

Are plant roots only “in” soil or are they “of” it? Roots, soil formation and function

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REVIEW**RUSSELL REVIEW****Are plant roots only “in” soil or are they “of” it? Roots, soil formation and function****Peter J. Gregory** 

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Abstract

Roots are near-ubiquitous components of soils globally but have often been regarded as separate from the soil rather than a substantial factor in determining what soil is and how it functions. The start of rapid soil formation commenced about 400 million years ago with the emergence of vascular plants and the evolution of roots and associated microbes. Roots and associated microorganisms contribute significantly to soil formation by altering rocks and soil minerals through a variety of biogeochemical processes and supply carbon to a depth that can have long residence times. Living root inputs of carbon via rhizodeposits are more efficient than shoot and root litter inputs in forming slow-cycling, mineral-associated soil organic carbon pools. The current functionality of soils in providing food and fuel and fibres, supplying plant nutrients, filtering water and flood regulation, and disease suppression are all dependent on the activities of plant roots. Roots are actively communicating and collaborating with other organisms for mutual benefit, and the signals underlying this modulation of the rhizosphere microbiome are being identified. In this review I examine how plant roots (an organ not an organism) affect soil formation and function and conclude that, from several perspectives, roots are not just “in” soil but “of” it and that definitions of soil should recognise this. A possible definition is: “Soils are altered surficial rock or sediment, composed of organic matter, minerals, fluids, and organisms whose formation and functionality are influenced by biogeochemical weathering and interactions of these components with plant roots.”

Highlights

- Paleoclimatic and paleosoil research shows the key role of roots and mycorrhiza in soil formation.
- Deep roots and living root inputs are substantial contributors to long-term C storage.
- Root/microbe signalling facilitates mutualistic symbioses, nutrient uptake and disease suppression.

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- Definitions of soil should explicitly include roots as an important component of the soil system.

KEYWORDS

arbuscular mycorrhiza, biogeochemical cycling, carbon sequestration, dynamics, N fixation, rhizodeposit, rhizosphere, root, soil acidity, soil aggregate, soil formation

1 | INTRODUCTION: “JUST WHERE DOES THE SOIL BEGIN?” (JENNY, 1941)

The advent of life on Earth not only changed the composition of the atmosphere but also resulted in the formation of soil (Dahl & Arens, 2020; Edwards et al., 2015; Kenrick et al., 2012; Schwartzman & Volk, 1989). The evolution of photosynthesising organisms about 850 million years ago as microbes and eukaryotes on land introduced organic carbon compounds into the surface sediments and began the development of proto-soils and palaeosoils (soils with little organic material and bioavailable elements; Dahl & Arens, 2020). Early land plants had no vascular systems and rhizoid-based rooting systems (Kenrick & Strullu-Derrien, 2014) but during the Devonian Period (416–360 million years ago) vascular plants evolved with roots and symbiotic associations with fungi. Together these facilitated the greater cycling of nutrients by accelerating the breakdown of minerals in soils and rocks, and the absorption of larger amounts of atmospheric carbon dioxide (Brundrett, 2002; Edwards et al., 2015). Simultaneously, plants oxygenated the atmosphere leading to the emergence of arthropods and oligochaetes that transformed and buried organic matter thereby enhancing soil formation (Ponomarenko, 2015).

Co-evolution of plant-fungal symbioses appears to have commenced in the Middle Ordovician era (470 million years ago). There is evidence for associations with rhizoids of liverworts and putative lichens, but the earliest evidence (411.5 million years ago) for mycorrhiza-like fungal symbioses with land plants is in early Devonian Rhynie Chert – before plants had evolved roots (Leake & Read, 2017; Remy et al., 1994). Studies of the Rhynie Chert show that fungal vesicles and highly branched structures appearing to be arbuscules evolved more than 400 million years ago and have changed little since (Leake & Read, 2017). The most recently evolved and diverse group of land plants, the Angiosperms (167–199 million years ago), are strongly mycorrhizal with over 85% forming the symbiosis (Brundrett, 2009). Arbuscular mycorrhizal fungi (AMF) are the dominant association with 72% of plant species forming such symbiotic relations. Other fungal symbioses include ectomycorrhizal associations with basidiomycetes and ascomycetes (2% of

plant species, mainly trees and woody shrubs) and ericoid mycorrhiza (1.4% of plant species; Leake & Read, 2017).

The exact contributions of non-vascular plants to geochemical cycling and the development of soils are still areas of contention both with regards to the roles of rhizoids of specific land-colonising plants (mosses, liverworts, lichens and their associated bacterial and fungal symbionts) and the amount of weathering they induced (Edwards et al., 2015; Lenton et al., 2012; Mitchell et al., 2016; Quirk et al., 2015). In microcosms containing either granite or andesite, studies with moss produced malic, citric, glyceric and succinic acids and released nearly 60 times more phosphorus than the controls without moss (Lenton et al., 2012). This increased phosphate weathering was postulated to contribute to the extensive phosphate deposits found in shallow water in the late Ordovician period and to the reduction in atmospheric CO₂ leading to the growth of ice sheets (Lenton et al., 2012). These conclusions were challenged by Quirk et al. (2015) who measured weathering by liverworts partnered by AMF from basalt grains that were amplified 3–7-fold for calcium and 9–13-fold for phosphorus. Allowing for the shallow depth of rhizoids and AMF this suggested only limited effects on land to ocean fluxes of P, Ca and Mg. A partial explanation for these differing results lies in the choice of non-vascular plant for the experiments. For example, Jackson (2015) showed that although all species of mosses and lichens enhanced weathering of granitic gneiss in a boreal forest, their secondary mineral-forming activities differed with differences also within species and genera of moss. Lichens altered silicates such as feldspars to clay minerals (illite and chlorite) more effectively than mosses but did not cause sufficiently intense leaching of Si and metals to produce kaolinite. Mosses typically produced a greater quantity of expandable clay minerals than lichens, but only mosses with high rock-derived element concentrations and high Mg:Ca ratios produced kaolinite (Jackson, 2015). Unlike the lichens, all but one of the moss species formed authigenic amphiboles and pyroxenes implying that not only are there major differences in the intensity of weathering between mosses and lichens but that the basic mechanisms of weathering and secondary mineral-forming processes are different (Jackson, 2015). Similarly, mosses and lichens also differ in their production of soluble phenolic compounds (PCs) with cyanobiont-containing lichens

having 3–5 times more soluble PCs than other lichens and mosses; such PCs are highly reactive with potentially important roles in humification and weathering (Zavarzina et al., 2019).

Fossil evidence indicates that early land colonisation involved communities of organisms comprising bacteria, arthropods, lichens, fungi, algae and small plants including liverworts, hornworts and mosses. These plants were similar to the components of modern cryptogamic ground covers (CGCs). Studies of CGCs from Iceland employing X-ray micro-computed tomography and microscopy show that while thalloid CGC organisms (liverworts, hornworts) developed thin (<1 cm) organic layers at the surface with limited subsurface structural development, leafy mosses and communities of mixed organisms formed thicker profiles (up to 7 cm) that were more complex structurally and more organic-rich (Mitchell et al., 2016; Mitchell et al., 2021). Smectite formed under liverwort, but not moss, CGC soils (Mitchell et al., 2016). These results show that the thickness and structure of proto-soils were determined by the type of colonising organism(s) and suggest that the shift from flattened to upright, leafy plant structures facilitated the evolution of more complex soils through the Palaeozoic period (Mitchell et al., 2021).

The evolution of plant life and associated rhizoids, roots and microbes had significant effects on weathering of rocks increasing its rate and the mobilisation of plant nutrients (especially P) by contacting a larger surface area of minerals and producing CO₂ via respiration that changed silicates to bicarbonates and hydroxides (Raven & Edwards, 2001). Nitrogen fixation by a range of organisms coupled with this increased weathering produced organic materials in fissures in rocks and a surface layer resembling soil. The further evolution of land-based plants with roots increased this weathering activity and led to a 10-fold reduction in atmospheric CO₂ concentration from 400 to 350 million years ago as C was transferred to plants and soil (Beerling & Berner, 2005; Raven & Edwards, 2001).

Given this acknowledged role of plants in the evolution of biogeochemical cycling and geomorphology, surprisingly little attention has been paid by soil scientists until recently to the part played by plant roots in the formation and development of soil and soil types. In his classic work on *Factors of Soil Formation*, Jenny (1941) treated soil as a physical system with properties that are functionally related to each other. To distinguish soil from other natural bodies, the properties can be assigned qualitative and/or quantitative limits but the boundary between soil and other natural bodies is often ill-defined. Jenny illustrates this with a figure of an ecosystem comprising a forest, soil and regolith and by posing the question where does the soil begin? Starting from the atmosphere and approaching the surface, is the forest litter part of the soil or of the surroundings (environment)?

This challenging question was posed to me on my first day as an undergraduate student of soil science in beech woodland near Reading by Dr John Dalrymple sparking lively debate. L, F and H horizons have been included as elements of soil profile descriptions so that the leaves and other dead parts of shoots are recognised as part of the soil and separate from the living plant. However, if the tree is approached from the bottom, the distinction between vegetation (root) and soil is less well defined and often arbitrary. Jenny acknowledged that living root hairs and fine roots are inseparable operationally from the soil so frequently included as components of soil properties. They are, in fact, part of a closely coupled soil/root/plant system that connects above- and below-ground domains facilitating the transfer of solar energy (Janzen, 2015; Jochum & Eisenhauer, 2022).

The purpose of this review is to explore and re-evaluate that close coupling. Plants cover about 80% of the Earth's terrestrial surface (forests 30%, grasslands 30% and tundra 20%) so that, apart from deserts and beneath ice sheets, most soil types are vegetated for at least part of a year (NASA, 2020). Recent recognition of the role of roots in generating a multiplicity of processes at root/soil interfaces has greatly increased our understanding of carbon and nutrient dynamics in soils (Gregory, 2006a and b; Jones et al., 2009; Moreau et al., 2019; Vetterlein et al., 2020) but much remains to be integrated into a full appreciation of how soils evolve and function. For example, Young and Bengough (2018) highlight that focussing on the microbiome as a measure of soil functioning ignores the substantial control that roots exert over their local environment and thus on the microbial community. These interactions are complex and may also be influenced by plant genotype, spatiotemporal dynamics of root growth and the composition of root exudates (Aira et al., 2010; Bonkowski et al., 2020; Young & Bengough, 2018). This review examines how roots of vascular plants (see Raven and Edwards (2001) and Kenrick and Strullu-Derrien (2014) for the characteristics of roots and their distinction from rhizoid-based rooting systems) affect processes involved in soil formation and function and discusses the question of whether they are merely in soil or a part of it.

