SOIL Discuss., 2, 265–289, 2015
www.soil-discuss.net/2/265/2015/
doi:10.5194/soild-2-265-2015

SOIL
Discussions
Open Access

Can we manipulate root system architecture to control soil erosion?

A. Ola, I. C. Dodd, and J. N. Quinton

Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

Received: 21 January 2015 – Accepted: 26 January 2015 – Published: 26 March 2015

Correspondence to: J. N. Quinton (j.quinton@lancaster.ac.uk)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Soil erosion is a major threat to soil functioning. The use of vegetation to control erosion has long been a topic for research. Much of this research has focused on the above ground properties of plants, demonstrating the important role that canopy structure and cover plays in the reduction of water erosion processes. Less attention has been paid to plant roots. Plant roots are a crucial yet under-researched factor for reducing water erosion through their ability to alter soil properties, such as aggregate stability, hydraulic function and shear strength. However, there have been few attempts to manipulate plant root system properties to reduce soil erosion. Therefore, this review aims to explore the effects that plant roots have on soil erosion and hydrological processes, and how plant root architecture might be manipulated to enhance its erosion control properties. We clearly demonstrate the importance of root system architecture for the control of soil erosion. We also demonstrate that some plant species respond to nutrient enriched patches by increasing lateral root proliferation. The soil response to root proliferation will depend upon its location: at the soil surface dense mats of roots may block soil pores thereby limiting infiltration, enhancing runoff and thus erosion; whereas at depth local increases in shear strength may reinforce soils against structural failure at the shear plane. Additionally, in nutrient deprived regions, root hair development may be stimulated and larger amounts of root exudates released, thereby improving aggregate stability and decreasing erodibility. Utilising nutrient placement at depth may represent a potentially new, easily implemented, management strategy on nutrient poor agricultural land or constructed slopes to control erosion, and further research in this area is needed.

1 Introduction

Soil erosion by water is a serious environmental problem. Approximately 430 million ha of arable land, representing 30 % of the globally available land for agricultural production, has been degraded by water erosion and a further 56 % is at risk (Jankauskas et al., 2008). The effect of above ground plant material on reducing soil erosion is well known. Plants intercept rainfall, some is stored in the canopy with the remainder evaporating or reaching the soil surface either directly as throughfall, or indirectly through stem flow or leaf drainage (Stocking and Elwell, 1976; Puigdefábregas, 2005). Water reaching the soil surface may be stored in small depressions on the soil surface or infiltrate into the soil. The remainder may move downhill as overland flow, entraining soil particles and transporting them, and may also concentrate to form rills and gullies. There are a number of factors controlling erosion, namely the erosivity of the eroding agent, slope angle, the nature of the plant cover and the erodibility of the soil (Morgan, 1986). Erosion may result in on-site soil degradation reducing the soil's productivity and water storage capacity, due to changes in soil structure, soil depth and losses of nutrients and organic matter (OM). This may lead to significant losses of crop yield (Lal, 2001; Pimentel, 2006; Jankauskas et al., 2008), posing a threat to food security or limiting the production of renewable biotic resources (Pimentel, 2006; Jankauskas et al., 2008). Off-site problems associated with downstream sedimentation include flooding, pollution, negative effects on biodiversity, as well as the loss of reservoir storage (Pimentel and Kounang, 1998; Lal, 2001; Pimentel, 2006). In the UK, the annual costs of both on-site and off-site problems were recently estimated to range between GBP 248 and GBP 469 million (Posthumus et al., 2013). Hence, there is a need to stabilize soils and preserve this crucial resource.

The importance of vegetation cover to control erosion has been demonstrated by many studies. Both linear and exponential decreases in erosion rates associated with vegetation cover have been observed, as the nature of the relationship varies for canopy and ground covers, or inter-rill and rill erosion (Boer and Puidgefábregas, 2005). Soil loss due to overland flow decreases exponentially with increasing percentage ground cover (Morgan, 1986; Gyssels et al., 2005). In Montana and Utah, for example, erosion rates increased ca. 200 times in response to a decrease in ground cover from 100 % to less than 1 % (Trimble and Mendel, 1995). A minimum of 10 %

plant coverage was required to significantly reduce erosion rates on a semi-arid hillslope in Arizona (Abrahams et al., 1988), however, the magnitude of the response ultimately depends on vegetation type and species (Bochet et al., 2006). Positive effects of the aerial biomass in controlling erosion are generally attributed to reduced overland flow velocities and reductions in the kinetic energy of raindrops (Stocking and Elwell, 1976; Puigdefábregas, 2005). Furthermore, vegetation covers modify intrinsic soil properties such as OM content, aggregate stability, shear strength, and infiltration capacity, which determine a soil's erodibility (Gyssels et al., 2005). The above ground biomass enhances the infiltration and soil water storage capacity by the interception of rainfall and water loss from leaves (Puigdefábregas, 2005; González-Pelayo et al., 2010), thereby increasing soil shear strength (Tengbeh, 1993; De Baets et al., 2008). In addition, vegetation cover creates a microclimate and supplies OM, influencing the activity of microorganisms, and therefore nutrient availability, resulting in a positive feedback on plant productivity. Both additional OM as well as microbial and fungal secretions enhance the formation of stable aggregates (Puidgefábregas, 2005; Vásquez-Méndez et al., 2010), which affect hydraulic conductivity and, hence water storage capacity (Puidgefábregas, 2005). Thus, the presence of vegetation influences soil erosion rates.

However, reduction in soil loss results from the combined effects of the above and below-ground biomass (Gyssels and Poesen, 2003). Concentrated flow erosion rates were reduced to almost zero within the 0–10 % soil cross-sectional occupation by grass roots, but decreased only by 25–50 % for the same increase in aerial cover (De Baets et al., 2006). Furthermore, a rainfall simulation experiment comparing erosion rates under ryegrass (*Lolium perenne*) after the above ground material was removed demonstrated that the below ground material of this species accounted for 90 % of the decrease in soil detachment 27 weeks after being sown in erosion pans (Zhou and Shangguan, 2007). Thus, the importance of roots to control erosion cannot be neglected. This paper aims to review available information about the effects of roots on soil properties determining the resistance of soil to water erosion with emphasis on root system architecture (RSA).

Furthermore, factors influencing RSA and the potential of deep fertilizer applications to control soil erosion will be discussed.

