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Plant root traits affecting the resistance of soils to concentrated flow erosion

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ABSTRACT: The effect of plant species on erosion processes may be decisive for long-term soil protection in degraded ecosystems. The identification of functional effect traits that predict species ability for erosion control would be of great interest for ecological restoration purposes. Flume experiments were carried out to investigate the effect of the root systems of three species having contrasted ecological requirements from eroded marly lands of the French Southern Alps [i.e. *Robinia pseudo acacia* (tree), *Pinus nigra austriaca* (tree) and *Achnatherum calamagrostis* (grass)], on concentrated flow erosion rates. Ten functional traits, describing plant morphological and biomechanical features, were measured on each tested sample. Analyses were performed to identify traits that determine plant root effects on erosion control. Erosion rates were lowest for samples of *Robinia pseudo acacia*, intermediate in *Achnatherum calamagrostis* and highest in *Pinus nigra austriaca*. The three species also differed strongly in their traits. Principal components analysis showed that the erosion-reducing potential of plant species was negatively correlated to root diameter and positively correlated to the percentage of fine roots. The results highlighted the role of small flexible roots in root reinforcement processes, and suggested the importance of high root surface and higher tensile strength for soil stabilization. By combining flume experiment to plant functional traits measurements, we identified root system features influencing plant species performance for soil protection against concentrated flow erosion. Plant functional traits related to species efficiency for erosion control represent useful tools to improve the diagnosis of land vulnerability to erosion, plant community resistance and the prediction of ecosystem functioning after ecological restoration.

KEYWORDS: concentrated runoff erosion; plant trait; flume experiment; soil fixation; root system

Introduction

During the past 15 years, researchers from various disciplinary fields have addressed the importance of ecosystems services (Millennium Ecosystem Assessment, 2005), defined as the benefits human populations derive from ecosystem processes (Costanza *et al.*, 1997), to human societies. Soil retention and erosion control are part of the regulation functions provided by vegetation (De Groot *et al.*, 2002) historically recognized since the nineteenth century and have become critically important in many ecosystems (Pimentel and Kounang, 1998).

Indeed, the loss of soil through water erosion is one of the greatest environmental issues affecting both agricultural and natural lands worldwide (Morgan, 1995; Pimentel *et al.*, 1995; Durán and Rodríguez, 2008). In the French Southern Alps, marly lands are subjected to severe water erosion and intense gullyng (Figure 1), ending in the formation of badlands (Poesen *et al.*, 2003), where concentrated runoff and shallow soil slippage processes cause considerable soil losses (3.5 cm yr⁻¹ in Lecompte *et al.*, 1998; 100 tons ha⁻¹ yr⁻¹ in Mathys *et al.*, 2003).

Vegetation has long been recognized as a factor significantly influencing erosion rates on slopes prone to instability (Thornes, 1990; Morgan, 1995) and has thus been used for decades in ecological restoration operations on degraded lands (e.g. Coutancier,

2004; Norris *et al.*, 2008; Stokes *et al.*, 2010). The effects of vegetation on concentrated flow erosion are manifold. Plant canopy intercepts rainfall, increases water infiltration and surface roughness (Styzcen and Morgan, 1995), thus reducing surface runoff and concentrated flow erosion. This protective effect of vegetation has mostly been related to vegetation cover without taking into account community composition and functional diversity (Garnier *et al.*, 2004). Yet, species with certain functional traits may be more efficient in soil stabilization than others and may have a stronger impact on erosive dynamics and ecosystem stability (De Baets *et al.*, 2009; Stokes *et al.*, 2009). Evidence has shown that ecosystem processes are strongly influenced by the functional traits of individual species that compose the community (Díaz and Cabido, 2001; Garnier *et al.*, 2004; Mokany *et al.*, 2008). Classifying species according to their impact on ecosystem processes and predicting ecosystem functioning from these so-called 'functional effect traits' that have a significant influence on ecosystems processes, is therefore a major challenge in applied ecology (Lavorel and Garnier, 2002). This approach has been used to determine plant traits that control litter decomposition rates (e.g. Cortez *et al.*, 2007; Cornwell *et al.*, 2008), primary productivity (e.g. Pontes *et al.*, 2007) or nitrogen cycling (e.g. Craine *et al.*, 2002) but can be generalized to other ecological processes including soil



Figure 1. Eroded marly land in the French Southern Alps (Draix, Alpes-de-Haute-Provence, France). This figure is available in colour online at wileyonlinelibrary.com/journal/esp

protection against concentrated flow erosion. In degraded areas in a context of ecosystem restoration, several authors have stressed the need to identify species and plant traits that contribute to the provision of ecosystem services (Díaz *et al.*, 2006; Luck *et al.*, 2009). In addition, it is becoming widely acknowledged that interdisciplinary studies, relating ecology and geomorphology are necessary (Osterkamp *et al.*, 2012; Stoffel and Wilford, 2012).

