RESEARCH ARTICLE

10.1002/2016JG003422

Key Points:

- Inoculation improved plant survival and altered root growth but delayed soil stabilization
- A temporal offset is detected between inoculation effects tested in glasshouse studies and field experiments
- Field experiments including continuous monitoring are needed to understand the plant-soil interactions in steep, coarse-grained environments

Correspondence to:

A. Bast,
alexander.bast@wsl.ch

Citation:

Bast, A., W. Wilcke, F. Graf, P. Lüscher, and H. Gärtner (2016), Does mycorrhizal inoculation improve plant survival, aggregate stability, and fine root development on a coarse-grained soil in an alpine eco-engineering field experiment?, *J. Geophys. Res. Biogeosci.*, 121, 2158–2171, doi:10.1002/2016JG003422.

Received 22 MAR 2016

Accepted 6 JUL 2016

Accepted article online 12 JUL 2016

Published online 24 AUG 2016

Does mycorrhizal inoculation improve plant survival, aggregate stability, and fine root development on a coarse-grained soil in an alpine eco-engineering field experiment?

A. Bast^{1,2}, W. Wilcke³, F. Graf^{1,4}, P. Lüscher¹, and H. Gärtner¹

¹Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland, ²Department of Geography, University of Zürich, Zurich, Switzerland, ³Institute of Geography and Geomorphology, Karlsruhe Institute of Technology, Karlsruhe, Germany, ⁴WSL Institute for Snow and Avalanche Research SLF, Davos Dorf, Switzerland

Abstract Steep vegetation-free talus slopes in high mountain environments are prone to superficial slope failures and surface erosion. Eco-engineering measures can reduce slope instabilities and thus contribute to risk mitigation. In a field experiment, we established mycorrhizal and nonmycorrhizal research plots and determined their biophysical contribution to small-scale soil fixation. Mycorrhizal inoculation impact on plant survival, aggregate stability, and fine root development was analyzed. Here we present plant survival ($n_{\text{total}} = 1248$) and soil core ($n_{\text{total}} = 108$) analyses of three consecutive years in the Swiss Alps. Soil cores were assayed for their aggregate stability coefficient (ASC), root length density (RLD), and mean root diameter (MRD). Inoculation improved plant survival significantly, but it delayed aggregate stabilization relative to the noninoculated site. Higher aggregate stability occurred only after three growing seasons. Then also RLD tended to be higher and MRD increased significantly at the mycorrhizal treated site. There was a positive correlation between RLD, ASC, and roots < 0.5 mm, which had the strongest impact on soil aggregation. Our results revealed a temporal offset between inoculation effects tested in laboratory and field experiments. Consequently, we recommend to establish an intermediate to long-term field experimental monitoring before transferring laboratory results to the field.

1. Introduction

Earth surface erosion and superficial slope failures are omnipresent in mountain systems. Typical features are shallow mass movements on vegetation-free, steep slopes where Leptosols occur. Climate change raises the likelihood of torrential rain [Frei *et al.*, 2006], therefore the frequency and magnitude of surface erosional processes and superficial slope failures [Crozier, 2010]. The consequence is a higher damage potential for infrastructure and society [Keiler *et al.*, 2010]. Eco-engineering measures, as link between civil engineering techniques and ecological principles to assess, design, construct, and maintain vegetation systems, might provide a suitable response to the emerging need for sustainable risk mitigation strategies [Stokes *et al.*, 2014].

Site-adapted and well-developed plant systems reduce splash erosion, diminish overland flow, and hence reduce water erosion [e.g., Zuazo and Pleguezuelo, 2008]. Root systems control soil hydrological, mechanical, and chemical properties and support soil microbial abundance and diversity [Gyssels *et al.*, 2005; De Baets *et al.*, 2007; Zuazo and Pleguezuelo, 2008; Haichar *et al.*, 2014; Stokes *et al.*, 2014]. Roots influence soil aggregate stability, and in turn soil shear strength [Fattet *et al.*, 2011], which is essential for assessing, calculating, and modeling the stability of slopes [Pollen and Simon, 2005; Mao *et al.*, 2013b]. Especially, fine roots reinforce the soil by increasing apparent cohesion, in particular when they traverse potential shear surfaces [Stokes *et al.*, 2009]. To quantify these root effects, root length density (RLD) is commonly used [Stokes *et al.*, 2009].

The inoculation with native and exotic mycorrhizal fungi is a common agricultural measure to improve plant survival and productivity [e.g., Pellegrino *et al.*, 2011; Verbruggen *et al.*, 2013]. In plant-fungi symbioses, fungi improve the acquisition of nutrients, in particular nitrogen and phosphorous, while plants return carbon compounds, produced during photosynthesis, to the fungi [e.g., Smith and Read, 2008].

Various laboratory experiments revealed that mycorrhizal fungi play an important role in stabilizing soil particles into macroaggregates by forming a complex network of hyphae in the subsurface [e.g., Rillig and

Mummey, 2006; Tisdall et al., 2012]. However, mycorrhizal fungi are rarely present in coarse-grained vegetation-free soils of young landslides [Amaranthus and Trappe, 1993; Azcón-Aguilar et al., 2003].

A number of surveys have shown the positive effects of eco-engineering measures on hillslope and soil aggregate stability in degraded high mountain environments [e.g., Stangl, 2007; Burri et al., 2009; Graf et al., 2009; Bischetti et al., 2010]. By contrast, only a few studies addressed the effect of mycorrhizal inoculation on aggregate stability as component of eco-engineering efforts [Graf, 1997; Beglinger et al., 2011; Graf and Frei, 2013]. Based on glasshouse experiments, these investigations identified an increase in aggregate stability and fine root development within a few months. On the contrary, Bast et al. [2014] demonstrated that on an alpine slope, mycorrhizal inoculated saplings did not have any additional effect on soil aggregate stability within 4 months.

Assuming that mycorrhizal inoculation under field conditions only produces significant effects in the longer run, we aimed to determine whether a commercial mycorrhizal inoculum enhances plant survival rates, aggregate stability, and fine root development in an eco-engineering field experiment during three consecutive growing seasons (2010–2012). We investigated 2400 planted saplings on two test sites located on a slope in the eastern Swiss Alps. One of the two test sites was treated with a commercial mycorrhizal inoculum to test if (i) mycorrhizal inoculation accelerates the positive hedge layer effect on aggregate stability, (ii) plant survival and fine root development will be stimulated by the inoculation, and (iii) the stimulated root development in turn influences aggregate stability positively.

2. Materials and Methods

2.1. Research Site

The study was conducted in the Arieschbach catchment, municipality of Fideris in the eastern Swiss Alps (Figure 1a), where suboceanic conditions with mild winters and temperate summers characterize the climate [Ott et al., 1997]. Mean annual air temperature is 4.6°C, and the average annual sum of rainfall is 1170 mm (period 1961 to 1990), estimated with the Daymed software [Thornton et al., 1997; Bast et al., 2014]. Quaternary sediments, derived from glacial and/or gravitative processes, cover the bedrock consisting of Prättigau flysch. The sediments provide the parent material for the dominating Cambisols, Luvisols, and Regosols [IUSS Working Group WRB, 2006] under a fir-spruce forest, which is the natural vegetation type in the catchment.