2 | ROOTS AND SOIL FORMATION

2.1 | Alteration of soil minerals

Interest in the role of roots in promoting biological weathering has been stimulated by the need to better understand historical changes in the Earth's climate and the cycling of carbon and nutrients on the land and in the oceans (Beerling & Berner, 2005; Comas et al., 2012;

Wen, Sullivan, et al., 2021). Evolutionary advances in plants and mycorrhizal associations have significantly affected geochemical carbon and plant nutrient cycles (Leake & Read, 2017; Finlay et al., 2020; Figure 1). Evidence for biologically-mediated alteration of minerals and rock types is now available including apatite (Calvaruso et al., 2013; Morra & Olsen, 2020), carbonates (Thorley et al., 2015; Wen, Sullivan, et al., 2021), kaolinite (Austin et al., 2018), olivine (Callot et al., 1987) and shales (Hasenmueller et al., 2017). These alterations are the consequence of a variety of root/microbe processes including acid and siderophore release, respiration, associated uptake of plant nutrients and physical fracturing with each operating in specific circumstances (Finlay et al., 2020; Hasenmueller et al., 2017).

Transformations of silicate minerals in soil by roots have a long history of study especially with respect to plant uptake of ions such as potassium, ammonium and magnesium. Kuchenbuch and Jungk (1984) measured potassium uptake by maize seedlings and found that up to 80% of the plant uptake was contributed by the root-induced release of non-exchangeable K derived from phyllosilicate lattices. In a laboratory study in which ryegrass and rape were grown in containers inducing a mat of roots to grow against a film of agar containing the K-rich mica phlogopite, the release of interlayer K and exchange with cations such as Ca and Mg resulted in the

transformation of the mica to vermiculite (Hinsinger, 1998; Hinsinger & Jaillard, 1993). Similarly, an increase in mixed-layer minerals was found when K release by a root mat of alfalfa was measured in soil containing illite (Vetterlein et al., 2013). While the rate of transformation was rapid in both of these laboratory studies, slower but significant rates have also been observed in field conditions. For example, Kodama et al. (1994) compared bulk and rhizosphere soil from maize crops at three sites and determined that the content of vermiculite and interstratified clay minerals was about 6% larger in the rhizosphere soil than the bulk soil; non-phyllosilicate and mica content was about 5% less in the bulk soil than the rhizosphere soil. Root-induced release of non-exchangeable ammonium from clay minerals such as smectites and vermiculite accompanied by the exchange of ammonium by H^+ can also leave the lattice in a more expanded state (Scherer & Ahrens, 1996). Similarly, uptake of Mg by wheat and oat from the Mg-rich clay mineral palygorskite was shown to result in kaolinite formation in pot experiments (Salehi & Tahamtani, 2012). In a field study in orange orchards in which X-ray diffraction (XRD) patterns of soil samples from bulk and rhizosphere regions were obtained, Shahrokh et al. (2020) showed that the ratio of kaolinite to palygorskite increased in the rhizosphere by 40% compared to the bulk soil as the age of the orchard increased from 5 to 10 to 20 years. Transmission

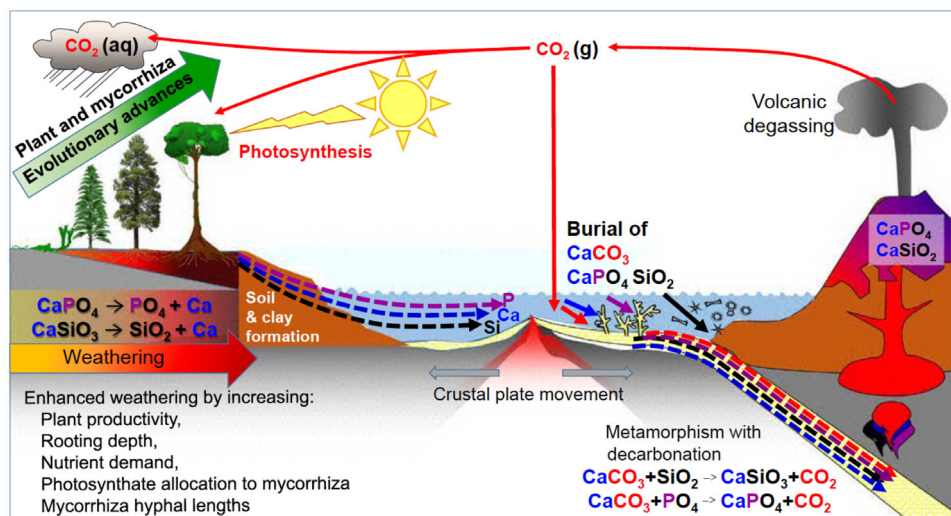


FIGURE 1 The effects of evolutionary advancement in plants and mycorrhizal associations in the geochemical carbon cycle, increasing the weathering of calcium (Ca)-, phosphorus (P)- and silicon (Si)- bearing minerals and generating clay minerals. Plants and their mycorrhizal fungi have increased the rates of dissolution of continental silicates, especially apatite ($CaPO_4$) and calcium silicate ($CaSiO_3$), but a portion of the Ca, P and Si is washed into the oceans increasing their productivity. Some of the Ca and P ends up in limestone and chalk deposits by marine organisms thereby sequestering carbon dioxide (CO_2) dissolved in the oceans into calcium carbonate ($CaCO_3$) rock for millions of years. Dissolved Si is used in sponges, radiolarians and diatoms that can accumulate on the sea floor. The ocean sediments are recycled by subduction or uplift by tectonic forces, with volcanic degassing and eruptions of base-rich igneous rocks such as basalt returning Ca, P, Si and other elements (e.g. magnesium, Mg) back to the continents, thereby reinvigorating ecosystems with new nutrient supplies through weathering. Reproduced with permission by Elsevier from Leake and Read (2017)

electron microscopy of the rhizosphere soil showed that this neoformed kaolinite had the typical hexagonal morphology of kaolinite. Interestingly, the same measurements in lemon orchards up to 50 years old grown on a similar soil type showed no significant neokaolinite formation in the rhizosphere. Whether this was an effect of the tree or a combination of tree/mycorrhizal association is unknown.

Changing land use, with associated changes in vegetation, can also alter the pattern of mineral transformation. As described above, the growth of annual crops tends to deplete K and other cations from clay mineral interlayers in the topsoil resulting in a higher abundance of clay minerals with expandable layers (Barré et al., 2007; Hinsinger, 1998). When cultivated soils are re-forested, this dynamic is reversed. For example, Austin et al. (2018) showed (by XRD) that planting of loblolly pines (*Pinus taeda*) on a previously cultivated kaolinite-dominated Ultisol increased the illite-like mineral abundance at the surface most likely because of K uplift by deep tree roots, biomass decomposition at the surface and subsequent storage of K in soil minerals.

Land use and associated vegetation affect rates of weathering because rooting depth is typically greater beneath forests than grasslands or annual arable crops (Jackson et al., 1996). Roots also affect weathering rates by changing regolith and soil structure and thereby hydrological processes. Roots and associated mycorrhizal fungi can physically fracture and etch rocks through the production of organic acids (Hasenmueller et al., 2017; Leake et al., 2008; Thorley et al., 2015) and, having opened up the rock, decaying roots leave a network of biopores through which water can move. This is particularly noticeable beneath shrublands and forests where deep and thick roots promote abundant macropores between the surface and deeper regolith enhancing the biotic generation of downward-propagating weathering agents (Billings et al., 2018) and increasing the drainage of water to depth (Pawlik et al., 2016). Pawlik et al. (2016) reviewed the many effects of tree roots on rates of weathering through biomechanical processes such as uprooting, root groove development, soil displacement and infilling of stump holes and root cavities together with biochemical processes. They concluded that many aspects are poorly understood especially the influence of specific tree species and their interactions with different environmental settings. Numerical simulation of multiple regulators of weathering on a limestone/mudstone bedrock found that weathering was enhanced by an order of magnitude when roots were present compared to without roots and that the deeper roots of forests compared to grasslands enhanced weathering by about 17% to 200% as infiltration rates increased by two orders of magnitude

(Wen, Sullivan, et al., 2021). Carbonate weathering can also be increased by roots as a result of the deeper distribution of carbon via root and microbial biomass leading to enhanced respiration and elevation of CO₂ concentration and associated acidity which increase carbonate solubility and hence weathering (Thorley et al., 2015; Wen, Sullivan, et al., 2021). The type of tree and associated mycorrhizae may also influence weathering of carbonates through a combination of root architecture and organic acid production by fungi. For instance, Thorley et al. (2015) found differences in calcite and dolomite weathering with the fastest rates in soils with an angiosperm tree/ectomycorrhizal combination.

2.2 | Inputs of carbon into soils via roots

The subject of root contributions of carbon to soil has received increasing interest both in relation to the evolution of land-based plants and their contribution to biogeochemical weathering and to the contribution that they might make in sequestering carbon and mitigating climate change (Pausch & Kuzyakov, 2018; Poirier et al., 2018; Sokol et al., 2019). Fine root production has been estimated to be 22% of global terrestrial net primary production (McCormack et al., 2015) with rhizodeposits (root cap cells, mucilage, exudates and lysates, and decaying root tissues) a major source of stable C inputs to soil (Rasse et al., 2005; Sokol et al., 2019; Keller et al., 2021).

A key element in improved understanding of C storage has been to gain better estimates of rooting depth and, particularly, the role and functions of deep roots (Canadell et al., 1996; Pierret et al., 2016; Poirier et al., 2018). Major uncertainties exist regarding the rooting depth of many plant species, vegetation types and ecosystems not least because of the difficulties in measuring them (Maeght et al., 2013; Pierret et al., 2016). Roots are rarely measured to their full depth so many published data are based on extrapolation of measurements in upper layers assuming an exponential decline of root density with depth (Jackson et al., 1996; Pierret et al., 2016). This can lead to substantial underestimates of the true rooting depth because, while root density typically declines exponentially with depth in upper layers of soils that are regularly rewetted, a few roots can grow to a considerable depth depending on soil depth, regolith structure and soil moisture status (Harper & Tibbett, 2013). This is especially the case for many trees and shrubs (see drawings by Kutschera, 1960 and Kutschera et al., 1997 for examples) but may also occur in crop species with pronounced taproots (e.g., cauliflower [Kage et al., 2000] and sugar beet [Brown & Biscoe, 1985]).

TABLE 1 Average maximum depth of rooting and depth of deepest root for 11 terrestrial biomes (from Canadell et al., 1996).

