer via roots will generate a whole new idea that will allow better decisions on the specific use of crop rotation, fertilization and other methods of soil amelioration. These approaches provide valuable tools for addressing many problems in both natural and agricultural soils. Carbon sequestration will certainly contribute in reducing atmospheric CO_2 concentration and will mitigate drought, salinity stress and desertification. It will certainly be the most viable approach towards sustainable agriculture. Thus, sequestered soil carbon may be used for agriculture, forestry, and will be a potential option to mitigate global change.

1. Sage, R. F., Was low atmospheric CO_2 during the pleistocene a limiting factor for the origin of agriculture. *Global Change Biol.*, 1995, **1**, 93–106.
2. Whipps, J. M., Carbon economy. In *The Rhizosphere* (ed. Lynch, J. M.), Wiley, New York, 1990, pp. 59–97.
3. Batjes, N. H., Total C and N in soils of the world. *Eur. J. Soil Sci.*, 1996, **47**, 151–163.
4. USEPA, Inventory of US greenhouse gas emissions and sinks, 1990–1994. Washington DC, 1995.
5. Bowen, G. D. and Rovira, A. D., The rhizosphere and its management to improve plant growth. *Adv. Agron.*, 1999, **66**, 1–102.
6. Kuzyakov, Y. and Domanski, G., Carbon input by plants into the soil. *Rev. J. Plant Nutr. Soil Sci.*, 2000, **163**, 421–431.
7. Darrah, P. R., The rhizosphere and plant nutrition: a quantitative approach. *Plant Soil*, 1993, **155/156**, 1–20.
8. Gregory, P. J. and Atwell, B. J., The fate of carbon in pulse labelled crops of barley and wheat. *Plant Soil*, 1991, **136**, 205–213.
9. Kuzyakov, Y., Kretzschmar, A. and Stahr, K., Contribution of *Lolium perenne* rhizodeposition to carbon turnover of pasture soil. *Plant Soil*, 1999, **231**, 127–136.
10. Paul, E. A. and Clark, F. E., *Soil Microbiology and Biochemistry*, Academic Press, CA, 1996, 2nd edn.
11. Jones, D. L., Organic acids in the rhizosphere – a critical review. *Plant Soil*, 1998, **205**, 25–44.

12. Kuzyakov, Y., Ehrensberger, H. and Stahr, K., Carbon partitioning and below-ground translocation by *Lolium perenne*. *Soil Biol. Biochem*., 2001, **33**, 61–74.
13. Haynes, R. J., Active ion uptake and maintenance of cation–anion balance: a critical examination of their role in regulating rhizosphere pH. *Plant Soil*, 1990, **126**, 247–264.
14. Arshad, M. and Frankenberger Jr. W. T., Plant growth-regulating substances in the rhizosphere: Microbial production and functions. *Adv. Agron*., 1998, **62**, 45–151.
15. Gahoonia, T. S. and Nielsen, N. E., The effect of root-induced pH change on the depletion of inorganic and organic phosphorus in the rhizosphere. *Plant Soil*, 1992, **143**, 183–189.
16. Jones, D. L. and Darrah, P. R., Role of root derived organic acids in the mobilization of nutrients from the rhizosphere. *Plant Soil*, 1994, **166**, 247–257.
17. Meharg, A. A. and Killham, K., Loss of exudates from the roots of perennial ryegrass inoculated with a range of micro-organisms. *Plant Soil*, 1995, **170**, 345–349.
18. Dakora, F. D. and Phillips, D. A., Root exudates as mediators of mineral acquisition in low-nutrient environments. In *Food Security in Nutrient-Stressed Environments: Exploring Plants' Genetic Capabilities* (ed. Adu-Gyamfi, J. J.), Kluwer, Dordrecht, 2000.
19. Lal, R. J. M., Kimble, R. F., Follett and Cole, C. V., The potential of US cropland to sequester carbon and mitigate the greenhouse effect. Ann Arbor Press, Chelsea, MI, 1998.
20. Nordt, L. C., Wilding, L. C. and Drees, L. R., Pedogenic carbonate transformations. In leaching soil systems: Implications for global change. In *Global Climate Change and Pedogenic Carbonates* (eds Lal, R. *et al.*), Lewis Publishers, Boca Raton, FL, 2000, pp. 43–64.
21. Bruce, J. P., Frome, M., Haites, E., Janzen, H., Lal, R. and Paustian, K., Carbon sequestration in soils. Soil and Water Conservation Society's Carbon Sequestration in Soils Workshop, Calgary, Alberta, Canada, 21–22 May 1998.
22. Bouwman, A. F. and Leemans, R., The role of forest soils in the global carbon cycle. In *Carbon Forms and Functions in Forest Soils* (eds McFee, W. W. and Kelly, J. M.), SSSA, Madison, WI, 1995, pp. 503–526.
23. Swinnen, J., Van Veen, J. A. and Merckx, R., Carbon fluxes in the rhizosphere of winter wheat and spring barley with conventional vs integrated farming. *Soil Biol. Biochem*., 1995, **27**, 811–820.
24. Zobel, R. W., Soil environmental constraints to root growth. *Adv. Soil Sci*., 1992, **19**, 27–51.
25. Nye, P. H., Changes of pH across the rhizosphere induced by roots. *Plant Soil*, 1981, **61**, 7–26.
26. Hinsinger, P., How do plant roots acquire mineral nutrients? Chemical processes involved in the rhizosphere. *Adv. Agron*., 1998, **64**, 225–265.

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