Can we manipulate root system architecture to control soil erosion?

Anne Ola[1], Ian C. Dodd[1] and John N. Quinton[1*]

[1] Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, United Kingdom

*corresponding author J.Quinton@lancaster.ac.uk

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 specifically 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 demonstrate the importance of root system architecture for the control of soil erosion. We also show that some plant species respond to nutrient enriched patches by increasing lateral root proliferation. The erosional response to root proliferation will depend upon its location: at the soil surface dense mats of roots may reduce soil erodiblity but block soil pores thereby limiting infiltration, enhancing runoff. 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 specific depths 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 representing a much greater threat to agricultural production than soil erosion by wind (Lal, 2010). Approximately 430 million ha of arable land, or 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 vegetation 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

1   recently estimated to range between £248 and £469 million (Posthumus *et al.,* 2013). Hence,

2   there is a need to stabilize soils and preserve this crucial resource.

3   The importance of vegetation cover to control erosion has been demonstrated by many

4   studies. Both linear and exponential decreases in erosion rates associated with vegetation

5   cover have been observed, as the nature of the relationship varies for canopy and ground

6   covers, or inter-rill and rill erosion (Boer and Puidgefábregas, 2005).. In Montana and Utah,

7   for example, overland flow erosion rates increased ca. 200 times in response to a decrease in

8   ground cover from 100% to less than 1% (Trimble and Mendel, 1995). A minimum of 10%

9   plant cover was required to significantly reduce erosion rates on a semi-arid hillslope in

10   Arizona (Abrahams *et al.,*1988), however, the magnitude of the response ultimately depends

11   on vegetation type and species (Bochet *et al*., 2006). Positive effects of the aerial biomass in

12   controlling erosion are generally attributed to reductions in the kinetic energy of raindrops

13   and reduced overland flow velocities (Stocking and Elwell, 1976; Puigdefábregas, 2005).

14   Furthermore, vegetation covers modify intrinsic soil properties determining a soil's erodibility

15   (Gyssels *et al.,* 2005) creating a microclimate and supplying OM, that affect the activity of

16   microorganisms, and therefore nutrient availability, resulting in a positive feedback on plant

17   productivity. Both additional OM as well as microbial and fungal secretions enhance the

18   formation of stable aggregates (Puidgefábregas, 2005, Vásquez-Méndez *et al.,* 2010), which

19   affect hydraulic conductivity and, hence, water storage capacity (Puidgefábregas, 2005) and

20   may increase soil shear strength (Tengbeh, 1993; De Baets *et al,* 2008).

21   Compared to studies on above ground plant properties and soil erosion, the effects of below

22   ground biomass have received relatively little attention. However, it is clear that the reduction

23   in soil loss due to vegetation results from the combined effects of the above and below ground

24   biomass (Gyssels and Poesen, 2003). Concentrated flow erosion rates were reduced to almost

25   zero within the 0-10% soil cross-sectional occupation by grass roots, but decreased only by

1   25-50% for the same increase in aerial cover (De Baets *et al.*, 2006). Furthermore, a rainfall

2   simulation experiment conducted 27 weeks after ryegrass (*Lolium perenne*) was sown in

3   erosion pans demonstrated (by removal of the above ground material) that the below ground

4   material of this species accounted for 90% of the decrease in soil detachment (Zhou and

5   Shangguan, 2007).

6   In this paper we take an interdisciplinary view of the plant root and its interaction with the

7   soil, ~~in line with the interdiciplinary nature of this journal (Brevik et al.,2015),~~ and review the

8   literature concerning the effects of roots on soil properties determining the resistance of soil

9   to water erosion (.concentrated and sheet flow) with emphasis on root system architecture

10   (RSA). We then explore the factors influencing RSA especially lateral root (LR) growth, and

11   finally the potential of fertilizer applications to stimulate LR proliferation, and thus form the

12   basis for a soil erosion control method, will be discussed.

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

14   Erodibility is the result of various mechanical, adhesive and cohesive bonding forces acting

15   within the soil matrix (Knapen et al., 2007) and should be regarded as a 'summation of a

16   highly complex response pattern, strongly influenced by intrinsic soil characteristics and

17   extrinsic variables' (Bryan, 2000). The erosion response may be influenced by any soil

18   property, but will be dominated by shear strength, aggregate stability and hydraulic funtion

19   (Bryan, 2000). Roots alter the erodibility of a soil through their effect on these soil properties

20   in a number of ways (Figure 1). Firstly, roots have a high tensile strength (Gyssels *et al.,*

21   2005; De Baets *et al.,* 2008) providing up to 100% of the cohesive strength of a root

22   permeated soil (Hales *et al.,* 2009), thus increasing soil shear strength. The additional tensile

23   strength associated with roots is responsible for the transfer of shear stresses via tensile

24   resistance or interface friction within the soil-root matrix (Prosser *et al*., 1995, De Baets *et al.,*

1 2008). There was a positive linear relationship between the cross-sectional area of barley

2 (*Hordeum vulgare*) roots at the shear plane and, subsequent increases in soil shear strength in

3 a silty clay loam soil (Waldron, 1977). In ryegrass, increasing root densities from 0.20 g cm^{-3}

4 to 1.80 g cm^{-3} also increased strength from 1 kPa to 5 kPa in a sandy clay loam (Tengbeh,

5 1993). Hence, the presence of roots considerably increases shear strength.