2 The effects of roots on soil erodibility

Roots influence the erodibility of a soil in a number of ways (Fig. 1). Firstly, the mechanical reinforcement of soils by roots was more effective in increasing soil shear strength, than the already mentioned hydrological effect associated with the entire plant system (Simon et al., 2006). Roots have a high tensile strength (Gyssels et al., 2005; De Baets et al., 2008) providing up to 100 % of the cohesive strength of a root permeated soil (Hales et al., 2009), thus increasing soil shear strength. The additional tensile strength associated with roots is responsible for the transfer of shear stresses via tensile resistance or interface friction within the soil-root matrix (Prosser et al., 1995; De Baets et al., 2008). There was a positive linear relationship between the cross-sectional area of barley (*Hordeum vulgare*) roots at the shear plane and, subsequent increases in soil shear strength in a silty clay loam soil (Waldron, 1977). In ryegrass, increasing root densities from 0.20 to 1.80 $\mathrm{g\,cm^{-3}}$ also increased strength from 1 to 5 kPa in a sandy clay loam (Tengbeh, 1993). Hence, the presence of roots considerably increases shear strength.

Secondly, roots prevent sediment transport by retaining soil particles (De Baets et al., 2006) and increasing the number of stable aggregates, due to their enmeshing effect (Haynes and Beare, 1997), which is also true for fungal hyphae (Haynes and Beare, 1995; Degens, 1997; Moreno-Espíndola et al., 2007), and the release of various organic and inorganic binding agents (Amezketa, 1999). Root exudates such as mucilage are considered the main mechanism by which plant roots enhance aggregate stability (Morel et al., 1991; Moreno-Espíndola et al., 2007). Root mucilage expands under wet conditions covering soil particles, while subsequent drying leads to the contraction of mucilage, pulling these soil particles tightly together to form a rhizosheath, and thereby reorienting clay particles parallel to the axis of the root (Oades, 1984; Watt et al., 1994; Amezketa, 1999; McCully, 1999). Moreover, root exudates are associated with the release of polyvalent cations that form strong bonds between organic molecules and clays (Oades, 1984; Pojasok and Kay, 1990; Amezketa, 1999). Increasing amounts of ions in solution after exudates were added limit clay dispersion and significantly increase aggregate stability (Pojasok and Kay, 1990). Decaying roots and fungal hyphae also represent a source of OM (Oades, 1984; Haynes and Beare, 1995; Amezketa, 1999) that contributes to aggregate stability. Thus aggregate stability is enhanced by biological activity (both plant and fungal) within the soil.

Root exudates represent 5 to 21 % of a plant's photosynthetically fixed carbon (C) (Walker et al., 2003) serving as a crucial energy source for microorganisms (Haynes and Beares, 1995; Amezketa, 1999). Both fungal and bacterial extracellular polymeric substances contribute to the cementation of aggregates, and, thus enhance aggregate persistence (Oades, 1984; Morel et al., 1991; Watt et al., 1994; Haynes and Beare, 1995; Bryan, 2000). However, the effect of roots on aggregate stability is species specific (Haynes and Beare, 1997; Amezketa, 1999) due to differences in root morphology (Pohl et al., 2009), turnover rates (Stokes et al., 2009), the quantity and chemical composition of the root exudates and the influence of differences in root exudates on microbial activity (Haynes and Beare, 1997; Bertin et al., 2003). Barley roots increased aggregate stability (Haynes and Beare, 1997), whilst there is contradicting evidence about the effects of roots of maize (*Zea mays*) on aggregate stability. Root mucilage of maize reportedly readily increased aggregation (Morel et al., 1991), but the release of chelating agents, such as organic acids (which destroy iron and aluminium bonds with OM) by maize decreased aggregate stability (Oades, 1984). These contrasting results may be attributed to genotypic variation in the chemistry of the root exudates. For example, within genotypes of barley three structural variations of mugineic acid (an organic ligand) have been found (Bertin et al., 2003). In addition, some organic compounds released by roots and microorganisms may also induce water repellency depending on soil matric potential and the number of wetting and drying cycles undergone (Hallett et al., 2003). However, OM and aggregate stability are crucial in the formation of macropores, which reduce bulk density and facilitate gaseous diffusion and improve infiltration rates (Gyssels and Poesen, 2003). Thus, the effects of root exudates vary with their composition.

Roots may also represent barriers to overland flow, and soil surface roughness provided by roots enhances infiltration rates (De Baets et al., 2006), while water uptake through roots (Macleod et al., 2007) and the creation of continuous pore spaces increase the infiltration capacity, reducing surface runoff (Bryan, 2000; Bronick and Lal, 2005; Macleod et al., 2007). Quinton et al. (2002) found a positive correlation between infiltration rates and root density for needle grass (*Stipa tenacissima*) and, to a lesser extent, for downy plantain (*Plantago albicans*), while unclear results were obtained for albaida (*Anthyllis cytisoides*) and white wormwood (*Artemisia herba-alba*). In alfalfa (*Medicago sativa*), 60 % of all flow paths are associated with the roots or the channels of decomposed roots allowing water to rapidly percolate through the soil matrix (Stokes et al., 2009). Shallow, fibrous root systems and rhizomatous mats of ryegrass and common bent grass (*Agrostis capillaris*), respectively, resulted in a low saturated hydraulic conductivity (Archer et al., 2002). Several authors (Mitchell et al., 1995; Meek et al., 1989; Archer et al., 2002; Devitt and Smith, 2002) suggest that living roots occupy available macropores for flow pathways, and enhance infiltration rates over time, as a result of channels created by decaying roots. Infiltration rates in a sandy loam, for instance, tripled within three years of alfalfa cultivation (Meek et al., 1989) and significantly increased infiltration rates were recorded for the last half of the growing season, and after harvest, of a maize crop (Archer et al., 2002). This is also supported by observations that the root effect of ryegrass on increasing infiltration rates (thus decreasing runoff) increased with time (Zhou and Shangguan, 2007). Moreover, the effects associated with cyclic shrinking-expanding of roots in accordance with water availability also created flow pathways over time (Archer et al., 2002). However, the effect of roots on flow pathways, and thus infiltration rates, differed under a number of Mediterranean species, due to differences in root morphology (Quinton et al., 2002), and turnover rates, as a result of differences in root diameter and chemical composition (Stokes et al., 2009). Thus, not only the presence of roots, but their physical arrangement within the soil, alters soil hydraulic properties.

