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Plant-induced changes in soil structure: Processes and feedbacks

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Abstract. Soil structure influences the growth and activity of organisms living in soil. In return, microbes, fauna, and plants affect structure. The objective of this paper is to review the role of plants in modifying soil structure. Vegetation affects structural form and stability at different scales and through various direct and indirect mechanisms. By penetrating the soil, roots form macropores which favour fluid transport. They also create zones of failure which contribute to fragment the soil and form aggregates. This phenomenon is enhanced by the wetting and drying cycles associated with plant growth. Drying also causes shrinkage and strengthening of the soil. Anchorage of roots and the exudation of cementing material stabilizes soil structure. Finally, as a source of C, roots and plant residues provide a food source to the microflora and fauna which contribute to structure formation and stabilization. In return, plant-induced changes in structure will affect plant growth mostly by modifying the root physical environment, and the water and nutrient cycles.

Introduction

Most soil chemical, biological and physical reactions and processes occur at the interface between the solid, liquid, and gas phases. It is the spatial arrangement of these three phases that defines soil structure. Structure is central to soil functioning as it controls water, gas and nutrient fluxes and storage, and therefore influences the activity and growth of living organisms. In return, microbes, fauna, and plants will affect structure in complex ways. The objective of this paper is to review the role of plants in modifying soil structure. Examples will show that vegetation affects soil structure at different scales and through a wide variety of mechanisms involving root activity, such as root penetration, water extraction, anchorage and exudation of compounds in the rhizosphere. Also, the whole plant, dead or alive, can be an important source of carbon, providing microbes and fauna with a substrate for the production of stabilizing material as well as providing physical protection of the soil surface against structure-altering processes like rainfall or compaction.

Most of our knowledge, and thus the examples presented in this review, come from observations and experiments performed on agricultural soils, but the generalization and basic principles discussed should apply to other ecosystems such as forest or range soils. However, it should be kept in mind that the effects of plants on soil structure in agricultural soils cannot always be distinguished easily from the management practices associated with cultivation. Hence, some of the effects reported here may result from complex interactions with other factors such as fertilization or tillage.

Soil structure

Conceptually, soil structure can be characterized by its form, stability and resiliency (Kay 1990). Structural form refers to the arrangement of solids and voids that exists at a given time, whereas the stability is the ability to retain this arrangement when exposed to different stresses. Resiliency is the capacity of the soil to recover some soil structural form or stability when an applied stress is removed.

Structural form can be investigated by considering either the spatial arrangement of the solid particles or that of the voids. The solid particles are usually present in soils as clusters called aggregates, peds or clods which may be separated from one another by planes of weakness or failure zones. Structural units vary in size from a few microns to a few centimeters; structural characteristics are therefore scale-dependent. The arrangement of the solids defines the size, shape, and organization of the voids (pores). Important characteristics of the pores are their size and number, which in turn determine the fluid storage capacity. Pores can be arbitrarily divided into macropores for which the lower size range varies from 30 to 1000 μm (Luxmoore 1981) and smaller micropores. Other important pore characteristics such as connectivity and continuity will also have a bearing on fluid transport. Total porosity provides an assessment of the total volume of soil available for storage but gives no indication of the pore organization. Visual and micromorphological methods as well as water desorption characteristics, and water and gas flow measurements are used to investigate soil pore space organization. Structural form is governed by the inherent soil properties (clay content and type), by climatic factors (wetting and drying, freezing and thawing), and by human and biological activity (tillage, roots, microflora and fauna). Soil structural form will thus evolve in time in response to the temporal variation of these factors.

The stability of the soil structure is most often characterized by its resistance to various stresses such as those caused by rapid wetting or mechanical compression. It is the strength of the failure zones between structural units that determines the stability of the structure at a given scale. This resistance is provided by stabilizing agents which vary in nature with soil type and scale. Soil aggregates are normally not a random arrangement of primary particles. Primary particles and aggregates of different sizes are usually arranged in a hierarchical fashion. Tisdall and Oades (1982) presented an aggregation model for Australian grassland soils which appears to apply to soils in which organic matter is the main aggregate stabilizing agent (Oades & Waters 1991). As earlier proposed by Edwards and Bremner (1967), the model suggests that the building blocks or elementary units are stable microaggregates (<250 μm) which are bound together to form stable macroaggregates (>250 μm). The cementing or binding agents of macroaggregates are relatively labile organic matter fractions such as fungal hyphae and fine roots (Tisdall & Oades 1982), polysaccharides (Angers & Mehuys 1989; Haynes & Swift 1990) or hydrophobic aliphatics (Capriel et al. 1990; Dinel et al. 1992). The binding material within microaggregates is composed of more recalcitrant organic matter and inorganic constituents (Tisdall & Oades 1982). Methods to determine structural stability have been described by Kemper and Rosenau (1986) and Angers and Mehuys (1993), among others. A major concern in soil structure research is the wide variation in the methods used in the different experiments and the lack of standardization which often make difficult and even preclude the generalization and modeling of the results.