6 Secondly, roots prevent sediment transport by retaining soil particles (De Baets *et al.* 2006)

7 and increasing the number of stable aggregates, due to their enmeshing effect (Haynes and

8 Beare, 1997), which is also true for fungal hyphae (Haynes and Beare, 1997; Degens, 1997;

9 Moreno-Espíndola *et al.* 2007), and the release of various organic and inorganic binding

10 agents (Amezketa, 1999). Root exudates such as mucilage are considered the main

11 mechanism by which plant roots enhance aggregate stability (Morel *et al*., 1991; Moreno-

12 Espíndola *et al.* 2007). Root mucilage expands under wet conditions covering soil particles,

13 while subsequent drying leads to the contraction of mucilage, pulling these soil particles

14 tightly together to form a rhizosheath, and thereby reorienting clay particles parallel to the

15 axis of the root (Oades, 1984; Watt *et al.,* 1994; Amezketa, 1999; McCully, 1999). Moreover,

16 root exudates are associated with the release of polyvalent cations that form strong bonds

17 between organic molecules and clays (Oades, 1984; Pojasok and Kay, 1990; Amezketa,

18 1999). Increasing amounts of ions in solution after exudates were added limit clay dispersion

19 and significantly increase aggregate stability (Pojasok and Kay, 1990). Decaying roots and

20 fungal hyphae also represent a source of OM (Oades, 1984; Haynes and Beare, 1997;

21 Amezketa, 1999) that contributes to aggregate stability. Thus aggregate stability is enhanced

22 by biological activity (both plant and fungal) within the soil.

23 Root exudates represent 5 to 21% of a plant's photosynthetically fixed carbon (C) (Walker *et*

24 *al.,* 2003) serving as a crucial energy source for microorganisms (Haynes and Beare, 1997;

25 Amezketa, 1999). Both fungal and bacterial extracellular polymeric substances contribute to

5

the cementation of aggregates, and, thus enhance aggregate persistence (Oades, 1984; Morel *et al.,* 1991; Watt *et al.,* 1994; Haynes and Beare, 1997; 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*). Root mucilage of maize reportedly 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 different barley genotypes, 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 between species and depend on their composition.

Roots may also provide soils with additional surface roughness enhancing 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

1   results were obtained for albaida (*Anthyllis cytisoides*) and white wormwood (*Artemisia*

2   *herba-alba*). Under alfalfa (*Medicago sativa*), 60% of all flow paths are associated with the

3   roots or the channels of decomposed roots allowing water to rapidly percolate through the soil

4   matrix (Stokes *et al.* 2009). Shallow, fibrous root systems and rhizomatous mats of ryegrass

5   and common bent grass (*Agrostis capillaris*), respectively, resulted in a low saturated

6   hydraulic conductivity (Morgan *et al.,* 1995). Several authors (Mitchell *et al.*, 1995; Meek *et*

7   *al.,* 1989; Archer *et al.,* 2002; Devitt and Smith, 2002) suggest that living roots occupy

8   available macropores for flow pathways, and enhance infiltration rates over time, as a result

9   of channels created by decaying roots. Infiltration rates in a sandy loam, for instance, tripled

10   within three years of alfalfa cultivation (Meek *et al.,* 1989) and significantly increased

11   infiltration rates were recorded for the last half of the growing season, and after harvest, of a

12   maize crop (Archer *et al.,* 2002). This is also supported by observations that the root effect of

13   ryegrass on increasing infiltration rates (thus decreasing runoff) increased with time (Zhou

14   and Shangguan, 2007). Moreover, the effects associated with cyclic shrinking-expanding of

15   roots in accordance with water availability also created flow pathways over time (Archer *et*

16   *al.,* 2002). However, the effect of roots on flow pathways, and thus infiltration rates, differed

17   under a number of Mediterranean species, due to differences in root morphology (Quinton *et*

18   *al.,* 2002), and turnover rates, as a result of differences in root diameter and chemical

19   composition (Stokes *et al.,* 2009). Thus, not only the presence of roots, but their physical

20   arrangement within the soil, alters soil hydraulic properties.

21   A frequently used root parameter, that sufficiently describes the effectiveness of a species to

22   control concentrated flow erosion rates (Burylo *et al.,* 2012), is root length density (RLD).

23   RLD is the total length of the roots divided by the volume of the root permeated soil sample

24   (De Baets *et al.,* 2006), thus providing information about the occupation of soil by roots

25   (Bauhus and Messier, 1999; De Baets *et al.,* 2006, De Baets *et al.,* 2007). 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

subjected to concentrated flow 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.,* 2006). 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 root characteristics

such as RLD, but also their distribution within the soil.

3.Root system architecture and its manipulation

RSA is the three-dimensional deployment of roots (Linkohr *et al.,* 2002; Basu *et al.,* 2011). In

eudicots, RSA is mainly determined by the extent and direction of root tip growth and the

positioning and frequency of LRs (Jones and Ljung, 2012). Therefore, in this review

'manipulating RSA' refers to alterations being made to the spatial configuration of the roots

of an individual plant in respect of LR growth (i.e. initiation, elongation, diameter, branching)

by stimulating proliferation of these roots at certain depths. RSA is constitutively 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 coarse (seminal – seed derived, or nodal – shoot derived) roots and fine

(lateral) roots (Ø <1mm) (LRs), which often develop root hairs (McCully, 1999) from the

trichoblasts in the meristematic zone (Gilroy & Jones, 2000). Although LRs are the major

sites of water and nutrient uptake, coarse roots are mainly responsible for anchorage, the

storage of nutrients, water and C, as well as 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 (De Beats *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 against concentrated flow than tap root systems with similar root mass (De Baets *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 and greater root length densities (RLD) associated with fibrous root systems compared to tap root systems (De Baets *et al.*, 2007).