A root parameter frequently measured in erosion studies is root length density (RLD). RLD is the total length of the roots divided by the volume of the root permeated soil sample (De Baets et al., 2006). Under cereal and grass plants in the loess belt of Belgium, concentrated flow erosion rates exponentially decreased with a linear increase in RLD (Gyssels and Poesen, 2003). Similar results were obtained by Mamo and Bubenzer (2001a, b) between erosion rates of a silt loam soil and RLD in maize and soybean (*Glycine max*), which reduced detachment rates by 50 % compared to fallow soils. A similar relation exists between RLD of barley and detachment rates (De Baets et al., 2007). However, increasing RLD either affects soil shear strength positively (Ghidey and Alberts, 1997; Mamo and Bubenzer, 2001a, b), or not at all, depending on species and soil type (Pierret et al., 2007). Furthermore, higher RLDs enhance soil aggregation in crop species (Haynes and Beare, 1997) and when comparing grass, forb and legume species from a natural grassland ecosystem (Rilling et al., 2002). However, the ability of roots to reinforce a soil is not only determined by RLD, but also by root system topology and the distribution of the roots within the soil profile.

3 Root system architecture and its manipulation

RSA is the three-dimensional deployment of roots (Linkohr et al., 2002) and is primarily influenced by genetic factors (Smucker, 1993; Malamy, 2005; Stokes et al., 2009), as demonstrated by mutants of maize lacking different root classes (Malamy, 2005). Mature cereal root systems consist mostly of long (seminal – seed derived, or nodal – shoot derived) roots and fine (lateral) roots (Ø < 1 mm) (LRs), which often develop root hairs (Mc Cully, 1999) from the trichoblasts in the meristematic zone (Gilroy and Jones, 2000). Although LRs are the major sites of water and nutrient uptake, the other root classes are mainly responsible for the storage of nutrients, water and C, as well as allowing the penetration of hard soils and deep horizons (Guerrero-Campo et al., 2006). LRs tend to have greater growth rates than other roots (Guerrero-Campo et al., 2006; Stokes et al., 2009) and account for ca. 90–98 % of the total root length of a root system (Engineer and Kranz, 2007; Pohl et al., 2009). Hence, total root length is mainly determined by the density of LRs (Guerrero-Campo et al., 2006; De Baets et al., 2007; Pierret et al., 2007). Thus RLD significantly increased with the percentage of LRs (Burylo et al., 2012), and decreased with increasing root diameters (Pohl et al., 2009). Moreover, different types of root system are often distinguished based on the presence of a primary root representing a single dominant axis with varying degrees of LR development, which is characteristic for primary or tap root systems (Fitter, 1987), whereas root systems lacking a primary root are referred to as a fibrous root system (DeBeats et al., 2007). Only a few studies have compared the effect of these different root systems on soil erosion rates, with fibrous root systems being more effective in reinforcing soils than tap root systems with similar root mass (DeBaets et al., 2007). In contrast, tap rooting species increase saturated hydraulic conductivity, which tends to be low under fibrous root systems (Archer et al., 2002; Quinton et al., 2002). These observations can be explained by the larger number of LRs associated with fibrous root systems compared to tap root systems (DeBaets et al., 2007).

The effect of roots on erodibility depends on the presence of LRs (Li et al., 1991). Increasing root diameter significantly increases a soil's erodibility when subjected to concentrated flow (De Baets et al., 2007, 2008). Similarly, soil detachment was positively correlated to root diameter of needle grass (*Achnatherum calamagrostis*) and two tree species (*Robinia pseudo acacia* and *Pinus nigra austriaca*) (Burylo et al., 2012). Root elasticity decreased with increasing lignin/cellulose ratio (Hathaway and Penny, 1975), as cellulose content is positively correlated with tensile strength and tends to be greater in LRs (Genet et al., 2005). This is is also reflected in exponential increases in tensile strength with decreasing root diameter, indicating that a high percentage of LRs may provide greater reinforcement at the shear plane (DeBaets et al., 2007; Loades et al., 2010; Burylo et al., 2012). Furthermore, Pohl et al. (2009) found that aggregate stability is correlated with the number of LRs, and that this correlation is stronger than that with other roots. LRs account for the majority of root tips in any root system, and are therefore the main source of root mucilage (McCully, 1999; Walker, 2003), thus potentially enhancing aggregate stability. LRs also tend to have greater turnover rates than other roots (Guerrero-Campo et al., 2006; Stokes et al., 2009), thus enhance the formation of fine OM (Archer et al., 2002). Gyssels et al. (2005) state that LRs significantly increase soil porosity and reduce the bulk density of a soil, depending on the nature of the soil and root diameter. Additionally, the root absorption capacity of water is associated with root length and density of the LRs (Guerrero-Campo et al., 2006). Thus LR abundance significantly alters both soil physical and hydrological properties.

Macleod et al. (2007) propose specific genetic selection and breeding for root traits, such as rooting depth, to improve soil hydraulic function. However, these root traits are under complex genetic control (Zhu et al., 2005; Macleod et al., 2007) even though alleles determining, for example, LR primordia development in thale cress (*Arabidopsis thaliana*) (Roycewicz and Malamy, 2014), as well as LR branching or length in maize (Zhu et al., 2005), have been identified. Limited knowledge of the root phenome, the “chaotic” nature of the interactions among phenes and environmental factors, ultimately determining crop performance and functional utility (Lynch and Brown, 2012), hinder the development of new crop varieties with altered root traits. Although RSA is genetically constrained, it is highly plastic in response to environmental cues. This means that genetically identical plants may differ in root density, growth rate, placement and growth direction (Müller and Schmidt, 2004; Malamy, 2005), as a result of adaptive responses (López-Bucio et al., 2003; Jones and Ljung, 2012) to the prevailing environmental conditions. The heterogeneous distribution of nutrients can increase LR length and initiation, as well as coordinate proliferation of LRs in soil regions where these resources are present (e.g. Fitter, 1987; Smucker, 1993; Stokes, 2009). Hence, the localized application of nutrients at deeper depths and associated LR proliferation offers an opportunity to manipulate LR distribution within the soil profile and a potential mechanism to promote RSAs that reduce soil erosion.

