

1 Can we manipulate root system architecture to control soil
2 erosion?

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7 **Abstract**

8 Soil erosion is a major threat to soil functioning. The use of vegetation to control erosion has
9 long been a topic for research. Much of this research has focused on the above ground
10 properties of plants, demonstrating the important role that canopy structure and cover plays in
11 the reduction of water erosion processes. Less attention has been paid to plant roots. Plant
12 roots are a crucial yet under-researched factor for reducing water erosion through their ability
13 to alter soil properties, such as aggregate stability, hydraulic function and shear strength.
14 However, there have been few attempts to specifically manipulate plant root system
15 properties to reduce soil erosion. Therefore, this review aims to explore the effects that plant
16 roots have on soil erosion and hydrological processes, and how plant root architecture might
17 be manipulated to enhance its erosion control properties. We demonstrate the importance of
18 root system architecture for the control of soil erosion. We also show that some plant species
19 respond to nutrient enriched patches by increasing lateral root proliferation. The erosional
20 response to root proliferation will depend upon its location: at the soil surface dense mats of
21 roots may reduce soil erodibility but block soil pores thereby limiting infiltration, enhancing
22 runoff. Additionally, in nutrient deprived regions, root hair development may be stimulated

1 and larger amounts of root exudates released, thereby improving aggregate stability and
2 decreasing erodibility. Utilising nutrient placement at specific depths may represent a
3 potentially new, easily implemented, management strategy on nutrient poor agricultural land
4 or constructed slopes to control erosion, and further research in this area is needed.

5 **1.Introduction**

6 Soil is a vital component of the earth system fundamental for many aspects of science
7 (Brevek et al., 2015). The damage caused to soils by soil erosion is therefore of considerable
8 concern. Soil erosion by water is a serious environmental problem representing a much
9 greater threat to agricultural production than soil erosion by wind (Lal, 2010). Approximately
10 430 million ha of arable land, or 30% of the globally available land for agricultural
11 production, has been degraded by water erosion and a further 56% is at risk (Jankauskas *et*
12 *al.*, 2008). The effect of vegetation on reducing soil erosion is well known. Plants intercept
13 rainfall, some is stored in the canopy with the remainder evaporating or reaching the soil
14 surface either directly as throughfall, or indirectly through stem flow or leaf drainage
15 (Stocking and Elwell, 1976; Puigdefábregas, 2005). Water reaching the soil surface may be
16 stored in small depressions on the soil surface or infiltrate into the soil. The remainder may
17 move downhill as overland flow, entraining soil particles and transporting them, and may also
18 concentrate to form rills and gullies. There are a number of factors controlling erosion,
19 namely the erosivity of the eroding agent, slope angle, the nature of the plant cover and the
20 erodibility of the soil (Morgan, 1986). Erosion may result in on-site soil degradation reducing
21 the soil's productivity and water storage capacity, due to changes in soil structure, soil depth
22 and losses of nutrients and organic matter (OM). This may lead to significant losses of crop
23 yield (Lal, 2001; Pimentel, 2006; Jankauskas *et al.*, 2008), posing a threat to food security or
24 limiting the production of renewable biotic resources (Pimentel, 2006; Jankauskas *et al.*,
25 2008). Off-site problems associated with downstream sedimentation include flooding,

1 pollution, negative effects on biodiversity, as well as the loss of reservoir storage (Pimentel
2 and Kounang, 1998; Lal, 2001; Pimentel, 2006). In the UK, the annual costs of both on-site
3 and off-site problems were recently estimated to range between £248 and £469 million
4 (Posthumus *et al.*, 2013). Hence, there is a need to stabilize soils and preserve this crucial
5 resource.