Biome	Average maximum rooting depth (m)	Deepest root (m)
Tundra	0.5 ± 0.1	0.9
Boreal forest	2.0 ± 0.3	3.3
Cropland	2.1 ± 0.2	3.7
Temperate grassland	2.6 ± 0.2	6.3
Temperate deciduous forest	2.9 ± 0.2	4.4
Tropical deciduous forest	3.7 ± 0.5	4.7
Temperate coniferous forest	3.9 ± 0.4	7.5
Sclerophyllous shrubs and trees	5.2 ± 0.8	40.0
Tropical evergreen forest	7.3 ± 2.8	18.0
Desert	9.5 ± 2.4	53.0
Tropical grassland/savanna	15.0 ± 5.4	68.0

Rooting depth ranged from 0.3 m for tundra species to 68 m for *Boscia albitrunca* in the central Kalahari in a survey of 253 woody and herbaceous species worldwide with 194 species with roots >2 m deep and 22 species with roots >10 m (Canadell et al., 1996). Maximum rooting depth averaged across plant species ranged from 0.5 ± 0.1 m for tundra to 15.0 ± 5.4 m for tropical grassland/savanna (Table 1). Averaged across biomes, and omitting annual crops, the average rooting depth was 7.0 ± 1.2 m for trees, 5.1 ± 0.8 m for shrubs and 2.6 ± 0.1 m for herbaceous plants (Canadell et al., 1996) so trees and shrubs, especially, can introduce C to substantial depths. Schenk and Jackson (2002) undertook a similar exercise but used a logistic model to extrapolate the depth of rooting from root mass/length data. They showed that the depth containing 95% of roots increased from 0.3 to 2.4 m as latitude decreased from 72 to 39° with deep rooting depths associated with water-limited environments. Soil texture influenced rooting depth with the depth containing 95% of roots being deeper on sandy soils than on clay or loam soils for five of the six vegetation types studied (Schenk & Jackson, 2002).

Inputs of C to soil come from plant shoot and root litter (i.e., dead plant material) and organic compounds released by living roots (rhizodeposits; Pausch & Kuzyakov, 2018). Until relatively recently, the focus of soil scientists (especially pedologists) has been on plant litter deposited on the soil surface (Rasse et al., 2005) but, more recently, the importance of roots and rhizodeposits in the formation of soil organic carbon (SOC) have received increased emphasis (Pausch & Kuzyakov, 2018; Sokol et al., 2019; Gherardi & Sala, 2020). Rhizodeposition is difficult to assess because:

(i) it occurs in a small zone close to roots; (ii) microbial utilisation and decomposition occur quickly; (iii) the organic C content is small compared to that of the bulk soil; and (iv) its composition is chemically similar to substances released by microbes that decompose soil organic matter (Kuzyakov & Domanski, 2000). Most work has been done with young cereal and grass plants using pulse labelling with a $^{13}\text{CO}_2$ or $^{14}\text{CO}_2$ atmosphere (e.g., Gregory & Atwell, 1991; Palta & Gregory, 1997; Paterson et al., 1999). Pausch and Kuzyakov (2018) used several approaches to estimate rhizodeposition under cereals and grasslands (281 datasets) and found that the annual crops generally retained more C (45% of assimilated labelled C) in shoots than the mainly perennial grasses (34%). Using data based on root sampling, they estimated that annual cereal crops (wheat, barley, oat, triticale) typically producing 36–67.5 g C m⁻² in root biomass would, with a rhizodeposition to root ratio of 0.5, give a net annual C input by rhizodeposition of 18–34 g C m⁻². Employing gross primary production (GPP) data from atmospheric flux data and generalised partitioning coefficients from pulse-labelling experiments, they estimated that net rhizodeposition of cereals with GPP of 1101 g C m⁻² year⁻¹ would be 3% of GPP equivalent to 33 g C m⁻² whereas that from grasslands with GPP of 1097 g C m⁻² year⁻¹ would be 5% of GPP equivalent to 55 g C m⁻² (Pausch & Kuzyakov, 2018). A review of carbon inputs into soils of lowland rice crops from continuous labelling studies estimated a total belowground C input of 160 g C m⁻² during one rice season, of which 40 g C m⁻² was rhizodeposition (Liu et al., 2019). Pulse-labelling studies gave values that were 15% smaller but the relative allocation to rhizodeposits was similar at about 26% with both methods (Liu et al., 2019).

Although direct estimates of plant-derived C inputs to soil are scarce (apart from annual cereal crops and some grasses), studies of the total C allocated belowground are becoming more common (Gherardi & Sala, 2020; Jackson et al., 2017). Gherardi and Sala (2020) collected data from 111 sites worldwide to calculate that belowground C allocation was, on average, 46% of terrestrial C fixation (total global belowground net primary productivity of 24.7 ± 5.7 Pg C year⁻¹) ranging from 32% ± 4% in croplands to 64% ± 5% in grasslands; the fraction of total net productivity allocated belowground was >50% in many terrestrial ecosystems (especially forests [except broadleaf], shrublands and grasslands). Total belowground productivity increased with precipitation but the fraction of total fixed C entering the soil decreased with precipitation from about 70% in arid ecosystems to about 35% in humid ecosystems (Gherardi & Sala, 2020). Similar climatic influences on C allocation belowground were found by Hui and Jackson (2006). In a survey of grasslands at 12 sites, the percentage of net primary production allocated belowground ranged from 40% at a savanna site in Kenya to 86% at a cold desert

steppe site in China. Belowground allocation was negatively correlated with means of annual temperature and precipitation although there was substantial interannual variability (Hui & Jackson, 2006).

Recent studies have suggested important differences between the forms of belowground C inputs for soil organic C formation. Sokol et al. (2019) conducted a manipulative experiment in mixed hardwood, temperate forest to follow living root and litter inputs in supplying soil food webs and soil organic C pools. They found that living root inputs were 2–13 times more efficient than litter inputs in forming both fast-cycling particulate organic C and slow-cycling mineral-associated soil organic C. Moreover, living root inputs were more efficiently used by the soil microbial community via the *in vivo* microbial turnover pathway resulting in additions to the mineral-associated soil organic C pool. This is consistent with the notions of a C pathway of dissolved organic C (root exudates) from living roots through the microbial biomass and into the mineral-associated soil organic C (Cotrufo et al., 2015). The form of mycorrhizal association may also play an important role in determining the formation of slow-cycling soil C especially beneath trees and in forests (Clemmensen et al., 2013). Keller et al. (2021) examined C fluxes in six temperate forests using $\delta^{13}\text{C}$ -enriched ingrowth cores and found that not only were root-derived C inputs ($199.5 \pm 14.7 \text{ g C m}^{-2} \text{ year}^{-1}$) greater than leaf litter inputs ($168.8 \pm 10.77 \text{ g C m}^{-2} \text{ year}^{-1}$) but that root-derived C was 54% greater in arbuscular mycorrhizal than ectomycorrhizal-associated trees. Despite the acknowledged importance of deep roots in transferring C to sites where long-term stabilisation might occur (Poirier et al., 2018), there are few quantitative studies of root C inputs and associated microbial utilisation and stabilisation in subsoils. Using a 4-m deep tower and ^{13}C pulse labelling, Peixoto et al. (2020) assessed rhizodeposition and incorporation of C into phospholipid fatty acids and amino sugars in three crop species (lucerne, *Medicago sativa*; kernza, *Thinopyrum intermedium*; and rosinweed, *Silphium integrifolium*). Rhizodeposition decreased with depth from 35% to 45% at 0–25 cm depth to 8.0%, 2.5% and 2.7% for lucerne, kernza and rosinweed, respectively, at 340–360 cm corresponding to inputs of 5, 0.5 and 2 mg C kg⁻¹ dry weight of soil. However, relative microbial stabilisation increased with depth leading the authors to conclude that even small amounts of C released by roots at depth (especially by crops like lucerne) can be stabilised and contribute to C storage (Peixoto et al., 2020).

It has long been recognised that SOC plays a key role in soil aggregation and structure formation (Emerson, 1959; Tisdall & Oades, 1982) and the processes by which C interacts with soil components to both form stable aggregates and stable C compounds are still topics of research. Cotrufo et al. (2015, 2019) postulated dual pathways of

SOC formation based on mineral-associated organic C (MAOC) formed of mainly simple compounds and particulate organic C (POC) formed of more complex compounds. Roots can contribute to both of these pathways through root litter and rhizodeposits. Reviewing experiments with litter incubation and living plants grown in soil, Villarino et al. (2021) found that while rhizodeposits had the highest MAOC formation efficiency (46% compared to about 7% for both roots and shoot litter inputs), root litter biomass had the highest POC efficiency (19% compared to 12% with combined root + rhizodeposits). Rhizodeposits reduced POC formation probably by increasing the decomposition rate of newly formed POC. The role of mycorrhiza in these studies is unclear but their secretions and microbial necromass may have contributed C inputs for MAOC formation (Frey, 2019).

2.3 | Mineralisation (decomposition) of organic materials

2.3.1 | Rhizodeposits

While roots can contribute to SOC stabilisation, through biochemical recalcitrance, mineral adsorption and physical inaccessibility (Poirier et al., 2018), they can also promote destabilisation by exposing previously protected C to microbial decomposition (Dijkstra et al., 2021). Microbially driven processes in soils, such as mineralisation of soil organic matter (SOM) and subsequent immobilisation and nitrification, are significantly affected by roots. Typically, the presence of roots increases SOM decomposition rates by up to 5-fold, although under some circumstances the rate can be reduced up to 50% (Cheng et al., 2014; Yin et al., 2019). Plant-derived rhizodeposits comprising sloughed root cells, mucilage, exuded organic compounds and senescing root tissues are substrates for microbial growth which, in turn, stimulate the synthesis of extracellular enzymes by rhizosphere organisms that accelerate SOM mineralisation (Cheng & Kuzyakov, 2005; Murphy et al., 2015; Paterson, 2003). This rhizosphere priming effect (RPE) has been widely reported and results from a combination of plant and soil factors (Cheng et al., 2014). Plant roots also release a range of enzymes (e.g., cellulases, chitinases, phosphatases and proteases) that can decompose SOM although their functional significance for plant nutrition is uncertain and highly dependent on whether they are root-surface bound, enter soil solution, or are rapidly decomposed by microbes (George et al., 2008; Greenfield et al., 2020).