Often neglected in soil erosion models, plant roots also have a number of hydrological and mechanical effects (Gyssels *et al.*, 2005). The effect of plant root systems on soil stability has received increasing attention in recent years. Small flexible roots lower pore water pressure, increase surface roughness and provide additional soil cohesion through root reinforcement (Reubens *et al.*, 2007). Concentrated flow erosion rates have been related to root traits such as root density (i.e. root mass per unit volume of soil – Li *et al.*, 1991; De Baets *et al.*, 2006; Gyssels *et al.*, 2006), root length density (i.e. root length per unit volume of soil – Mamo and Bubenzer, 2001; De Baets *et al.*, 2006; De Baets *et al.*, 2007), root system type (heart versus tap root system – De Baets *et al.*, 2007) and root surface area density (i.e. root surface per unit volume of soil – Zhou and Shangguan, 2005). Li *et al.* (1991) also reported that root reinforcement of soils depends on the number of fibrous roots less than 1 mm in diameter, the most resistant to tension (Gray and Sotir, 1996).

Although the literature on the effects of plant roots on soil erosion by runoff is well documented, information remains rather descriptive. Quantitative research and laboratory experiments on hydraulic flume remains sparse (Mamo and Bubenzer, 2001; De Baets *et al.*, 2006), primarily because of methodological difficulties. Moreover, experimental studies have been carried out on different species, traits and soil conditions, and different relationships between plant traits and erosion rates have been obtained. So far, generalizing on the functional traits that can explain or predict the effect of plant species on soil stability against concentrated flow is not achievable. Previous studies related erosion rates to *ad hoc* chosen or easy to measure root variables, whereas this study measured a complete set of root variables potentially influencing soil erosion rates and investigated their correlation with erosion-reducing potential of plant root systems, in order to present the root variables that relate best to the erosion-reducing potential of plant root systems in early growth stages.

The present study, focusing on the erosion processes in the marly badlands of the French Southern Alps, aims to expand

our knowledge on plant functional traits that are involved in root reinforcement of soils and in reducing concentrated flow erosion rates. To meet this objective, we conducted flume experiments to simulate concentrated runoff similar to the ones that can be observed in gully beds during intense rainfalls. Tests were carried out on soil samples with laboratory grown plant species to evaluate the influence of the root system of three different species on soil resistance to incision by concentrated flow erosion. Soil detachment rates were assessed and 10 plant traits related to root biomass, root morphology and root mechanical properties were measured. Results are discussed in order to identify the relevant traits to evaluate and predict species performance for soil reinforcement against concentrate flow erosion.

Materials and Methods

Plant material

Three species were selected according to the following criteria: they are pioneer species prevalent in eroded marly lands, they include different root system types to have different root traits values, they are, or were, used for land restoration. Added to availability constraints in the field or in nurseries and to experimental constraints, three species were studied: two tree species, *Pinus nigra austriaca* and *Robinia pseudo acacia* and the grass *Achnatherum calamagrostis*. The two tree species are both exotic species native to Austria and North America respectively but they did not show invasive development in marly lands of the French Southern Alps since they were first introduced during restoration operations at the end of the nineteenth century (Vallauri *et al.*, 2002).

In April 2009, seeds of the two tree species were germinated in vermiculite, a chemically inert mineral substrate, for four weeks in a growth chamber at 25 °C /15 °C day/night temperature and 70% relative humidity. For the grass species, individual tussocks were collected in the field in autumn and cultivated in common garden during winter. Ramets were then isolated in April 2009, cut to 3 cm and 5 cm for aerial parts and roots respectively, and planted in vermiculite.