Soil structural resiliency has been much less studied than form or stability. One example of structural form resiliency is the recovery of porosity after the removal of a mechanical stress. The resiliency of the structural form is also illustrated in the case of self-mulching soils. Due to their intrinsic properties, these soils have the ability, after having been dispersed or puddled, to form a granular structure after repeated wetting and drying cycles. Finally, resiliency is also illustrated by the age hardening phenomenon and the thixotropic behaviour of soils (Dexter et al. 1988) in which stability is recovered or gained with time following application or occurence of weakening stresses.

Plant effects on soil structure

Root penetration

Growing in existing pores or through the soil matrix, roots create compressive and shear stresses which can reach 2 MPa (Goss 1991). Radial pressure exerted by the growing roots will compress the soil in their vicinity (Dexter 1987) and decrease the porosity in that zone (Guidi et al. 1985; Bruand et al. 1996). Dorioz et al. (1993) observed a closer packing of the clay particles in the immediate vicinity of the roots. The compression of soil around roots results in the enlargement of existing pores and the creation of new ones. A large proportion of the pores formed by roots would fall into the macropore range (>30 μm) (Gibbs & Reid 1988). Macropores play a major role in the preferential flow phenomenon (Beven & Germann 1982), by which water or other fluids by-pass the soil matrix. Macropore flow can take place during active plant growth but water movement through the soil profile can be limited compared to decayed root systems (Mitchell et al. 1995). Infiltration rates can actually be reduced by actively growing roots (Barley 1954). Mitchell et al. (1995) observed dye tracer on ped faces connected to living root crowns down to a 16-cm soil depth, while in a decayed root crown, the dye extended below 55 cm. The flow along living roots has been attributed to the presence of a saturated film of water on the outer surface of the roots and to root shrinkage. As decay occurs, tissue remnants and the associated microflora remain as pore coatings on channel walls which enhance water transport efficiency (Barley 1954).

Alfalfa (*Medicago sativa* L.) is characterized by a large-diameter, long and almost straight tap root and has been reported to be particularly efficient in promoting macropore flow (Meek et al. 1990; Mitchell et al. 1995; Caron et al. 1996a). Meek et al. (1989) reported that under alfalfa 27% of the pores in the 0–20 cm depth extended to 50 cm. As mentioned earlier, Mitchell et al. (1995) observed dye tracer to depths in excess of 55 cm in decayed alfalfa root channels. Meek et al. (1989 and 1990) clearly showed a progressive increase in water infiltration in the soil with the number of years under alfalfa (Figure 1). Preferential flow under branching-type root systems such as corn (*Zea mays* L.), may also be significant, although in this case it may be associated with earthworm activity (Edwards et al. 1989). The process of pore formation by roots is believed to be particularly important in undisturbed or no-till soils, as tillage tends to disrupt the continuity of the pore system. In such soils, plant roots and litter will also contribute indirectly to macropore formation by serving as food to the fauna and in particular earthworms which have a well-documented impact on channel formation (e.g. Ehlers 1975; Edwards et al. 1989).

Root penetration is also often associated with soil fragmentation as it creates zones of failure, and therefore induces soil loosening and aggregate formation. Bui Hui Tri (1968) observed that plant roots can fragment initially compact soils. Materechera et al. (1994) suggested that the higher proportion of small aggregates in planted than in unplanted soils could have resulted from breakdown of the large aggregates by penetrating roots. Although soil fragmentation due to root growth is believed to be mostly associated with the modification of the moisture regime (Gerard et al. 1972; Caron et al. 1992a), work of Materechera et al. (1994) showed that fragmentation can occur even