Plant factors such as plant biomass, root-derived CO₂ (positively related to rhizodeposition) and plant N acquisition are often positively related to RPE (Dijkstra et al., 2006; Zhu & Cheng, 2013) with enhanced RPE

increasingly recognised as a nutrient acquisition strategy of plants to exchange carbon to soil microorganisms for N and other nutrients (Jones et al., 2009; Kuzyakov & Xu, 2013; Sun et al., 2021). In annual cereals, the quantity of carbon allocated belowground changes during the growing season with typically 25% as rhizodeposits during early growth decreasing to <5% during grain-filling (Gregory & Atwell, 1991; Meng et al., 2013; Pausch & Kuzyakov, 2018; Swinnen et al., 1995). Root biomass rarely increases in cereals after flowering as assimilates are prioritised for grain filling so that the amount of C available in the rhizosphere to promote mineralisation is small and RPE declines. Sun et al. (2021) grew maize in plots with different plant densities and found that plant growth stage had significant effects on soil SOM, C and N dynamics resulting from a combination of phenological changes in rates of root growth and rhizodeposition coupled with changes in root morphology and in soil properties (e.g. water content and nutrients). In this study, C and N mineralisation rates were modulated by root morphology at higher plant densities with mineralisation rates directly related to specific root length (Sun et al., 2021). They suggested that a higher specific root length might facilitate the occupation of a larger soil volume and extend the distribution of rhizodeposits to support microbial activity; it might also alter soil properties such as aggregation. Although root exudation is passive in nature (diffusion-driven), there is increasing evidence that both plants and microbes can affect this process by modifying concentration gradients depending on their nutritional status (Canarini et al., 2019). Moreover, because exudation of primary metabolites occurs close to the root tip, changes in concentration at the root tip can be sensed and signals translated to modify the rhizosphere microbiome and root system architecture (Vetterlein et al., 2020).

2.3.2 | Soil structure and porosity

The size and distribution of aggregates and the dimensions and connectivity of soil pores, have large effects on SOM mineralisation through influences on both the accessibility of microbial substrates and the distribution and activity of microbial biomass (Kravchenko et al., 2021; Six et al., 2004; Wang, Dijkstra, et al., 2020). Soil structure can be viewed from the complementary perspectives of both the solid (aggregate) and pore spaces but the latter is often more useful in considering soil functions (Rabot et al., 2018). Zhang et al. (2018) and Lucas et al. (2019) used X-ray computed tomography to distinguish biopores formed by roots and soil fauna from non-biopores. Zhang et al. (2018) found that the contribution of biopores to subsoil (20–30 cm depth) macroporosity was

affected by fertiliser treatment ranging from 30.1% to 58% in rainfed fields used for maize production and 66.3% to 74.1% in paddy fields used for rice production. On a chronosequence of loess used for reclamation, Lucas et al. (2019) found that the density of biopores increased with time after the start of reclamation reaching equilibrium after about 6 years in the topsoil (0–20 cm) and 12 years at 40–60 cm depth. At depth, only 10% of biopores were filled with roots similar to the findings of White and Kirkegaard (2010) who found that while 30%–40% of wheat roots were clumped in large pores and cracks (formed by a combination of a previous lucerne crop, soil fauna and drying) in the upper 60 cm of a Kandosol, only 20% of pores were occupied. In the subsoil (>60 cm) 85%–100% of roots were in large pores but only 5% of such pores were occupied. Lucas et al. (2019) concluded that roots can rapidly trigger biopore formation reaching an equilibrium at a time-dependent on root density and soil management and that once a well-connected network of biopores has been established this can be used by subsequent plants.

While roots can increase the supply of labile C to rhizosphere microbes thereby increasing rates of SOM mineralisation, their growth may also enhance aggregate destruction leading to the release of previously inaccessible, protected C (Dijkstra et al., 2021); both these effects enhance RPE (Cheng et al., 2014). Using a soil rich in C₄ SOM, Wang, Dijkstra, et al. (2020) grew a C₃ grass (*Agropyron cristatum*) for 35 days in pots of sieved aggregates of different sizes and found that the grass increased RPE in all aggregate sizes (from 47% to 106%) but the effect was significantly smaller in the small aggregates. Planting also significantly increased microbial N immobilisation especially in the small aggregates and aggregate destruction in the medium-sized aggregates. These findings suggest a role for plant/soil structure feedback in C and N cycling (Wang, Dijkstra, et al., 2020).

Long-term C storage in soils is a consequence of both physical inaccessibility within aggregates and association with various minerals especially iron and aluminium oxides (Dungait et al., 2012; Kleber et al., 2015) and is enhanced by deposition by deep roots or burial deep in the soil, where conditions limit decomposition (Beniston et al., 2014; Fontaine et al., 2007; Kell, 2011). Plant roots can destabilise SOM associated with minerals via several mechanisms including simple physical disruption, acting as conduits to relieve limiting factors (e.g., oxygen, water, nutrients), and through the specific release of root exudates (Jilling et al., 2018; Keiluweit et al., 2015; Rumpel, 2014; Rumpel & Kögel-Knabner, 2011). Li et al. (2021) examined the ability of three exudate types (ligands, reductants and simple sugars) to release carbon from glucose adsorbed to two iron and two aluminium oxides in incubation studies.

The strong ligand, oxalic acid, caused rapid mineralisation by sorption and dissolution of minerals (a direct mobilisation mechanism) whereas the simple sugar, glucose, caused slower mineralisation but increased microbial activity and metabolite production (an indirect microbially-mediated mobilisation mechanism), and the reductant, catechol, promoted both mechanisms (Li et al., 2021). The molecular structure of the carbon compounds in the soil or associated with minerals may also influence the response to inputs of root-derived C. For example, Moore et al. (2019) employed mesocosm and modelling studies to demonstrate that complex forms of soil C were more sensitive to root/microbe interactions than simple C structures. In a broadleaf boreal ecosystem, roots stimulated the decomposition of leaf material but not that of starch. They postulated that increased root density increased the decomposition of leaves by alleviating the limitations of active microbial biomass whereas starch decomposition was not increased because microbes grew efficiently on the simple substrate without the need for root-derived inputs (Moore et al., 2019).

2.4 | Acidification of soils by roots

In addition to acidic precipitation and deposition from the atmosphere of acidifying gases such as sulphur dioxide and ammonia, soil acidification is also caused by nutrient uptake and root exudation, nitrogen fixation by legumes and mineralisation of organic matter (Goulding, 2016). pH changes in the rhizosphere have been demonstrated widely with alterations of 0.5–1 unit within 1–2 mm of the root surface common (Hinsinger et al., 2003). Such root-mediated changes are induced by a range of processes including imbalance of cation/anion uptake by plants, the release of organic anions (especially carboxylates), root respiration and microbial production of acids from root exudates (Gregory, 2006b; Hinsinger et al., 2003).

In the context of soil formation, acidification is important because it is a mechanism for altering minerals and releasing ions that are essential for plant and microbial nutrition. Carboxylates released from roots enhance P release from minerals and its supply to plants through the dissolution of P that is strongly bound to iron and aluminium oxides, mobilisation of organic P and via their strong affinity for sorption sites allowing P to move into solution. They can also act as a substrate for microbes and enhance the activity of P-solubilising bacteria (Kirk et al., 1999; Pang et al., 2021). The consequences of carboxylate production are most evident in plants that occupy severely P-impoverished soils where such production is more efficient than mycorrhizas at securing P (Lambers et al., 2008; Raven et al., 2018). The release of citrate and malate by

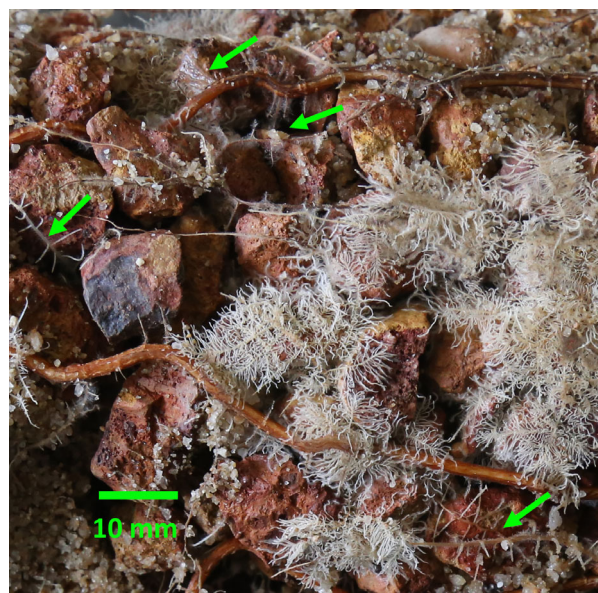


FIGURE 2 Cluster roots of *Banksia attenuate* intimately interacting with lateritic gravel from which they mobilise sparingly available phosphorus by releasing carboxylates (mainly citrate, malate and trans-aconitate). New cluster roots (indicated by the green arrows) grow in the gaps between stone particles and on their surfaces. Reproduced with permission by PNAS from Lambers et al. (2019)

many plants has been widely reported (Gregory, 2006b), but of particular interest is the excretion of organic anions by plants that form proteoid or cluster roots (Lamont, 2003; Shane & Lambers, 2005). Cluster roots exist in many Proteaceae, Lupinus and Alnus species with functionally similar, but morphologically different, specialised roots also occurring in some Cactaceae, Cyperaceae and Velloziaceae (Lambers et al., 2008; Lambers et al., 2013; Lambers et al., 2019). Figure 2 shows cluster roots of *Banksia attenuata* growing on the surface of grains of a lateritic gravel from which P was mobilised by carboxylates (Shi et al., 2020). Similarly, Teodoro et al. (2019) demonstrated that vellozioid roots of *Barbacenia tomentosa* in the *campos rupestres* of Brazil grew inside quartzite rock and mobilised nutrients (especially P and Mn) by carboxylate release. The weathered rock subsequently produces sand grains, soil and a range of microhabitats supporting Velloziaceae with different root specialisations and means of acquiring P (Abrahão et al., 2019).

Symbiotic N fixation by legumes is frequently associated with rhizosphere acidification because the high ratio of cation/anion uptake results in proton release (Marschner, 2012; Ch 14.4.1). Uncharged N_2 enters the roots and is converted to NH_4^+ which, accompanied by uptake of other macronutrient cations, results in a net release of H^+ . Over time, N fixation can lead to acidification of the bulk soil especially where legumes are grown as a regular

component of farm rotational practices, such as in parts of Australia (Tang et al., 1997). In a study of 12 pasture legume species grown in solution culture, Tang et al. (1997) found that the quantity of protons released was positively correlated with the concentrations of excess cations over anions and ash alkalinity. However, there were differences between species (proton excretion ranged from 143 to 265 cmol H⁺/kg dry matter) with *Trifolium tomentosum* and *Trifolium glomeratum* excreting more per unit of dry matter than *Medicago* species and *Trifolium subterraneum*, and all these more than *Ornithopus* species. A similar correlation between the quantity of protons released per unit of dry matter produced and concentrations of excess cations and ash alkalinity was also found in a range of 10 crop legumes (McLay et al., 1997). Although soil acidification produced by nitrate leaching from surface layers is typically greater than that produced by N fixation (Nemecek et al., 2008), subsoil acidification by legumes has numerous implications for weathering including the release of Mn and Al (by acidic subsoils) and of rock phosphate fertilisers.