Four weeks after germination and multiplication, seedlings, similar in size and shape, were transplanted into plastic pots (16 cm square × 23 cm deep) filled with marly substrate collected from the field (Draix experimental site, Alpes de Haute Provence department, France, 44° 8'N, 6° 20'E). At the

same time, bare soil pots were prepared to serve as control. The soil from this site corresponded to the detrital and regolith layers that deposited after removal by erosion processes and was made of structureless marl fragments and colluvial materials. These marls have relatively low carbonate content (from 20 to 35%) their effective cohesion ranges from 6 to 12 kPa (Antoine *et al.*, 1995; Maquaire *et al.*, 2003).

Pots were planted with 10 seedlings regularly distributed and then randomly placed in the experimental garden, with a 20 cm distance, where plants were let to grow. Root growth and root density were checked weekly by excavating soil samples from additional pots and flume experiment took place eight weeks later (July 2009) when root density was assumed sufficient to have a significant effect on soil stability

Hydraulic flume experiment

Flume experiments were conducted in July 2009, on three month old seedlings. Before each test, soil samples were prepared as follows: the above-ground biomass was removed (clipped level at the soil surface) and samples were placed in a container filled with water to wet the entire soil column and ensure similar soil moisture content between the samples. After soaking, samples were left to drain for 12 hours.

Before the experiment, the bottom of the pots was cut and thin plates of polystyrene were added to raise the soil surface at the upper rim of the pot. Pots were placed in an open box at the bottom of the flume (Figure 2) and adhesive tape was stuck straddling the rims of the pot and the bottom of the flume to prevent edge effects. Samples were then exposed to a concentrated flow at a constant discharge (Q) of $0.0015 \text{ m}^3 \text{ s}^{-1}$ during 60 seconds. This duration was determined after preliminary tests had shown that soil detachment mainly occurred during the first 60 seconds of the experiment. The corresponding flow shear stress (τ), which was used to evaluate the erosive force of the concentrated flow (Gimenez and Govers, 2002; De Baets *et al.*, 2006), was 5.2 Pa (see Appendix for details), which falls within the range of values needed for

incipient motion of soil particles (1.8–10.6 Pa, Poesen *et al.*, 2003). Detached soil particles were collected at the bottom end of the flume in two 50 L buckets every 30 seconds to calculate erosion rates. Tests were repeated on 10 pots per species. Ten tests were also carried out on bare soil samples (control).

Soil detachment rate

After the flume experiments, the collected sediments were left to decant, and then separated from the water, dried (48 hours at 70 °C) and weighed. Relative soil detachment (RSD) rate was calculated for each test as the ratio of the mass of sediment detached from root-permeated samples to the average mass of sediment detached from bare soil samples (control).

Morphological traits measurement

The above-ground parts of plants, cut before the flume experiments, were dried (48 hours at 70 °C) and weighed. After the tests, samples were cleaned by gently removing the soil by hand with a water jet, and conserved in ethanol 50% (v/v) until analysis. Root traits were measured using WinRHIZO PRO (version 2003b, Regent Instrument, Quebec, Canada) following the protocol described in Bouma *et al.* (2000). The roots were stained with blue methylene (5 g L^{-1}) in order to increase contrast and then scanned at a resolution of 400 dpi. WinRHIZO was then used to determine root mean diameter (D), root length (L), external root surface (RSA), volume (V) and the percentage of fine roots with a diameter less than 0.5 mm (FR). Roots were then dried for 48 hours at 70 °C and weighed.

Root density (root mass per unit volume of root-permeated soil, RD in kg m^{-3}), root tissue density (RTD in g cm^{-3}), specific root length (SRL in m g^{-1}) and root length density (root length per unit volume of root-permeated soil, RLD in km m^{-3}) were calculated. Finally, root to shoot ratio (R/S) was obtained by dividing dry root mass by dry shoot mass.