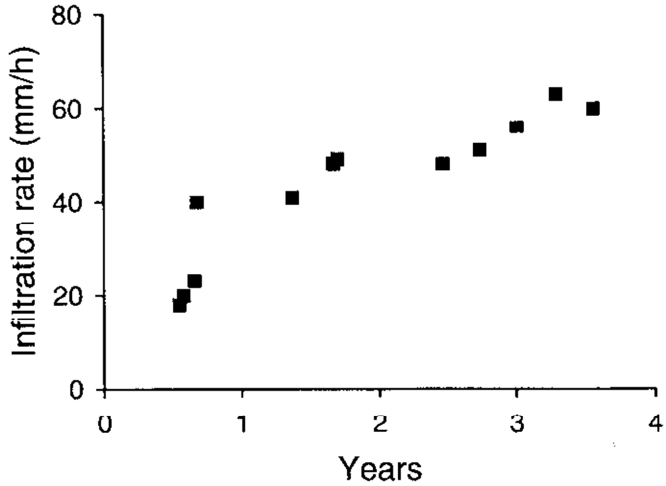

Figure 1. Changes in infiltration rate under alfalfa culture with time (after Meek et al. 1989, with permission).

at constant soil moisture content. Dorioz et al. (1993) also observed that microfissures created by roots occurred in continuously moist conditions.

Modifying the soil water regime

In many soils, the soil structural form is greatly affected by soil water. Depending on their clay content and type, soils show variable potential to shrink and swell. The loss of volume upon drying leads to the development of cracks which can be as large as 5 cm and can extend to considerable depths, up to 80 cm or more, depending on the soil and climatic conditions as well as the presence and type of vegetation (Ravina 1983). Grevers and De Jong (1990) found differences in macropore structure of a swelling clay soil between grass species which they attributed to differences in water uptake between plants and thus differential dessication of the soil. It was found that the greater was the plant biomass production, the greater were the area and length of macropores (cracks). Since plant distribution varies in space because of associated cultural practices, the cracking pattern will also vary in relation to plants. For row crops, water is used firstly at the row and quarter row position (Van Weesenbeek & Kachanoski 1988) and the cracking pattern will develop at the interrow position (Fox 1964; Chan & Hodgson 1984). For other crops, which have a uniform or random spatial distribution, the cracking pattern develops at the outer boundaries of the rooted volume (Mitchell & Van Genuchten 1992).

Wetting and drying cycles also influence the extent of soil fragmentation and aggregate formation. Drying produces cracks and induces fracture of aggregates. Rapid wetting can also induce micro-cracks which can make the soil more friable (Dexter 1991). Plant growth will influence the magnitude, frequency and effects of these cycles on aggregation (Semmel et al. 1990; Caron et al. 1992a; Materechera et al. 1992). For instance, Materechera et al. (1992) observed that repeated wetting/drying cycles associated with root growth resulted in the production of smaller aggregates. They attributed this observation partly to cracking of soil caused by the heterogeneity of water extraction giving rise to tensile stress patterns within the grid of roots.

Soil structural stability is also influenced by soil water content and its variations with time. Soil cohesion and strength usually increase with decreasing soil water content as a result of increased contact points and capillary forces (Kemper & Rosenau 1984; Horn et al. 1994). Water uptake by the plant will therefore usually result in an increase in soil strength (Horn & Dexter 1989). Resistance to compression in undisturbed soil cores, a measure of mechanical strength, was greater in a cropped soil which contained less water than a bare soil (Lafond et al. 1992). At the aggregate level, soil cohesion was greatly enhanced by decreasing water contents and the dispersion of clay-size material decreased accordingly (Caron & Kay 1992). This explained the increased stability of aggregates observed in the field under bromegrass relative to a fallow since bromegrass periodically dried the soil to a greater extent than did a bare soil (Caron et al. 1992b).

The drying of soil by the roots may also act synergistically with the aggregate binding material produced in the rhizosphere and increase soil structural stability. As will be discussed later, organic materials released by the roots and microbial population of the rhizosphere can be efficient in cementing soil particles. Dorioz et al. (1993) observed that the adsorption of water by the roots promoted a reorganization of the clay, characterized by oriented and compacted clay particles, and that this microenvironment was very rich in root mucilage. The drying that occurs in the zone of mucilage production contributes to the efficiency of the binding agents through increased sorption of the binding material onto colloid surfaces (Reid & Goss 1981; Caron et al. 1992c).