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 function (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 *et al.* 2009). Hence, the localized application of nutrients at prescribed depths and associated LR proliferation offers an opportunity to manipulate LR distribution within the soil profile, thereby promoting 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). Lack of 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) (Figure 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

1   similar results (Granato and Raper, 1989). Furthermore, a concentration of 1 mM NO_3^-

2   stimulated LR branching and increased LR diameters in both maize and barley (Drew, 1975;

3   Granato and Raper, 1989), possibly due to increases in stele diameter and the numbers of cells

4   in the root cortex and stele (Forde and Lorenzo, 2001). When thale cress was grown on

5   vertical agar plates with a NO_3^--enriched band halfway down the plate, LR lengths increased

6   2-3 fold, although there was no evidence for enhanced LR initiation (Zhang and Forde, 1998).

7   However, nutrient solutions containing NH_4^+ as primary N source lead to higher root

8   densities and increased root elongation in maize compared to solutions containing NO_3^- (Jing

9   *et al.* 2010). The localized availability of P often also results in increased LR extension

10   (Drew, 1975; Robinson, 1994) and sometimes increased LR initiation within this zone (Drew,

11   1975). However, Drew (1975) highlights the importance of the presence of both nutrients, N

12   and P, in stimulating LR proliferation. In addition, LR proliferation has been reported in

13   response to organic and inorganic N and P, although the response to the former is determined

14   by the extent and rate in which mineralization has occurred (Robinson, 1994). Thus LR

15   proliferation in response to localised nutrient patches is well documented in many species

16   grown in different artificial (not soil) media.

17   Root proliferation is believed to be triggered partly by shoot-to-root signalling, as the

18   developmental response to localized increased NO_3^- was most pronounced with plants of low

19   N status (Forde and Lorenzo, 2001; Forde, 2002). High NO_3^- levels result in increased auxin

20   concentration in the LR tip stimulating LR growth, while high NH_4^+ levels enhance higher

21   order root branching. The presence of both forms of N results in a complementary response

22   (Forde, 2002; Jones & Ljung, 2012). However, if NO_3^- concentrations are too high, LR

23   growth tends to be inhibited (Zhang and Forde, 1998; Linkohr *et al.,* 2002), which is mediated

24   by abscisic acid (López-Bucio *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 cm 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 0-15cm 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 15-30cm (Jing *et al.,* 2010). However, the responsiveness of plants to localized nutrient availability varies between different species and genotypes (Robinson, 1994).

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

Beyond the selection of different plant species, little consideration has been given to the potential for manipulating RSA for soil erosion control, despite it being known that the distribution of LRs within the top 50cm 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; De Baets *et al.,* 2008). However, it has been argued higher RLDs at deeper soil depths would be particularly beneficial, as this increases possible water uptake and evapotranspiration rates, thus infiltration rates (Stokes *et al.,* 2009) and would provide reinforcement to deeper soil layers in situations where concentrated flow erosion is problematic. In addition, longer vertical roots, that increase RLD at depth, provide conduits to deeper soil layers (Archer *et al.,* 2002; Devitt and Smith, 2002; Quinton *et al.,* 2002) and directly affect water storage capacity of the effective soil depth (Macleod *et al.,* 2007; Stokes *et al.,* 2009). 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.,* 2008). Although Mediterranean shrubs typically 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 (Reubens *et al.,* 2007; De Baets *et al.,* 2008).

1   Plants may also respond to heterogeneous nutrient supply with compensatory root growth

2   (Drew, 1975; Robinson, 1994). Compensatory growth means that proliferation within the N

3   or P enriched zone compensates, and may be proportional to, the inhibitory effect of the

4   limited availability of these nutrients on LR development outside this zone (Robinson, 1994).

5   In this case, soil properties at different soil layers may change accordingly to the proportion of

6   LRs present within these layers. Reduced LR growth on the soil surface, when nutrients are

7   only available at deeper depths, could reduce resistance to surface erosion, but could

8   potentially increase the water storage capacity of a soil, as the number of blocked pores by

9   LRs at the soil surface would be reduced. Furthermore, although the diameter of LR increases

10   in nutrient enriched zones (Drew, 1975; Granato and Raper, 1989; Forde and Lorenzo, 2001),

11   LR proliferation may still increase shear strength locally (De Baets *et al.,* 2008; Loades *et al.,*

12   2010) and could help to reinforce soils at the shear plane. In addition, aggregate stability may

13   be improved within the nutrient poor patch, as larger quantities of mucilage may be released

14   within this zone to mobilise scarcely available P (Bertin *et al.,* 2003). In contrast, Paterson *et*

15   *al.* (2006) showed that LR proliferation in response to localized availability of NO_3^- resulted

16   only in a locally increased release of root exudates in barley. Compensatory growth may also

17   enhance root hair development in the nutrient poor zone, and root hairs contribute to soil

18   aggregation in the rhizosphere and are crucial for rhizosheath development (Hochholdinger *et*

19   *al.,* 2004; Moreno-Espíndola *et al.*, 2007). Root hair length increased from 0.1-0.2 to 0.7 mm

20   and density by a factor of 2-4 when spinach (*Spinacia oleracea*), tomato (*Solanum*

21   *lycopersicum*) and rapeseed (*Brassica napus*) were grown in nutrient solutions with

22   concentrations of 2 μM P compared to concentrations of 1000 μM P (Foehse and Junk, 1983).