6 The importance of vegetation cover to control erosion has been demonstrated by many
7 studies, from plot (Quinton *et al.*, 1997) to basin scale (Zhao *et al.*, 2013); it plays a
8 significant role in the recovery of degraded land following anthropogenic and climatic stress
9 (Cerdà & Doerr, 2005; Zhao *et al.*, 2013) Both linear and exponential decreases in erosion
10 rates associated with vegetation cover have been observed, as the nature of the relationship
11 varies for canopy and ground covers, or inter-rill and rill erosion (Boer and Puidgefábregas,
12 2005). In Montana and Utah, for example, overland flow erosion rates increased ca. 200 times
13 in response to a decrease in ground cover from 100% to less than 1% (Trimble and Mendel,
14 1995). A minimum of 10% plant cover was required to significantly reduce erosion rates on a
15 semi-arid hillslope in Arizona (Abrahams *et al.*, 1988), however, the magnitude of the
16 response ultimately depends on vegetation type and species (Bochet *et al.*, 2006). Positive
17 effects of the aerial biomass in controlling erosion are generally attributed to reductions in the
18 kinetic energy of raindrops and reduced overland flow velocities (Stocking and Elwell, 1976;
19 Puigdefábregas, 2005). Furthermore, vegetation covers modify intrinsic soil properties
20 determining a soil's erodibility (Gyssels *et al.*, 2005) creating a microclimate and supplying
21 OM, that affect the activity of microorganisms, and therefore nutrient availability, resulting in
22 a positive feedback on plant productivity. Both additional OM as well as microbial and fungal
23 secretions enhance the formation of stable aggregates (Puidgefábregas, 2005, Vásquez-
24 Méndez *et al.*, 2010), which affect hydraulic conductivity and, hence, water storage capacity

1 (Puidgefábregas, 2005) and may increase soil shear strength (Tengbeh, 1993; De Baets *et al*,
2 2008).

3 Compared to studies on above ground plant properties and soil erosion, the effects of below
4 ground biomass have received relatively little attention. However, it is clear that the reduction
5 in soil loss due to vegetation results from the combined effects of the above and below ground
6 biomass (Gyssels and Poesen, 2003). Concentrated flow erosion rates were reduced to almost
7 zero within the 0-10% soil cross-sectional occupation by grass roots, but decreased only by
8 25-50% for the same increase in aerial cover (De Baets *et al.*, 2006). Furthermore, a rainfall
9 simulation experiment conducted 27 weeks after ryegrass (*Lolium perenne*) was sown in
10 erosion pans demonstrated (by removal of the above ground material) that the below ground
11 material of this species accounted for 90% of the decrease in soil detachment (Zhou and
12 Shangguan, 2007).

13 In this paper we take an interdisciplinary view of the plant root and its interaction with the
14 soil, and review the literature concerning the effects of roots on soil properties determining
15 the resistance of soil to water erosion (concentrated and sheet flow) with emphasis on root
16 system architecture (RSA). We then explore the factors influencing RSA especially lateral
17 root (LR) growth, and finally the potential of fertilizer applications to stimulate LR
18 proliferation, and thus form the basis for a soil erosion control method, will be discussed.

19 **2.The effects of roots on soil erodibility**

20 Erodibility is the result of various mechanical, adhesive and cohesive bonding forces acting
21 within the soil matrix (Knapen *et al.*, 2007) and should be regarded as a ‘summation of a
22 highly complex response pattern, strongly influenced by intrinsic soil characteristics and
23 extrinsic variables’ (Bryan, 2000). The erosion response may be influenced by any soil
24 property, but will be dominated by shear strength, aggregate stability and hydraulic function

1 (Bryan, 2000). Roots alter the erodibility of a soil through their effect on these soil properties
2 in a number of ways (Figure 1). Firstly, roots have a high tensile strength (Gyssels *et al.*,
3 2005; De Baets *et al.*, 2008) providing up to 100% of the cohesive strength of a root
4 permeated soil (Hales *et al.*, 2009), thus increasing soil shear strength. The additional tensile
5 strength associated with roots is responsible for the transfer of shear stresses via tensile
6 resistance or interface friction within the soil-root matrix (Prosser *et al.*, 1995, De Baets *et al.*,
7 2008). There was a positive linear relationship between the cross-sectional area of barley
8 (*Hordeum vulgare*) roots at the shear plane and, subsequent increases in soil shear strength in
9 a silty clay loam soil (Waldron, 1977). In ryegrass, increasing root densities from 0.20 g cm⁻³
10 to 1.80 g cm⁻³ also increased strength from 1 kPa to 5 kPa in a sandy clay loam (Tengbeh,
11 1993). Hence, the presence of roots considerably increases shear strength.

