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1	Arbuscular mycorrhizal fungal hyphae reduce soil erosion by surface water flow in							
2	a greenhouse experiment							
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20								
21	Abstract							
22								
23	The role of arbuscular mycorrhizal fungi (AMF) in resisting surface flow soil erosion has							

24	never been tested experimentally. We set up a full factorial greenhouse experiment using						
25	Achillea millefolium with treatments consisting of addition of AMF inoculum and non-						
26	microbial filtrate, non-AMF inoculum and microbial filtrate, AMF inoculum and						
27	microbial filtrate, and non-AMF inoculum and non-microbial filtrate (control) which						
28	were subjected to a constant shear stress in the form of surface water flow to quantify the						
29	soil detachment rate through time. We found that soil loss can be explained by the						
30	combined effect of roots and AMF extraradical hyphae and we could disentangle the						
31	unique effect of AMF hyphal length, which significantly reduced soil loss, highlighting						
32	their potential importance in riparian systems.						
33							
34	Keywords: Soil erosion, concentrated flow, soil detachment rate, AMF						
35							
36	The rate of soil loss by erosion has been accelerated due to various human activities at a						
37	global scale (Grimm et al., 2002), with negative effects including loss of topsoil, decrease						
38	in soil organic matter, and pollution of surface waters (Lal, 2001). Soil erosion is related						
39	to the susceptibility of soil to both detachment and transport of soil particles (Gyssels et						
40	al., 2005). Vegetation biomass, both above and belowground, has been identified to play a						
41	role in decreasing soil erosion (Prosser et al., 1995; Gyssels and Poesen, 2003). The role						
42	of soil biota has not often been subjected to empirical tests, but it is assumed that						
43	members of the soil biota indirectly decrease soil erosion through the formation and						
44	stabilization of soil aggregates (Tisdall and Oades, 1982; Rillig and Mummey, 2006). For						
45	example, arbuscular mycorrhizal fungi (AMF) are root associated fungi known for their						
46	role in increasing soil aggregation (Tisdall and Oades, 1982; Mardhiah et al., 2014;						

48	(Tisdall and Oades, 1982; Rillig and Mummey, 2006) and by stimulating root growth						
49	(Bearden and Petersen, 2000).						
50							
51	In order to quantify the role of AMF hyphae in reducing soil erosion, we measured at the						
52	end of a greenhouse experiment the difference in soil detachment rate (g soil 10 s ⁻¹) under						
53	a constant flow of water across a fixed area of soil surface (63.6 cm^2) at successive points						
54	in time, comparing different treatments (AMF treatment, microbial filtrate treatment,						
55	AMF and microbial filtrate treatment and control). Achillea millefolium seeds were						
56	surface sterilized in 70% ethanol and 5% commercial bleach. We added 5 seeds per pot						
57	and then thinned to two plants per pot. We used a sandy loam alluvial soil (73% sand,						
58	18% silt and 7% clay (Rillig et al., 2010)), which was autoclaved twice (121°C, 20						
59	minutes) and was re-mixed before placing into each pot (1.3 kg of soil per pot). Pots in						
60	AMF treatments received 150 Glomus intraradices (Rhizophagus irregularis) spores;						
61	non-AMF treatment pots received the same amount of sterile carrier material. We						
62	prepared the microbial filtrate, which might introduce saprobic fungi and bacteria, by						
63	passing a suspension of the soil used in the study (200 g L^{-1}) through a 20 μ m size sieve						
64	and used the slurry as microbial filtrate treatment. Pots in microbial filtrate treatments						
65	received 2 ml of the slurry, while those in non-microbial filtrate treatment received the						
66	same amount of sterile slurry. The greenhouse temperature was 16-22°C and the						
67	experiment lasted for ~ 23 weeks. The plants were of similar size by the end of the						
68	experiment.						