The experimental research plots were established on the east-northeast exposed *Patjänja Rüfe* (46°53' 43.41 N, 9°44'30"E) (Figure 1b), an instable and erosion-prone, 37°–50° inclined hillslope, ranging between 1220 and 1400 m above sea level (Figure 1b). The occurring soil is a skeletal Leptosol [IUSS Working Group WRB, 2006]. Before the experiment was implemented, soil texture analyses were performed (Figure 1d and Table 1) [Bast et al., 2014]. On average 79% of the soil particles were larger than 2 mm (Table 1), and all soil samples were classified as poorly graded gravel with silt (GP-GM) [ASTM-D2487-00, 2000]. Vegetation is sparse, restricted to local spots, and formed by pioneer plants (e.g., *Tussilago farfara* L. and *Saxifraga aizoides* L.).

2.2. Experimental Setup and Sampling Design

In May 2010, two sites (10 m × 32 m each) were stabilized with hedge layers (Figure 1b). At each site, a walking excavator dug 15 small terraces of 10 m length and approximately 0.5 m depth into the slope. At the bottom of these, four saplings of alder (*Alnus viridis* (CHAIX) DC. and *Alnus incana* (L.) MOENCH.), two of willow (*Salix purpurea* L., *Salix spp.*), and one further tree and shrub species (Figure 1c) were planted per running meter resulting in a total of 1200 saplings per site. At one of the two sites 40 mL of a commercial mycorrhizal inoculum (INOQ Forst) was added to the roots of each sapling [Bast et al., 2014; INOQ GmbH, 2014, www.inoq.de/downloads/Forest_e.pdf]. In the following, the stabilized, mycorrhizally treated site is referred to as *sm*, the stabilized nonmycorrhizally treated site to *snm*. A site of the same size (10 m × 32 m) next to the two treated sites serves as control (*c*) and reflects natural, unstabilized conditions. In total, the experimental site is covering an area of approximately 1000 m². For sampling and further statistical analysis, the control and each treated site were split into three research plots (I–IX) (Figure 1d). A 2 m buffer zone around each test site was used to reduce edge effects (Figure 1d).

Figure 1. (a, b) Study site, (c) used plant assortment, (d) sketch map of the sampling design, and (e) schematic of growth of a green alder (*Alnus viridis* (CHAIX) DC.) and sample extraction. Figure 1a shows map of Switzerland with indication of the study site (Fideris/Eastern Swiss Alps). Figure 1b shows photograph of the Patjänja Rüfe showing the environmental setting in the vicinity of the field experiment (September 2013). The bold, white dashed line highlights the upper erosion scar of the Patjänja Rüfe. The black and white framed rectangles illustrate the position of the treated sites (sm: stabilized with plants, mycorrhizal treated; snm: stabilized with plants, nonmycorrhizal treated) and the control (c). White dotted lines mark the contour lines. In Figure 1c an assortment of eight saplings per running meter was used (for plant rows see Figure 1d). Figure 1d shows sketch map of the sampling design. For the position of the treated sites and the control within the Patjänja Rüfe, compare Figure (1b). Roman numerals (I–IX) are placed in the middle of the research plots, indicated by the black boxes. The light grey colored, outer parts mark the nonsampled crossover areas. The grey lines within the two treated sites illustrate the 15 plant rows (80 saplings per row) of each treatment. Black squares show the soil sampling location for grain size analyses. Grey dots show the soil sampling position for aggregate and root analyses. The black triangle flags the data logger location, where soil temperature and moisture were logged. Figure 1e shows schematic graph of the growth of a green alder, which was excavated in 2012 (for position see Figure (1c)). Soil samples were taken at a distance of 30–50 cm uphill a green alder with a HUMAX probe up to a depth of 20 cm below ground surface.

Table 1. Particle-Size Distribution for the Soil Samples (Depth Layer: 0–35 cm), Taken Prior to the Experiment Started (May 2010)

Grain Size	Plot I	Plot III	Plot IV	Plot VI	Plot VII	Plot IX	Mean ± s.e.
Gravel (g kg ⁻¹)	813	748	733	821	852	785	792 ± 19
Sand (g kg ⁻¹)	131	180	170	135	84	136	140 ± 14
Silt (g kg ⁻¹)	40	54	65	33	42	59	49 ± 5
Clay (g kg ⁻¹)	16	16	31	10	22	19	19 ± 3

Figure 2. Soil temperature and volumetric water content (VWC) at 10 cm depth. The length of each growing season and dormant period in days is at the very top and delineated through the green colors in the background. The length of the first growing period was not assigned. (a) Soil temperature: daily averages (black line) $\pm$ standard deviation (grey shade). Monthly averages (red squares and red line). Monthly maximum and minimum (shade in light red). Average of the growing season and dormant period are stated on top. (b) VWC: daily averages (black line) $\pm$ standard deviation (grey shade). Monthly averages (blue squares and blue line). Monthly maximum and minimum (shade in light blue). Average of the growing season and dormant period are stated on top.

At the end of each growing season (2010–2012), 36 soil cores (0–20 cm depth) were taken (four per research plot) to analyze aggregate stability and fine root development (Figure 1d), resulting in a total of 108 soil samples. In 2010, sampling points were randomly chosen within a distance of 30–50 cm uphill a green alder (*Alnus viridis* (CHAIX) DC.) (Figure 1e). In 2011 and 2012, the same locations were revisited. Soil cores were extracted with a HUMAX probe and a 5 kg sledge hammer (Figure 1e) [Bast et al., 2015]. Samples were directly pushed in a PVC plastic tube (length = 25 cm, diameter = 5 cm) to extract an undisturbed soil core (Figure 1e). Sampling was possible up to a maximum length of 20 cm due to the coarse texture of the experimental site. If cores were shorter than 16 cm, only the first 10 cm were analyzed. The soil core samples were kept in a cold storage room at 3.5°C until further processing.

From July 2010 to September 2012, temperature was logged once every 60 min, and volumetric water content (VWC) is triplicated every 60 min at a depth of 10 cm (Figure 1d) using the Decagon sensors EC-5 and 5TM (Decagon Devices Inc., 2014, <http://www.decagon.com/products/>). For each growing season and dormant period, respectively, statistical key figures were computed and graphically explored (Figure 2). Growing season was defined as the period between the date at which the diurnal mean soil temperature at 10 cm depth exceeds and dropped below 3.2°C [Körner and Paulsen, 2004].

2.3. Plant Survival

Plant survival was determined on the six research plots (plots IV–IX) of the treated sites at the end of each growing season by counting all living plants. The research plots did not include the buffer zone (Figure 1d). As a consequence, the number of originally planted individuals in the analyzed research plots was 624 per test site.

2.4. Soil Aggregate Stability Measurements

Aggregate stability was expressed by an aggregate stability coefficient (ASC), ranging from 0, reflecting complete dispersion during the test, to 1, indicating a totally stable sample [Bast et al., 2015].