12 Secondly, roots prevent sediment transport by retaining soil particles (De Baets *et al.* 2006)
13 and increasing the number of stable aggregates, due to their enmeshing effect (Haynes and
14 Beare, 1997), which is also true for fungal hyphae (Haynes and Beare, 1997; Degens, 1997;
15 Moreno-Espíndola *et al.* 2007), and the release of various organic and inorganic binding
16 agents (Amezketá, 1999). Root exudates such as mucilage are considered the main
17 mechanism by which plant roots enhance aggregate stability (Morel *et al.*, 1991; Moreno-
18 Espíndola *et al.* 2007). Root mucilage expands under wet conditions covering soil particles,
19 while subsequent drying leads to the contraction of mucilage, pulling these soil particles
20 tightly together to form a rhizosheath, and thereby reorienting clay particles parallel to the
21 axis of the root (Oades, 1984; Watt *et al.*, 1994; Amezketá, 1999; McCully, 1999). Moreover,
22 root exudates are associated with the release of polyvalent cations that form strong bonds
23 between organic molecules and clays (Oades, 1984; Pojasok and Kay, 1990; Amezketá,
24 1999). Increasing amounts of ions in solution after exudates were added limit clay dispersion
25 and significantly increase aggregate stability (Pojasok and Kay, 1990). Decaying roots and

1 fungal hyphae also represent a source of OM (Oades, 1984; Haynes and Beare, 1997;
2 Amezketta, 1999) that contributes to aggregate stability. Thus aggregate stability is enhanced
3 by biological activity (both plant and fungal) within the soil.

4 Root exudates represent 5 to 21% of a plant's photosynthetically fixed carbon (C) (Walker *et*
5 *al.*, 2003) serving as a crucial energy source for microorganisms (Haynes and Beare, 1997;
6 Amezketta, 1999). Both fungal and bacterial extracellular polymeric substances contribute to
7 the cementation of aggregates, and, thus enhance aggregate persistence (Oades, 1984; Morel
8 *et al.*, 1991; Watt *et al.*, 1994; Haynes and Beare, 1997; Bryan, 2000). However, the effect of
9 roots on aggregate stability is species specific (Haynes and Beare, 1997; Amezketta, 1999) due
10 to differences in root morphology (Pohl *et al.*, 2009), turnover rates (Stokes *et al.*, 2009), the
11 quantity and chemical composition of the root exudates and the influence of differences in
12 root exudates on microbial activity (Haynes and Beare, 1997, Bertin *et al.*, 2003). Barley
13 roots increased aggregate stability (Haynes and Beare, 1997), whilst there is contradicting
14 evidence about the effects of roots of maize (*Zea mays*). Root mucilage of maize reportedly
15 increased aggregation (Morel *et al.*, 1991), but the release of chelating agents, such as organic
16 acids (which destroy iron and aluminium bonds with OM) by maize decreased aggregate
17 stability (Oades, 1984). These contrasting results may be attributed to genotypic variation in
18 the chemistry of the root exudates. For example, within different barley genotypes, three
19 structural variations of mugineic acid (an organic ligand) have been found (Bertin *et al.*,
20 2003). In addition, some organic compounds released by roots and microorganisms may also
21 induce water repellency depending on soil matric potential and the number of wetting and
22 drying cycles undergone (Hallett *et al.*, 2003). However, OM and aggregate stability are
23 crucial in the formation of macropores, which reduce bulk density and facilitate gaseous
24 diffusion and improve infiltration rates (Gyssels and Poesen, 2003). Thus, the effects of root
25 exudates vary between species and depend on their composition.

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

1 A frequently used root parameter, that sufficiently describes the effectiveness of a species to
2 control concentrated flow erosion rates (Burylo *et al.*, 2012), is root length density (RLD).
3 RLD is the total length of the roots divided by the volume of the root permeated soil sample
4 (De Baets *et al.*, 2006), thus providing information about the occupation of soil by roots
5 (Bauhus and Messier, 1999; De Baets *et al.*, 2006, De Baets *et al.*, 2007). Under cereal and
6 grass plants in the loess belt of Belgium, concentrated flow erosion rates exponentially
7 decreased with a linear increase in RLD (Gyssels and Poesen, 2003). Similar results were
8 obtained by Mamo and Bubenzer (2001a, b) between erosion rates of a silt loam soil
9 subjected to concentrated flow and RLD in maize and soybean (*Glycine max*), which reduced
10 detachment rates by 50% compared to fallow soils. A similar relation exists between RLD of
11 barley and detachment rates (De Baets *et al.*, 2006). However, increasing RLD either affects
12 soil shear strength positively (Ghidey and Alberts, 1997; Mamo and Bubenzer, 2001a, b), or
13 not at all, depending on species and soil type (Pierret *et al.*, 2007). Furthermore, higher RLDs
14 enhance soil aggregation in crop species (Haynes and Beare, 1997) and when comparing
15 grass, forb and legume species from a natural grassland ecosystem (Rilling *et al.*, 2002).
16 However, the ability of roots to reinforce a soil is not only determined by root characteristics
17 such as RLD, but also their distribution within the soil.

