#### **Dear Artemi**

Many thanks for your comments on the paper.

I have had a look at the PDF that you marked up and at the comments in your original remarks again.

Thanks for directing my attention to the papers below and those in the PDF you marked up.

I have gone through each of them carefully to check whether they have something to say about vegetation, particularly the below ground elements, and erosion - my comments on each of the papers are below the references. I have also annotated the PDF.

You will see that two of the papers here and one you mentioned in the PDFhave been included, that this has necessitated me to add a further paper to make the point about vegetation and scale.

I have uploaded a revised manuscript which I hope you will find acceptable.

With best wishes

John

**Topiccal Editor Initial Decision: Reconsider after major revisions** (24 Jun 2015) by Prof. Artemi Cerdà Comments to the Author:

Dear author The paper is of quality in my opinion Please, follow the advises of the reviewers Sincerely Artemi Cerdà

Non-public comments to the Author: Dear author Dear John I found your paper of interest and necessary, You just need to try to satisfy (difficult) some of the comments which in my opinion are not 100 % necessary to critize the paper I did some reference review and update to help in the last review of the paper and I found the

And the introduction needs to show how your paper contribute to an interdisciplinary view of the Soil Science

following that can make the paper more scientifically sound and of interest

Brevik, E. C., Cerdà, A., Mataix-Solera, J., Pereg, L., Quinton, J. N., Six, J., and Van Oost, K.: The interdisciplinary nature of SOIL, SOIL, 1, 117-129, doi:10.5194/soil-1-117-2015, 2015.

This is already quoted in the introduction

#### And the use of this view into applied science

van Leeuwen, J. P., Lehtinen, T., Lair, G. J., Bloem, J., Hemerik, L., Ragnarsdóttir, K. V., Gísladóttir, G., ewton, J. S., and de Ruiter, P. C.: An ecosystem approach to assess soil quality in organically and conventionally managed farms in Iceland and Austria, SOIL, 1, 83-101, doi:10.5194/soil-1-83-2015, 2015.

This is a paper that contrasts organic farming with conventional farming. Apart from root crops and the removal of roots before soil analysis roots are not methioned. I don't think this is appropriate to quote.

Zornoza, R., Acosta, J. A., Bastida, F., Domínguez, S. G., Toledo, D. M., and Faz, A.: Identification of sensitive indicators to assess the interrelationship between soil quality, management practices and human health, SOIL, 1, 173-185, doi:10.5194/soil-1-173-2015, 2015.

And the paper of Bochet that link plants and soil erosion

E. Bochet 2015 The fate of seeds in the soil: a review of the influence of overland flow on seed removal and its consequences for the vegetation of arid and semiarid patchy ecosystems SOIL, 1, 131-146, 2015

This is a really good paper, but deals with how erosion moves seeds around the landscale not how erosion is affected by vegetation and particularly below ground rooting structures

and the relation between vegetation and erosion

Palacio, R.G., Bisigato, A.J., Bouza, B.J. 2014. Soil erosion in three grazed plant communities in northeastern Patagonia. Land Degradation and Development, in press. DOI: 10.1002/ldr.2289

This paper considers shrub and grassland communities and considers their effect on erosion and deposition. Apart from stating that different plants communities have a different affects I'm not sure what quoting this paper contributes to the paper. We already make the point that vegetation is important and quote a number of studies that have adopted a more mechanistic approach.

Qian, J., Wang, Z., Liu, Z., & Busso, C. A. (2014). BELOWGROUND BUD BANK RESPONSES TO GRAZING INTENSITY IN THE INNER-MONGOLIA STEPPE, CHINA. Land Degradation & Development. | DOI: 10.1002/ldr.2300

Again, an interesting paper, but this is a paper about budding in rhizomes and bulbs. The authors don't discuss erosion at all.

This paper show the importance of vegetation at basin scale to control soil erosion Zhao, G., Mu, X., Wen, Z., Wang, F., and Gao, P. Soil erosion, conservation, and Eco-environment changes in the Loess Plateau of China. Land Degradation & Development, 24: 499- 510. 2013. DOI 10.1002/ldr.2246

*I have now quoted this in the introduction to make the point that vegetation is important at all scales.* 

and the soil structure and vegetation

Cerdà, A. 2000. Aggregate stability against water forces under different climates on agriculture land and scrubland in southern Bolivia. Soil and Tillage Research, 36, 1-8.

This paper focusses on the effects of landuse on aggregate stability. It concludes that agriculture is the driving force, but it doesn't discuss roots, apart from a reference to the Oades 1984 paper which we also quote. I don't think it is relevant.