Soil cores were detached from the plastic tubes and cut into two parts of approximately 10 cm length (Figure 1e). Both subsamples were placed consecutively on a sieve having a mesh size of 20 mm. The sieve

Figure 3. Kaplan-Meier survival curves for the treated sites calculated from the presence/absence of all initially planted species in May 2010 within the research plots IV–VI (sm: stabilized, mycorrhizally treated; black lines; $n = 624$) and VII–IX (snm: stabilized with plants, nonmycorrhizally treated; grey lines; $n = 624$). Black and grey dashed lines illustrate the upper and lower 95% confidence interval. The black and grey solid lines do show a significant difference to each other according to the Mantel-Haenszel test ($P < 0.001$).

scanned [Bast et al., 2014] to quantify root length and diameter with WinRHIZO [Réagents Instruments Inc., 2003]. Root length density (RLD) was determined by summing up root lengths of the sample and dividing this value by the volume of the corresponding soil cylinder. RLD of the roots was grouped into four root diameter classes [Pohl et al., 2009]: *very fine roots* (<0.5 mm), *fine roots* (≥ 0.5 – <1.0 mm), *fibrous roots* (≥ 1.0 – <1.5 mm), and *coarse roots* (≥ 1.5 mm). Root diameter was expressed as mean root diameter (MRD).

2.6. Statistical Analysis

All statistical analyses were performed with R, version 3.0.2 [R Core Team, 2013]. Kaplan-Meier survival analysis was performed to illustrate and test the inoculation effect on plant survival. The Kaplan-Meier estimator is a nonparametric maximum likelihood estimate of the survival probability $S(t)$ [Kaplan and Meier, 1958; Tableman and Kim, 2003]. $S(t)$ for any particular sapling of the time period t is specified by the number of saplings at risk (n_i) at the beginning of a time period t_i and the number of saplings (d_i), which died during the time period t_i (equation (1)) [Tableman and Kim, 2003]:

$$S(t) = \prod_{t_i \leq t} \frac{n_i - d_i}{n_i} \quad (1)$$

Based on the Kaplan-Meier estimate, the difference between the survival curves of the two treated sites was tested by using the Mantel-Haenszel test [Harrington and Fleming, 1982]. Survival analysis was implemented with the R package *survival* [Therneau, 2014].

To detect treatment effects on ASC, RLD, and MRD within the growing seasons, linear mixed effect models were applied [Bast et al., 2014]. The factor plot was used as random effect in random intercept models. ASC, RLD, and MRD were used as response vectors for observations and treatment (sm and snm) and control (c) as fixed effects. Tukey's HSD (honestly significant differences) was applied to test a posteriori contrasts with the R package *multcomp* [Hothorn et al., 2008], which allows a multiple comparison in mixed models by estimating a variable following an asymptotic multivariate normal distribution and a consistent estimate of its covariance matrix [Hothorn et al., 2008].

The influence of RLD, MRD, and the root diameter classes on ASC was also tested by linear mixed effect models by setting up random intercept slope models [Zuur et al., 2009]. The random part of the models included

was centered in a drainable pail, which was rapidly filled up with tap water until the sample was completely covered. After 5 min of slaking, the water was drained. Soil material, trapped within the sieve, as well as the material that passed the sieve, was flushed into bowls and left for sedimentation. After 24 h water was sucked off, the remaining material was dried for 24 h at 105°C and thereafter weighed. To correct for stone content, stones larger than 20 mm were removed and weighed separately.

ASC was determined as the proportion of the mass of the soil material trapped by the sieve to the mass of the total soil sample, whereas the mass of the stones was subtracted for stone correction. The average of the two subsamples was calculated in order to express the ASC of the 0–20 cm depth layer.

2.5. Root Measurements

Before the bowls were left for sedimentation, roots were extracted, rinsed, and

Figure 4. (a) Average aggregate stability coefficient (ASC), (b) root length density (RLD), and (c) mean root diameter (MRD) for the treated sites (sm: stabilized with plants, mycorrhizally treated; snm: stabilized with plants, nonmycorrhizally treated) and the control (c) at the end of each growing season from 2010 to 2012 shown as bars with error (mean $\pm$ standard error of the mean; $n = 12$ per bar; depth layer: 0–20 cm). Bars within the same growing season and a different lowercase letter do show a statistically significant difference according to Tukey's HSD test, $P \leq 0.05$. For p values see Table 2.

Table 2. p Values of the Performed Tukey's HSD Test^a

Parameter	Year	c Versus sm	c Versus snm	sm Versus snm
Aggregate stability (ASC)	2010	0.60	0.04	0.27
	2011	0.04	0.52	0.39
	2012	<0.001	0.03	0.05
Root length density (RLD)	2010	0.85	0.16	0.41
	2011	0.004	0.22	0.30
	2012	<0.001	0.01	0.64
Mean root diameter (MRD)	2010	0.07	0.65	0.38
	2011	0.99	0.96	0.94
	2012	0.005	0.84	0.03

^aDifferences were tested based on linear mixed effect models (sm: stabilized with plants, mycorrhizally treated; snm: stabilized with plants, nonmycorrhizally treated); c: control). Statistically significant differences are shown in bold typeface ($P \leq 0.05$).

both plot and year. Year was nested in plot. In a first model (mod 1), ASC was used as response variable, whereas RLD, MRD, and the interaction RLD:MRD were fixed factors. Since a significant interaction prohibited the interpretation of the main effects, two separate models for RLD (mod 2) and MRD (mod 3) were implemented. In a last model (mod 4), the effects of the root diameter classes were identified.

Tukey's first aid transformations were used to meet the model assumptions [Tukey, 1957]. Hence, ASC was arcsine square root, RLD, and MRD and the RLD of the root classes very fine roots and fine roots were log transformed. Since RLD of the classes fibrous roots and coarse roots includes zero values, its RLDs were logst transformed; i.e., small and zero observations are modified to gain finite values for a subsequently applied log 10 transformation [Stahel, 2011]. Residual analyses were performed to ensure model quality. All linear mixed effect models were conducted with the R package *nlme* [Pinheiro et al., 2014].

Lowess smoothers, based on a robust locally weighted regression, were used to visualize the relation between ASC and RLD, as well as between ASC and MRD [Cleveland, 1979]. ASC was arcsine square root transformed, and RLD and MRD were log transformed.

3. Results

3.1. Plant Survival

Kaplan-Meier analysis showed that plants at the sm site achieve significantly greater survival probabilities than at the snm site (Figure 3). In September 2010, survival probabilities were about 70% (436 living saplings) at the sm site and about 43% (271 living saplings) at the snm site. Relative to this, in the following two growing seasons mortality at both sites was minor. Between September 2010 and 2011, further, 27 saplings died back at the sm site and 37 at the snm site, and between September 2011 and 2012, 23 versus 28 saplings died back at the sm and snm sites, respectively. Hence, survival probabilities were 66% (September 2011) and 62% (September 2012) at the sm site versus 38% (September 2011) and 33% (September 2012) at the snm site.