18 **3.Root system architecture and its manipulation**

19 RSA is the three-dimensional deployment of roots (Linkohr *et al.*, 2002; Basu *et al.*, 2011). In
20 eudicots, RSA is mainly determined by the extent and direction of root tip growth and the
21 positioning and frequency of LRs (Jones and Ljung, 2012). Therefore, in this review
22 ‘manipulating RSA’ refers to alterations being made to the spatial configuration of the roots
23 of an individual plant in respect of LR growth (i.e. initiation, elongation, diameter, branching)
24 by stimulating proliferation of these roots at certain depths. RSA is constitutively influenced
25 by genetic factors (Smucker, 1993; Malamy, 2005; Stokes *et al.*, 2009), as demonstrated by

1 mutants of maize lacking different root classes (Malamy, 2005). Mature cereal root systems
2 consist mostly of coarse (seminal – seed derived, or nodal – shoot derived) roots and fine
3 (lateral) roots ($\varnothing < 1\text{mm}$) (LRs), which often develop root hairs (McCully, 1999) from the
4 trichoblasts in the meristematic zone (Gilroy & Jones, 2000). Although LRs are the major
5 sites of water and nutrient uptake, coarse roots are mainly responsible for anchorage, the
6 storage of nutrients, water and C, as well as the penetration of hard soils and deep horizons
7 (Guerrero-Campo *et al.* 2006). LRs tend to have greater growth rates than other roots
8 (Guerrero-Campo *et al.*, 2006; Stokes *et al.*, 2009) and account for ca. 90-98% of the total
9 root length of a root system (Engineer and Kranz, 2007; Pohl *et al.*, 2009). Hence, total root
10 length is mainly determined by the density of LRs (Guerrero-Campo *et al.*, 2006; De Baets *et*
11 *al.*, 2007; Pierret *et al.*, 2007). Thus RLD significantly increased with the percentage of LRs
12 (Burylo *et al.*, 2012), and decreased with increasing root diameters (Pohl *et al.*, 2009).

13 Moreover, different types of root system are often distinguished based on the presence of a
14 primary root representing a single dominant axis with varying degrees of LR development,
15 which is characteristic for primary or tap root systems (Fitter, 1987), whereas root systems
16 lacking a primary root are referred to as a fibrous root system (De Baets *et al.*, 2007). Only a
17 few studies have compared the effect of these different root systems on soil erosion rates, with
18 fibrous root systems being more effective in reinforcing soils against concentrated flow than
19 tap root systems with similar root mass (De Baets *et al.*, 2007). In contrast, tap rooting species
20 increase saturated hydraulic conductivity, which tends to be low under fibrous root systems
21 (Archer *et al.*, 2002; Quinton *et al.*, 2002). These observations can be explained by the larger
22 number of LRs and greater root length densities (RLD) associated with fibrous root systems
23 compared to tap root systems (De Baets *et al.*, 2007).

24 Macleod *et al.* (2007) propose specific genetic selection and breeding for root traits, such as
25 rooting depth, to improve soil hydraulic function. However, these root traits are under

1 complex genetic control (Zhu *et al.*, 2005; Macleod *et al.*, 2007) even though alleles
2 determining, for example, LR primordia development in thale cress (*Arabidopsis thaliana*)
3 (Roycewicz and Malamy, 2014), as well as LR branching or length in maize (Zhu *et al.*,
4 2005), have been identified. Limited knowledge of the root phenome, the ‘chaotic’ nature of
5 the interactions among phenes and environmental factors, ultimately determining crop
6 performance and function (Lynch and Brown, 2012), hinder the development of new crop
7 varieties with altered root traits. Although RSA is genetically constrained, it is highly plastic
8 in response to environmental cues. This means that genetically identical plants may differ in
9 root density, growth rate, placement and growth direction (Müller and Schmidt, 2004;
10 Malamy, 2005), as a result of adaptive responses (López-Bucio *et al.*, 2003; Jones and Ljung,
11 2012) to the prevailing environmental conditions. The heterogeneous distribution of nutrients
12 can increase LR length and initiation, as well as coordinate proliferation of LRs in soil regions
13 where these resources are present (e.g. Fitter, 1987; Smucker, 1993; Stokes *et al.* 2009).
14 Hence, the localized application of nutrients at prescribed depths and associated LR
15 proliferation offers an opportunity to manipulate LR distribution within the soil profile,
16 thereby promoting RSAs that reduce soil erosion.