# Can we manipulate root system architecture to control soilerosion?

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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 properties of plants, demonstrating the important role that canopy structure and cover plays in 10 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 roots have on soil erosion and hydrological processes, and how plant root architecture might 16 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 erodiblity but block soil pores thereby limiting infiltration, enhancing 22 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.

#### 5 **1.Introduction**

6 Soil erosion by water is a serious environmental problem representing a much greater threat to 7 agricultural production than soil erosion by wind (Lal, 2010). Approximately 430 million ha 8 of arable land, or 30% of the globally available land for agricultural production, has been 9 degraded by water erosion and a further 56% is at risk (Jankar set al., 2008). The effect of 10 vegetation on reducing soil erosion is well known. Plants intercept rainfall, some is stored in 11 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; 13 Puigdefábregas, 2005). Water reaching the soil surface may be stored in small depressions on 14 the soil surface or infiltrate into the soil. The remainder may move downhill as overland flow, 15 entraining soil particles and transporting them, and may also concentrate to form rills and 16 gullies. There are a number of factors controlling erosion, namely the erosivity of the eroding 17 agent, slope angle, the nature of the plant cover and the erodibility of the soil (Morgan, 1986). 18 Erosion may result in on-site soil degradation reducing the soil's productivity and water 19 storage capacity, due to changes in soil structure, soil depth and losses of nutrients and 20 organic matter (OM). This may lead to significant losses of crop yield (Lal, 2001; Pimentel, 21 2006; Jankauskas et al., 2008), posing a threat to food security or limiting the production of 22 renewable biotic resources (Pimentel, 2006; Jankauskas et al., 2008). Off-site problems 23 associated with downstream sedimentation include flooding, pollution, negative effects on 24 biodiversity, as well as the loss of reservoir storage (Pimentel and Kounang, 1998; Lal, 2001; 25 Pimentel, 2006). In the UK, the annual costs of both on-site and off-site problems were

recently estimated to range between £248 and £469 million (Posthumus *et al.*, 2013). Hence,
 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 affect hydraulic conductivity and, hence, water storage capacity (Puidgefábregas, 2005) and 19 may increase soil shear strength (Tengbeh, 1993; De Baets et al, 2008). 20

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

In this paper we take an interdisciplinary view of the plant root and its interaction with the soil, in line with the interdicipliary nature this journal (Brevik et al.,2015), and review the literature concerning the effects of roots on soil properties determining the resistance of soil to water erosion (.concentrated and sheet flow) with emphasis on root system architecture (RSA). We then explore the factors influencing RSA especially lateral root (LR) growth, and finally the potential of fertilizer applications to stimulate LR proliferation, and thus form the 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 function 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 strength associated with roots is responsible for the transfer of shear stresses via tensile 23 24 resistance or interface friction within the soil-root matrix (Prosser et al., 1995, De Baets et al.,

2008). There was a positive linear relationship between the cross-sectional area of barley
(*Hordeum vulgare*) roots at the shear plane and, subsequent increases in soil shear strength in
a silty clay loam soil (Waldron, 1977). In ryegrass, increasing root densities from 0.20 g cm<sup>-3</sup>
to 1.80 g cm<sup>-3</sup> also increased strength from 1 kPa to 5 kPa in a sandy clay loam (Tengbeh,
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 between organic molecules and clays (Oades, 1984; Pojasok and Kay, 1990; Amezketa, 17 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.

Root exudates represent 5 to 21% of a plant's photosynthetically fixed carbon (C) (Walker *et al.*, 2003) serving as a crucial energy source for microorganisms (Haynes and Beare, 1997;
Amezketa, 1999). Both fungal and bacterial extracellular polymeric substances contribute to

1 the cementation of aggregates, and, thus enhance aggregate persistence (Oades, 1984; Morel 2 et al., 1991; Watt et al., 1994; Haynes and Beare, 1997; Bryan, 2000). However, the effect of 3 roots on aggregate stability is species specific (Haynes and Beare, 1997; Amezketa, 1999) due 4 to differences in root morphology (Pohl et al., 2009), turnover rates (Stokes et al., 2009), the 5 quantity and chemical composition of the root exudates and the influence of differences in 6 root exudates on microbial activity (Haynes and Beare, 1997, Bertin et al., 2003). Barley 7 roots increased aggregate stability (Haynes and Beare, 1997), whilst there is contradicting 8 evidence about the effects of roots of maize (Zea mays). Root mucilage of maize reportedly 9 increased aggregation (Morel et al., 1991), but the release of chelating agents, such as organic 10 acids (which destroy iron and aluminium bonds with OM) by maize decreased aggregate 11 stability (Oades, 1984). These contrasting results may be attributed to genotypic variation in 12 the chemistry of the root exudates. For example, within different barley genotypes, three 13 structural variations of mugineic acid (an organic ligand) have been found (Bertin et al., 14 2003). In addition, some organic compounds released by roots and microorganisms may also 15 induce water repellency depending on soil matric potential and the number of wetting and 16 drying cycles undergone (Hallett et al., 2003). However, OM and aggregate stability are 17 crucial in the formation of macropores, which reduce bulk density and facilitate gaseous 18 diffusion and improve infiltration rates (Gyssels and Poesen, 2003). Thus, the effects of root 19 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.