3.2. Soil Aggregate Stability

In September 2010, ASC was 17% higher at the sm and 45% higher at the snm, compared to the c site (Figure 4a). However, only the difference between the snm and c sites was significant (Table 2). In September 2011, the order changed: ASC was 247% higher at the sm, and 108% higher at the snm compared to the c site. The difference between the sm and c sites was significant (Table 2). At the end of the third growing season, in September 2012, ASC showed significant differences between the two treated sites as well as between each treated and the c site (Table 2). Compared to the c site, ASC was 162% higher at the sm site and 81% higher at the snm site, respectively. ASC was 45% higher at the sm site than at the snm site. ASC was lowest in September 2011 of the three observation years at all three study sites (Figure 4a).

3.3. Fine Root Development

In September 2010, there were no significant differences in RLD among the sites although both the sm and snm sites tended to have higher RLD values (Figure 4b and Table 2). In September 2011, RLD was 167%

Table 3. Mean Proportion of the Root Length Density (RLD) (%) of the Root Diameter Classes (Very Fine Roots (<0.5 mm), Fine Roots (≥ 0.5 –<1.0 mm), Fibrous Roots (≥ 1.0 –<1.5 mm), and Coarse Roots (≥ 1.5 mm)) Related to the Whole RLD (All Classes) Within the Depth Layer 0–20 cm

Treatment	Year	Very Fine Roots	Fine Roots	Fibrous Roots	Coarse Roots
Control (c)	2010	95.720	3.778	0.425	0.077
	2011	99.319	0.663	0.017	0.001
	2012	97.998	1.837	0.150	0.015
Stabilized, mycorrhizally treated (sm)	2010	93.766	5.076	0.825	0.333
	2011	99.342	0.627	0.030	0.001
	2012	96.551	3.063	0.287	0.099
Stabilized, nonmycorrhizally treated (snm)	2010	95.915	3.730	0.304	0.052
	2011	99.331	0.579	0.080	0.012
	2012	96.774	2.841	0.296	0.090

higher at the sm and 101% higher at the snm compared to the c site. The difference between the sm and c sites was significant (Table 2). In September 2012, RLD was significantly higher at the sm (316%) and the snm (182%) compared to the c site (Table 2). The temporal development of RLD showed a decrease in September 2011 at the c, sm, and snm sites (Figure 4b).

In September 2010 and 2011, MRD did not differ significantly among the sites (Figure 4c and Table 2). However, the sm site tended to show increased MRD values. In September 2012, MRD at the sm site was significantly higher than at the snm (22%) and the c sites (33%) (Table 2). Compared to September 2010 and 2012, in September 2011 MRD was lower at the c, sm, and snm sites (Figure 4c).

As indicated by the average MRD (Figure 4c), most of the roots can be classified as very fine roots. From September 2010 to 2012, the mean proportion of RLD of the very fine roots related to the entire RLD exceeded 93% (Table 3). The proportion of RLD of the fibrous roots and coarse roots was negligible. RLD of the fine roots at the sm site (2010: 5.1%; 2012: 3.1%) was slightly higher in September 2010 and 2012 compared to the snm (2010: 3.7%; 2012: 2.8%) and c sites (2010: 3.8%; 2012: 1.8%).

3.4. Relationship Between Fine Roots and Aggregate Stability

There was a significant positive correlation between RLD and ASC, as well as between MRD and ASC, respectively (Figure 5). RLD (mod 2) and MRD (mod 3) had a significant influence on ASC (Table 4). As visualized by the lowess line smoothers, at the sm site, ASC was consistently higher and had a smaller variation compared to the snm and c sites seen over all 3 years (Figure 5). Furthermore, RLD at the sm site showed a smaller variation than the snm and c sites (Figure 5a). Samples with a lower MRD showed a higher ASC at the sm site (Figure 5b).

Figure 5. Relation between aggregate stability coefficient (ASC) and (a) root length density (RLD) and (b) mean root diameter (MRD) respectively over a period of the observed years 2010–2012 ($n_{\text{total}} = 108$). Note the transformation of the variables. Symbols illustrate the treated sites (sm: stabilized with plants, mycorrhizally treated, $n_{\text{sm}} = 36$, black circles; snm: stabilized with plants, nonmycorrhizally treated, $n_{\text{snm}} = 36$, grey triangles) and the control (c, $n_{\text{c}} = 36$, light grey squares). Solid lines are the appendant lowess smoothers.

Table 4. Summary of the Linear Mixed Effect Models of the Roots Impact on Aggregate Stability^a

Model	Fixed Effect	Estimate	Standard Error	Degrees of Freedom	t Value	P
mod 1	Intercept	1.472	0.285	96	5.169	<0.001
	log (RLD)	−0.124	0.178	96	−1.067	0.289
	log (MRD)	0.743	0.116	96	4.183	<0.001
	log (RLD) : log (MRD)	− 0.185	0.076	96	− 2.424	0.017
mod 2	Intercept	0.269	0.060	98	4.501	<0.001
	log (RLD)	0.184	0.025	98	7.410	<0.001
mod 3	Intercept	1.438	0.152	98	9.459	<0.001
	log (MRD)	0.524	0.095	98	5.531	<0.001
mod 4	Intercept	1.933	0.262	94	7.370	<0.001
	log (MRD)	0.376	0.168	94	2.240	0.028
	log (RLD.veryfine)	3.967	1.457	94	2.724	0.008
	log (RLD.fine)	0.001	0.054	94	0.011	0.991
	logst (RLD.fibrous)	0.101	0.061	94	1.650	0.102
	logst (RLD.coarse)	0.067	0.036	94	1.888	0.062

^aBold facetype indicate significant levels ($P \leq 0.05$). RLD: root length density. MRD: mean root diameter. RLD.veryfine: ratio between RLD of the class very fine roots (<0.5 mm) and RLD. RLD.fine: ratio between RLD of the class fine roots (≥ 0.5 – <1.0 mm) and RLD. RLD.fibrous: ratio between RLD of the class fibrous roots (≥ 1.0 – <1.5 mm) and RLD. RLD.coarse: ratio between RLD of the class coarse roots (≥ 1.5 mm) and RLD. log: transforms the data by natural logarithm. logst: transforms the data by a logarithm with base 10 and modifying small and zero observations, yielding in finite values. Note that interaction terms of mod 4 are not listed since none of the 26 interactions were significant ($P > 0.05$).

Portioning the RLD into the different diameter classes (mod 4) reveals that only the very fine roots had a significant effect on ASC (Table 4), whereas the three other groups did not significantly influence ASC (Table 4).