Soil enmeshment

The root systems of many plant species form a dense network in soils. The effect of such a network in stabilizing soil profiles is well documented. Kleinfelder et al. (1992) found herbaceous roots to be efficient in stabilizing streambank soils; unconfined compressive strength was related to fine root-length density. Grass, legume and tree roots were shown to increase the shearing resistance of soil (Waldron & Dakessian 1982). In general, alfalfa and grass roots had a more rapid effect than woody species (Waldron & Dakessian 1982). However, older pine roots (54 months old) were clearly superior to younger alfalfa roots (14-month-old) in strengthening soil at the 60-cm soil depth (Waldron et al. 1983). Shearing resistance was generally proportional to the diameter and number of pine roots (Waldron et al. 1983). Waldron's shear tests were performed under saturated conditions and therefore plant-induced increases in resistance were not attributable to soil water removal by plants (Waldron & Dakessian 1982). The direct action of plant roots in enmeshing and anchoring the soil was also invoked as being responsible for the reduced shrinkage observed in cropped soils (alfalfa and wheat) compared to a bare soil (Mitchell & van Genuchten 1992).

At a smaller scale, it has been suggested that plant roots and root hairs can also directly enmesh and stabilize soil aggregates of millimeter size (Tisdall & Oades 1982). Visual (Figure 2) and microscopic observations (Foster & Rovira 1976; Tisdall & Oades 1982; Forster 1990; Dormaar & Foster 1991) clearly show that aggregates are formed and stabilized in the immediate vicinity of plant roots. Field and greenhouse studies have demonstrated that growing plants induce the rapid formation and stabilization of soil aggregates (Tisdall & Oades 1979; Reid & Goss 1981; Dufey et al. 1986; Angers & Mehuys 1988; Stone & Buttery 1989). Statistical correlations have been found between root length or mass and soil aggregation (Thomas et al. 1986; Dufey et al. 1986; Miller & Jastrow 1990). Although fine roots can form a dense network which can probably entangle or enmesh soil particles and form aggregates, indirect effects such as associated microbial activity or the release of binding material have most often been invoked to explain the apparent relationship between fine roots and aggregate stability.

Rhizosphere effects

Plant roots can promote soil aggregation by releasing material which can directly stabilize soil particles or by favoring microbial activity in the rhizosphere which in turn will affect soil structure. Morel et al. (1991) provided evidence that intact mucilage released by maize root tips significantly increased soil aggregate stability and they showed that this increase was independent of any microbial activity since it occurred immediately after the incorporation of the exudates in the soil (Figure 3). However, this effect was not long lasting except in one soil (silty clay) which maintained higher stability than the control even after the mucilage supply was exhausted. The authors proposed that the sticking effect of the mucilage was replaced by binding provided by newly synthesized microbial polysaccharides. Using ultra thin sections of perennial ryegrass (*Lolium perenne* L.) rhizosphere, Dormaar and

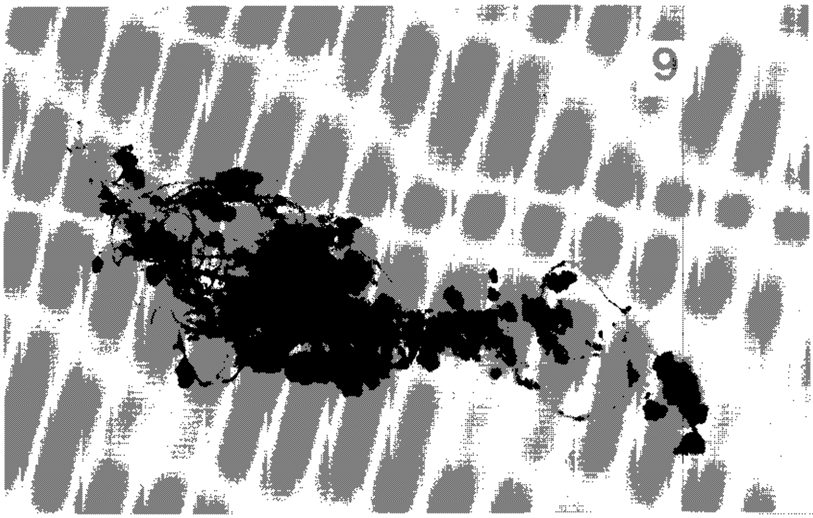

Figure 2. Soil aggregates adhering to timothy (*Phleum pratense* L.) roots.