4 Lateral root proliferation in response to local nutrient availability

The local proliferation of LRs allows the optimal exploitation of locally available nutrient reserves (Smucker, 1993; Robinson, 1994; Hodge, 2006). Nitrogen (N), as well as phosphorus (P), often limits growth (Linkohr et al., 2002; López-Bucio et al., 2003). Nitrate (NO_3^-) is the major source of N for most plants and is, as well as ammonium (NH_4^+), readily available to plants (Engineer and Kranz, 2007). A series of studies by Drew and co-workers investigated the response of barley roots to local nutrient enrichment. Although a heterogeneous distribution of potassium (K) did not affect RSA (Drew, 1975; Robinson, 1994), LR initiation and extension increased within a 4 cm long segment of a seminal root exposed to 100 times greater concentrations of NO_3^- and NH_4^+ than the remainder of the root system, where nutrient-limited conditions inhibited LR development (Drew et al., 1973; Drew, 1975; Drew and Staker 1975) (Fig. 2). The same is true for wheat (*Triticum aestivum*) (Drew, 1975; Forde and Lorenzo, 2001) and maize grown in a flowing nutrient culture whereby two nodal roots were exposed to different NO_3^- concentrations revealed similar results (Granato and Raper, 1989). Furthermore, a concentration of 1 mM NO_3^- stimulated LR branching and increased LR diameters in both maize and barley (Drew, 1975; Granato and Raper, 1989), possibly due to increases in stele diameter and the numbers of cells in the root cortex and stele (Forde and Lorenzo, 2001). When thale cress was grown on vertical agar plates with a NO_3^--enriched band halfway down the plate, LR lengths increased 2–3 fold, although there was no evidence for enhanced LR initiation (Zhang and Forde, 1998). However, nutrient solutions containing NH_4^+ as primary N source lead to higher root densities and increased root elongation in maize compared to solutions containing NO_3^- (Jing et al., 2010). The localized availability of P often also results in increased LR extension (Drew, 1975; Robinson, 1994) and sometimes increased LR initiation within this zone (Drew, 1975). However, Drew (1975) highlights the importance of the presence of both nutrients, N and P, in stimulating LR proliferation. In addition, LR proliferation has been reported in response to organic and inorganic N and P, although the response to the former is determined by the extent and rate in which mineralization has occurred (Robinson, 1994). Thus LR proliferation in response to localised nutrient patches is well documented in many species grown in different artificial (not soil) media.

Root proliferation is believed to be triggered partly by shoot-to-root signalling, as the developmental response to localized increased NO_3^- was most pronounced with plants of low N status (Forde and Lorenzo, 2001; Forde, 2002). High NO_3^- levels result in increased auxin concentration in the LR tip stimulating LR growth, while high NH_4^+ levels enhance higher order root branching. The presence of both forms of N results in a complementary response (Forde, 2002; Jones and Ljung, 2012). However, if NO_3^- concentrations are too high, LR growth tends to be inhibited (Zhang and Forde, 1998; Linkohr et al., 2002), which is mediated by abscisic acid (López-Bucio et al., 2003). Thus a 30-fold increase of the NPK concentration of a nutrient solution decreased seminal root lengths and increased number of LRs in wheat (Trapeznikov et al., 2003). A detailed discussion of the molecular mechanisms responsible for LR proliferation in nutrient-rich zones is beyond the scope of this paper, but the topic has been recently reviewed by Jones and Ljung (2012).

However, the growth media used in these studies (agar, hydroponics) do not necessarily reflect natural conditions and it is important to determine whether such responses occur in soil. Paradoxically, when wheat plants were grown in soil-filled rhizotrons (1.4 m deep) with nutrients (both N and P) banded at 0–40 or 60–100 cm below the soil surface and the soil allowed to dry (simulating a terminal drought stress), the greatest RLD detected at 1.4 m occurred with the surface fertiliser application (Jin et al., 2015). However, fertiliser banding (stratification) and local placement (patches) can elicit different responses. LRs of thale cress in a NO_3^- enriched patch in a heterogeneous soil were only marginally longer than in the corresponding patch under homogeneous conditions (Linkohr et al., 2002). Nevertheless, LR proliferation has been observed in the field (Sattelmacher et al., 1993; Robinson, 1994). A recent study in North China showed that banding NH_4^+ and P at 10 cm depth resulted in a 23–30 % increase in total root length and higher RLD at a depth of 0–15 cm in maize compared to broadcast application, or banding of P only while NH_4^+ was broadcast. Moreover, banding of both nutrients also increased RLD at a depth of 15–30 cm (Jing et al., 2010). However, the responsiveness varies between different species and genotypes (Robinson, 1994).

5 Manipulating root system architecture with deep fertilizer placement to control erosion

Beyond the selection of different plant species, little consideration has been given to the potential for manipulating plant RSA for soil erosion control, although the distribution of LRs within the top 50 cm of the soil is crucial in determining the effect of roots on the resistance of soils to concentrated flow erosion (Li et al., 1991). Dense mats of LRs are commonly found at the soil surface (Pierret et al., 2007) and the abundance of roots gradually declines with increasing soil depth (Quinton et al., 2002; DeBaets et al., 2008). However, it has been argued higher RLDs at deeper soil depths would be particularly beneficial, as this increases water uptake and evapotranspiration rates, thus infiltration rates (Macleod et al., 2007; Stokes et al., 2009). In addition, longer vertical roots and, thus, higher RLD at deeper depths, provide conduits to deeper soil layers (Archer et al., 2002; Devitt and Smith, 2002; Quinton et al., 2002) and directly affect storage capacity of the effective soil depth. Improvements in aggregate stability tend to be particularly pronounced in, if not spatially limited to, the rhizosphere (Oades, 1994; Foster, 1988; Morel et al., 1991; Haynes and Beare, 1997), so the extent of the root system determines its effect on soil aggregation (Haynes and Beare, 1997). The effects of roots of the grasses *Stipa bungeana* and *Bothriochlon ischaemum* on the properties of a Chinese loess soil (SOM and aggregate stability, especially in large diameter classes) decreased with increasing depth, as RLD deminished (Li and Li, 2011). The higher sediment load derived from deep soil horizons associated with the higher susceptibility of these soil horizons to erosional forces was further enhanced by increasing runoff discharge and slope gradient (Li and Li, 2011) and was particularly critical during concentrated flow erosion. Furthermore, soil cohesion provided by roots is also limited to the rooting depth of the vegetation, consequently soil reinforcement decreases with increasing depth (Gyssels et al., 2005; De Baets et al., 2007). Although Mediterranean shrubs only stabilize the top 50 cm of gully walls and hillslopes, failures may occur at deeper depths and increases in soil strength depend on the number of LRs that cross the potential shear plane (De Baets et al., 2007). These effects of increased RLD and rooting depths on erodibility may be seen in some fibrous species in response to deep fertilizer placement (Robinson, 2001).