4. Discussion

4.1. The Effect of Eco-Engineering and Mycorrhizal Inoculation on Aggregate Stability

In our study, 4 months after the establishment of the hedge layers ASC increased (Figure 4a) confirming previous reports of fast responses from laboratory studies, where nonmycorrhizal treated plantlets of pot experiments were tested [e.g., *Graf and Frei*, 2013]. The finding that ASC increased faster at the snm than at the sm site was surprising because the literature suggested the contrary. A number of laboratory and glasshouse experiments with plant-specific mycorrhizae suggested a significant increase in aggregate stability within 4 to 5 months after mycorrhizal inoculation [*Beglinger et al.*, 2011; *Graf and Frei*, 2013]. In our study, we were not able to confirm these findings within a period of 4 months when using a commercial mycorrhizal inoculum, cultivated for forest applications. However, after 3 years, mycorrhizal inoculum indeed increased ASC significantly (Figure 4a and Table 2). Differences between laboratory and field experiments can also be expected on the basis of the study of *van de Voorde et al.* [2012] who reported that preparing the soil and the inoculum in the laboratory has a strong influence on the observed plant-soil effect. Our results suggest that the effect of mycorrhizal inoculation establishes later in the field than in laboratory/glasshouse experiments and caution is advised against the untested transfer of slope stabilization methods from the laboratory/glasshouse to the field scale.

4.2. The Effect of Mycorrhizal Inoculation on Plant Survival and Fine Root Development

RLD showed a similar temporal and treatment-related development as ASC (Figure 4b). After three growing seasons, RLD was significantly higher at the treated sites than at the control site (Figure 4b and Table 2). This is in line with findings of *Burri et al.* [2009] who demonstrated that RLD of a 25 years old eco-engineered measure on morainic material of a mountain torrent catchment was 6 to 10 times higher compared to an untouched control.

Although there is no significant difference between the two test sites, the mycorrhizal treated specimens tended to show a higher RLD, however, with considerable variation (Figure 4b and Table 2). It has been shown in many studies and for many host plants that arbuscular and ectomycorrhiza stimulated root growth [*Smith and Read*, 2008]. For eco-engineering, this was also demonstrated in laboratory experiments. *Alnus incana* (L.) Moench grows in sieved (≤ 10 mm) morainic soil material and inoculated with the mycorrhizal fungus *Melanogaster variegatus* s.l. produced within 20 weeks more than twice the RLD compared to

noninoculated samples [Graf and Frei, 2013]. On the field experimental scale, even after 28 months, we could not find evidence for a similar effect.

The discrepancy between the laboratory and the field experiment might be explained by the finding of Poorter *et al.* [2012], indicating that root development depends on the space available for root spread and thus on the size of pots used in laboratory experiments. Consequently, differences in the available rooting space between laboratory and field experiments might have caused different responses to mycorrhizal inoculation.

Nevertheless, plant survival probability was about twice as high at the sm site compared to the snm site at the end of the first growing season (Figure 3). Experiments in tree nurseries and agriculture have demonstrated that the colonization by different mycorrhizal fungi increases water and nutrient uptake of the host plants, which results in better growth and higher survival rates [Jakobsen *et al.*, 1994; Berta *et al.*, 1995]. In our study, we found a significantly higher survival rate but no significant increase in RLD at the sm site than the snm site (Figures 3 and 4b). Species-specific differences of alder, willow, and other species were not considered since it was not possible to disentangle the fine roots within the soil cores and assign them to their corresponding sapling.

At the end of the third growing season, MRD was significantly higher at the sm than at the snm and c sites, without a significant difference in MRD between the two latter (Figure 4c and Table 2). These differences were also reflected in the mean contributions of the four diameter classes to total RLD. An alteration of the root diameter in response to mycorrhization was already reported by several authors. A study on myrobalan (*Prunus cerasifera* L.) revealed that inoculation with the mycorrhizal fungus *Glomus intraradices* increased the diameter of primary, secondary, and tertiary roots significantly [Berta *et al.*, 1995]. The mycorrhizal infection of leek (*Allium porrum* L.) resulted in a more branched root system, containing shorter branched adventitious roots of larger diameter [Berta *et al.*, 1993; Atkinson *et al.*, 1994]. Also, Fan *et al.* [2011] stated that inoculation with the fungus *Glomus irregulare* significantly changed the root morphology of three strawberry varieties (*Fragaria sp.*) and increased the length of roots with a greater diameter.

The alteration of the root system architecture by the mycorrhizal inoculation can be interpreted by a different behavior in nutrient acquisition and water uptake. The mycorrhizal fungi contribute to an increased nutrient and water uptake from the soil by extending their extraradical hyphae [Atkinson *et al.*, 1994; Allen, 2007; Smith and Read, 2008], and the host plants do not have to forage farther away into the soil by fine roots. Rousseau *et al.* [1994] stated that external mycelium comprised up to 75% of the uptake potential of 8 week old loblolly pines (*Pinus taeda* L.). After the root tips were infected by mycorrhiza, their linear growth ceased [Shishkova *et al.*, 2008], resulting in a lower RLD per individual, while secondary root growth continued [Shishkova *et al.*, 2008], leading to an increased MRD. Furthermore, the improved nutrient and water uptake may contribute to higher plant survival rates. Therefore, we suggest that the tendency of the increased RLD at the mycorrhizally treated site is driven by the increased number of individuals which survived.

Secondary growth and the associated increase in (fine) root thickness produces advantages for plant survival: thicker roots are an indicator of root longevity as well as bending stiffness, potentially promoting soil penetration [Stokes *et al.*, 2009]. The longevity of thicker roots, and by consequence the reduction of turnover, can result in an increased likelihood that the roots will be further colonized by a mycorrhizal fungus [Reinhardt and Miller, 1990]. Even fine roots can store starch as well as nutrients, and the bigger the diameter, the more important this function is [Danjon *et al.*, 2013]. When the photosynthesis rate is not sufficient, the stored starch can be used for root growth in times of low supplies, like early spring or winter season [Danjon *et al.*, 2013; Mao *et al.*, 2013a, 2013b].

4.3. The Relationship Between Fine Roots and Aggregate Stability

A significant influence of RLD on ASC (Figure 5a) was reported in several previous studies [e.g., Pohl *et al.*, 2009; Fattet *et al.*, 2011; Graf and Frei, 2013]. Mycorrhizal inoculation had a significant influence on ASC at the end of the third growing season (Figure 4a). For the aggregate size class with an equivalent diameter of 1–2 mm a correlation of hyphal length of the mycorrhizal fungi with aggregate stability was reported [Bearden and Petersen, 2000], which might be attributable to the hyphal enmeshment and entanglement of soil particles [Tisdall and Oades, 1982; Tisdall *et al.*, 2012]. However, in contrast to the latter studies

conducted on fine-grained substrates, we assessed soil aggregate stability in alpine Leptosols, where primary particles commonly exceed 2 mm.

The coherent decrease of ASC and RLD at the end of the second growing season seems to be climatically controlled. This assumption is supported by field measurements, showing low soil temperatures and more dry soil conditions during the dormant period 2010/2011 (Figure 2). Comparable relations between root growth/development and (soil) climate were discussed in several studies [e.g., Pregitzer *et al.*, 2000; Alvarez-Uria and Körner, 2007; Mao *et al.*, 2013a, 2013b]. Both the coherent decrease of ASC and RLD (Figures 4a and 4b) and the significant relationship between ASC and RLD suggest (Figure 5a) that RLD is crucial for the formation of water-stable aggregates in our experiment. This may partly result from the fact that the mycorrhizal hyphae do not produce enough mechanical force to bind the large soil particles of coarse-grained soil together, whereas the fine roots do. Linear mixed effect modeling revealed that only the very fine roots were significantly important for binding the soil particles together (Table 4). As evidenced by the positive correlation between MRD and ASC (Figure 5b), within that class thicker roots are more influential. Hence, we assume that MRD does not have a significant influence on the improvement of ASC, when exceeding a certain threshold of approximately 0.5 mm.