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

# 13

#### 3.Root system architecture and its manipulation

RSA is the three-dimensional deployment of roots (Linkohr et al., 2002; Basu et al., 2011). In 14 15 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 16 17 'manipulating RSA' refers to alterations being made to the spatial configuration of the roots 18 of an individual plant in respect of LR growth (i.e. initiation, elongation, diameter, branching) 19 by stimulating proliferation of these roots at certain depths. RSA is constitutively influenced 20 by genetic factors (Smucker, 1993; Malamy, 2005; Stokes et al., 2009), as demonstrated by 21 mutants of maize lacking different root classes (Malamy, 2005). Mature cereal root systems 22 consist mostly of coarse (seminal - seed derived, or nodal - shoot derived) roots and fine 23 (lateral) roots ( $\emptyset$  <1mm) (LRs), which often develop root hairs (McCully, 1999) from the trichoblasts in the meristematic zone (Gilroy & Jones, 2000). Although LRs are the major 24 25 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).

8 Moreover, different types of root system are often distinguished based on the presence of a 9 primary root representing a single dominant axis with varying degrees of LR development, 10 which is characteristic for primary or tap root systems (Fitter, 1987), whereas root systems 11 lacking a primary root are referred to as a fibrous root system (De Beats et al., 2007). Only a 12 few studies have compared the effect of these different root systems on soil erosion rates, with 13 fibrous root systems being more effective in reinforcing soils against concentrated flow than 14 tap root systems with similar root mass (De Baets et al., 2007). In contrast, tap rooting species 15 increase saturated hydraulic conductivity, which tends to be low under fibrous root systems 16 (Archer et al., 2002; Quinton et al., 2002). These observations can be explained by the larger 17 number of LRs and greater root length densities (RLD) associated with fibrous root systems 18 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

1 performance and function (Lynch and Brown, 2012), hinder the development of new crop 2 varieties with altered root traits. Although RSA is genetically constrained, it is highly plastic 3 in response to environmental cues. This means that genetically identical plants may differ in 4 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, 5 6 2012) to the prevailing environmental conditions. The heterogeneous distribution of nutrients 7 can increase LR length and initiation, as well as coordinate proliferation of LRs in soil regions 8 where these resources are present (e.g. Fitter, 1987; Smucker, 1993; Stokes et al. 2009). 9 Hence, the localized application of nutrients at prescribed depths and associated LR 10 proliferation offers an opportunity to manipulate LR distribution within the soil profile, 11 thereby promoting RSAs that reduce soil erosion.

12

# 4.Lateral root proliferation in response to local nutrient availability

13 The local proliferation of LRs allows the optimal exploitation of locally available nutrient 14 reserves (Smucker, 1993; Robinson, 1994; Hodge, 2006). Lack of nitrogen (N), as well as 15 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 16 17 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 18 19 heterogeneous distribution of potassium (K) did not affect RSA (Drew, 1975; Robinson, 20 1994), LR initiation and extension increased within a 4 cm long segment of a seminal root 21 exposed to 100 times greater concentrations of  $NO_3^-$  and  $NH_4^+$  than the remainder of the root 22 system, where nutrient-limited conditions inhibited LR development (Drew et al., 1973; 23 Drew, 1975; Drew and Staker 1975) (Figure 2). The same is true for wheat (Triticum 24 aestivum) (Drew, 1975; Forde and Lorenzo, 2001) and maize grown in a flowing nutrient 25 culture whereby two nodal roots were exposed to different NO<sub>3</sub><sup>-</sup> concentrations revealed

similar results (Granato and Raper, 1989). Furthermore, a concentration of 1 mM NO<sub>3</sub><sup>-</sup> 1 stimulated LR branching and increased LR diameters in both maize and barley (Drew, 1975; 2 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<sub>3</sub><sup>-</sup>-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). However, nutrient solutions containing NH<sub>4</sub><sup>+</sup> as primary N source lead to higher root 7 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 developmental response to localized increased NO3<sup>-</sup> was most pronounced with plants of low 18 19 N status (Forde and Lorenzo, 2001; Forde, 2002). High NO<sub>3</sub><sup>-</sup> levels result in increased auxin concentration in the LR tip stimulating LR growth, while high NH<sub>4</sub><sup>+</sup> levels enhance higher 20 21 order root branching. The presence of both forms of N results in a complementary response (Forde, 2002; Jones & Ljung, 2012). However, if NO<sub>3</sub><sup>-</sup> concentrations are too high, LR 22 23 growth tends to be inhibited (Zhang and Forde, 1998; Linkohr et al., 2002), which is mediated by abscisic acid (López-Bucio et al. 2003). A detailed discussion of the molecular 24