23   Split-root system experiments demonstrated root hair development of spinach in high P

24   concentrations is not affected if the remainder of the root system is exposed to low P

25   concentrations. In contrast, the magnitude of the positive effect on root hair development of

26   limited NO_3^- varied between species. However, further research is needed into the effects of

1 differences in LR growth dynamics in response to localized fertilizer application on soil

2 properties and subsequently erosion rates.

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

4 Potential effects of LR proliferation on above ground biomass production are crucial to

5 achieve high agricultural production, but may also be important in soil erosion control as

6 mentioned before. Recent estimates suggest root proliferation is a relative low cost strategy

7 adapted by plants to effectively absorb available ions and water in heterogeneous

8 environments, requiring only an additional 0.2% of the plant's daily carbon gain (Hodge,

9 2006). Only roots with small diameters proliferate (Drew, 1975; Granato and Raper, 1989;

10 Smucker, 1993; McCully, 1999), as fine roots represent less resistance to the flow of ions and

11 water during the uptake of these resources (Smucker, 1993). However, net C costs will be

12 determined by factors such as rooting volume, photosynthetic supply and may be even zero if

13 compensatory growth occurs (Robinson, 2001). This should buffer potential negative effects

14 of limited nutrient availability within some soil areas on above ground biomass, although

15 biomass partitioning ultimately depends on shoot nutrient status (Drew, 1975; Drew and

16 Saker, 1975; Robinson, 1994). LR proliferation either increases or has no effect on root to

17 shoot ratios (Robinson, 1994). Shoot development may be slightly retarded, which is reflected

18 in lower shoot biomass of barley grown under heterogeneous nutrient availability compared to

19 the controls (Drew and Saker, 1975). This shoot growth inhibition was attributed to initial

20 nutrient deficiencies until the roots reached the nutrient-rich zone (Drew and Saker, 1975). In

21 addition, placement of N fertilizer (calcium ammonium nitrate) at 10 cm depth compared to

22 surface mixing significantly increased dry matter production and grain yield at maturity of

23 wheat grown in a loamy sand soil (Sharma and Chaudhary,1983). However, there is a large

24 variability between species (Robinson, 1994; Hodge, 2006) and genotypes (Sattelmacher *et*

25 *al.,* 1993; Forde and Lorenzo, 2001) in their shoot responsiveness, which depends on

1 differences in nutrient uptake and utilization efficiency (Sattelmacher *et al.,* 1993).

2 Nevertheless, LR proliferation may occur without limiting above ground growth (and yield).

3 **7.Conclusion**

4 In conclusion, plant roots are crucial in reducing soil erosion rates due to overland flow, as

5 their presence affects soil properties such as aggregate stability, hydraulic function and shear

6 strength. However, the effect of roots on soil erodibility is determined by RLD, and, thus, LR

7 density and length, and the distribution of roots within the soil. It has been argued that a

8 higher RLD would be particularly beneficial in reducing soil erosion rates and that fertilizer

9 placement may be one way of achieving this In nutrient poor soils, the local availability of

10 high N or P may result in LR proliferation, although the response will depend on plant

11 species, and may include a general increase in rooting depth or compensatory growth.

12 However, research is needed to determine whether the localized application of N and P at

13 specific soil depths may represent a potential management technique to control erosion of

14 degraded agricultural soils with low nutrient levels. Investigations should therefore aim to

15 explore the effects of LR distribution at varying depths on soil properties, and, hence, soil

16 erodibility. Trade offs between reduced erodibility due to LR proliferation and potentila

17 reductions in soil hydraulic conductivity need to be explored. In addition, responsiveness of

18 different crops, grasses and shrubs (and different genotypes within a species) to

19 heterogeneous nutrient availability should be determined. Moreover, suitable depth(s) for

20 deep fertilizer placement should be established (with reference to practical implementation)

21 and the effects of varying environmental conditions, such as soil type, slope and flow

22 characteristics, on the erosion reducing effect of this potential management technique needs to

23 be assessed.

24

8.References

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

Amezketa, E. (1999). Soil aggregate stability: a review. *Journal of Sustainable Agriculture,* **14**, 83–151.

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

Basu, P., Brown, K.M. and Pal, A. (2011). Detailed Quantitative Analysis of Architectural Traits of Basal Roots of Young Seedlings of Bean in Response to Auxin and Ethylene. *Plant Physiology,* **155**, 2056–2065.

Bauhus, J. and Messier, C. (1999). Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. *Canadian Journal of Forest Research,* **29**, 260–273.

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

Boer, M. and Puidgefábregas, J. (2005). Effects of spatially structured vegetation patterns on hillslope erosion in a semiarid Mediterranean environment: a simulation study. *Earth Surface Processes and Landforms,* **30**, 149-167.

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

1 Brevik, E. C., A. Cerdà, J. Mataix-Solera, L. Pereg, J. N. Quinton, J. Six and K. Van Oost

2 (2015). The interdisciplinary nature of SOIL. SOIL 1(1): 117-129.

3 Bronick, C.J. and Lal, R. (2005). Soil structure and management: a review. *Geoderma*, **124**, 3

4 –22.

5 Bryan, R.B. (2000). Soil erodibility and processes of water erosion on hillslope.

6 *Geomorphology*, **32**, 385–415.