In tropical forests, too, N fixation by leguminous trees results in localised acidification with associated enhanced silicate weathering resulting in improved access to nutrients such as P, Fe and Mo compared to non-fixing trees (Epihov et al., 2017). In a field study on P-poor, deep Oxisols and Inceptisols in Panama, Epihov et al. (2021) showed that N fixing trees enhanced weathering through their effects on soil pH, C and N cycling (through combined effects of increased nitrate leaching and nodulation) which enriched genes of particular classes of microbes thereby linking energy metabolism to inorganic mineral nutrient cycling. This accelerated mineral weathering was linked with the enhanced growth and recruitment of the N fixing trees in early secondary succession but also had similar effects on nearby non-N fixing trees by influencing their soil/root microbiomes (Epihov et al., 2021).

3 | ROOTS AND SOIL FUNCTIONALITY

The notion that soil provides many functions simultaneously is now well-established and encompassed in a variety of terms such as multifunctional landscapes (O'Farrell & Anderson, 2010) and ecosystem services (Hopkins & Gregorich, 2013). Constanza et al. (1997) included soil formation in the list of ecosystem services provided by soil in addition to those of food and fibre production, climate regulation, air and water quality, nutrient cycling and biodiversity conservation, and cultural and aesthetic recreational needs of humans. Such multifunctionality is necessarily complex with different soil properties being foremost for particular functions. Attempts to simplify this complexity

with notions such as soil quality and soil health have been largely unsuccessful (Bünemann et al., 2018; Fierer et al., 2021; Sojka & Upchurch, 1999) and the difficulties of quantifying these terms have led to a re-awakening of the fact that they, and any derived indicators, only have meaning if linked to a specific function (Baveye, 2021; Powlson, 2020). This section focuses on the ways in which roots interact with soils to acquire nutrients, suppress plant diseases, pests and pathogens, and filter water.

3.1 | Nutrient acquisition for food production

Much soil science literature has focussed on the role of soil in supporting the production of agricultural products (e.g., Gregory & Nortcliff, 2013). Roots have been viewed as the means by which plants extract nutrients and water from the soil and thereby grow. What has changed relatively recently is the awareness that in most natural vegetation, and in several crop production contexts, roots are actively communicating and collaborating with other organisms for mutual benefit (Cameron, 2010; Harris et al., 2020; Oldroyd, 2013) – they are not simply exploiting soil nutrient resources. There are many examples of plant roots interacting with rhizobacteria, both rhizobia and free-living nitrogen-fixing bacteria, to form endophytic associations to fix nitrogen (e.g., *Rhizobium leguminosarum* with rice [Yanni & Dazzo, 2010] and *Azospirillum* with *Bracharia* grasses [Reis et al., 2001]), but most attention has been given to symbiotic associations in which bacteria and fungi reside within the root. However, what is common to all such associations is the need for signals to be exchanged between the plant and microbe to modulate plant defence responses and to facilitate the establishment of a physical niche for the microbe that reduces competition with other microbes.

As stated earlier, the successful colonisation of land 450 million years ago was aided by the formation of symbiotic associations with arbuscular mycorrhizal fungi (AMF). This first symbiosis was followed by the evolution of alternative or additional symbionts including associations between: (i) ascomycetes and basidiomycetes with orchids and Ericales to form specific intracellular structures as an alternative to arbuscular mycorrhizal symbiosis; (ii) nitrogen-fixing soil bacteria to form discrete root nodules (either with *Frankia* in actinorhizal nodulation or rhizobia in rhizobium-legume nodulation) – an evolution that occurred in the last common ancestor of Fabales, Fagales, Cucurbitales and Rosales; (iii) ectomycorrhizae with several gymnosperm and angiosperm lineages to form an extracellular symbiosis sometimes as an alternative to AMF and sometimes as an addition; and

(iv) cyanobacteria with diverse species within the embryophytes, in hornworts, liverworts, ferns, gymnosperms and angiosperms located in the intercellular spaces of plant tissues (Radhakrishnan et al., 2020). These different types of mutualistic symbioses have in common the ability of the microorganisms involved to capture nutrients that limit plant growth in exchange for carbon sources derived from photosynthesis (Jones et al., 2009; Oldroyd, 2013). Crucial in the formation of these associations are the signalling pathways that allow the plant and the microbe to recognise each other and to promote colonisation. Most work on identifying these signals has been undertaken with AMF and rhizobia leading to the identification of the chemical signals involved. Strigolactones released by plant roots signal to the AMF while flavonoids signal to rhizobia (Zipfel & Oldroyd, 2017). In response the AMF produce mycorrhizal factors (Myc factors) and the rhizobia nodulation factors (Nod factors) which are recognised by the host plant thereby activating a common symbiosis signalling pathway that promotes either root

invasion or formation of nodules, respectively (Figure 3; Mathesius, 2003; Oldroyd, 2013). Nod and Myc factors both incorporate short chains of chitin with a lipid tail (lipochitooligosaccharides, LCO) with a variety of substitutions (methyl, acetyl, fucosyl and sulphate). These chemical differences and variations in chain length facilitate specificity of interaction and recognition between different rhizobia and host legume species (Dénarié et al., 1996). In contrast to rhizobia, AMF typically has a broader host range with LCOs being generic or produced as a mixture of different LCOs with different plants recognising different LCOs in the mixture (Oldroyd, 2013). The signal molecules for *Frankia* and ericoid mycorrhiza are currently unknown but that for *Frankia* is thought not to be an LCO (Harris et al., 2020).

These mutualistic symbioses deliver large quantities of nutrients (especially N and P) to support plant growth. Estimates of global nutrient uptake by vegetation are uncertain with values for nitrogen fixation prior to extensive human activity ranging between 90 and 140 Tg

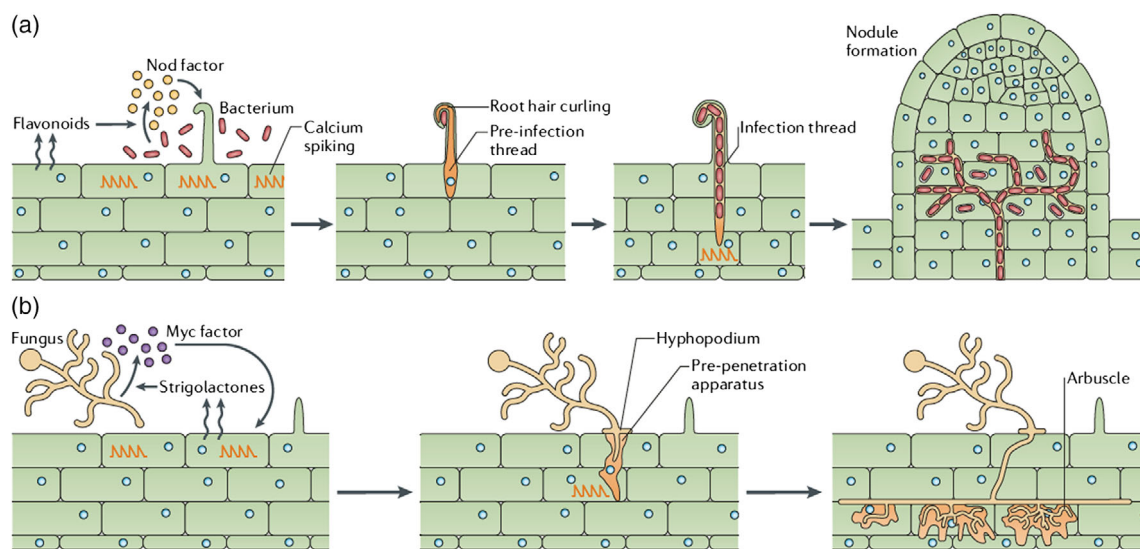


FIGURE 3 Rhizobial (a) and mycorrhizal (b) colonisation of roots. (a) Flavonoids released by the plant root signal to rhizobia in the rhizosphere, which in turn produce nodulation factors (nod factors) that are recognised by the plant. Nod factor perception activates the symbiosis signalling pathway leading to calcium oscillations, initially in epidermal cells but later in cortical cells preceding their colonisation. Rhizobia gain entry into the plant by root hair cells which grow around the bacteria attached at the root surface, trapping the bacteria inside a root hair curl. Infection threads are invasive invaginations of the plant cell, initiated at the site of root hair curls, that facilitate invasion of the rhizobia into the root tissue. The nucleus relocates to the site of infection and a pre-infection thread forms that predicts the path of the infection thread. Nodules initiate below the site of bacterial infection and form by de novo initiation of a nodule meristem in the root cortex. The infection threads grow towards the emergent nodules and ramify within the nodule tissue. Sometimes the rhizobia remain inside the infection threads, but more often they are released into membrane-bound compartments inside the cells of the nodules where they differentiate into a nitrogen-fixing state. (b) Strigolactone release by the plant root signals to arbuscular mycorrhizal fungi (AMF) in the rhizosphere. Perception of strigolactones promotes spore germination and hyphal branching. AMF produce mycorrhizal factors (Myc factors), including lipochitooligosaccharide (LCOs) and, possibly, signals that activate the symbiosis signalling pathway in the root, leading to calcium oscillations. AMF invasion involves an infection peg from the hyphopodium that allows fungal hyphal growth into the root epidermal cell. The route of hyphal invasion in the plant cell is predicted by a pre-penetration apparatus in a zone of the cell below the first point of fungal contact. The fungus colonises the plant root cortex through intercellular hyphal growth. Arbuscules are formed in inner root cortical cells from the intercellular hyphae. Reproduced with permission by Springer Nature from Oldroyd (2013)

N/year (Vitousek et al., 1997). Human activity has had substantial effects on plant N uptake through both the selection of leguminous crops which are estimated to have increased N fixation by 32–53 Tg N/year (Galloway et al., 1995) and the intensification of production systems for food and fibre by the application of about 110 Tg N/year of fertilisers in 2020/21 (IFA, 2020). While the quantity of P fertilisers applied to plants is known (about 17.5 Tg P/year), values for the uptake of P by mycorrhiza are very uncertain because although most vascular plant families can be mycorrhizal, not all species in a family are, and not all mycorrhizal roots are active in P acquisition (Albornoz et al., 2021). In soils with high P status, suppression of AMF has been widely reported so that benefits to crops given P fertiliser are typically small or absent (Ryan & Graham, 2018). Such suppression is also common in soils with very low P availability (Bolan et al., 1987). Albornoz et al. (2021) argue that AMF is important for P acquisition only in soils within a narrow range of soil P availability (as first suggested by Parfitt, 1979). At very low P availability, while mycorrhizal roots are common (Zemunik et al., 2015), the dominant mechanism of P mobilisation is root exudation of combinations of carboxylates and phosphatases (Raven et al., 2018). This makes assigning values of P uptake to specific root or root/symbiont mechanisms difficult.