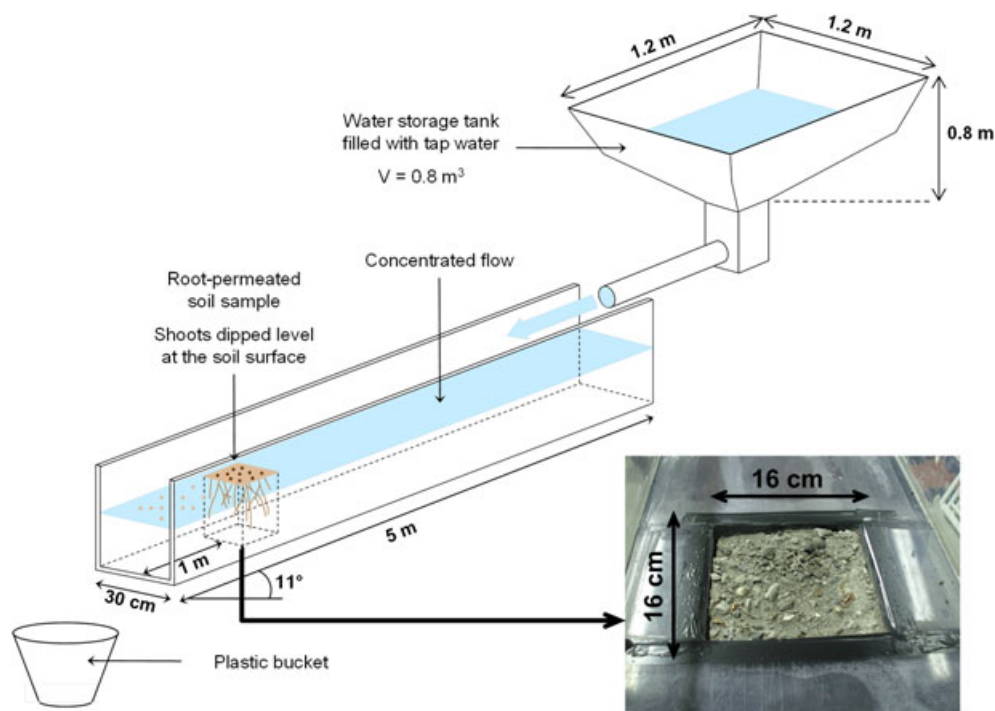


Figure 2. Schematic diagram of the hydraulic flume during concentrated flow tests. This figure is available in colour online at wileyonlinelibrary.com/journal/esp

Root tensile strength

Root samples were collected on another set of pots not used in the flume experiments. Roots were cleaned and undamaged root fragments were selected for tensile tests on a tensile-strength meter built on the basis of Hendry and Grime (1993). Before testing, root diameter was measured at three points along the root length. Once the root had broken, root tensile strength T_R (in MPa) was calculated as the peak force (N) needed to break the root per unit of cross-sectional area (in mm^2). For each species, at least 30 tests were performed on roots with diameters ranging from 0.06 to 0.88 mm.

Data analysis

Variations in soil detachment rates and trait values between species were investigated using one-way analysis of variance (ANOVA). Root tensile strength values were analysed through analysis of co-variance (ANCOVA) with root diameter as a covariate. The assumption of normality was verified prior to analysis (Shapiro–Wilk's test) and significant differences were assessed with Tukey's HSD test.

Principal components analysis (PCA) was performed to relate plant traits to erosion rates. All measured traits, except T_R which was not calculated on the same samples, were included untransformed in the analyses.

Analyses were carried out with STATISTICA (version 8.0 for Windows, Statsoft, 2008).

Results

Soil detachment rates

Erosion occurred in all soil samples but the presence of roots greatly reduced erosion rates (Figure 3). However, there were large differences in RSD rates between the three species studied and through time. *Robinia pseudo acacia* showed the strongest effect and reduced soil detachment by more than 95% since the first 30 seconds (no sediment was collected in the last 30 seconds of the test) compared with control. The grass species, *Achnatherum calamagrostis*, and the tree species *Pinus nigra*, also substantially stabilized the soil but to a lesser extent. RSD rates decreased with time for *Achnatherum calamagrostis* but stayed constant for *Pinus nigra*.