Clay and silt are also well known to promote the formation of water-stable aggregates, whereas sand and gravel favor disaggregation [e.g., Tisdall and Oades, 1982; Amezketa, 1999; Pohl *et al.*, 2009]. Applying a structural equation modeling approach, which was based on data of 27 grasslands, it was shown that biotic factors are less important than abiotic factors, like soil texture [Barto *et al.*, 2010]. Since the quantity of fine soil particles in the analyzed soil samples is low (Table 1), we assume that in coarse-grained, alpine Leptosols biotic parameters gain in importance regarding soil aggregation with increasing time after the establishment of a vegetation cover.

4.4. Effectiveness of the Inoculation and the Potential Influence of Actinomycetae

Mycorrhizal inoculation was used as a factorial variable in the applied statistical analysis. In degraded environments mycorrhizae are mostly absent [Smith and Read, 2008] and the mycorrhizae infection potential is drastically reduced in disturbed systems [Biondini *et al.*, 1985]. At the Patjänja Rufe a humus-accumulated topsoil horizon, where active mycorrhizal propagules are usually located [Amaranthus and Trappe, 1993], is absent and the corresponding host plants are missing. Consequently, it can be assumed that the presence or preexistence of mycorrhizae was negligibly small [Parke *et al.*, 1984]. The INOQ Forst inoculum used in the present study was developed for forest applications including restoration (INOQ GmbH, 2014, www.inoq.de/downloads/Forest_e.pdf). The company tested the product to guarantee its quality, which included tests on mycorrhizal fungi species to inspect their effectiveness. Thus, based on the literature and the fact that the mycorrhizal inoculum forms a symbiotic mutualism with the plants of the assortment used, we assume that the mycorrhizal inoculum infected the plant roots without directly controlling this effect.

Besides mycorrhizae, soil bacteria play an important role to determine soil properties. The soil cores used in this study were taken uphill a green alder. Alders are, in general, infected by both mycorrhizae and actinomycetae. Many alder species form a symbiosis with the N₂-fixing actinomycete *Frankia* and also with several ectomycorrhizae and arbuscular mycorrhizae [e.g., Monzón and Azcón, 2001; Isopi *et al.*, 1994]. However, the natural symbiosis with *Frankia* is in the same way possible at the noninoculated site within our experiment. Within a glasshouse experiment, Frei [2009] demonstrated that the infection rates of inoculated and noninoculated alder root nodules by actinomycete *Frankia* were the same. Hence, we can assume that the results revealed in our field experiment are due to the mycorrhizal inoculation. Furthermore, the quantified root development and aggregation is influenced not only by the appendant green alder but also by the surrounding inoculated species.

5. Conclusions and Outlook

The establishment of hedge layers on a steep vegetation-free slope with coarse-grained Leptosols increased aggregate stability significantly. Inoculation with mycorrhizae did not accelerate the positive hedge layer effect on aggregate stability until the end of the first growing season but had promoted aggregate stability significantly at the end of the third growing season. Plant survival was significantly improved by

inoculation with mycorrhiza and was approximately twice the rate at the nonmycorrhizally treated site. Fine root development was stimulated by inoculation, but not immediately. At the end of the third growing season, there was a tendency to higher RLD and a significant larger MRD at the inoculated site. RLD and ASC were correlated positively, and the very fine roots were most influential. A positive correlation between MRD and ASC indicates that roots having a larger MRD are more influential within the class of the very fine roots.

The application of a commercial mycorrhizal inoculum is a valuable promoter in mitigating slope instability and surface erosion and hence in protecting slopes against superficial slope failures. The temporal offset in the results between laboratory and field experiments underlines the importance of environmental field monitoring.

Acknowledgments

The authors wish to thank the Federal Office for the Environment (FOEN) and the Wolfermann-Nägeli-Stiftung (Zürich) for funding the project (BAFU 09.0027.PJ/1211-3446). Furthermore, we would like to thank the two anonymous reviewers and the Editors for their useful comments that helped to improve the manuscript. The data used in this paper will be provided on request by A. Bast (alexander.bast@wsl.ch) or H. Gärtner (holger.gaertner@wsl.ch).