17 **4.Lateral root proliferation in response to local nutrient availability**

18 The local proliferation of LRs allows the optimal exploitation of locally available nutrient
19 reserves (Smucker, 1993; Robinson, 1994; Hodge, 2006). Lack of nitrogen (N), as well as
20 phosphorus (P), often limits growth (Linkohr *et al.*, 2002; López-Bucio *et al.*, 2003). Nitrate
21 (NO_3^-) is the major source of N for most plants and is, as well as ammonium (NH_4^+), readily
22 available to plants (Engineer and Kranz, 2007). A series of studies by Drew and co-workers
23 investigated the response of barley roots to local nutrient enrichment. Although a
24 heterogeneous distribution of potassium (K) did not affect RSA (Drew, 1975; Robinson,
25 1994), LR initiation and extension increased within a 4 cm long segment of a seminal root

1 exposed to 100 times greater concentrations of NO_3^- and NH_4^+ than the remainder of the root
2 system, where nutrient-limited conditions inhibited LR development (Drew *et al.*, 1973;
3 Drew, 1975; Drew and Staker 1975) (Figure 2). The same is true for wheat (*Triticum*
4 *aestivum*) (Drew, 1975; Forde and Lorenzo, 2001) and maize grown in a flowing nutrient
5 culture whereby two nodal roots were exposed to different NO_3^- concentrations revealed
6 similar results (Granato and Raper, 1989). Furthermore, a concentration of 1 mM NO_3^-
7 stimulated LR branching and increased LR diameters in both maize and barley (Drew, 1975;
8 Granato and Raper, 1989), possibly due to increases in stele diameter and the numbers of cells
9 in the root cortex and stele (Forde and Lorenzo, 2001). When thale cress was grown on
10 vertical agar plates with a NO_3^- -enriched band halfway down the plate, LR lengths increased
11 2-3 fold, although there was no evidence for enhanced LR initiation (Zhang and Forde, 1998).
12 However, nutrient solutions containing NH_4^+ as primary N source lead to higher root densities
13 and increased root elongation in maize compared to solutions containing NO_3^- (Jing *et al.*
14 2010). The localized availability of P often also results in increased LR extension (Drew,
15 1975; Robinson, 1994) and sometimes increased LR initiation within this zone (Drew, 1975).
16 However, Drew (1975) highlights the importance of the presence of both nutrients, N and P,
17 in stimulating LR proliferation. In addition, LR proliferation has been reported in response to
18 organic and inorganic N and P, although the response to the former is determined by the
19 extent and rate in which mineralization has occurred (Robinson, 1994). Thus LR proliferation
20 in response to localised nutrient patches is well documented in many species grown in
21 different artificial (not soil) media.

22 Root proliferation is believed to be triggered partly by shoot-to-root signalling, as the
23 developmental response to localized increased NO_3^- was most pronounced with plants of low
24 N status (Forde and Lorenzo, 2001; Forde, 2002). High NO_3^- levels result in increased auxin
25 concentration in the LR tip stimulating LR growth, while high NH_4^+ levels enhance higher

1 order root branching. The presence of both forms of N results in a complementary response
2 (Forde, 2002; Jones & Ljung, 2012). However, if NO_3^- concentrations are too high, LR
3 growth tends to be inhibited (Zhang and Forde, 1998; Linkohr *et al.*, 2002), which is mediated
4 by abscisic acid (López-Bucio *et al.* 2003). A detailed discussion of the molecular
5 mechanisms responsible for LR proliferation in nutrient-rich zones is beyond the scope of this
6 paper, but the topic has been recently reviewed by Jones and Ljung (2012).