On many soils, especially those to which manures and fertilisers have been applied to aid crop and tree production, several traits in root systems have been identified that benefit nutrient acquisition. In short, these can be summarised as mining and/or foraging strategies (Lynch, 2007). White (2019) lists these as follows: (i) high-affinity/high-capacity transport systems for nutrient uptake, which reduce nutrient concentrations and accelerate diffusion and solubilisation of nutrients in the rhizosphere; (ii) modification of rhizosphere pH through a variety of mechanisms (described earlier in this review), which increase rates of nutrient solubilisation; (iii) root distribution in the soil profile and root proliferation in nutrient-rich patches, which improve the quantity and efficiency of nutrient acquisition; (iv) root growth rate and allocation of biomass to root systems, which affects early plant vigour and ability to compete with other plants for nutrient resources; (v) architectural and anatomical characteristics of the root system, which affect the volume of soil explored and the surface area available for uptake; and (vi) root/microbe interactions, which lead to mutually beneficial symbioses and/or microbiomes that facilitate the nutrient acquisition.

Identification of these traits has led to a range of ideas as to how these might be incorporated into crop improvement and sustainable production programmes (Lynch, 2019; Oldroyd & Leyser, 2020; Wang, Whalley, et al.,

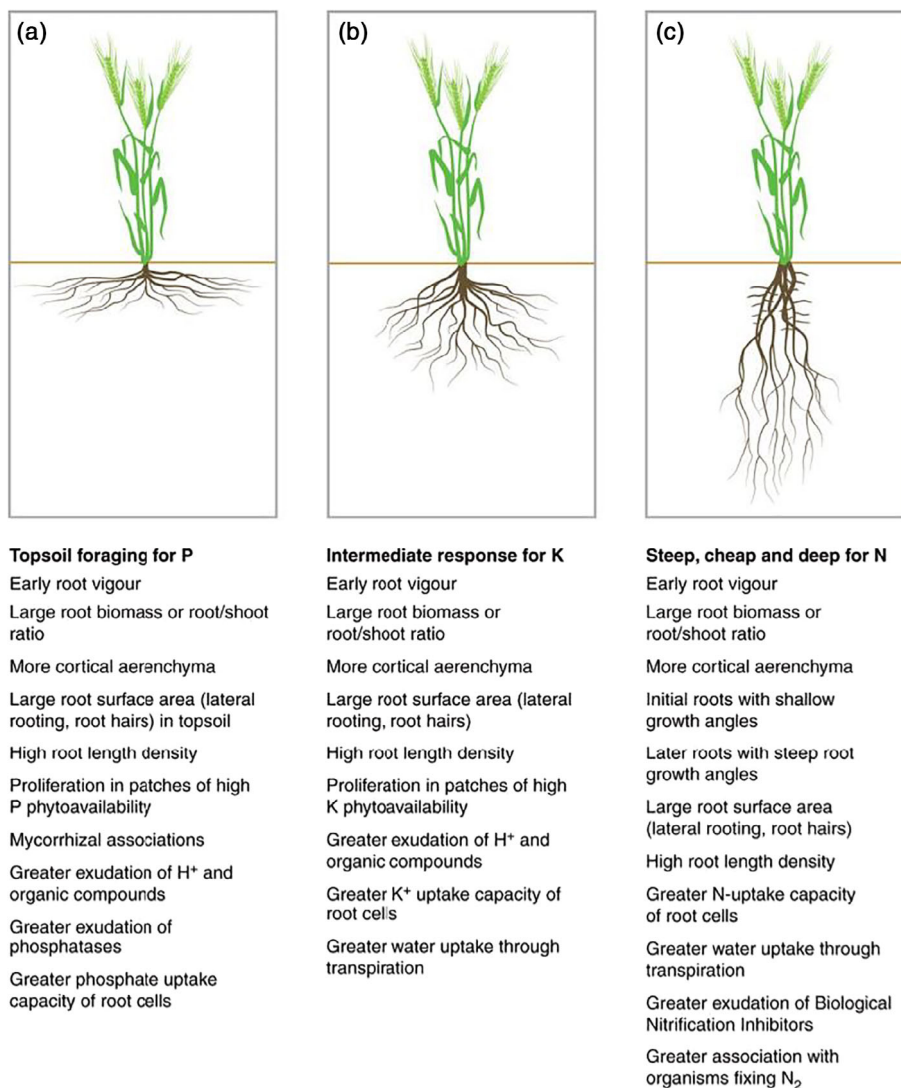
2020; White et al., 2013). Ideotypes for root systems have been developed based on the distribution and mobility of nutrient ions and water in soils (Figure 4) and different root system architectural (RSA) phenes targeted in many genotypic studies via identification of quantitative trait loci (QTL; e.g., Zhang et al., 2016; Tuberosa et al., 2021). Among RSA traits frequently targeted have been root hairs (for uptake of immobile nutrients like P; Gregory et al., 2009; Brown et al., 2013; Wissuwa et al., 2016), root growth angle (influencing the rate at which shallow and deep water and nutrient resources become accessible; Hargreaves et al., 2009; Maccaferri et al., 2016; BurrIDGE et al., 2019), and the ability to root deeply (influencing water availability and nutrient accessibility and availability; Price et al., 2002; Lilley & Kirkegaard, 2011; Arai-Sanoh et al., 2014; Tracy et al., 2020). Many of these ideas have yet to be realised through breeding programmes but marker-assisted breeding has resulted in the release of deep-rooted, drought-tolerant upland rice cultivars (Steele et al., 2013) and root ideotype breeding of common bean has increased production on smallholder farms (BurrIDGE et al., 2019). Further developments in RSA breeding are anticipated but currently limited by the ability to phenotype large numbers of genotypes under field conditions and the need to take account of RSA plasticity in response to soil conditions (Schneider & Lynch, 2020; Tuberosa et al., 2021).

3.2 | Disease, pest and pathogen suppression for food production

Besides nutrient acquisition, root/microbe communication is also important in the ecology of soil-borne plant pests, pathogens and plant health. Some pathogens (e.g., oomycetes) have been able to usurp the plant-derived strigolactone and fungal LCO signalling pathway utilised by AMF (described above) to recognise the plant surface and to promote infection structures (Wang et al., 2012). More generally though, plants are able to influence their rhizosphere microbiome to benefit plant health (Berendsen et al., 2012). Such studies are in their infancy, but there is increasing evidence that plant roots are able to promote specific microorganisms to prosper in their rhizosphere so that while microbial populations are higher than in the bulk soil their diversity is less (Berendsen et al., 2012; Huang et al., 2019).

Disease suppression is a general feature of soils and is usually effective against a broad spectrum of pests and pathogens but is not transferrable from soil to soil (Schlatter et al., 2017). Specific rhizodeposits (including exudates and volatile compounds) lead to the development of particular rhizosphere communities as, for example, in

FIGURE 4 Root ideotypes for efficient acquisition of phosphorus (a), potassium (b) and nitrogen (c). Reproduced with permission from Oxford University Press from White et al. (2013)



the development of disease suppressive soils (Schlatter et al., 2017). In such soils, a pathogen may either not establish or persist, or establish but cause little disease, or establish and cause disease initially but decline in severity with time (Weller et al., 2002). An example of this phenomenon is the widely observed decline with time of effects of the yield-reducing, soil-borne, fungal pathogen of wheat take-all (*Gaeumannomyces graminis*). A key role in the long-term suppression of this disease is played by the rhizosphere recruitment of fluorescent *Pseudomonas* spp. and, in particular, by those species that produce the antibiotic 2,4-diacetylphloroglucinol (DAPG; Raaijmakers & Weller, 1998). Variations in the time of development of this specific suppression could be due to the differential ability of wheat genotype roots to recruit and support the DAPG-producing pseudomonads and DAPG production (Kwak et al., 2012; Mazzola et al., 2004).

Repeated plantings of monocultures can induce changes in the root microbiome that recruit beneficial microbiota which reduce soilborne pathogens and promote

plant growth. For example, Yin et al. (2021) repeatedly grew wheat on soil infected with *Rhizoctonia solani* AG8 and found that bacterial communities recruited to the infected rhizosphere were distinct from those without infection. Infection increased the abundance of genera such as *Chitinophaga*, *Pseudomonas*, *Chryseobacterium*, *Flavobacterium* and *Serratia* that have suppressive or antagonistic functions and a group of plant growth-promoting (PGP) and nitrogen-fixing microbes including *Pedobacter*, *Variovorax* and *Rhizobium*. Initially, infection with *R. solani* decreased shoot growth but, over a cycle of nine repeated wheat plantings, disease suppression was apparent at the fifth cycle and by the ninth cycle there were no significant differences in shoot length and fresh weight between the uninfected control and the infected treatments. These results show that root pathogens can promote the production of beneficial microbes in the rhizosphere that, in turn, suppress the pathogen (Yin et al., 2021).

Foliar pathogens have also been demonstrated to modify root exudation of long-chain fatty acids and amino

acids recruiting microbes in the rhizosphere that reduce the severity of the pathogen (Yuan et al., 2018). As with take-all, recruitment of specific *Pseudomonas* populations appears to play a key role in reducing the severity of infection of some foliar pathogens (Wen, Zhao, et al., 2021). Compounds released by roots also act as signals to soil-dwelling organisms such as nematodes. When roots of maize are attacked by larvae of the beetle *Diabrotica virgifera virgifera* (western corn rootworm, WCR) they release a sesquiterpene (E)- β -caryophyllene (E β C) which attracts entomopathogenic nematodes (EPNs) that infect and kill the larva (Hiltpold et al., 2010). This signalling mechanism has been exploited to explore the development of more effective strains of nematodes to control the pest (Hiltpold et al., 2012). However, the insect has evolved a variety of defensive abilities to resist the EPN including the sequestration of secondary metabolites such as the benzoxazinoids abundant in young maize tissues (Bruno et al., 2020). Screening of EPN isolates from Mexico (the likely source of WCR) showed substantial variability in their capacity to infect WCR although most were adapted to benzoxazinoid-related defences suggesting that the larvae possess other defence mechanisms that help to resist EPN (Bruno et al., 2020).