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 3 4 reflect natural conditions and it is important to determine whether such responses occur in 5 soil. Paradoxically, when wheat plants were grown in soil-filled rhizotrons (1.4 m deep) with 6 nutrients (both N and P) banded at 0-40 cm or 60-100 cm below the soil surface and the soil 7 allowed to dry (simulating a terminal drought stress), the greatest RLD detected at 1.4 m 8 occurred with the surface fertiliser application (Jin et al., 2015). However, fertiliser banding 9 (stratification) and local placement (patches) can elicit different responses. LRs of thale cress 10 in a  $NO_3^-$  enriched patch in a heterogeneous soil were only marginally longer than in the 11 corresponding patch under homogeneous conditions (Linkohr et al. 2002). Nevertheless, LR 12 proliferation has been observed in the field (Sattelmacher et al., 1993; Robinson, 1994). A 13 recent study in North China showed that banding  $NH_4^+$  and P at 10 cm depth resulted in a 23-14 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 15 both nutrients also increased RLD at a depth of 15-30cm (Jing et al., 2010). However, the 16 17 responsiveness of plants to localized nutrient availability varies between different species and 18 genotypes (Robinson, 1994).

# 19 5.Manipulating root system architecture with nutrient placement to control 20 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

1 commonly found at the soil surface (Pierret et al., 2007) and the abundance of roots gradually 2 declines with increasing soil depth (Quinton et al., 2002; De Baets et al., 2008). However, it 3 has been argued higher RLDs at deeper soil depths would be particularly beneficial, as this 4 increases possible water uptake and evapotranspiration rates, thus infiltration rates (Stokes et 5 al., 2009) and would provide reinforcement to deeper soil layers in situations where 6 concentrated flow erosion is problematic. In addition, longer vertical roots, that increase RLD 7 at depth, provide conduits to deeper soil layers (Archer et al., 2002; Devitt and Smith, 2002; 8 Quinton et al., 2002) and directly affect water storage capacity of the effective soil depth 9 (Macleod et al., 2007; Stokes et al., 2009). Improvements in aggregate stability tend to be 10 particularly pronounced in, if not spatially limited to, the rhizosphere (Oades, 1994; Foster, 11 1988; Morel et al., 1991; Haynes and Beare, 1997), so the extent of the root system 12 determines its effect on soil aggregation (Haynes and Beare, 1997). The effects of roots of the 13 grasses Stipa bungeana and Bothriochlon ischaemum on the properties of a Chinese loess soil 14 (SOM and aggregate stability, especially in large diameter classes) decreased with increasing 15 depth, as RLD deminished (Li and Li, 2011). The higher sediment load derived from deep soil 16 horizons associated with the higher susceptibility of these soil horizons to erosional forces 17 was further enhanced by increasing runoff discharge and slope gradient (Li and Li, 2011) and 18 was particularly critical during concentrated flow erosion. Furthermore, soil cohesion 19 provided by roots is also limited to the rooting depth of the vegetation, consequently soil 20 reinforcement decreases with increasing depth (Gyssels et al., 2005; De Baets et al., 2008). 21 Although Mediterranean shrubs typically only stabilize the top 50 cm of gully walls and 22 hillslopes, failures may occur at deeper depths and increases in soil strength depend on the 23 number of LRs that cross the potential shear plane (Reubens et al., 2007; De Baets et al., 24 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). In this case, soil properties at different soil layers may change accordingly to the proportion of 5 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<sub>3</sub><sup>-</sup> 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 limited NO<sub>3</sub><sup>-</sup> varied between species. However, further research is needed into the effects of 26

differences in LR growth dynamics in response to localized fertilizer application on soil
 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 variability between species (Robinson, 1994; Hodge, 2006) and genotypes (Sattelmacher et 24 25 al., 1993; Forde and Lorenzo, 2001) in their shoot responsiveness, which depends on differences in nutrient uptake and utilization efficiency (Sattelmacher *et al.*, 1993).
 Nevertheless, LR proliferation may occur without limiting above ground growth (and yield).

## 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.

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

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- 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