7 However, the growth media used in these studies (agar, hydroponics) do not necessarily
8 reflect natural conditions and it is important to determine whether such responses occur in
9 soil. Paradoxically, when wheat plants were grown in soil-filled rhizotrons (1.4 m deep) with
10 nutrients (both N and P) banded at 0-40 cm or 60-100 cm below the soil surface and the soil
11 allowed to dry (simulating a terminal drought stress), the greatest RLD detected at 1.4 m
12 occurred with the surface fertiliser application (Jin *et al.*, 2015). However, fertiliser banding
13 (stratification) and local placement (patches) can elicit different responses. LR of thale cress
14 in a NO_3^- enriched patch in a heterogeneous soil were only marginally longer than in the
15 corresponding patch under homogeneous conditions (Linkohr *et al.* 2002). Nevertheless, LR
16 proliferation has been observed in the field (Sattelmacher *et al.*, 1993; Robinson, 1994). A
17 recent study in North China showed that banding NH_4^+ and P at 10 cm depth resulted in a 23-
18 30 % increase in total root length and higher RLD at a depth of 0-15cm in maize compared to
19 broadcast application, or banding of P only while NH_4^+ was broadcast. Moreover, banding of
20 both nutrients also increased RLD at a depth of 15-30cm (Jing *et al.*, 2010). However, the
21 responsiveness of plants to localized nutrient availability varies between different species and
22 genotypes (Robinson, 1994).

23 **5.Manipulating root system architecture with nutrient placement to control** 24 **erosion**

1 Beyond the selection of different plant species, little consideration has been given to the
2 potential for manipulating RSA for soil erosion control, despite it being known that the
3 distribution of LRs within the top 50cm of the soil is crucial in determining the effect of roots
4 on the resistance of soils to concentrated flow erosion (Li *et al.*, 1991). Dense mats of LRs are
5 commonly found at the soil surface (Pierret *et al.*, 2007) and the abundance of roots gradually
6 declines with increasing soil depth (Quinton *et al.*, 2002; De Baets *et al.*, 2008). However, it
7 has been argued higher RLDs at deeper soil depths would be particularly beneficial, as this
8 increases possible water uptake and evapotranspiration rates, thus infiltration rates (Stokes *et*
9 *al.*, 2009) and would provide reinforcement to deeper soil layers in situations where
10 concentrated flow erosion is problematic. In addition, longer vertical roots, that increase RLD
11 at depth, provide conduits to deeper soil layers (Archer *et al.*, 2002; Devitt and Smith, 2002;
12 Quinton *et al.*, 2002) and directly affect water storage capacity of the effective soil depth
13 (Macleod *et al.*, 2007; Stokes *et al.*, 2009). Improvements in aggregate stability tend to be
14 particularly pronounced in, if not spatially limited to, the rhizosphere (Oades, 1994; Foster,
15 1988; Morel *et al.*, 1991; Haynes and Beare, 1997), so the extent of the root system
16 determines its effect on soil aggregation (Haynes and Beare, 1997). The effects of roots of the
17 grasses *Stipa bungeana* and *Bothriochlon ischaemum* on the properties of a Chinese loess soil
18 (SOM and aggregate stability, especially in large diameter classes) decreased with increasing
19 depth, as RLD diminished (Li and Li, 2011). The higher sediment load derived from deep soil
20 horizons associated with the higher susceptibility of these soil horizons to erosional forces
21 was further enhanced by increasing runoff discharge and slope gradient (Li and Li, 2011) and
22 was particularly critical during concentrated flow erosion. Furthermore, soil cohesion
23 provided by roots is also limited to the rooting depth of the vegetation, consequently soil
24 reinforcement decreases with increasing depth (Gyssels *et al.*, 2005; De Baets *et al.*, 2008).
25 Although Mediterranean shrubs typically only stabilize the top 50 cm of gully walls and
26 hillslopes, failures may occur at deeper depths and increases in soil strength depend on the

1 number of LRs that cross the potential shear plane (Reubens *et al.*, 2007; De Baets *et al.*,
2 2008).

3 Plants may also respond to heterogeneous nutrient supply with compensatory root growth
4 (Drew, 1975; Robinson, 1994). Compensatory growth means that proliferation within the N
5 or P enriched zone compensates, and may be proportional to, the inhibitory effect of the
6 limited availability of these nutrients on LR development outside this zone (Robinson, 1994).
7 In this case, soil properties at different soil layers may change accordingly to the proportion of
8 LRs present within these layers. Reduced LR growth on the soil surface, when nutrients are
9 only available at deeper depths, could reduce resistance to surface erosion, but could
10 potentially increase the water storage capacity of a soil, as the number of blocked pores by
11 LRs at the soil surface would be reduced. Furthermore, although the diameter of LR increases
12 in nutrient enriched zones (Drew, 1975; Granato and Raper, 1989; Forde and Lorenzo, 2001),
13 LR proliferation may still increase shear strength locally (De Baets *et al.*, 2008; Loades *et al.*,
14 2010) and could help to reinforce soils at the shear plane. In addition, aggregate stability may
15 be improved within the nutrient poor patch, as larger quantities of mucilage may be released
16 within this zone to mobilise scarcely available P (Bertin *et al.*, 2003). In contrast, Paterson *et*
17 *al.* (2006) showed that LR proliferation in response to localized availability of NO_3^- resulted
18 only in a locally increased release of root exudates in barley. Compensatory growth may also
19 enhance root hair development in the nutrient poor zone, and root hairs contribute to soil
20 aggregation in the rhizosphere and are crucial for rhizosheath development (Hochholdinger *et*
21 *al.*, 2004; Moreno-Espíndola *et al.*, 2007). Root hair length increased from 0.1-0.2 to 0.7 mm
22 and density by a factor of 2-4 when spinach (*Spinacia oleracea*), tomato (*Solanum*
23 *lycopersicum*) and rapeseed (*Brassica napus*) were grown in nutrient solutions with
24 concentrations of 2 μM P compared to concentrations of 1000 μM P (Foehse and Junk, 1983).
25 Split-root system experiments demonstrated root hair development of spinach in high P