3.3 | Water movement and filtration

Plant roots have profound effects on hydrological processes in soils through their roles in aggregation and soil structure formation, and the generation of continuous macropores which facilitate aeration, water movement and storage, and further root growth (Angers & Caron, 1998). Occupation of fractures in bedrock and generation of macropores in soil and regolith by roots results in a network of connected biopores through which water, nutrients and particulate matter can move (Hasenmueller et al., 2017; Lucas et al., 2019; Watson & Luxmoore, 1986; Wen, Sullivan, et al., 2021). Watson and Luxmoore (1986) were among the first to use tension infiltrometers to show that wide, continuous pores occupying only a small proportion of the total soil volume contributed most of the water flow although whether these pores were biopores is unknown. Their results demonstrated that 95% of the flow occurred in pores $>250\ \mu\text{m}$ diameter occupying only 0.32% of the pore volume. Such preferential flow, which bypasses most of the soil matrix, has important practical consequences for the movement of solutes and pollutants from land to watercourses; behaviour that is not well captured by the dominant Richards equation approach to soil water movement (Beven & Germann, 2013).

Given the close connection between roots and the formation of macropores, it might reasonably be expected

that root size and system architecture would have effects on water flow in soil. This has rarely been explored, but Cheng et al. (2011) explored preferential flow under three different land uses using dye tracer. They found that the vertical distribution of dye differed between farmland used for crops, shrubland (mainly grass-covered) and forest, with farmland and shrubland having more preferential flow paths in the topsoil compared to forest. The dense rooting of grass in the upper soil layers promoted the formation of horizontally oriented macropores which facilitated near-surface lateral flow. In contrast, the deeper and thicker roots of the forest allowed high connectivity to the subsurface permitting rapid drainage to depth (as also found by Pawlik et al., 2016). Cheng et al. (2011) concluded that “root characteristics are important in the formation of preferential flow paths” with roots of $<5\ \text{mm}$ particularly effective. Similarly, Macleod et al. (2013) demonstrated that the rooting behaviour of the hybrid grass *Festulolium* contributed to a reduction in runoff of 43%–51% compared with the parent grasses when grown on clay-rich soil. This was due to intense initial root growth to $>1\ \text{m}$ initially followed by rapid senescence that left biopores that transmitted water to depth (Macleod et al., 2013). Root architecture is also important in fluvial ecosystems affecting both subsurface flow paths and the flow velocity resulting in increased water residence times (Nikolakopoulou et al., 2018). Tracer breakthrough curves showed that the helophytes (*Iris pseudacorus*, *Phragmites australis* and *Scirpus lacustris*) all increased water residence time and that hydraulic retention increased as the relative volume of fine roots increased but decreased in the presence of thick roots (Nikolakopoulou et al., 2018).

Trees have many effects on hydrology. While they frequently increase the rate of water infiltration and drainage via the influence of macropores, they can also decrease the surface flow and runoff of sediments to water courses. However, there are differences between tree species in root system architecture and morphology and in their response to edaphic and climatic growing conditions (Förster et al., 2021) so there is potential to select tree species to undertake specific roles (USDA, 2012).

Deep rooting to reduce the leaching of dissolved solutes and recycle nutrients to topsoil has been examined in many environments. Shepherd et al. (2000) showed that the integration of perennial, deep-rooted trees and shrubs and the rotation of annual and perennial crops can tighten N cycling in the agricultural landscapes of Kenya. Mean nitrate concentrations at 0.5–4 m depth were $<0.2\ \text{mg kg}^{-1}$ soil beneath hedgerows and woodlots but $1.0\text{--}2.1\ \text{mg kg}^{-1}$ beneath poor maize crops. Similarly, woody tree species in Cerrado, Brazil were found to take up labelled nitrate from deep in the profile although

this differed between the three trees studied (Pinheiro et al., 2021). *Xylopia aromatica* took up nitrate from a depth of 9 m and from a distance of up to 5 m from the trunk whereas uptake by both *Coussarea hydrangeifolia* and *Miconia albicans* was confined to a depth of 1.5 m and a lateral spread of 2 m. Improved agronomic nitrogen use efficiency has been demonstrated by exploiting differences in crop rooting patterns (Thorup-Kristensen, 2006). Deep-rooted crops (such as fodder radish or white cabbage) or catch crops (such as chicory) can be used to recover nitrate leached during the growing season from crops such as wheat and barley, with catch crops able to lift nitrate into shallower layers where many crops have their roots (Thorup-Kristensen, 2006; Thorup-Kristensen et al., 2020). Deep rooting can also be employed in crop rotations to raise other nutrients such as potassium and phosphorus from the subsoil to topsoil. Han et al. (2021) showed that deep-rooted crops such as lucerne and chicory increased available K in the topsoil by 27 mg kg⁻¹ over 3 years and increased yields of subsequent spring wheat crops by up to 14%, and P uptake by 19% and K uptake by 14%. In many environments, the use of perennial crops to regulate water, nutrient and carbon cycles to enhance the sustainability of arable crop production and reduce nutrient loads to freshwater bodies has been shown to be beneficial (Kell, 2011; Thorup-Kristensen et al., 2020).

4 | DISCUSSION: ARE ROOTS MERELY IN SOIL OR OF IT?

4.1 | Roots in soil

Clearly, living roots are plant organs and have a separate identity from the mineral matter, water, air, decayed organic material and living organisms and microorganisms constituting the bulk of soil. Proto-soils formed as autotrophic bacteria and algae transferred carbon compounds into surface layers (Mitchell et al., 2021) but it was the evolution of plants with roots that enhanced this process (Kenrick & Strullu-Derrien, 2014). Roots receive photosynthate from the shoot and use this to fuel numerous processes including interaction with other organisms in the rhizosphere and accessing water and nutrients to the benefit of the plant overall. This distinction between root and soil is maintained in the evolutionarily ancient symbiosis of plants with AMF and in that with nitrogen-fixing bacteria (Zipfel & Oldroyd, 2017). Both symbioses are intracellular with AMF located in specialised host-membrane compartments in root cortical cells forming arbuscules, and rhizobia confined to root-derived nodules (Oldroyd, 2013). Plant membranes and their associated

signalling pathways are key to successful symbiosis, to the defence against root-infecting plant pathogens and the interplay of immunity and symbiosis signalling (Couto & Zipfel, 2016).

The evolution of plants to form symbioses with many microorganisms including AMF, ectomycorrhiza, actinorhiza, rhizobia and plant-growth-promoting rhizobacteria has led to an appreciation that roots are part of an assemblage of organisms comprising a holobiont (Finlay et al., 2020). These various holobionts play a significant role in the weathering of soil parent material and thus on patterns of nutrient mobilisation at multiple scales (Figure 1; Sverdrup, 2009; Finlay et al., 2020). Concomitant with the evolution of symbioses has been the evolution of root traits in woody species to enhance weathering rates. Comas et al. (2012) undertook phylogenetic analyses and demonstrated that angiosperm taxa that diversified since the early Cretaceous have thinner roots with greater length per unit of biomass than earlier diverging taxa. These thinner roots may have allowed plants to forage more efficiently for soil water and nutrients and, with the evolution of ectomycorrhizas during the Cretaceous and Cenozoic, contributed to increased rates of mineral weathering.

Inputs of dead plant components into the soil have frequently focussed on leaves and other shoot residues (litter), but more recently the role of roots and rhizodeposits have received greater attention because of potential for carbon sequestration (Poirier et al., 2018; Rasse et al., 2005). Deep-rooted trees and the evolution of angiosperms have depleted CO₂ from the atmosphere and placed C at depths of up to several metres below the land surface (Berner, 1997; Kell, 2011). Living roots in the soil produce rhizodeposits that fuel many microbial processes and the production of mineral-associated organic carbon (MAOC) fractions (Sokol et al., 2019; Villarino et al., 2021). Several studies in forests now demonstrate that living roots, not leaf and root litter inputs, drive soil C dynamics (Keller et al., 2021; Sokol et al., 2019) with the suggestion that rhizodeposits and roots appear to play opposite but complementary roles for building MAOC and particulate organic carbon (POC) fractions (Villarino et al., 2021).

4.2 | Roots as a component of soil

Jenny (1941) stated that in his opinion “the distinction between soil and environment is arbitrary; it exists only in our minds, not in nature. The often-quoted axiom that soil is ‘independent natural bodies’ is misleading, and little is gained by trying to establish tight compartments between pedology and related sciences”. This review demonstrates that rapid soil formation commenced with

the evolution of vascular plants and that many soil processes including weathering, accreting carbon, shaping of microbial communities, transporting nutrients and water are crucially dependent on plant roots – the roots (an element of Jenny's environment) are of a soil's characteristics. Perhaps because, in the last century or so, much soil science was focussed on agriculture and mostly annual plants, this reality has been overlooked. The native vegetation of the semiarid ecosystems of south-west Western Australia affords numerous examples of how pedogenic features in soils result from the bioengineering undertaken by roots and their associated microorganisms (Verboom & Pate, 2006). Pedogenetic creates cemented by amorphous or microcrystalline compounds such as calcium carbonate (calcretes), iron (ferricretes), aluminium (alcretes) or oxides of silicon (silcretes) may exist distinctly or grade chemically from one to another without changes in parent rock but associated with roots of different plants especially those forming cluster roots (Pate et al., 2001). Production of hydrophobic compounds and rhizosheaths by roots, coupled with root architecture determining the distribution of root-associated pores, all affect water and solute movement and the resultant soil profiles (Verboom & Pate, 2006), with the “spearheading” of water immediately beneath root boles of large taxa especially obvious.