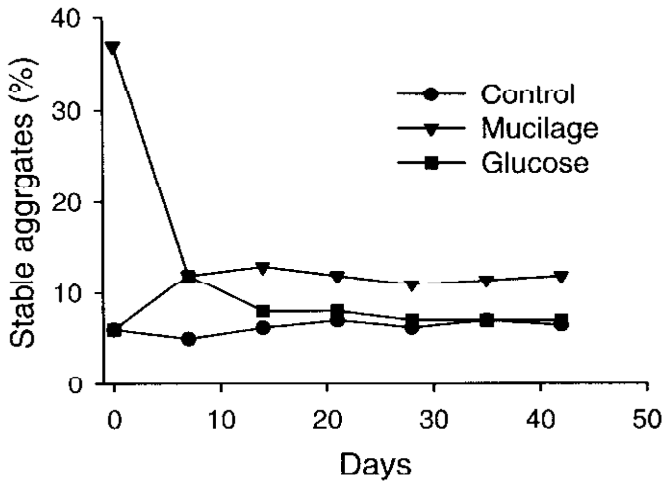

Figure 3. Evolution of water-stable aggregates during incubation of unamended, glucose- and corn mucilage-amended silty clay (after Morel et al. 1991, with permission).

Foster (1991) observed that microaggregates (2–20 μm) were formed *de novo* by the association of mineral particles, root gel, root fragments and microbial extra-cellular polysaccharides.

Plant roots can also affect the chemical and ionic environment of the soil with various possible consequences on the soil structure. Reid et al. (1982) observed a decrease in the stability of two soils following the early growth of corn which they attributed to the destruction of the linkages between organic matter, iron or aluminium, and mineral particles by the roots. Pojasok and Kay (1990) found that the release of nutrient ions and carbon in the exudates of bromegrass and corn roots increased aggregate stability. This positive effect of root exudate C on soil aggregation agrees with the observations of Morel et al. (1991).

The effect of roots on aggregation has often been associated with vesicular-arbuscular mycorrhiza (VAM) supported by the root systems of many plant species (Tisdall & Oades 1979; Thomas et al. 1986; Jastrow 1987; Miller & Jastrow 1990). This role was also demonstrated in studies of revegetation of unstable maritime sand dunes (Sutton & Sheppard 1976; Forster 1990). Sand aggregates can be efficiently stabilized by cross-linking of the sand particles by short lengths of hyphae (Degens et al. 1996). There has been some controversy as to whether it is the roots or the VAM, or both that are actually binding the soil particles into aggregates (Thomas et al. 1986; Miller & Jastrow 1990). Using a statistical path analysis, Miller and Jastrow (1990) suggested that the effect of fine roots on soil aggregation was related to their association with VAM. Thomas et al. (1986) found a correlation between plant-induced changes in soil aggregation and VAM, but could not conclude that VAM were responsible for this effect since VAM had also increased root length. In an attempt to separate the respective role of roots and their associated VAM, Thomas et al. (1993) grew split-root soybeans (*Glycine max* L. Merr.) in containers with one side of the root system colonized by VAM and the other not. They concluded that in their system, the direct effect of VAM hyphae on soil aggregation was significant and at least equivalent to that of the roots alone. Tisdall and Oades (1979) suggested that fungal hyphae are covered by a layer of amorphous material, probably polysaccharides, to which soil particles are attached. Wright and Upadhyaya (1996) proposed that a glycoprotein secreted by VAM could be responsible for their aggregating and stabilizing effect.

The rhizosphere presents a very diverse and high level of microbial activity largely induced by root exudation and mucilage, root sloughing and favourable aeration and water conditions in the root vicinity (Bowen & Rovira 1991). The presence of mycorrhiza in the rhizosphere of many plant species is noticeable and their role in soil aggregation has been discussed. Few studies have looked at the contribution of other specific rhizosphere microorganisms to soil aggregation. Inoculation of wheat roots with a rhizosphere strain of *Bacillus polymyxa* increased the mass of soil adhering to the roots (Gouzou et al. 1993). Microbial extracellular polysaccharides are found in the rhizosphere of plants (Bowen & Rovira 1991) and could act as cementing material. However, their effect cannot be distinguished easily from that of plant mucilages. Rhizobia are present in the rhizosphere of many plant species, especially legumes. Rhizobial polysaccharides have been shown to be efficient in promoting soil aggregation (Clapp et al. 1962). Much remains to be determined about the mechanisms of aggregate formation and stabilization in the plant rhizosphere, and the respective contribution of roots and specific rhizosphere microorganisms is still unclear. Moreover, both biological and physical processes such as drying contribute to the formation and stabilization of aggregates in the immediate vicinity of the roots.