Leifheit et al., 2014) through their extended extraradical hyphae in the rhizosphere

70 To measure the soil erosion due to water flowing over the soil surface, a hydraulic flume, 71 2 m in length and 0.1 m wide, was constructed using a transparent Plexi glass wall at the 72 University of Trento, Italy. At 20 cm before the end of the flume, a hole with a 9 cm 73 external diameter was created to hold the soil core. A sharpened PVC pipe (inner 74 diameter = 9 cm), made to fit the flume hole, was used as a corer and was carefully 75 placed at the centre of each of the pots and pushed through the soil from the top until it 76 reached the bottom of each pot. The corer was then pushed through from below and 77 towards the surface of the flume bottom using a piston so that the soil surface was 78 maintained in line with the flume bed through each experiment (Suppl. Mat. Figure S1). 79 The flume was set at a slope of 18° , and a flow of tap water was discharged into the flume at a constant rate (0.0003 m³ s⁻¹). Mean flow velocity (1.17 ± 0.01 m s⁻¹) was measured 80 81 every day and yielded a mean flow shear stress on the soil surface of 7.75 Pa (Suppl. Mat. 82 Equation S1).

83

84 Ten replicate samples were prepared according to each treatment. Samples were prepared 85 with methods adjusted from De Baets et al. (2006). The samples were retained within a 86 constant water level environment (4.5 cm below the soil surface) to allow slow capillary 87 rise and all above ground biomass was clipped. The samples were drained immediately 88 prior to being introduced to the flume, where they were subjected to a constant discharge 89 for 145 seconds. Following an initial flow period of 20 seconds, samples of the water 90 draining from the flume were taken every 15 seconds for 10 seconds, providing a total of 91 five successive 10 second samples (R1-R5). The samples were left to settle before 92 decanting the water, which was oven dried at 65°C and then the residue was weighed.

93	Soil which was left in the corer was carefully retained and dried. To ensure that
94	measurements of the soil left in the corer did not include soil and roots exposed by the
95	soil erosion experiment, we carefully scraped a thin layer of the surface layer off each
96	cored soil. After sieving the soil through a 4-mm sieve, aggregate stability was measured
97	by re-wetting 4.0 g of soil using capillary action and sieving for 5 minutes on a 250 μm
98	sieve before drying at 65°C. The dried material was then crushed and passed through the
99	sieve, separating the stable aggregates from the coarse fraction. Root biomass was
100	extracted and measured using an extraction-flotation method (Cook et al., 1988). Root
101	length grouped by diameter (Barto et al., 2010) was measured by analyzing scanned
102	images using WinRhizo Pro 2007d (Regent Instruments Inc., Quebec City, Canada).
103	Hyphae were extracted from 4.0 grams of dried soil using a protocol adapted from
104	Jakobsen et al. (1992) and then stained with Trypan Blue. AMF and non-AMF
105	extraradical hyphal length were measured according to Rillig et al. (1999).
106	
107	We used the Kruskal Wallis test to quantify the difference of soil detachment rate (g soil
108	10 s ⁻¹) between treatments at each of the five successive time points during the flume
109	experiments. We also ran linear models correlating total soil loss with soil detachment
110	rate determinants (percent water stable aggregates (% WSA), root biomass, very fine, fine
111	and coarse root length, AMF and non-AMF extraradical hyphal length) tested as main
112	effect and interaction. We calculated variation in partitioning of root biomass and AMF
113	extraradical hyphal length using redundancy analysis. All statistical analyses were
114	conducted using version 2.14.0 of the R statistics software (R Development Core Team,
115	2012).