1 concentrations is not affected if the remainder of the root system is exposed to low P
2 concentrations. In contrast, the magnitude of the positive effect on root hair development of
3 limited NO_3^- varied between species. However, further research is needed into the effects of
4 differences in LR growth dynamics in response to localized fertilizer application on soil
5 properties and subsequently erosion rates.

6 **6.Effects of LR proliferation on aerial growth**

7 Potential effects of LR proliferation on above ground biomass production are crucial to
8 achieve high agricultural production, but may also be important in soil erosion control as
9 mentioned before. Recent estimates suggest root proliferation is a relative low cost strategy
10 adapted by plants to effectively absorb available ions and water in heterogeneous
11 environments, requiring only an additional 0.2% of the plant's daily carbon gain (Hodge,
12 2006). Only roots with small diameters proliferate (Drew, 1975; Granato and Raper, 1989;
13 Smucker, 1993; McCully, 1999), as fine roots represent less resistance to the flow of ions and
14 water during the uptake of these resources (Smucker, 1993). However, net C costs will be
15 determined by factors such as rooting volume, photosynthetic supply and may be even zero if
16 compensatory growth occurs (Robinson, 2001). This should buffer potential negative effects
17 of limited nutrient availability within some soil areas on above ground biomass, although
18 biomass partitioning ultimately depends on shoot nutrient status (Drew, 1975; Drew and
19 Saker, 1975; Robinson, 1994). LR proliferation either increases or has no effect on root to
20 shoot ratios (Robinson, 1994). Shoot development may be slightly retarded, which is reflected
21 in lower shoot biomass of barley grown under heterogeneous nutrient availability compared to
22 the controls (Drew and Saker, 1975). This shoot growth inhibition was attributed to initial
23 nutrient deficiencies until the roots reached the nutrient-rich zone (Drew and Saker, 1975). In
24 addition, placement of N fertilizer (calcium ammonium nitrate) at 10 cm depth compared to
25 surface mixing significantly increased dry matter production and grain yield at maturity of

1 wheat grown in a loamy sand soil (Sharma and Chaudhary,1983). However, there is a large
2 variability between species (Robinson, 1994; Hodge, 2006) and genotypes (Sattelmacher *et*
3 *al.*, 1993; Forde and Lorenzo, 2001) in their shoot responsiveness, which depends on
4 differences in nutrient uptake and utilization efficiency (Sattelmacher *et al.*, 1993).
5 Nevertheless, LR proliferation may occur without limiting above ground growth (and yield).

6 **7.Conclusion**

7 In conclusion, plant roots are crucial in reducing soil erosion rates due to overland flow, as
8 their presence affects soil properties such as aggregate stability, hydraulic function and shear
9 strength. However, the effect of roots on soil erodibility is determined by RLD, and, thus, LR
10 density and length, and the distribution of roots within the soil. It has been argued that a
11 higher RLD would be particularly beneficial in reducing soil erosion rates and that fertilizer
12 placement may be one way of achieving this In nutrient poor soils, the local availability of
13 high N or P may result in LR proliferation, although the response will depend on plant
14 species, and may include a general increase in rooting depth or compensatory growth.