7 Burylo, M., Rey, F., Mathys, N. and Dutoit, T. (2012). Plant root traits affecting the resistance

8 of soils to concentrated flow erosion. *Earth Surface Processes and Landforms,* **37**, 1436-

9 1470.

10 De Baets, S., Poesen, J., Gyssels, G. and Knapen, A. (2006). Effects of grass roots on the

11 erodibility of topsoil during concentrated flow. *Geomorphology,* **76**, 54-67.

12 De Baets, S., Poesen, J., Knapen, A. and Galindo, P. (2007). Impact of root architecture on

13 the erosion-reducing potential of roots during concentrated flow. *Earth Surface Processes and*

14 *Landforms,* **32**, 1323-1345.

15 De Baets, S.; Poesen, J.; Reubens, B.; Wemans, K.; De Baerdemaeker, J. and Muys, B.

16 (2008). Tensile strength and root distribution of typical mediterranean plant species and their

17 contribution to soil shear strength. *Plant and Soil,* **305**, 207-226.

18 Degens, B. P. (1997). Macro-aggregation of soils by biological bonding and binding

19 mechanisms and the factors affecting these: A review. *Australian Journal of Soil Research*,

20 **35**, 431-459.

21 Devitt, D.A. and Smith, S.D. (2002). Root channel macropores enhance downward movement

22 of water in a Mojave Desert ecosystem. *Journal of Arid Environments,* **50**, 99-108.

Di Tomaso, J.M. (1995). Approaches for Improving Crop Competitiveness through the Manipulation of Fertilization Strategies. *Weed Science,* **43**, 491-497.

Drew, M.C. (1975). 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.

Drew, M.C. and Saker, L.R. (1975). 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. *Journal of Experimental Botany*, **26**, 79–90.

Drew, M.C., Saker, L.R. and Ashley, T.W. (1973). 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. *Journal of Experimental Botany*, **24**, 1189–1202.

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

Fitter, A.H. (1987). An architectural approach to the comparative ecology of plant root systems. *New Phytologist,* **106**, 61-77.

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

Forde, B.G. (2002). Local and long-range signaling pathways regulating plant responses to nitrate. *Annual Review of Plant Biology,* **53**, 203-224.

1   Forde, B.G. and Lorenzo, H. (2001). The nutritional control of root development. *Plant and*

2   *Soil,* **232**, 51-68.

3   Foster, R.C. (1988). Microenvironments of soil microorganisms. *Biology and Fertility of*

4   *Soils,* **6**, 189-203.

5   Genet, M., Stokes, A., Salin, F., Mickovski, S.B., Fourcaud, T., Dumail, J. and van Beek, R.

6   (2005). The influence of cellulose content on tensile strength in tree roots. *Plant and Soil,*

7   **278**,1‑9.

8   Ghidey, F. and Alberts, E.E. (1997). Plant root effects on soil erodibility, splash detachment,

9   soil strength,and aggregate stability. *Transactions of the American Society of Agricultural*

10   *Engineers,* **40**, 129–35.

11   Gilroy, S. and Jones, D.L. (2000). Through form to function: root hair development and

12   nutrient uptake. *Trends in Plant Science,* **2**, 56-60.

13   González-Pelayo, O., Andreu, V., Gimeno-García, E. and Rubio, J.L. (2010). Rainfall

14   influence on plot-scale runoff and soil loss from repreated burning in a Mediterranean-shrub

15   ecosystem, Valencia, Spain. *Geomorphology,* **118**, 444-452.

16   Granato, T.C. and Raper JR, D. (1989). Proliferation of maize *(Zea mays* L.) roots in response

17   to localized supply of nitrate. *Journal of Experimental Botany,* **40**, 263-275.

18   Guerrero-Campo, J., Palacio, S., Pérez-Rontomé, C. and Montserrat-Martí, G. (2006). Effect

19   of root system morphology on root-sprouting and shoot-rooting abilities in 123 plant species

20   from eroded lands in North-east Spain. *Annals of Botany,* **98**, 439-447.

21   Gyssels, G. and Poesen, J. (2003). The importance of plant root characteristics in controlling

22   concentrated flow erosion rates. *Earth Surface Processes and Landforms,* **28**, 371–384.

1   Gyssels, G., Poesen, J., Bochet, E. and Li, Y. (2005). Impact of plant roots on the resistance

2   of soils to erosion by water: a review. *Progress in Physical Geography*, **29**, 189-217.

3   Hales, T.C., Ford, C.R., Hwang, T., Vose, J.M. and Band, L.E. (2009). Topographic and

4   ecological controls on root reinforcement. *Journal of Geophysical Research,* **114**, 1-17.

5   Hallett, P.D., Gordon, D.C. and Bengough, A.G. (2003). Plant influence on rhizosphere

6   hydraulic properties: direct measurements using a miniaturized infiltrometer. *New*

7   *Phytologist,* **157,** 597–603

8   Hathaway, R.L. and Penny, D. (1975). Root strength in some populus and salix clones. *New*

9   *Zealand Journal of Botany*, **13**, 333–344.

10   Haynes, R.J. and Beare, M.H. (1997). Influence of six crop species on aggregate stability and

11   some labile organic matter fractions. *Soil Biology and Biochemistry,* **29**, 1647-1653.