117 In general, soil loss decreased through time (Suppl. Mat. Figure S2). A possible 118 explanation is that initially, relatively loose surface soil which came into contact with the 119 erosion flow was rapidly detached; soil loss then slowed, possibly because of more 120 intense effects of roots with or without fungal hyphae. We found that AMF treatments 121 decreased soil loss most effectively compared to the control (Figure 1). Total soil loss can 122 be explained by the joint effect of total root biomass (17%) and AMF extraradical hyphae 123 (16%) (Table 1). AMF extraradical hyphal length significantly decreased total soil loss 124 when used in linear models as a singular main effect and in interaction with root biomass 125 (Suppl. Mat. Table S1, Figure 2). This is to our knowledge, the first time that AMF 126 extraradical hyphal length has been shown to have a direct effect in reducing surface soil 127 erosion due to surface flow. The role of AMF seems to be due to the ability of AMF to 128 produce extraradical hyphae. The addition of microbial filtrate did not reduce the soil 129 detachment rate compared to the control and even reduced the effectiveness of AMF 130 treatment. We also did not find a significant difference of %WSA between treatments 131 (Suppl. Mat. Table S3) and no significant correlations between the soil detachment rate 132 and % WSA in our models (data not shown). This implies that soil aggregate stability in 133 our system was not an important factor for preventing soil erosion due to concentrated 134 flow. Studies showed that besides soil aggregates, microtopography (surface roughness) 135 and soil cohesion due to a dense root mat, can decrease surface soil erosion (Campbell 136 et.al., 1989; Prosser et al., 1995; Prosser and Dietrich, 1995; Hu et al., 2002). Our study 137 implies that, rather than the role in formation or maintenance of stable soil aggregates, the 138 role of AMF hyphae -which might also include the formation of a hyphal network which

139	further increases soil cohesion- might be more important in reducing surface soil erosion.
140	Although the microbial filtrate might contain saprobic fungi which also produced hyphae,
141	their minimal effect towards reduced soil erosion in this study might imply that the
142	hyphae of both fungal groups behave differently. AMF tend to produce more persistent,
143	coarser and thicker extraradical hyphae compared to many saprobic fungal hyphae
144	(Klironomos and Kendrick, 1996; Klironomos et al., 1999; Allen, 2006). Saprobic fungi
145	can also produce enzymes degrading soil carbon, an ability which AMF lack; this taken
146	together could explain the significant role of AMF in reducing soil erosion in our
147	experiment. Overall, our results highlight the role of AMF in potentially stabilizing soils
148	in riparian systems.
149	
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151	
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- 242

Table 1. Variation partitioning based on redundancy analysis was used to explain the

- 244 pattern of total soil loss in relation to explanatory variables: AMF extraradical hyphal
- length and root biomass. All percentages explained were significant (p-values < 0.05).
- 246

Response variable:	df	Fraction explained (%)
Total soil loss (g soil in 50 s)		
Explanatory variables:		
AMF extraradical hyphal length fraction	1	16
(with covariable: root biomass)		
Root biomass fraction	1	17
(with covariable: AMF extraradical hyphal length)		
Total	2	28
Shared fraction	0	4.1
Residuals	-	76
AMF extraradical hyphal length (without covariable)	1	9.7
Root biomass (without covariable)	1	10.2

247

248 Figure captions

249

250 Figure 1. Linear models fitted using the generalized least squares (GLS) method

251 corrected for heterogeneity of variances (var = varIdent(form= \sim 1|fcategorical)) were used

to plot cumulative soil detachment rate through time (R1, R2, R3, R4, R5) for different

253 treatments ("control", "AMF treatment", "AMF and microbial filtrate treatment" and

254 "microbial filtrate treatment"). Figure shows fitted lines with significant differences

between each treatment levels (Suppl. Mat. Table S2). Different symbols indicate

256 different treatments (control = Δ , AMF treatment = \bullet , AMF and microbial filtrate

257 treatment = \circ , microbial filtrate treatment = +). The highest data point (microbial filtrate

- treatment, ranging 12.15-30.03 g soil 10 s⁻¹, R1-R5) was omitted to enable clear
- visualization of data.
- 260

- 262 Figure 2. A linear model fitted using the generalized least square (GLS) method corrected
- 263 for heterogeneity of variances (var = varIdent(form=~1|fcategorical)) and spatial
- autocorrelation was used to correlate total soil loss (y axis) to AMF extraradical hyphal
- length (x axis).