Plants may also respond to heterogeneous nutrient supply with compensatory root growth (Drew, 1975; Robinson, 1994). Compensatory growth means that proliferation within the N or P enriched zone compensates, and may be proportional to, the inhibitory effect of the limited availability of these nutrients on LR development outside this zone (Robinson, 1994). In this case, soil properties at different soil layers may change accordingly to the proportion of LRs present within these layers. Reduced LR growth on the soil surface, when nutrients are only available at deeper depths, could potentially increase the water storage capacity of a soil, as the number of blocked pores by LRs at the soil surface would be reduced. Furthermore, although the diameter of LR increases in nutrient enriched zones (Drew, 1975; Granato and Raper, 1989; Forde and Lorenzo, 2001), LR proliferation may still increase shear strength locally (De Baets et al., 2008; Loades et al., 2010) and could help to reinforce soils at the shear plane. In addition, aggregate stability may be improved within the nutrient poor patch, as larger quantities of mucilage may be released within this zone to mobilise scarcely available P (Bertin et al., 2003). In contrast, Paterson et al. (2006) showed that LR proliferation in response to localized availability of NO_3^- resulted only in a locally increased release of root exudates in barley. Compensatory growth may also enhance root hair development in the nutrient poor zone, and root hairs contribute to soil aggregation in the rhizosphere and are crucial for rhizosheath development (Hochholdinger et al., 2004; Moreno-Espíndola et al., 2007). Root hair length increased from 0.1–0.2 to 0.7 mm and density by a factor of 2–4 when spinach (*Spinacia oleracea*), tomato (*Solanum lycopersicum*) and rapeseed (*Brassica napus*) were grown in nutrient solutions with concentrations of 2 μM P compared to concentrations of 1000 µM P (Foehse and Junk, 1983). Split-root system experiments demonstrated root hair development of spinach in high P concentrations is not affected if the remainder of the root system is exposed to low P concentrations. In contrast, the magnitude of the positive effect on root hair development of limited NO_3^- varied between species. However, further research is needed into the effects of differences in RSA development in response to deep fertilizer application on soil properties and subsequently erosion rates.

6 Effects of LR proliferation on the above-ground material

Roots with larger diameters do not proliferate (Drew, 1975; Granato and Raper, 1989; Smucker, 1993; McCully, 1999). More C is required to produce and maintain respiration within these roots, due to the increased number of cortical cells within them, in addition to increased C consumption rates caused by spatially limited nutrient availability per se. Consequently, the relative high demand of plant photosynthates required by roots with large diameters may negatively impact on above ground biomass production (Drew, 1975; Smucker, 1993). Recent estimates suggest root proliferation is a relative low cost strategy adapted by plants to effectively absorb available ions and water in heterogeneous environments, requiring only an additional 0.2 % of the plant's daily carbon gain (Hodge, 2006). Obviously, smaller root diameters represent less resistance to the flow of ions and water during the uptake of these resources (Smucker, 1993). However, net C costs will be determined by factors such as rooting volume, photosynthetic supply and may be even zero if compensatory growth occurs (Robinson, 2001). This should buffer potential negative effects of limited nutrient availability within some soil areas on above ground biomass although biomass partitioning ultimately depends on shoot nutrient status (Drew, 1975; Drew and Saker, 1975; Robinson, 1994). LR proliferation either increases or has no effect on root to shoot ratios (Robinson, 1994). Shoot development may be slightly retarded, which is reflected in differences in absolute biomass reported in barley grown under heterogeneous nutrient availability and the controls, although both treatments yielded similar total biomass (Drew and Saker, 1975). The authors attribute this observation to initial nutrient deficiencies until the roots have reached the nutrient-rich zone (Drew and Saker, 1975). In addition, placement of N fertilizer (calcium ammonium nitrate) at 10 cm depth compared to surface mixing significantly increased dry matter production and grain yield at maturity of wheat grown in a loamy sand soil (Sharma and Chaudhary, 1983). However, there is a large variability between species (Robinson, 1994; Hodge, 2006) and genotypes (Sattelmacher et al., 1993; Forde and Lorenzo, 2001) in their shoot responsiveness, which depends on differences in nutrient uptake and utilization efficiency (Sattelmacher et al., 1993). Nevertheless, LR proliferation may occur without limiting above-ground growth (and yield).

7 Conclusion

In conclusion, plant roots are crucial in reducing erosion rates when subjected to concentrated flow, as their presence affects soil properties such as aggregate stability, hydraulic function and shear strength. However, the effect of roots on soil erodibility is determined by RLD, and, thus, LR density and length, and the distribution of roots within the soil. It has been argued that a higher RLD at greater depths would be particularly beneficial in reducing soil erosion rates. In nutrient poor soils, the local availability of high N or P at deeper soil depths may result in LR proliferation, although the response will depend on plant species, and may include a general increase in rooting depth or compensatory growth. Increased rooting depths and/or the proliferation of LR at deeper depths on agricultural land can be achieved by banding fertilizer at the desired soil depth either before sowing, during tillage or by injection after seedling emergence. Alternatively, nutrient solutions supplied via access holes may be used to stabilize constructed slopes (Robinson, 1994). Further benefits of the deep application of fertilizer may include the enhanced competitive ability of crops against weeds (Di Tomaso, 1995). In addition, the extent of the root system, and thus rhizosphere, influences the degradation capability for pollutants as well as the ability of plants to extract pollutants from a soil (Wenzel, 2009). Hence, deep fertilizer applications may be used to stabilise and reclaim contaminated sites.

However, research is needed to determine whether the localized application of N and P at deeper soil depths may represent a potential management technique to control erosion of degraded agricultural soils with low nutrient content and engineered slopes. Investigations should therefore aim to explore the effects of LR distribution at varying depths on soil properties, and, hence, erodibility. In addition, responsiveness of different crops, grasses and shrubs (and different genotypes within a species) to heterogeneous nutrient availability should be determined. Moreover, suitable depth(s) for deep fertilizer placement should be established (with reference to practical implementation) and the effects of varying environmental conditions, such as soil type, slope and flow characteristics, on the erosion reducing effect of this potential management technique needs to be assessed.

References

Abrahams, A. D., Parsons, A. J., and Luk, S. H.: Hydrologic and sediment responses to simulated rainfall on desert hillslopes in southern Arizona, Catena, 15, 103–117, 1988.

Amezketa, E.: Soil aggregate stability: a review, J. Sust. Agric., 14, 83–151, 1999.

Archer, N. A. L., Quinton, J. N., and Hess, T. M.: Below-ground relationships of soil texture, roots and hydraulic conductivity in two-phase mosaic vegetation in South-east Spain, J. Arid Environ., 52, 535–553, 2002.

Bertin, C., Yang, X., and Weston, L.: The role of root exudates and allelochemicals in the rhizosphere, Plant Soil, 256, 67–83, 2003.