15 However, research is needed to determine whether the localized application of N and P at
16 specific soil depths may represent a potential management technique to control erosion of
17 degraded agricultural soils with low nutrient levels. Investigations should therefore aim to
18 explore the effects of LR distribution at varying depths on soil properties, and, hence, soil
19 erodibility. Trade offs between reduced erodibility due to LR proliferation and potential
20 reductions in soil hydraulic conductivity need to be explored. In addition, responsiveness of
21 different crops, grasses and shrubs (and different genotypes within a species) to
22 heterogeneous nutrient availability should be determined. Moreover, suitable depth(s) for
23 deep fertilizer placement should be established (with reference to practical implementation)
24 and the effects of varying environmental conditions, such as soil type, slope and flow

1 characteristics, on the erosion reducing effect of this potential management technique needs to
2 be assessed.

3

4 **8.References**

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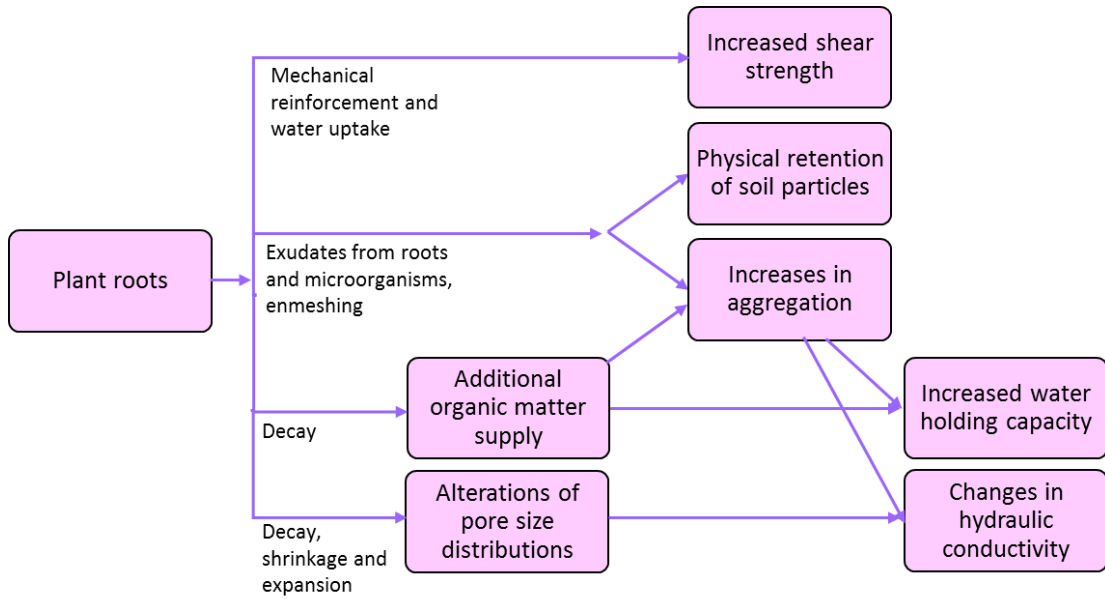


Figure 1. Key mechanisms by which plant roots influence soil physical properties

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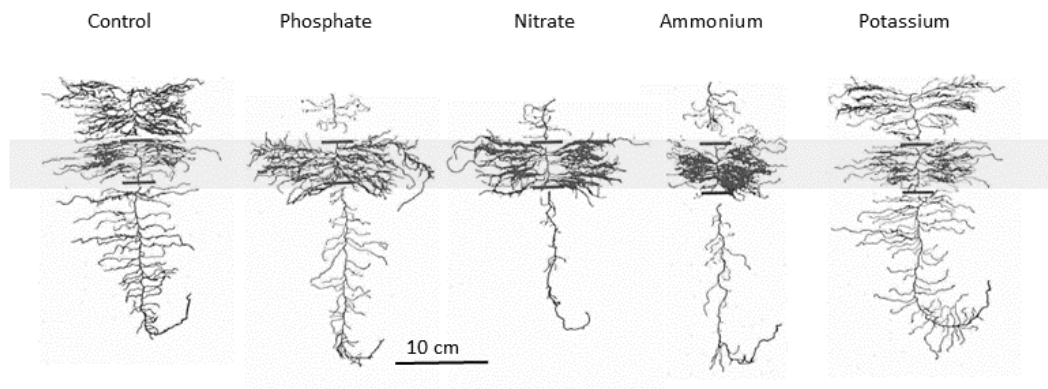


Figure 2. Effect of a localised supply of phosphate, nitrate, ammonium, and potassium on root form. Control plants received the complete nutrient solution to all parts of the root system. The other roots received the complete nutrient solution only in the middle zone (shaded), the top and bottom being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

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