Another pedological feature directly associated with roots is rhizoliths (Jaillard et al., 1991; Klappa, 1980) which are especially common in sandy and silty calcareous soils. Most plants require less calcium and magnesium relative to major nutrients such as potassium and phosphate so, in soils in which solution concentrations of Ca and Mg are high, these ions accumulate around roots and, with time, in root tissues (Huguet et al., 2020). Formation mechanisms and their timescales for rhizoliths are still a topic of active research (Huguet et al., 2020; Sun et al., 2020) and important in assisting paleoenvironmental reconstructions (Becze-Deák et al., 1997; Li et al., 2015). Calcified root formation commences with carbonate accretion around live fine roots but as the root ages, calcium carbonate can precipitate around phloem and xylem cells. When the root dies and decays, CO₂ production reduces pH and leads to further carbonate weathering and the eventual precipitation of carbonate in voids between several fine roots resulting in one large rhizolith (see Huguet et al., 2020 for details). In the Tengri Desert of north-west China, pristine rhizoliths only formed around *Artemisia* roots and were absent around other plant roots suggesting that both the specific biochemical composition of dead roots and the associated microbial communities determine whether rhizoliths will form (Sun et al., 2020; Tang et al., 2020).

These clear examples of pedogenic features resulting from the presence of roots and associated microbes suggest

that roots are not merely in the soil but of it. Verboom and Pate (2006) introduced the term “phytotarium” to denote the outcomes of biotic influences in the construction and maintenance of niches specific to particular vegetation types and their manifestations in soil profiles. They also drew attention to the work of the early Russian soil scientist R.V. Rizpolozhenskii (summarised with other Russian work by Ackert, 2013) who concluded that soil formation involved the interaction of two primary factors, all living organisms and rock, with “the seizure of food by organisms from the unorganized environment and its reciprocal return” paramount. Soil for Rizpolozhenskii represented “a border between the chaotic environment and the world of order” with state factors such as climate and topography viewed only as external conditions (quotation from Lapenis et al., 2000). This view of soil formation chimes with the recent paleoclimatic and paleosol research mentioned earlier that demonstrates the key role of roots and their associated microorganisms in rock weathering (Edwards et al., 2015; Mitchell et al., 2021). Such thinking contrasts with the focus on state factors which have received greater attention than living organisms perhaps because of the relative difficulty of characterising and quantifying these compared with climatic variables and topographic features.

Arguably nowhere has the exclusion of roots as an element of real soil behaviour been more detrimental to progress than in the development of theories to characterise water and solute movement. Beven and Germann (2013) lament the lack of “an adequate physical theory linking all types of flow” (in soil), but while the first figure in their paper highlights the correspondence of preferential flow and grassroots around soil peds, the word root appears only four times and the modelling approaches described are largely concerned with the physical boundary and flow conditions of the water rather than the inclusion of biologically relevant root (and other living organisms) parameters. Admittedly, this is a challenging topic but the increasing ability to characterise root system architecture (RSA) in models (e.g., Postma and Black (2021) for crops; Tobin et al. (2007) for trees) coupled with the experimental evidence that RSA and root growth patterns affect preferential flow (Cheng et al., 2011) and flood incidence (Macleod et al., 2013) suggests that this could be a worthwhile realm to explore. RSA and rhizosphere properties such as mucilage and bulk density are being incorporated into models of plant water uptake (Daly et al., 2018; Landl et al., 2021), but effects on macropore flow are yet to be included.

Hiltner (1904) coined the term rhizosphere to explain his observations that specific processes were occurring at the root/soil interface that was different from those in the bulk soil. He noted that materials exuded from roots of different legumes attracted

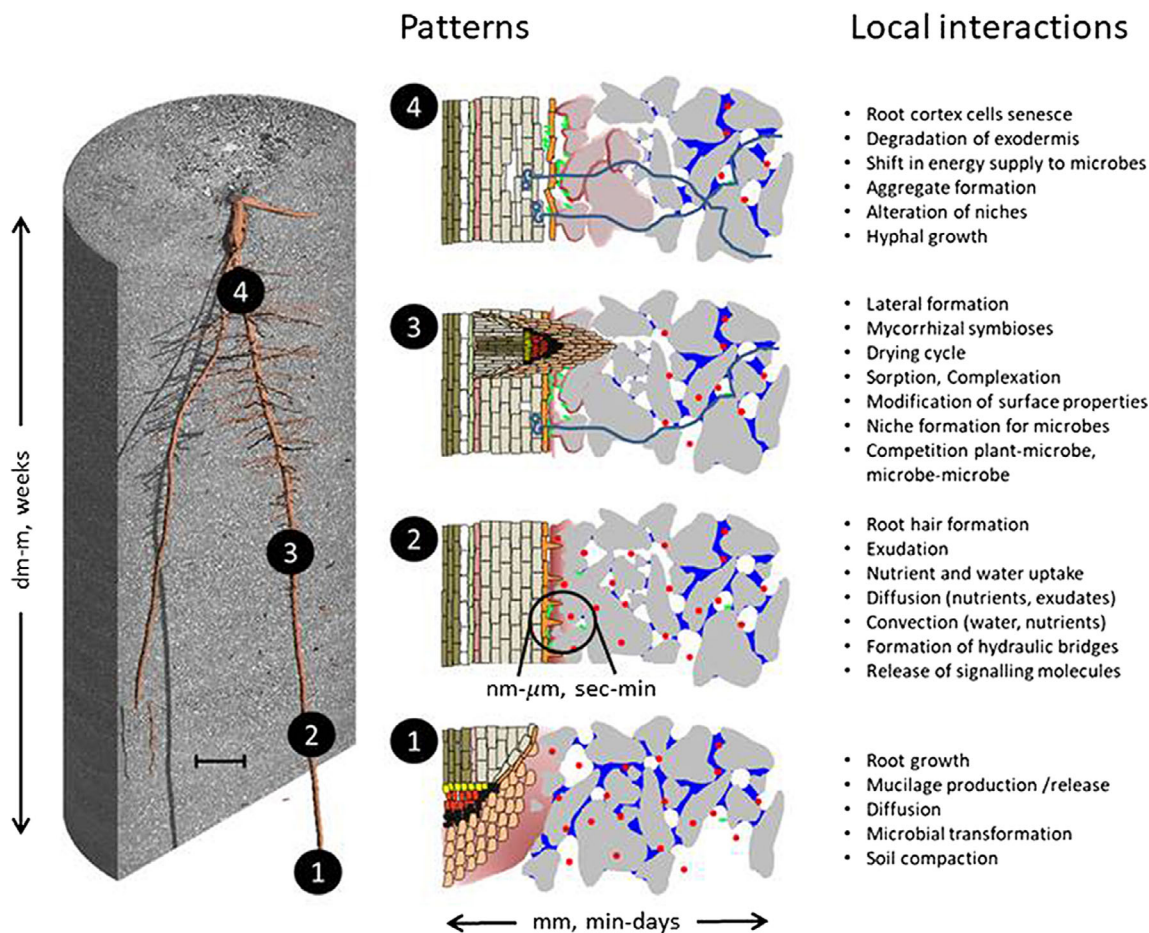


FIGURE 5 Hypothetical patterns (not to scale) reflecting rhizosphere self-organisation at different levels. Shown are mucilage (pink) and water distribution (blue), compaction of soil particles (grey) and aggregate formation (grey-pink), colonies of microorganisms (green), depletion of phosphorus (red) and their potential changes with root ontogeny. The latter is illustrated on the left for a 7-day old *Zea mays* root system growing in loam (scale bar 10 mm). Local interactions are given according to their potential importance at particular developmental stages although they may also be relevant at other stages. Reproduced with permission from Vetterlein et al. (2020)

organisms that were different than roots of non-legumes and that each legume species attracted organisms that had specific benefits for that species. Recent methodological developments have facilitated both the characterisation of this root microbiome (Young & Bengough, 2018) and, as described earlier, of the chemical signals that are being exchanged between the root and organisms in the soil (Mathesius, 2003; Zipfel & Oldroyd, 2017). However, while the rhizosphere is an easily understood mind picture, perhaps it would be helpful to recognise more explicitly that the influence of roots pervades much of soil because different processes result in chemical, physical and microbial gradients of different sizes that operate over different timescales (Hinsinger et al., 2005; Vetterlein et al., 2020). Gregory (2006a) noted that for mobile nutrients, water and volatile compounds, the density of root beneath many arable crops and grasslands means that most soil in the upper profile could be regarded as rhizosphere soil. Similarly, the

mycorrhizal networks of most native vegetation influence much of the soil profile (Gregory, 2006b).

The significance of many the processes and functions operating at and through root/soil interactions depend on the spatial and temporal scales at which they are viewed (Vetterlein et al., 2020; Figure 5). For example, understanding how signalling molecules operating over short distances influence microbial populations around the root and nutrient acquisition at larger distances and over prolonged periods is essential for developing management practices that allow the soil to be resilient to disturbance and change. Similarly, improving local nutrient-sensing capabilities in crop roots to optimise the use of limited nutrients (Oldroyd & Leyser, 2020) and the possible manipulation of the volatile plant hormone ethylene that acts as an early warning of compacted soil (Pandey et al., 2021) could assist the development of more robust and sustainable systems of crop production. At an ecosystem level, roots and their associated traits

and biotic interactions play key roles in the transformation and circulation of many elements and compounds and in the formation, maintenance and stability of soils (Freschet et al., 2021).

5 | CONCLUSIONS

Soil has been defined in many ways and, as Jenny (1941) acknowledges “it is problematic whether any definition of soil could be formulated to which everyone would agree”. Nevertheless, there is consensus that soil is different from rocks and sediments because of biogeochemical weathering with the definition offered by Amundson (2014) currently widely employed: “Soils are altered surficial rock or sediment, composed of organic matter, minerals, fluids, and organisms that develop through chemical weathering and deposition of litter.” It is noteworthy that this definition while including organisms, excludes plant roots (which are organs, not organisms) despite their near-ubiquity in soils globally. Moreover, the material presented earlier in this review demonstrates the crucial role of roots in soil formation (in both geological and anthropogenic timeframes) and the functions and services that soil provides. Simply adding roots to Amundson’s list of soil components is unsatisfactory because they are also clearly a component of another living system – the plant. However, in addition to what soil is composed of, this definition could easily be supplemented by a statement of what roots contribute such as: “Soils are altered surficial rock or sediment, composed of organic matter, minerals, fluids, and organisms whose formation and functionality are influenced by biogeochemical weathering and interactions of these components with plant roots.”

To conclude, the formation and functioning of soil are dependent on the presence of roots and their associated organisms. For some purposes, roots can be regarded as merely in soil but for many purposes, they are a vital component of the soil system and of its functioning and should be specifically recognised in the definition of soil. As we understand more about the signalling and communication between roots and organisms and the chemical, physical and biological changes occurring as a result of root/soil interactions, we shall gain an increased understanding of the processes influencing the genesis of soil profiles (Verboom & Pate, 2006), the interaction of pedogenesis and plant diversity (Laliberté et al., 2013), and how the plant/soil system might be better managed.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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