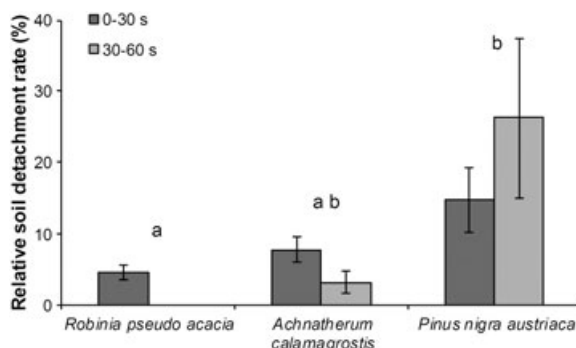


Figure 3. Relative soil detachment rates between species. Results are presented in two 30 second time periods to show the evolution of soil detachment through time. Analyses of variance found species effect on soil detachment significant both in the first 30 seconds (0–30 seconds: $F=3.7$, $p=0.03$) and in the last 30 seconds (30–60 seconds: $F=5.6$, $p=0.009$) of the tests. Bars are means \pm standard errors. Letters indicate significant differences between species (ANOVA, Tukey's HSD test, $\alpha=0.05$)

Plant traits and root tensile strength

All traits measured were significantly different between species except root volume (Table I), traducing important morphological differences in species root systems. *Achnatherum calamagrostis* had the more developed root system (RD, RLD and RSA) and presented the roots with highest tissue density (RTD), before *Robinia pseudo acacia* and *Pinus nigra austriaca*. However, *Robinia pseudo acacia* had finer roots [D, SRL and percentage of fine roots (%FR)] than *Achnatherum calamagrostis* and *Pinus nigra austriaca*, the later one having the thickest and shorter roots.

Root biomechanical properties were also different between species (Figure 4). As revealed by tensile strength tests, root tensile strength decreased as root diameter increased ($r=-0.51$, $p<0.001$). Analysis of covariance ($D: F=52.8$, $p<0.000$; Species: $F=16.6$, $p<0.000$) showed that *Achnatherum calamagrostis* had roots more resistant to traction than the two tree species, that had similar responses to traction (*post-hoc* Tukey's HSD test).

Relationship between erosion rates and functional traits

Multivariate analysis revealed distinct clustering of the three species (Figure 5) according to the two first axes of the PCA, accounting for 46% and 30% of the variation in the data set respectively.

Robinia pseudo acacia occupied the lower end of axis 2 whereas *Pinus nigra austriaca* occupied the lower end of axis 1 and the upper end of axis 2. *Achnatherum calamagrostis* was located in the upper end of axis 1 and along the entire axis 2. RSD rate variation was consistent with the results of analysis of variance, high erosion rates being graphically associated to *Pinus nigra* and low erosion rates to *Robinia pseudo acacia*.

The analysis showed relationship between RSD rates and some functional traits (Figure 5 and Table II). RSD rate was positively correlated to mean root diameter and negatively correlated to the proportion of fine roots. However, root mass (RD and V), root length density and external root surface did not directly influence erosion rates.

There were also significant relationships between D and %FR and other root traits that must be considered to interpret the relationship between plant traits and the effect on erosion rates (Table II). Both D and %FR were strongly correlated to RLD, RSA and SRL, the former negatively and the latter positively. Therefore, for a given root biomass, species with thinner roots tend to have higher root–soil contact thanks to longer roots.

Discussion

Species effect on concentrated flow erosion rates

The present study clearly demonstrated that plant root systems substantially decreased concentrated flow erosion rates, even at very low densities at the first stages of plant development (Table I and Figure 3). Here, we reported decreases of soil detachment rates in the first 30 seconds of the tests ranging from 72% (*Pinus nigra*) to 95% (*Robinia pseudo acacia*) on average, with root densities of only 0.03 kg m^{-3} . These values are higher than those reported by Mamo and Bubenzer (2001) and De Baets *et al.* (2006), who measured similar decreases but for root densities higher than 1 kg m^{-3} . These differences may be attributed to differences in experimental parameters such as flow shear stress and soil properties. Indeed, in our study, we applied a flow shear stress of 5.2 Pa on marly

Table 1. Mean values \pm standard errors of traits for the three species studied, and results of one-way ANOVA (Statistic test *F*).