12   Hochholdinger, F., Woll, K., Sauer, M. and Dembinsky, D. (2004). Genetic dissection of root

13   formation in Maize (*Z. mays*) reveals root-type specific developmental programmes. *Annals*

14   *of Botany,* **93**, 359-368.

15   Hodge, A. (2006). Plastic plants and patchy soils. *Journal of Experimental Botany,* **57**, 401-

16   411.

17   Jankauskas, B., Jankauskiene, G. and Fullen, M.A. (2008). Soil erosion changes in the

18   physical properties of Lithuanian Eutric Albeluvisols under different land use systems. *Acta*

19   *Agriculturae Scandinavian Section B – Soil and Plant Science*, **58**, 66-76.

20   Jin, K., Shen, J., Ashton, R.W., White, R.P., Dodd, I.C., Parry, M.A.J. and Whalley, W.R.

21   (2015). Wheat root growth responses to horizontal stratification of fertiliser in a water-limited

22   environment. *Plant and Soil,* **386***, 77-88.

1   Jing, J., Rui, Y., Zhang, F., Rengel, Z. and Shen, J. (2010). Localized application of

2   phosphorus and ammonium improves growth of maize seedlings by stimulating root

3   proliferation and rhizosphere acidification. *Field Crops Research,* **119**, 355-364.

4   Jones, B. and Ljung, K. (2012). Subterranean space exploration: the development of root

5   system architecture. *Current Opinion in Plant Biology*, **15**, 97–102.

6   Knapen, A., Poesen, J., Govers, G., Gyssels, G. and Nachtergaele, J. (2007). Resistance of

7   soils to concentrated flow erosion: A review, *Earth-Science Reviews*, **80**, 75–109.

8   Lal, R. (2001). Soil degradation by erosion, *Land Degradation and Development,* **12**, 519-

9   539.

10 Lal, R. (2010). Managing soils for a warming earth in a food-insecure and energy-starved

11 world, *Journal of Plant Nutrition and Soil Science,***173**, 4-15.

12 Li, Y., Zhu, X.-M. and Tian, J.-Y. (1991). Effectiveness of plant roots to increase the anti-

13 scourability of soil on the Loess Plateau. *Chinese Science Bulletin,* **36**, 2077–2082.

14 Li, P. and Li, Z. (2011). Soil reinforcement by a root system and its effects on sediment yield

15 in response to concentrated flow in the loess plateau. *Agricultural Sciences,* **2,** 86-93.

16 Linkohr, B.I., Williamson, L.C., Fitter, A.H. and Leyser, O. (2002). Nitrate and phosphate

17 availability and distribution have different effects on root system architecture of *Arabidopsis.*

18 *The Plant Journal,* **29**, 751-760.

19 Loades, K.W., Bengough, A.G., Bransby, M.F. and Hallet, P.D. (2010). Plant density

20 influence on fibrous root reinforcement of soils. *Ecological Engineering,* **36**, 276-284.

21 Lynch, J.P. and Brown, K.M. (2012). New roots for agriculture: exploiting the root phenome.

22 *Philosophical Transactions of the Royal Society B,* **367**, 1598–1604.

1   López-Bucio, J., Cruz-Ramírez, A. and Estrella-Herrera, L. (2003). The role of nutrient

2   availability in regulating root architecture. *Current Opinion in Plant Biology,* **6**, 280-287.

3   Macleod, C.J.A., Binley, A., Hawkins, S.L., Humphreys, M.W., Turner, L.B., Whalley, W.R.

4   and Haygarth, P.M. (2007). Genetically modified hydrographs: what can grass genetics do for

5   temperate catchment hydrology? *Hydrological Processes,* **21**, 2217-2221.

6   Malamy, J.E. (2005). Intrinsic and environmental response pathways that regulate root system

7   architecture. *Plant, Cell and Environment,* **28**, 67-77.

8   Mamo, M. and Bubenzer, G.D. (2001a). Detachment rate, soil erodibility and soil strength as

9   influenced by living plant roots: Part II. Field study. *American Society of Agricultural*

10 *Engineers*, **44**, 1175– 1181.

11 Mamo, M. and Bubenzer, G.D. (2001b). Detachment rate, soil erodibility and soil strength as

12 influenced by living plant roots: Part I. Laboratory study. *American Society of Agricultural*

13 *Engineers*, **44**, 1167–1174.

14 McCully, M.E. (1999). Roots in soil: unearthing the complexities of roots and their

15 rhizospheres. *Annual Review of Plant Physiology and Plant Molecular Biology*, **50**, 695-718.

16 Meek, B.D., Rechel, E.A., Carter, L.M. and De Tar, W.R. (1989). Changes in infiltration

17 under alfalfa as influenced by time and wheel traffic. *Soil Science Society of America Journal*,

18 **53**, 238–241.

19 Mitchell, A.R., Ellsworth, T.R. and Meek, B.D. (1995). Effects of root systems on preferential

20 flow in swelling soils. *Communication in Soil Science and Plant Analysis,* **26**, 2655-2666.

21 Morel, J.L., Habib, L., Plantureux, S. and Guckert, A. (1991). Influence of maize root

22 mucilage on soil aggregate stability. *Plant and Soil,* **136**, 111-119.

1   Moreno-Espíndola, I.P., Rivera-Becerril, F., De Jésus Ferrera-Guerrero, M. and De Léon-

2   González, F. (2007). Role of root-hairs and hyphae in adhesion of sand particles. *Soil Biology*

3   *and Biochemistry,* **39**, 2520-2526.