Roots and litter as carbon inputs

Aside from the immediate and short-term effects of roots on the soil structure which have already been described, plant roots and litter also have a longer-term influence through their contribution to soil organic matter. A large proportion of the C fixed by the plants is allocated below ground. Consequently, in many ecosystems, plant roots constitute the most important source of organic matter in the soil, and so have a predominant effect on biologically-induced changes in the soil structure. Moreover, in many ecosystems, a large part of the above-ground plant is returned to the soil as litter or crop residues which also constitutes an important C source. Although the exact mechanisms are subject to debate, the role of organic matter and biological activity in controlling aggregation in most soils is well recognized (Oades 1984 and 1993).

Decomposing plant residues promote soil aggregation and the magnitude of the effect is related to the decomposability of the material (Tisdall et al. 1978 and Figure 4). Golchin et al. (1994) presented a model for aggregate formation and stabilization during plant debris decomposition. They proposed that plant-derived particulate organic matter entering the soil is initially colonized by the microbial population which together with exudates adsorb mineral particles. As plant fragments are encrusted by mineral particles, they become the centre of water-stable aggregates and are thereby protected from rapid decomposition. Decaying plant residues and their associated microbial products located inside aggregates modify the physical environment of the aggregates. They can obstruct intra-aggregate pores, which can result in a slower rate of water entry within the aggregates and reduce aggregate disruption due to rapid wetting (Caron et al. 1996b).

Plant roots and litter will also indirectly influence soil structure by serving as food to the soil fauna and in particular to earthworms which contribute to aggregate formation and stabilization through various mechanisms such as clay orientation (Marinissen et al. 1996) and microbial activity such as fungi (Marinissen & Dexter 1990). Their role on pore formation was briefly discussed earlier. The quantity and quality of plant residues influence earth-

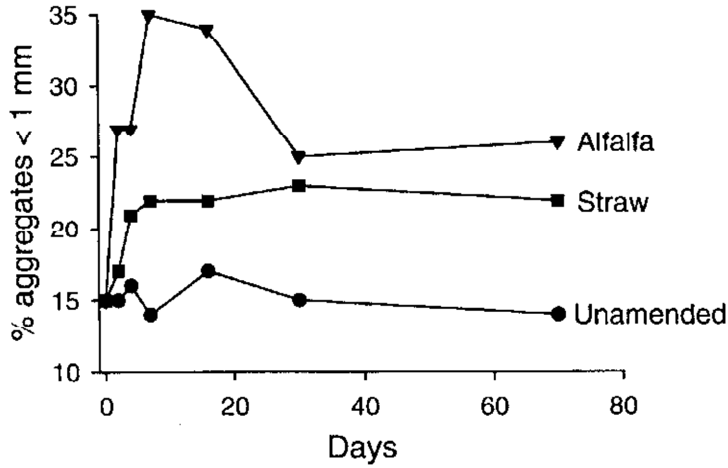

Figure 4. Dynamics of water-stable aggregates of a silty loam following additions of two plant residues (Lafond et al. 1993).

worm population and activity (Shipitalo et al. 1988) with consequent variable effects on structural stability (Shipitalo & Protz 1988).

Dufey et al. (1986) measured the effects of ryegrass (*Lolium multiflorum* Lmk.) and clover (*Trifolium pratense* L.) on aggregate stability both during and after plant growth. Both crops increased soil stability during the growing period. After growth, a further increase in stability was observed which was assumed to be due to biological factors and was analogous to the effect of the addition of fresh organic matter to the soil. Roberson et al. (1991, 1995) compared the efficiency of cover crops in improving soil aggregation and hydraulic conductivity over two years. They suggested that by providing carbon to the microbial biomass cover crops promote the production of microbial polysaccharides which increases soil aggregation. The net effect of various plant species after a few years of growth is the result of a large number of interacting factors. Soil water-stable macroaggregation usually increases rapidly in an exponential fashion following the establishment of perennial grasses or legumes (Kay 1990; Angers 1992). Comparative studies have shown that differences in aggregating and stabilizing efficiency varies not only between plant species (e.g. Drury et al. 1991; Chantigny et al. 1997) but also between cultivars or varieties within a given species (Carter et al. 1994). Considering the wide variety in growing conditions and the large number of interacting factors, it is not surprising that, in addition to physical factors, the effects of various plant species on stable aggregation after several years of growth have been related to different organic matter fractions: fungal biomass or hyphal length (Tisdall & Oades 1979; Miller & Jastrow 1990; Chantigny et al. 1997), labile polysaccharides (Angers & Mehuys 1989; Haynes & Francis 1993), hydrophobic aliphatics (Capriel et al. 1990) and microbial biomass (Drury et al. 1991; Haynes & Francis 1993). It is likely that under given growing conditions any of these fractions will be closely related to the total amount of C deposited in the soil both in the form of roots and above-ground residues returned to the soil.