	<i>Robinia pseudo acacia</i>	<i>Achnatherum calamagrostis</i>	<i>Pinus nigra austriaca</i>	ANOVA (<i>F</i> -statistic)
<i>R/S</i>	0.21 \pm 0.03	0.28 \pm 0.03	0.31 \pm 0.02	4.21*
RD (kg m ⁻³)	0.03 \pm 0.00	0.09 \pm 0.01	0.03 \pm 0.00	20.35***
<i>V</i> (cm ³)	1.15 \pm 0.09	1.53 \pm 0.21	1.25 \pm 0.10	2.05 ns
<i>D</i> (mm)	0.39 \pm 0.01	0.37 \pm 0.01	0.60 \pm 0.02	100.7***
RLD (km m ⁻³)	1.56 \pm 0.15	2.06 \pm 0.21	0.73 \pm 0.07	22.14***
RSA (cm ²)	114.15 \pm 9.75	145.6 \pm 15.35	81.5 \pm 6.64	8.92**
SRL (m g ⁻¹)	49.76 \pm 3.53	27.14 \pm 4.59	23.17 \pm 0.87	21.27***
RTD (g cm ⁻³)	0.16 \pm 0.01	0.33 \pm 0.01	0.15 \pm 0.01	59.92***
%FR	86.57 \pm 1.00	78.08 \pm 2.80	48.17 \pm 2.51	91.37***

Note: *R/S*, root to shoot biomass ratio; RD, root density; *V*, root volume; *D*, root diameter; RLD, root length density; RSA, external root surface; SRL, specific root length; RTD, root tissue density; %FR, percentage of fine roots. Levels of significance are: ns, non significant; **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

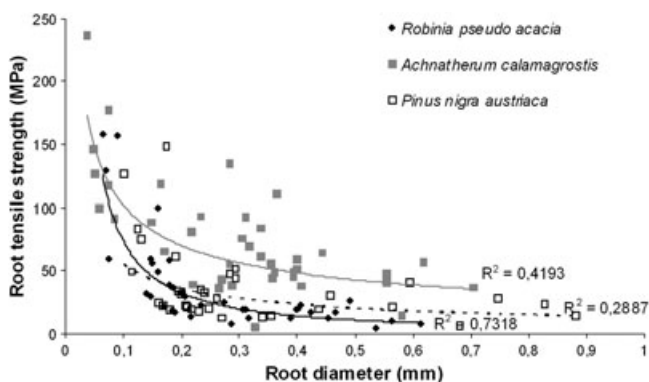


Figure 4. Relationship between root diameter and root tensile strength and differences between species.

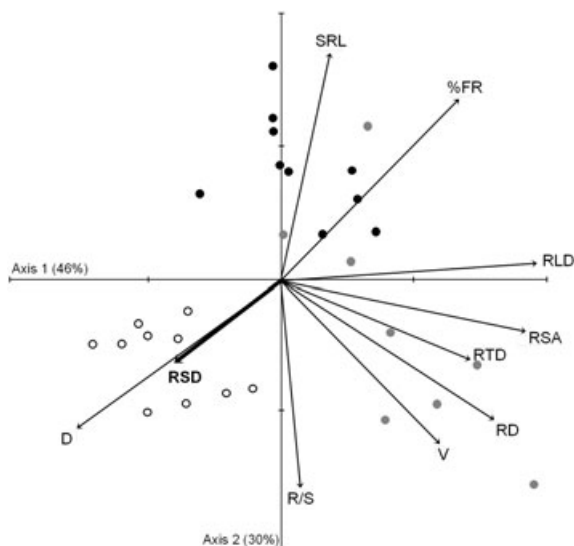


Figure 5. Principal component analysis joint plot ordination of functional traits, relative soil detachment and the three species studied (●, *Robinia pseudo acacia*; ■, *Achnatherum calamagrostis*; ○, *Pinus nigra austriaca*). RSD, relative soil detachment; *D*, root diameter; *R/S*, root to shoot biomass ratio; *V*, root volume; RD, root density; RTD, root tissue density; RSA, external root surface; RLD, root length density; %FR, percentage of fine roots; SRL, specific root length.

samples, whereas values ranged from 1.1 to 2.2 Pa on silt loam in Mamo and Bubenzer (2001), and from 9 to 45 Pa on sandy loam in De Baets *et al.* (2006). In addition, the flume bed and the tape, have a different bed roughness than the soil sample, which may cause higher flow velocities upslope of the sample.

This, also called clear water effect, may increase the vulnerability of bare soil samples (control) to soil detachment, and thus lead to an overestimation of the erosion reduction values. In future experiments, such effect should be reduced by increasing the roughness of the flume bed.

The use of a flume experiment presents some obvious advantages such as the control of environmental parameters. The observation of the effect of one species or individual on erosion rates at a time, which is barely possible in the field, is also easier as well as the reproducibility of the observations. However, the method has some limitations, on top of which the possible lack of connection with field processes which may lead to difficulties when extrapolating the results. In addition, the pot size used here would be insufficient to investigate the effectiveness of juvenile tree species roots, and bigger samples would be required. Therefore, these results, which refer to plants in the early stages of their development, must be interpreted with caution and could be validated by further experiments or field observations.