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

5   Morgan, R.P.C., Quinton, J.N. & Edwards, J. (1995). 3.05 Vegetation strategies for

6   combating desertification. MEDALUS II Project 3 Managing Desertification. Contract

7   EV5V-CT92-0165. Final Report covering the period 1 January 1991 to 30 September 1995.

8   Müller, M. and Schmidt, W. (2004). Environmentally induced plasticity of root hair

9   development in Arabidopsis. *Plant Physiology,* **134***, 409–419.

10   Oades, J.M. (1984). Soil organic matter and structural stability: mechanisms and implications

11   for management. *Plant and Soil,* **76**, 319-337.

12   Paterson, E., Sim, A., Standing, D., Dorward, M. and McDonald, A.J.S. (2006). Root

13   exudation from *Hordeum vulgare* in response to localized nitrate supply. *Journal of*

14   *Experimental Botany,* **57**, 2413-2420.

15   Pierret, A.; Latchackak, K.; Chathanvongsa, P.; Sengtaheuanghoung, O. and Valentin, C.

16   (2007). Interactions between root growth, slopes and soil detachment depending on land use:

17   a case study of a small mountain catchment in Northern Laos. *Plant and Soil,* **301**, 51-64.

18   Pimentel, D. (2006). Soil erosion: a food and environmental threat. *Environment,*

19   *Development and Sustainability*, 8, 119-137.

20   Pimentel, D. and Kounang, N. (1998). Ecology of soil erosion in ecosystems. *Ecosystems,* **1**,

21   416-426.

1   Pohl, M., Alig, D., Körner, C. and Rixen, C. (2009). Higher plant diversity enhances soil

2   stability in disturbed alpine ecosystems. *Plant and Soil*, **324**, 91‑102.

3   Pojasok, T. and Kay, B.D. (1990). Effect of root exudates from corn and bromegrass on soil

4   structural stability. *Canadian Journal of Soil Science,* **70**, 351 – 362.

5   Posthumus, H., Deeks, L.K., Rickson, R.J. and Quinton, J.N. (2013). Costs and benefits of

6   erosion control measures in the UK. *Soil Use and Management,* DOI: 10.1111/sum.12057

7   Prosser, I.P., Dietrich, W.E. and Stevenson, J. (1995). Flow resistance and sediment transport

8   by concentrated overland flow in a grassland valley. *Geomorphology*, **13**, 71–86.

9   Puigdefábregas, J. (2005). The role of vegetation patterns in structuring runoff and sediment

10 fluxes in drylands. *Earth Surface Processes and Landforms,* **30**, 133-147.

11 Quinton, J.N., Morgan, R.P.C., Archer, N.A., Hall, G.M., Green, A. (2002). Bioengineering

12 principles and desertification mitigation. In: Brandt, C.J., Geeson, N.A., Thornes, J.B. (Eds.)

13 Mediterranean desertification, A mosaic of processes and responses. John Wiley and Sons,

14 Chichester, p.93-105.

15 Reubens, B., Poesen, J., Danjon, F., Geudens, G. and Muys, B. (2007). The role of fine and

16 coarse roots in shallow slope stability and soil erosion control with a focus on root system

17 architecture: a review. *Trees,* **21**, 385-402.

18 Rilling, M.C., Wright, S.F. and Eviner, V.T. (2002). The role of arbuscular mycorrhizal fungi

19 and glomalin in soil aggregation: comparing effects of five plant species. *Plant and Soil,* **238**,

20 325-333.

21 Robinson, D. (1994). The response of plants to non-uniformus supplies of nutrients. *New*

22 *Phytologist,* **127**, 635-674.

1 Robinson, D. (2001). Root proliferation, nitrate inflow and their carbon costs during nitrogen

2 capture by competing plants in patchy soil. *Plant and Soil,* **232**, 41-50.

3 Roycewicz, P.S. and Malamy, J.E. (2014). Cell wall properties play an important role in the

4 emergence of lateral root primordia from the parent root. *Journal of Experimental Botany*, **65**,

5 2057–2069.

6 Sattelmacher, B., Gerendas, J., Thoms, K., Brück, H. and Bagdady, N.H. (1993). Interaction

7 between root growth and mineral nutrition. *Environmental and Experimental Botany,* **33**, 63-

8 73.

9 Sharma, B.R. and Chaudhary, T.N. (1983). Wheat root growth, grain yield and water uptake

10 as influenced by soil water regime and depth of nitrogen placement in a loamy sand soil.

11 *Agricultural Water Management,* **6**, 365-373.

12 Smucker, A.J.M. (1993). Soil environmental modifications of root dynamics and

13 measurement. *Annual Review of Phytopathology*, **31**, 191-216.

14 Stocking, M. and Elwell, H. (1976). Vegetation and erosion: A review. *Scottish Geographical*

15 *Magazine*, **92**, 4-16.

16 Stokes, A., Atger, C., Bengough, A.G., Fourcaud, T. and Sidle, R.C. (2009). Desirable plant

17 root traits for protecting natural and engineered slopes against landslides. *Plant and Soil*, **324**,

18 1–30.

19 Tengbeh, G. T. (1993). The effect of grass roots on shear strength variations with moisture

20 content. *Soil Technology*, **6**, 287-295.

21 Trimble, S.W. and Mendel, A.C. (1995). The cow as a geomorphic agent – a critical review.

22 *Geomorphology,* **13**, 233-253.