Bochet, E., Poesen, J., and Rubio, J. L.: Runoff and soil loss under individual plants of a semi-arid Mediterranean shrubland: influence of plant morphology and rainfall intensity, Earth Surf. Proc. Landforms, 31, 536–549, 2006.

Boer, M. and Puidgefábregas, J.: Effects of spatially structured vegetation patterns on hillslope erosion in a semiarid Mediterranean environment: a simulation study, Earth Surf. Proc. Landforms, 30, 149–167, 2005.

Bronick, C. J. and Lal, R.: Soil structure and management: a review, Geoderma, 124, 3–22, 2005.

Bryan, R. B.: Soil erodibility and processes of water erosion on hillslope, Geomorphology, 32, 385–415, 2000.

Burylo, M., Rey, F., Mathys, N., and Dutoit, T.: Plant root traits affecting the resistance of soils to concentrated flow erosion, Earth Surf. Proc. Landforms, 37, 1436–1470, 2012.

De Baets, S., Poesen, J., Gyssels, G., and Knapen, A.: Effects of grass roots on the erodibility of topsoil during concentrated flow, Geomorphology, 76, 54–67, 2006.

De Baets, S., Poesen, J., Knapen, A., and Galindo, P.: Impact of root architecture on the erosion-reducing potential of roots during concentrated flow, Earth Surf. Proc. Landforms, 32, 1323–1345, 2007.

De Baets, S., Poesen, J., Reubens, B., Wemans, K., De Baerdemaeker, J., and Muys, B.: Tensile strength and root distribution of typical mediterranean plant species and their contribution to soil shear strength, Plant Soil, 305, 207–226, 2008.

Degens, B. P.: Macro-aggregation of soils by biological bonding and binding mechanisms and the factors affecting these: A review, Aust. J. Soil Res., 35, 431–459, 1997.

Devitt, D. A. and Smith, S. D.: Root channel macropores enhance downward movement of water in a Mojave Desert ecosystem, J. Arid Environ., 50, 99–108, 2002.

Di Tomaso, J. M.: Approaches for Improving Crop Competitiveness through the Manipulation of Fertilization Strategies, Weed Sci., 43, 491–497, 1995.

Drew, M. C.: Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley, New Phytologist, 75, 479–490, 1975.

Drew, M. C. and Saker, L. R.: Nutrient supply and the growth of the seminal root system of barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system, J. Exp. Bot., 26, 79–90, 1975.

Drew, M. C., Saker, L. R., and Ashley, T. W.: Nutrient supply and the growth of the seminal root system in barley. I. The effect of nitrate concentration on the growth of axes and laterals, J. Exp. Bot., 24, 1189–1202, 1973.

Engineer, C. B. and Kranz, R. G.: Reciprocal leaf and root expression of *AtAmt1.1* and root architectural changes in response to nitrogen starvation, Plant Physiol., 143, 236–250, 2007.

Fitter, A. H.: An architectural approach to the comparative ecology of plant root systems, New Phytologist, 106, 61–77, 1987.

Foehse, D. and Jungk, A.: Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants, Plant Soil, 74, 359–368, 1983.

Forde, B. G.: Local and long-range signaling pathways regulating plant responses to nitrate, Annu. Rev. Plant Biol., 53, 203–224, 2002.

Forde, B. G. and Lorenzo, H.: The nutritional control of root development, Plant Soil, 232, 51–68, 2001.

Foster, R. C.: Microenvironments of soil microorganisms, Biol. Fert. Soils, 6, 189–203, 1988.

Genet, M., Stokes, A., Salin, F., Mickovski, S. B., Fourcaud, T., Dumail, J., and van Beek, R.: The influence of cellulose content on tensile strength in tree roots, Plant Soil, 278, 1–9, 2005.

Ghidey, F. and Alberts, E. E.: Plant root effects on soil erodibility, splash detachment, soil strength,and aggregate stability, Trans. Am. Soc. Agric. Eng., 40, 129–35, 1997.

Gilroy, S. and Jones, D. L.: Through form to function: root hair development and nutrient uptake, Trends Plant Sci., 2, 56–60, 2000.

González-Pelayo, O., Andreu, V., Gimeno-García, E., and Rubio, J. L.: Rainfall influence on plot-scale runoff and soil loss from repreated burning in a Mediterranean-shrub ecosystem, Valencia, Spain, Geomorphology, 118, 444–452, 2010.

Granato, T. C. and Raper Jr., D.: Proliferation of maize *(Zea mays* L.) roots in response to localized supply of nitrate, J. Exp. Bot., 40, 263–275, 1989.

Guerrero-Campo, J., Palacio, S., Pérez-Rontomé, C., and Montserrat-Martí, G.: Effect of root system morphology on root-sprouting and shoot-rooting abilities in 123 plant species from eroded lands in North-east Spain, Ann. Botany, 98, 439–447, 2006.

Gyssels, G. and Poesen, J.: The importance of plant root characteristics in controlling concentrated flow erosion rates, Earth Surf. Proc. Landforms, 28, 371–384, 2003.

Gyssels, G., Poesen, J., Bochet, E., and Li, Y.: Impact of plant roots on the resistance of soils to erosion by water: a review, Prog. Phys. Geogr., 29, 189–217, 2005.

Hales, T. C., Ford, C. R., Hwang, T., Vose, J. M., and Band, L. E.: Topographic and ecological controls on root reinforcement, J. Geophys. Res., 114, 1–17, 2009.

Hallett, P. D., Gordon, D. C., and Bengough, A. G.: Plant influence on rhizosphere hydraulic properties: direct measurements using a miniaturized infiltrometer, New Phytologist, 157, 597–603, 2003.

Hathaway, R. L. and Penny, D.: Root strength in some populus and salix clones, New Zealand J. Bot., 13, 333–344, 1975.

Haynes, R. J. and Beare, M. H.: Influence of six crop species on aggregate stability and some labile organic matter fractions, Soil Biol. Biochem., 29, 1647–1653, 1997.

Hochholdinger, F., Woll, K., Sauer, M., and Dembinsky, D.: Genetic dissection of root formation in Maize (*Z. mays*) reveals root-type specific developmental programmes, Ann. Botany, 93, 359–368, 2004.

Hodge, A.: Plastic plants and patchy soils, J. Exp. Bot., 57, 401–411, 2006.

Jankauskas, B., Jankauskiene, G., and Fullen, M. A.: Soil erosion changes in the physical properties of Lithuanian Eutric Albeluvisols under different land use systems, Acta Agric. Scandinavian Section B – Soil and Plant Science, 58, 66–76, 2008.