Plant morphological and biomechanical traits

The three species selected in our study presented important morphological and ecological differences that appeared in the trait values (Table 1). *Achnatherum calamagrostis*, a grass species successfully colonizing badland areas (Guàrdia *et al.*, 2000) and presenting a heart root system with many fibrous roots developing from the base of the tussocks, had a high fine roots content, high RLD and RSA. The tree species *Robinia pseudo acacia* and *Pinus nigra austriaca*, both have a tap root system, characterized at the seedling stage, by a strong vertical root and many laterals. However, these two species had opposite values on several traits. The former was characterized by small diameters and high values of %FR, SRL, RLD and RSA while the latter had opposite features. These morphological differences may result from contrasted species growth patterns: *Robinia pseudo acacia* (Fabaceae) being a fast-growing invasive species particularly vigorous in poor and dry environments (Boring and Swank, 1984), and *Pinus nigra* having a rather slow-growing behaviour. Indeed, fast-growing woody species generally have smaller diameters and greater SRL allowing successful resource foraging and acquisition (Comas and Eissenstat, 2004). In addition, SRL has been positively correlated to root proliferation (Eissenstat, 1991), and may be relevant to assess species ability to capture nutrients in nutrient-rich patches in otherwise poor soils (Hodge, 2004) and to colonize newly restored areas.

Table II. Correlation matrix between functional traits and relative soil detachment (RSD).

	RSD	R/S	RD	V	D	RLD	RSA	SRL	RTD	%FR
RSD	1	—	—	—	—	—	—	—	—	—
R/S	0.13	1	—	—	—	—	—	—	—	—
RD	-0.11	0.38*	1	—	—	—	—	—	—	—
V	-0.13	0.51**	0.77***	1	—	—	—	—	—	—
D	0.37*	0.37	-0.34	0.02	1	—	—	—	—	—
RLD	-0.33	0.06	0.70***	0.58***	-0.74***	1	—	—	—	—
RSA	-0.29	0.25	0.80***	0.82***	-0.52**	0.93***	1	—	—	—
SRL	-0.30	-0.53**	-0.40*	-0.26	-0.53**	0.32	0.14	1	—	—
RTD	-0.08	0.19	0.83***	0.33	-0.54**	0.59***	0.53**	-0.38*	1	—
%FR	-0.38*	-0.42*	0.15	-0.09	-0.95***	0.68***	0.46*	0.69***	0.33	1

Note: RSD, relative soil detachment; R/S: root to shoot biomass ratio; RD, root density; V, root volume; D, root diameter; RLD, root length density; RSA, external root surface; SRL, specific root length; RTD, root tissue density; %FR, percentage of fine roots.

Indicated are correlation coefficient r and significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Species also differed regarding their biomechanical properties (Figure 4). Root tensile strength decreased as root diameter increased, indicating that fine roots are the most resistant in tension (Bischetti *et al.*, 2005; De Baets *et al.*, 2008; Burylo *et al.*, 2011). This relationship has been attributed to differences in root structure and in particular to higher cellulose concentrations in small roots (Genet *et al.*, 2005). Hathaway and Penny (1975) demonstrated that root elasticity decreased with increasing lignin/cellulose ratio. Therefore, roots of tree species might be weaker in tension than fibrous roots of grasses because of their higher lignin content.

Erosion-reducing potential and plant traits

Our results highlighted significant correlations between concentrated flow erosion rates and functional traits (Figure 5 and Table I). RSD rate was positively correlated to root diameter and negatively correlated to the percentage of fine roots: the higher fine root content, the lower erosion rates. This result confirmed the importance of small flexible roots (< 2 mm) that hold soil particles together and increase soil shear strength (Stokes *et al.*, 2009). As fine roots are stronger in tension than thick roots (Figure 4), many fine roots will be more efficient than a few coarse roots to prevent soil erosion from concentrated flow. In addition, D and %FR are significantly correlated to RLD, RSA and SRL, suggesting that these traits may also indirectly influence erosion rates. Indeed, high values of RLD, RSA and SRL imply more fine roots and more root–soil contact. Several studies demonstrated the influence of RLD (De Baets *et al.*, 2006; De Baets *et al.*, 2007) and RSA (Li *et al.*, 1991) on RSD rate but, to our knowledge, SRL has not yet been related to erosion rates during concentrated flow.