1 Vásquez-Méndez, R., Ventura-Ramos, E., Oleschko, K., Hernández-Sandoval, L., Parrot, J.-

2 F. and Nearing, M.A. (2010). Soil erosion and runoff in different vegetation patches from

3 semiarid Central Mexico. *Catena,* **80**, 162-169.

4 Waldron, L. J. (1977). Shear resistance of root-permeated homogenous and stratified soil. *Soil*

5 *Science Society of America Journal,* **41**, 843-849

6 Walker, T.S., Harsh, P.B., Grotewold, E. and Vivanco, J.M. (2003). Root exudates and

7 rhizosphere biology. *Plant Physiology,* **132**, 44-51.

8 Watt, M., McCully, M.E. and Canny, M.J. (1994). Formation and stabilization of rhizosheats

9 of *Z. mays* L. *Plant Physiology,* **106**, 179-186.

10 Wenzel, W.W. (2009). Rhizosphere processes and management in plant-assisted

11 bioremediation (phytoremediation) of soils. *Plant and Soil*, **321**, 385–408.

12 Zhang, H. and Forde, B.G. (1998) An Arabidopsis MADS box gene that controls nutrient-

13 induced changes in root architecture. *Science*, **279**, 407-409.

14 Zhou, Z.C. and Shangguan, Z.P. (2007). The effects of ryegrass roots and shoots on loess

15 erosion under simulated rainfall. *Catena,* **70**, 350-355.

16 Zhu, J., Kaeppler, S. and Lynch, J.P. (2005). Mapping of QTLs for lateral root branching and

17 length in maize (*Zea mays* L.) under differential phosphorus supply. *Theoretical and Applied*
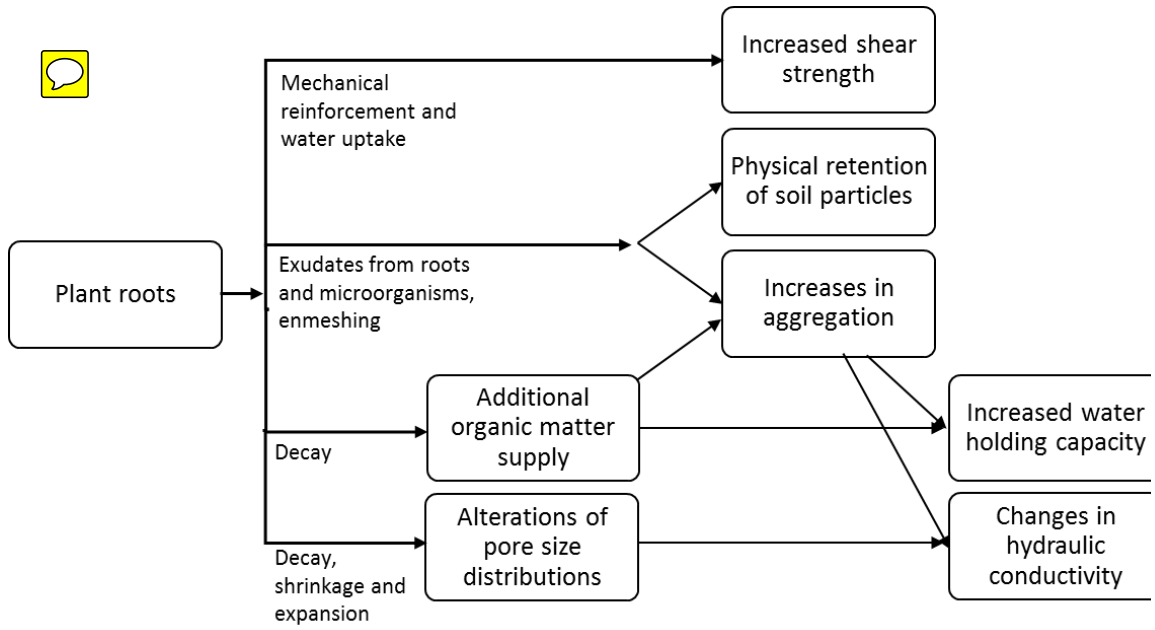
18 *Genetics*, **111**, 688–695.

19

20

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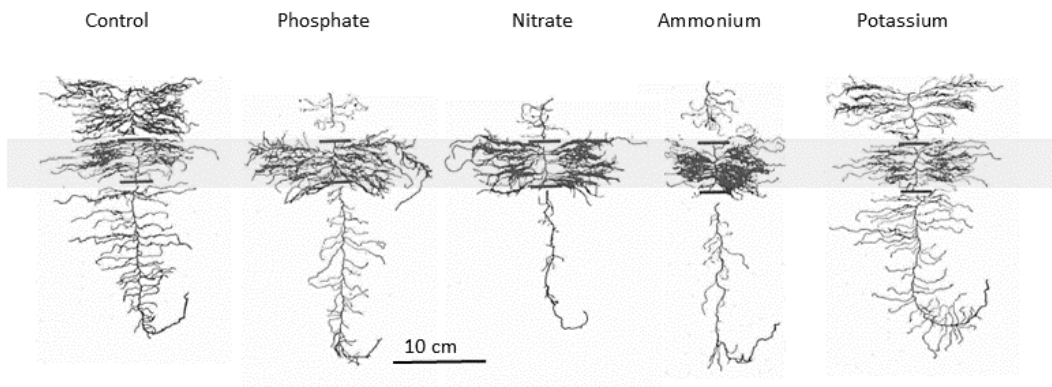
1

2

3

4

1

2

3

4

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

5