Jin, K., Shen, J., Ashton, R. W., White, R. P., Dodd, I. C., Parry, M. A. J., and Whalley, W. R.: Wheat root growth responses to horizontal stratification of fertiliser in a water-limited environment, Plant Soil, 386, 77–88, doi:10.1007/s11104-014-2249-8, 2015.

Jing, J., Rui, Y., Zhang, F., Rengel, Z., and Shen, J.: Localized application of phosphorus and ammonium improves growth of maize seedlings by stimulating root proliferation and rhizosphere acidification, Field Crops Res., 119, 355–364, 2010.

Jones, B. and Ljung, K.: Subterranean space exploration: the development of root system architecture, Current Opinion Plant Biology, 15, 97–102, 2012.

Lal, R.: Soil degradation by erosion, Land Deg. Develop., 12, 519–539, 2001.

Li, P. and Li, Z.: Soil reinforcement by a root system and its effects on sediment yield in response to concentrated flow in the loess plateau, Agric. Sci., 2, 86–93, 2011.

Li, Y., Zhu, X.-M., and Tian, J.-Y.: Effectiveness of plant roots to increase the anti-scourability of soil on the Loess Plateau, Chinese Sci. B., 36, 2077–2082, 1991.

Linkohr, B. I., Williamson, L. C., Fitter, A. H., and Leyser, O.: Nitrate and phosphate availability and distribution have different effects on root system architecture of *Arabidopsis*, The Plant J., 29, 751–760, 2002.

Loades, K. W., Bengough, A. G., Bransby, M. F., and Hallet, P. D.: Plant density influence on fibrous root reinforcement of soils, Ecol. Eng., 36, 276–284, 2010.

Lynch, J. P. and Brown, K. M.: New roots for agriculture: exploiting the root phenome, Phil. Trans. Roy. Soc. B., 367, 1598–1604, 2012.

López-Bucio, J., Cruz-Ramírez, A., and Estrella-Herrera, L.: The role of nutrient availability in regulating root architecture, Current Opinion Plant Biol., 6, 280–287, 2003.

Macleod, C. J. A., Binley, A., Hawkins, S. L., Humphreys, M. W., Turner, L. B., Whalley, W. R., and Haygarth, P. M.: Genetically modified hydrographs: what can grass genetics do for temperate catchment hydrology?, Hydrol. Processes, 21, 2217–2221, 2007.

Mamo, M. and Bubenzer, G. D.: Detachment rate, soil erodibility and soil strength as influenced by living plant roots: Part II. Field study, Am. Soc. Agric. Eng., 44, 1175–1181, 2001a.

Mamo, M. and Bubenzer, G. D.: Detachment rate, soil erodibility and soil strength as influenced by living plant roots: Part I. Laboratory study, Am. Soc. Agric. Eng., 44, 1167–1174, 2001b.

McCully, M. E.: Roots in soil: unearthing the complexities of roots and their rhizospheres, Annu. Rev. Plant Physiol. Plant Molec. Biol., 50, 695–718, 1999.

Meek, B. D., Rechel, E. A., Carter, L. M., and De Tar, W. R.: Changes in infiltration under alfalfa as influenced by time and wheel traffic, Soil Sci. Soc. Am. J., 53, 238–241, 1989.

Mitchell, A. R., Ellsworth, T. R., and Meek, B. D.: Effects of root systems on preferential flow in swelling soils, Comm. Soil Sci. Plant Anal., 26, 2655–2666, 1995.

Morel, J. L., Habib, L., Plantureux, S., and Guckert, A.: Influence of maize root mucilage on soil aggregate stability, Plant Soil, 136, 111–119, 1991.

Moreno-Espíndola, I. P., Rivera-Becerril, F., De Jésus Ferrera-Guerrero, M., and De Léon-González, F.: Role of root-hairs and hyphae in adhesion of sand particles, Soil Biol. Biochem., 39, 2520–2526, 2007.

Morgan, R. P. C.: Soil Erosion Conservation (2nd ed.), Longman, Harlow, UK, 1986.

Müller, M. and Schmidt, W.: Environmentally induced plasticity of root hair development in Arabidopsis, Plant Physiology, 134, 409–419, 2004.

Oades, J. M.: Soil organic matter and structural stability: mechanisms and implications for management, Plant Soil, 76, 319–337, 1984.

Paterson, E., Sim, A., Standing, D., Dorward, M., and McDonald, A. J. S.: Root exudation from *Hordeum vulgare* in response to localized nitrate supply, J. Exp. Bot., 57, 2413–2420, 2006.

Pierret, A., Latchackak, K., Chathanvongsa, P., Sengtaheuanghoung, O., and Valentin, C.: Interactions between root growth, slopes and soil detachment depending on land use: a case study of a small mountain catchment in Northern Laos, Plant Soil, 301, 51–64, 2007.

Pimentel, D.: Soil erosion: a food and environmental threat, Environ., Develop. Sust., 8, 119–137, 2006.

Pimentel, D. and Kounang, N.: Ecology of soil erosion in ecosystems, Ecosystems, 1, 416–426, 1998.

Pohl, M., Alig, D., Körner, C., and Rixen, C.: Higher plant diversity enhances soil stability in disturbed alpine ecosystems, Plant Soil, 324, 91–102, 2009.

Pojasok, T. and Kay, B. D.: Effect of root exudates from corn and bromegrass on soil structural stability, Can. J. Soil Sci., 70, 351–362, 1990.

Posthumus, H., Deeks, L. K., Rickson, R. J., and Quinton, J. N.: Costs and benefits of erosion control measures in the UK, Soil Use Manag., published online first, doi:10.1111/sum.12057, 2013.

Prosser, I. P., Dietrich, W. E., and Stevenson, J.: Flow resistance and sediment transport by concentrated overland flow in a grassland valley, Geomorphology, 13, 71–86, 1995.

Puigdefábregas, J.: The role of vegetation patterns in structuring runoff and sediment fluxes in drylands, Earth Surf. Proc. Landforms, 30, 133–147, 2005.

Quinton, J. N., Morgan, R. P. C., Archer, N. A., Hall, G. M., and Green, A.: Bioengineering principles and desertification mitigation, in: Mediterranean desertification, A mosaic of processes and responses, edited by: Brandt, C. J., Geeson, N. A., and Thornes, J. B., John Wiley and Sons, Chichester, p. 93–105, 2002.

Rilling, M. C., Wright, S. F., and Eviner, V. T.: The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species, Plant Soil, 238, 325–333, 2002.