However, although RD was previously found a relevant parameter to predict the erosion-reducing effect of grasses (De Baets *et al.*, 2006), we found no direct relationship with root density. This suggests that RD alone is not sufficient to compare species effect on erosion rates and that other traits must be considered, which is in accordance with the findings of De Baets and coworkers (De Baets *et al.*, 2007; De Baets and Poesen, 2010) who stated that to compare the effectiveness of species with contrasted root architectures, an interaction term between RD and root diameter is needed.

Nevertheless, further laboratory and field experiments on larger sets and mixture of species would bring a valuable insight on the trait–erosion relationship. Moreover, we focused on the mechanical effects of roots and only measured morphological traits whereas the effect of the rhizosphere on soil stability include a wide range of processes (Angers and Caron,

1998), such as the exudation of cementing material (mucilage, polysaccharides) or a strong biological activity (microbial or mycorrhizal), that must be kept in mind when comparing species suitability for erosion control.

The findings of our study could find useful implications, for restoration purposes, in predicting plant root effects on erosive dynamics and in identifying the most efficient species for erosion control. This would make the diagnosis of ecosystem vulnerability to environmental constraints and the evaluation of ecosystem functioning after restoration more operational. The results presented here suggest that fast-growing species, having higher fine roots contents, could be efficient at the early stages of plant development for soil reinforcement. Moreover, such species have fast growth both above and below ground, which could also make them interesting for fast vegetation cover development after restoration. However, further investigations are necessary to confirm these interpretations that remain speculative based on a small scale study. In addition, while the results are interesting, the influence of plant species and functional traits on erosion control and ecosystem functioning as the plants, especially tree species, mature, must be taken into consideration for a long-term sustainable management of degraded lands. For example, as the trees grow, root system morphological and architectural features change (Chiatante *et al.*, 2003), which may modify plant effects on soil processes. The development of fast-growing pioneer species can quickly restore some of the damaged or lost ecosystem services, here erosion control and soil retention, but restoring one particular service, can modify environmental conditions and can be detrimental to the provision of other services (Ehrenfeld, 2000).

Understanding and predicting vegetation response to environmental change and the effects of plant species on ecosystem processes is a major challenge in applied ecology. During the last decade, trait-based approaches have multiplied in theoretical as well as in applied ecology to meet this objective. In eroded areas, it is necessary to identify functional traits related both to species response to erosive constraints and to species effects on erosive processes. Lavorel and Garnier (2002) formalized this idea and proposed the conceptual response-and-effect framework, in which a varying degree of overlap exists between response and effect traits.

The present study highlighted the role of fine roots in reducing erosion rates due to concentrated flow. In particular, the percentage of fine roots was related to relative soil detachment rates. In a previous study on species response to uprooting by erosive forces (Burylo *et al.*, 2009), percentage of fine roots was identified as a relevant trait to evaluate and predict species resistance to uprooting. In a context of land restoration, this match between functional response and effect traits is promising, and further comparisons should be carried out.

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Nomenclature

τ = flow shear stress (Pa)
 ρ_w = water density (kg m^{-3})
 g = acceleration due to gravity (m s^{-2})
 R = hydraulic radius (m)
 S = $\sin(\alpha)$ (—)
 α = slope angle of the flume (deg)
 a = flume width (m)
 d = depth of water in the flume (m)
 q = unit flow discharge ($\text{m}^2 \text{s}^{-1}$)
 Q = flow discharge ($\text{m}^3 \text{s}^{-1}$)
 u = mean flow velocity (m s^{-1})

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Appendix

Detailed flow shear stress calculation

Flow shear stress (τ) was calculated to evaluate the erosive force of the concentrated flow simulated by the flume experiment (De Baets *et al.*, 2006, 2007) and to relate to erosion in actively eroded gullies (Gimenez and Govers, 2002).

The following equations were used:

$$\tau = \rho_w g R S \quad (1)$$

$$R = \frac{ad}{a + 2d} \quad (2)$$

$$d = q/u \quad (3)$$

$$q = Q/a \quad (4)$$