References

- Allen, M. F. (2007), Mycorrhizal fungi: Highways for water and nutrients in arid soils, *Vadose Zone J.*, 6(2), 291–297, doi:10.2136/vzj2006.0068.
- Alvarez-Uria, P., and C. Körner (2007), Low temperature limits of root growth in deciduous and evergreen temperate tree species, *Funct. Ecol.*, 21(2), 211–218, doi:10.1111/j.1365-2435.2007.01231.x.
- Amaranthus, M., and J. Trappe (1993), Effects of erosion on ecto- and VA-mycorrhizal inoculum potential of soil following forest fire in southwest Oregon, *Plant Soil*, 150(1), 41–49, doi:10.1007/BF00779174.
- Amezket, E. (1999), Soil aggregate stability: A review, *J. Sustain. Agric.*, 14(2–3), 83–151, doi:10.1300/J064v14n02_08.
- ASTM-D2487-00 (2000), Standard practice for classification of soils for engineering purpose (Unified Soil Classification System), Ann. b. ASTM standards, sect. four, 04.08, 238–248.
- Atkinson, D., G. Berta, and J. E. Hooker (1994), Impact of mycorrhizal colonisation on root architecture, root longevity and the formation of growth regulators, in *Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems*, edited by S. Gianinazzi and H. Schüepp, pp. 89–99, Birkhauser Verlag, Basel.
- Azcón-Aguilar, C., J. Palenzuela, A. Roldán, S. Bautista, R. Vallejo, and J. M. Barea (2003), Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened Mediterranean shrublands, *Appl. Soil Ecol.*, 22(1), 29–37, doi:10.1016/S0929-1393(02)00107-5.
- Barto, E. K., F. Alt, Y. Oelmann, W. Wilcke, and M. C. Rillig (2010), Contributions of biotic and abiotic factors to soil aggregation across a land use gradient, *Soil Biol. Biochem.*, 42(12), 2316–2324, doi:10.1016/j.soilbio.2010.09.008.
- Bast, A., W. Wilcke, F. Graf, P. Lüscher, and H. Gärtner (2014), The use of mycorrhiza for eco-engineering measures in steep alpine environments: Effects on soil aggregate formation and fine-root development, *Earth Surf. Processes Landforms*, 39, 1753–1763, doi:10.1002/esp.3557.
- Bast, A., W. Wilcke, F. Graf, P. Lüscher, and H. Gärtner (2015), A simplified and rapid technique to determine an aggregate stability coefficient in coarse grained soils, *CATENA*, 127, 170–176, doi:10.1016/j.catena.2014.11.017.
- Bearden, B., and L. Petersen (2000), Influence of arbuscular mycorrhizal fungi on soil structure and aggregate stability of a vertisol, *Plant Soil*, 218(1), 173–183, doi:10.1023/a:1014923911324.
- Beglinger, K., T. Sieber, and F. Graf (2011), Effects of endophytic and mycorrhizal fungi associated with *Salix appendiculata* on soil aggregate stability, *Geophys. Res. Abstr.* EGU2011–9654, vol. 13.
- Berta, G., A. Fusconi, and A. Trotta (1993), VA mycorrhizal infection and the morphology and function of root systems, *Environ. Exp. Bot.*, 33(1), 159–173, doi:10.1016/0098-8472(93)90063-L.
- Berta, G., et al. (1995), Arbuscular mycorrhizal induced changes to plant growth and root system morphology in *Prunus cerasifera*, *Tree Physiol.*, 15(5), 281–293, doi:10.1093/treephys/15.5.281.
- Biondini, M., C. Bonham, and E. Redente (1985), Secondary successional patterns in a sagebrush (*Artemisia tridentata*) community as they relate to soil disturbance and soil biological activity, *Vegetatio*, 60(1), 25–36, doi:10.1007/BF00053909.
- Bischetti, G. B., E. A. Chiaradia, V. D'Agostino, and T. Simonato (2010), Quantifying the effect of brush layering on slope stability, *Ecol. Eng.*, 36(3), 258–264, doi:10.1016/j.ecoleng.2009.03.019.
- Burri, K., F. Graf, and A. Boell (2009), Revegetation measures improve soil aggregate stability: A case study of a landslide area in Central Switzerland, *For. Snow Landscape Res.*, 82(1), 45–60.
- Cleveland, W. S. (1979), Robust locally weighted regression and smoothing scatterplots, *J. Am. Stat. Assoc.*, 74(368), 829–836, doi:10.2307/2286407.
- Crozier, M. J. (2010), Deciphering the effect of climate change on landslide activity: A review, *Geomorphology*, 124(3–4), 260–267, doi:10.1016/j.geomorph.2010.04.009.
- Danjon, F., A. Stokes, and M. R. Bakker (2013), Root systems of wood plants, in *Plant Roots. The Hidden Half*, 4th ed., edited by A. Eshel and T. Beekman, pp. 29–21–29–26, CRC Press - Taylor & Francis Group, Boca Raton, Fla.
- De Baets, S., J. Poesen, A. Knapen, G. G. Barbera, and J. A. Navarro (2007), Root characteristics of representative Mediterranean plant species and their erosion-reducing potential during concentrated runoff, *Plant Soil*, 294(1–2), 169–183, doi:10.1007/s1104-007-9244-2.
- Fan, L., Y. Dalpe, C. Q. Fang, C. Dube, and S. Khanzadeh (2011), Influence of arbuscular mycorrhizae on biomass and root morphology of selected strawberry cultivars under salt stress, *Botany*, 89(6), 397–403, doi:10.1139/b11-028.
- Fattet, M., Y. Fu, M. Ghestem, W. Ma, M. Foulonneau, J. Nespoulous, Y. Le Bissonnais, and A. Stokes (2011), Effects of vegetation type on soil resistance to erosion: Relationship between aggregate stability and shear strength, *CATENA*, 87(1), 60–69, doi:10.1016/j.catena.2011.05.006.
- Frei, C., R. Schöll, S. Fukutome, J. Schmidli, and P. L. Vidale (2006), Future change of precipitation extremes in Europe: Intercomparison of scenarios from regional climate models, *J. Geophys. Res.*, 111, D06105, doi:10.1029/2005JD005965.
- Frei, M. (2009), Validation of a new approach to determine vegetation effects on superficial soil movements, PhD Thesis, Diss. ETH No. 18455, ETH Zurich, Zurich, 259 pp.
- Graf, F. (1997), Ectomycorrhiza in alpine soil bioengineering, *Rev. Valdôtaine Hist. Nat., Suppl.*, 51, 225–342.
- Graf, F., and M. Frei (2013), Soil aggregate stability related to soil density, root length, and mycorrhiza using site-specific *Alnus incana* and *Melanogaster variegatus* s.l., *Ecol. Eng.*, 57, 314–323, doi:10.1016/j.ecoleng.2013.04.037.