Robinson, D.: The response of plants to non-uniformus supplies of nutrients, New Phytologist, 127, 635–674, 1994.

Robinson, D.: Root proliferation, nitrate inflow and their carbon costs during nitrogen capture by competing plants in patchy soil, Plant Soil, 232, 41–50, 2001.

Roycewicz, P. S. and Malamy, J. E.: Cell wall properties play an important role in the emergence of lateral root primordia from the parent root, J. Exp. Bot., 65, 2057–2069, 2014.

Sattelmacher, B., Gerendas, J., Thoms, K., Brück, H., and Bagdady, N. H.: Interaction between root growth and mineral nutrition, Environ. Exp. Bot., 33, 63–73, 1993.

Sharma, B. R. and Chaudhary, T. N.: Wheat root growth, grain yield and water uptake as influenced by soil water regime and depth of nitrogen placement in a loamy sand soil, Agric. Water Manag., 6, 365–373, 1983.

Simon, A., Pollen, N., and Langendoen, E.: Influence of two woody riparian species on critical conditions for streambank stability: upper Truckee river, California, J. Am. Water Resour. Assoc., 42, 99–113, 2006.

Smucker, A. J. M.: Soil environmental modifications of root dynamics and measurement, Annu. Rev. Phytopathol., 31, 191–216, 1993.

Stocking, M. and Elwell, H.: Vegetation and erosion: A review, Scottish Geographical Magazine, 92, 4–16, 1976.

Stokes, A., Atger, C., Bengough, A. G., Fourcaud, T., and Sidle, R. C.: Desirable plant root traits for protecting natural and engineered slopes against landslides, Plant Soil, 324, 1–30, 2009.

Tengbeh, G. T.: The effect of grass roots on shear strength variations with moisture content, Soil Technol., 6, 287–295, 1993.

Trapeznikov, V. K., Ivanov, I. I., and Kudoyarova, G. R.: Effect of heterogeneous distribution of nutrients on root growth, ABA content and drought resistance of wheat plants, Plant Soil, 252, 207–214, 2003.

Trimble, S. W. and Mendel, A. C.: The cow as a geomorphic agent – a critical review, Geomorphology, 13, 233–253, 1995.

Vásquez-Méndez, R., Ventura-Ramos, E., Oleschko, K., Hernández-Sandoval, L., Parrot, J.-F., and Nearing, M. A.: Soil erosion and runoff in different vegetation patches from semiarid Central Mexico, Catena, 80, 162–169, 2010.

Waldron, L. J.: Shear resistance of root-permeated homogenous and stratified soil, Soil Sci. Soc. Am. J., 41, 843–849, 1977.

Walker, T. S., Harsh, P. B., Grotewold, E., and Vivanco, J. M.: Root exudates and rhizosphere biology, Plant Physiology, 132, 44–51, 2003.

Watt, M., McCully, M. E., and Canny, M. J.: Formation and stabilization of rhizosheats of *Z. mays* L., Plant Physiology, 106, 179–186, 1994.

Wenzel, W. W.: Rhizosphere processes and management in plant-assisted bioremediation (phytoremediation) of soils, Plant Soil, 321, 385–408, 2009.

Zhang, H. and Forde, B. G.: An Arabidopsis MADS box gene that controls nutrient-induced changes in root architecture, Science, 279, 407–409, 1998.

Zhou, Z.-C. and Shangguan, Z.-P.: Soil anti-scouribility enhanced by plant roots, J. Int. Plant Biol., 47, 676–682, 2005.

Zhu, J., Kaeppler, S., and Lynch, J. P.: Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply, Theor. Appl. Genetics, 111, 688–695, 2005.

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◂◂ ▸▸
◂ ▸
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

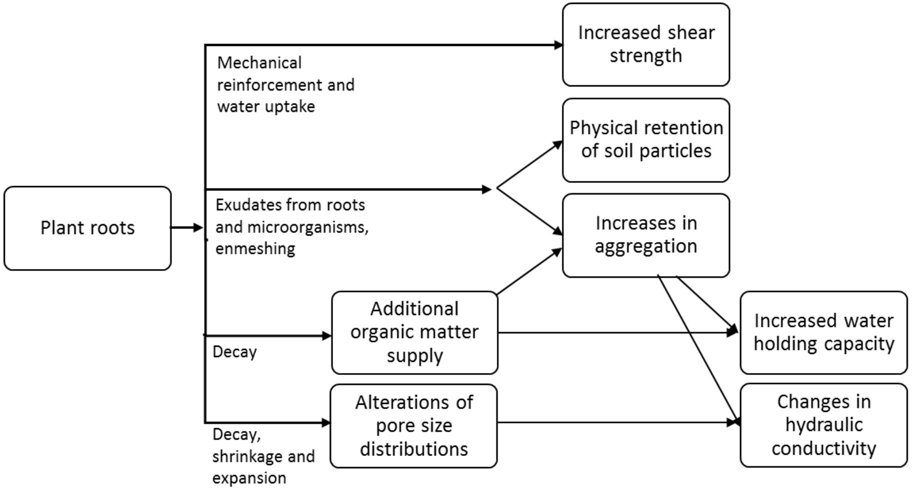

Figure 1. Key mechanisms by which plant roots influence soil physical properties.

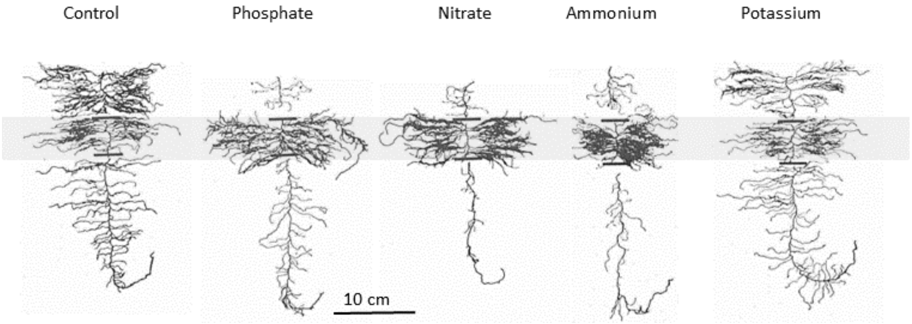

Figure 2. Effect of a localised supply of phosphate, nitrate, ammonium, and potassium on root form. Control plants received the complete nutrient solution to all parts of the root system. The other roots received the complete nutrient solution only in the middle zone (shaded), the top and bottom being supplied with a solution deficient in the specified nutrient. Adapted and reproduced with permission from Drew (1975). ©John Wiley and Sons.