Feedbacks and conclusions

Soil structure is one of the many factors influencing plant growth. Although much research has been devoted to understand the soil physical controls of plant growth, direct field evidence of the feedback effects of plant-induced changes in soil structure on plants is scarce. Further, critical or threshold values of soil physical and structural properties with regard to plant growth are not well defined. Plant roots are very adaptable and changing structure changes many other factors. An approach to characterize soil structural quality with respect to plant growth was recently developed which defines non- or least-limiting water contents (Letey 1985; da Silva et al. 1994). The critical physical properties of a soil controlling plant growth have been identified as resistance to root penetration, water availability and aeration.

One of the most significant plant-induced changes in soil structural form is the formation of continuous macropores by penetrating roots. These macropores facilitate aeration and water movement and storage in the soil as well as decreasing resistance to further root growth. These changes are likely to result in positive feedback effects on plant growth as roots can grow into these macropores (Van Noordwijk et al. 1993). Jakobsen and Dexter (1988) have predicted from crop modelling that biopores can presumably increase crop yields. Another important element is the formation of water-stable aggregates. Aggregation is important for many aspects of soil functioning related to plant growth. It has been suggested that ideal conditions for a seedbed are produced by stable aggregates not less than 0.5–1.0 mm and not greater than 5–6 mm diam. (Russell 1973). Soils with more stable aggregates are also more resistant to surface crusting (Le Bissonnais & Arrouays 1997) and to compaction (Angers et al. 1987), and thus are more favourable to seedling emergence, root growth and water infiltration and storage.

Soil structure may also influence plant growth by controlling biological activity and nutrient cycling. Location of substrate in soil pores controls its accessibility to decomposers (Elliott et al. 1980; Ladd et al. 1996). Encrustation of plant residues with minerals provides protection from decomposition (Golchin et al. 1994). In systems such as a new alfalfa stand (Angers 1992) or prairie restoration (Jastrow 1996), early increases in aggregation are believed to contribute to organic matter build-up and thus nutrient storage. Angers et al. (1997) have shown that plant residue-derived N accumulates rapidly in stable aggregates during decomposition. Organic matter present in aggregates is partly physically protected (Elliott 1986) and can be mineralized upon aggregate mechanical disruption or wetting and drying cycles (Rovira & Greacen 1957; Sorensen 1974; Elliott 1986) and contribute to nutrient supply to plants. Further, organic matter present in various aggregate size classes is believed to have different turnover rates (Buyanovsky et al. 1994). The importance of plant-induced changes in soil structure on nutrient storage and turnover, and their eventual feedback impact on plant growth is undoubtedly significant and deserves to be studied further.

There are other plant-related factors that can affect the soil structure which have not been discussed in this paper. For instance, live material or litter present at the soil surface can absorb the kinetic energy of rainfall and reduce the effect of compaction by vehicular traffic (Soane 1990). Plant debris also affects soil mechanical properties by providing increased resistance to deformation (Rawitz et al. 1994) and elasticity (Guérif 1979), thus increasing the resiliency of the soil structure. Also, the presence of litter or crop residues at the soil surface can modify the soil water content and indirectly influence the soil structure through processes already described.

Plants are part of the ecosystem and have a significant impact on their environment. The influence of the plant/root system on soil properties and functioning is well demonstrated. However, the exact mechanisms involved are still poorly understood. In particular, much remains to be determined about the respective role of rhizosphere organisms and plant roots on the soil structure. The contributions of physical and biological processes are very difficult to separate. The influence of plants on water and solute transport also deserves more attention. Although there is no doubt that structure affects plant growth, there is still little direct evidence of the feedback effects of plant-induced changes in soil structure on plant growth. Soil structure is one of the important but least understood processes by which plants influence the biogeochemical cycles. This understanding is necessary for sustainable land management and improved knowledge of ecosystems evolution.

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