- Graf, F., M. Frei, and A. Boell (2009), Effects of vegetation on the angle of internal friction of a moraine, *For. Snow Landscape Res.*, 82(1), 61–77.
- Gyssels, G., J. Poesen, E. Bochet, and Y. Li (2005), Impact of plant roots on the resistance of soils to erosion by water: A review, *Prog. Phys. Geogr.*, 29(2), 189–217, doi:10.1191/0309133305pp443ra.
- Haichar, F. E. Z., C. Santaella, T. Heulin, and W. Achouak (2014), Root exudates mediated interactions belowground, *Soil Biol. Biochem.*, 77, 69–80, doi:10.1016/j.soilbio.2014.06.017.
- Harrington, D. P., and T. R. Fleming (1982), A class of rank test procedures for censored survival data, *Biometrika*, 69(3), 553–566, doi:10.1093/biomet/69.3.553.
- Hothorn, T., F. Bretz, and P. Westfall (2008), Simultaneous inference in general parametric models, *Biom. J.*, 50(3), 346–363, doi:10.1002/bimj.200810425.
- Isopi, R., E. Lumini, M. Frattegiani, G. Puppi, M. Bosco, F. Favilli, and E. Buresti (1994), Inoculation of *Alnus cordata* with selected microsymbionts: Effects of *Frankia* and *Glomus spp.* on seedling growth and development, *Symbiosis*, 17, 237–245.
- IUSS Working Group WRB (2006), World reference base for soil resources 2006, 128 pp., World Soil Resour. Rep. No. 103., FAO, Rome.
- Jakobsen, I., E. J. Jøner, and J. Larsen (1994), Hyphal phosphorus transport, a keystone to mycorrhizal enhancement of plant growth, in *Impact of Mycorrhizal Colonisation on Root Architecture, Root Longevity and the Formation of Growth Regulators*, edited by S. Gianinazzi and H. Schüepp, pp. 133–146, Birkhäuser Verlag, Basel.
- Kaplan, E. L., and P. Meier (1958), Nonparametric estimation from incomplete observations, *J. Am. Stat. Assoc.*, 53(282), 457–481, doi:10.1080/01621459.1958.10501452.
- Keiler, M., J. Knight, and S. Harrison (2010), Climate change and geomorphological hazards in the eastern European Alps, *Philos. Trans. R. Soc. A*, 368(1919), 2461–2479, doi:10.1098/rsta.2010.0047.
- Körner, C., and J. Paulsen (2004), A world-wide study of high altitude treeline temperatures, *J. Biogeogr.*, 31(5), 713–732, doi:10.1111/j.1365-2699.2003.01043.x.
- Mao, Z., M.-L. Bonis, H. Rey, L. Saint-André, A. Stokes, and C. Jourdan (2013a), Which processes drive fine root elongation in a natural mountain forest ecosystem?, *Plant Ecol. Diversity*, 6(2), 231–243, doi:10.1080/17550874.2013.788567.
- Mao, Z., C. Jourdan, M. L. Bonis, F. Pailler, H. Rey, L. Saint-André, and A. Stokes (2013b), Modelling root demography in heterogeneous mountain forests and applications for slope stability analysis, *Plant Soil*, 363(1–2), 357–382, doi:10.1007/s11104-012-1324-2.
- Monzón, A., and R. Azcón (2001), Growth responses and N and P use efficiency of three *Alnus* species as affected by arbuscular-mycorrhizal colonisation, *Plant Growth Regul.*, 35(1), 97–104, doi:10.1023/A:1013875501259.
- Ott, E., M. Frehner, H.-U. Frey, and P. Lüscher (1997), *Gebirgsnadelwälder. Ein praxisorientierter Leitfaden für eine standortgerechte Waldbehandlung*, 287 pp., Paul Haupt Verlag, Bern, Stuttgart, Wien.
- Parke, J. L., R. G. Linderman, and J. M. Trappe (1984), Notes: Inoculum potential of ectomycorrhizal fungi in forest soils of southwest Oregon and Northern California, *For. Sci.*, 30, 300–304.
- Pellegrino, E., S. Bedini, L. Avio, E. Bonari, and M. Giovannetti (2011), Field inoculation effectiveness of native and exotic arbuscular mycorrhizal fungi in a Mediterranean agricultural soil, *Soil Biol. Biochem.*, 43(2), 367–376, doi:10.1016/j.soilbio.2010.11.002.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team (2014), nlme: Linear and nonlinear mixed effects models, R package version 3.1-117, edited.
- Pohl, M., D. Alig, C. Körner, and C. Rixen (2009), Higher plant diversity enhances soil stability in disturbed alpine ecosystems, *Plant Soil*, 324(1), 91–102, doi:10.1007/s11104-009-9906-3.
- Pollen, N., and A. Simon (2005), Estimating the mechanical effects of riparian vegetation on stream bank stability using a fiber bundle model, *Water Resour. Res.*, 41, W07025, doi:10.1029/2004WR003801.
- Poorter, H., J. Bühler, D. van Dusschoten, J. Climent, and J. A. Postma (2012), Pot size matters: A meta-analysis of the effects of rooting volume on plant growth, *Funct. Plant Biol.*, 39(11), 839–850, doi:10.1071/FP12049.
- Pregitzer, K. S., J. A. King, A. J. Burton, and S. E. Brown (2000), Responses of tree fine roots to temperature, *New Phytol.*, 147(1), 105–115, doi:10.1046/j.1469-8137.2000.00689.x.
- R Core Team (2013), R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available at <http://www.R-project.org/>.]
- Réagents Instruments Inc. (2003), WinRhizo 2003b - for washed root measurements. Réagents Instruments Inc, Canada. [Available at www.regentinstruments.com.]
- Reinhardt, D. R., and R. M. Miller (1990), Size classes of root diameter and mycorrhizal fungal colonization in two temperate grassland communities, *New Phytol.*, 116(1), 129–136, doi:10.1111/j.1469-8137.1990.tb00518.x.
- Rillig, M. C., and D. L. Mummey (2006), Mycorrhizas and soil structure, *New Phytol.*, 171(1), 41–53, doi:10.1111/j.1469-8137.2006.01750.x.
- Rousseau, J. V. D., D. M. Sylvia, and A. J. Fox (1994), Contribution of ectomycorrhiza to the potential nutrient-absorbing surface of pine, *New Phytol.*, 128(4), 639–644, doi:10.1111/j.1469-8137.1994.tb04028.x.
- Shishkova, S., T. L. Rost, and J. G. Dubrovsky (2008), Determinate root growth and meristem maintenance in angiosperms, *Ann. Bot.*, 101(3), 319–340, doi:10.1093/aob/mcm251.
- Smith, S. E., and D. J. Read (2008), *Mycorrhizal Symbiosis*, 3rd ed., 787 pp., Academic Press, Cambridge, U. K.
- Stahel, W. A. (2011), *regR: Building regression models*. R package version 1.0-2, edited.
- Stangl, R. (2007), *Hedge Brush Layers and Live Crib Walls—Stand Development and Benefits*, pp. 287–296, Springer, Dordrecht.
- Stokes, A., C. Atger, A. G. Bengough, T. Fourcaud, and R. C. Sidle (2009), Desirable plant root traits for protecting natural and engineered slopes against landslides, *Plant Soil*, 324(1–2), 1–30, doi:10.1007/s11104-009-0159-y.
- Stokes, A., et al. (2014), Ecological mitigation of hillslope instability: Ten key issues facing researchers and practitioners, *Plant Soil*, 377, 1–23, doi:10.1007/s11104-014-2044-6.
- Tableman, M., and J. S. Kim (2003), *Survival Analysis Using S: Analysis of Time-to-Event Data*, 280 pp., Chapman & Hall/CRC Texts in Statistical Sci., CRC Press, Boca Raton, Fla.
- Therneau, T. M. (2014), A package for survival analysis in S. R package version 2.37-7, edited.
- Thornton, P. E., S. W. Running, and M. A. White (1997), Generating surfaces of daily meteorological variables over large regions of complex terrain, *J. Hydrol.*, 190(3–4), 214–251, doi:10.1016/s0022-1694(96)03128-9.
- Tisdall, J. M., and J. M. Oades (1982), Organic matter and water-stable aggregates in soils, *J. Soil Sci.*, 33(2), 141–163, doi:10.1111/j.1365-2389.1982.tb01755.x.
- Tisdall, J. M., S. E. Nelson, K. G. Wilkinson, S. E. Smith, and B. M. McKenzie (2012), Stabilisation of soil against wind erosion by six saprotrophic fungi, *Soil Biol. Biochem.*, 50, 134–141, doi:10.1016/j.soilbio.2012.02.035.
- Tukey, J. W. (1957), On the comparative anatomy of transformations, *Ann. Math. Stat.*, 28(3), 602–632, doi:10.1214/aoms/1177706875.

- van de Voorde, T. F. J., W. H. van der Putten, and T. M. Bezemer (2012), Soil inoculation method determines the strength of plant–soil interactions, *Soil Biol. Biochem.*, *55*, 1–6, doi:10.1016/j.soilbio.2012.05.020.
- Verbruggen, E., M. G. A. van der Heijden, M. C. Rillig, and E. T. Kiers (2013), Mycorrhizal fungal establishment in agricultural soils: Factors determining inoculation success, *New Phytol.*, *197*(4), 1104–1109, doi:10.1111/j.1469-8137.2012.04348.x.
- Zuazo, V. H. D., and C. R. R. Pleguezuelo (2008), Soil-erosion and runoff prevention by plant covers. A review, *Agron. Sustain. Dev.*, *28*(1), 65–86, doi:10.1051/agro:2007062.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith (2009), *Mixed Effects Models and Extensions in Ecology With R*, 574 pp., Springer, New York.