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Linking plant morphological traits to uprooting resistance in eroded marly lands (Southern Alps, France)

M. Burylo · F. Rey · C. Roumet · E. Buisson · T. Dutoit

Abstract In marly catchments of the French Southern Alps, soils are subjected to harsh water erosion that can result in concentrated flows uprooting small plants. Evaluating and predicting plant resistance to uprooting from simple plant traits is therefore highly important so that the most efficient plant strategy for future restoration of eroded slopes can be defined. Twelve species growing on marly land were studied. For each species, *in-situ* lateral uprooting tests were conducted and morphological plant traits were measured on small plants at the early stages of their development. The results show that maximum uprooting force was most positively correlated with stem basal diameter. Resistance to uprooting depends on a combination of several traits. Tap root length, the proportion of fine lateral roots and root topology were the best predictors of anchorage strength.

Keywords Response traits · Uprooting · Erosion · Marls

Abbreviations
D	Stem basal diameter at the root-shoot junction
H	Plant height
DBH	Diameter at Breast Height
DW_R	Total root dry weight
DW_{R1}	Tap root dry weight
L	Total root length measured using WinRHIZO
L_{R1}	Length of the tap root measured using WinRHIZO
V	Total root system volume measured using WinRHIZO
Surf	External root surface area calculated with WinRHIZO
μ	Magnitude: number of external links
a	Altitude: number of links in the longest single path from an external link to the base link
E(a)	Expected altitude calculated from μ on the assumption of random patterns of root branching using the algorithm taken from Werner and Smart (1973)
F_{max}	Maximum force reached before plant uprooting
σ	Critical stress calculated as the ratio of F_{max} to plant basal cross-sectional area

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Introduction

Extensive areas of the French Southern Alps are covered with Black Marl formations. In a Mediterranean and mountainous climate, with wetting–drying cycles, frost in winter and high-intensity rainfalls in summer, these marly lands are subjected to intense hydric erosion resulting in torrential floods heavily loaded with sediment (Oostwoud Wijdenes and Ergenzinger 1998; Descroix and Mathys 2003; Mathys et al. 2005). This erosion is responsible for the sedimentation of river systems and the silting of regional reservoirs. Land rehabilitation using vegetation, through reforestation projects with Austrian Black pine dating from the late 19th century (Vallauri et al. 2002), or more recent ecological engineering methods using bioengineering works (Rey 2005), has proved effective in reducing erosion and restoring a certain ecological functioning. In particular, the new methods using vegetation barriers allow significant quantities of sediment to be retained, by installing bioengineering works specifically in gully floors. These methods are low-cost solutions for ecological rehabilitation, because they guarantee efficient sediment control with as few interventions as possible. These solutions use living material (cuttings and plants) and favor immediate natural vegetation colonization on the sediment trapped (Rey et al. 2005; Burylo et al. 2007).

Nevertheless, erosive constraints still limit the sustainability of natural vegetation colonization (Cohen and Rey 2005). Concentrated runoff loaded with sediment can uproot plants that have established after restoration and that could have otherwise stabilized the slopes. Understanding and predicting plant resistance to uprooting at the early stages of their development is therefore a major objective for both scientists and practitioners. Explaining plant resistance in terms of plant traits is essential so that taxon-free generalizations of the results can be made and species compared beyond the local study site.

Over the past 20 years, many studies have been conducted on the mechanisms of plant anchorage (Table 1) contributing a great deal of information on the factors influencing anchorage strength. To withstand external constraints, plants must transfer the force into the soil via their roots. Plant anchorage depends on a combination of root system type and root system morphology (Dupuy et al. 2005b), soil

Table 1 List of morphological traits positively correlated with anchorage strength according to the type of study

Type of material	Factors affecting anchorage	Key references
Live material		
Temperate mature trees	DBH, Height, Stem mass, Root system depth, Root area, Root bending resistance	Crook and Ennos (1996), Cucchi et al. (2004), Mickovski and Ennos (2002), Nicoll et al. (2006)
Temperate juvenile trees	Root volume, Stem biomass, Tap root length	Karrenberg et al. (2003), Khuder et al. (2007)
Tropical trees	DBH	Crook and Ennos (1998)
Herbaceous dicots	Stem basal diameter, Root biomass, Root bending resistance	Ennos et al. (1993a), Goodman et al. (2001), Toukura et al. (2006)
Grasses	Height, Lateral root spread, Biomass, Lateral root number, Lateral root volume, Root bending resistance	Bailey et al. (2002), Crook and Ennos (1993), Ennos et al. (1993b), Mickovski et al. (2005), Stokes et al. (2007)
Aquatic macrophytes	Root number, Root area	
Schutten et al. (2005)		
Physical model	Root system depth, Root length, Root branching, root stiffness	Mickovski et al. (2007), Stokes et al. (1996)
Numerical model	Root system type, Root system depth, Lateral root spread, Root number, Root diameter, Root branching	Dupuy et al. (2005a, b)

properties (Ennos 1990), and type of constraint, i.e. vertical uprooting or lateral loading (Ennos 1993). Several types of anchorage systems (plate, tap, coronal), growth forms (trees, shrubs, herbs), and type of soil or type of constraint (grazing, wind

loading, hydrological forces) have been investigated. Experiments on physical and numerical models have made it easier to isolate the effects of a few root parameters on the entire plant's resistance to uprooting. Among plant traits, plant size (DBH, height, stem basal diameter, biomass), root system size (depth and lateral spread), root number, root length, and root branching are the most important traits related to plant anchorage (Table 1).

It has also been demonstrated that when subjected to mechanical stress such as wind loading, some species have higher numbers of roots and greater lateral root branching (Stokes et al. 1997; Mickovski and Ennos 2003), root length (Tamasi et al. 2005), lateral root basal cross-sectional area and root rigidity (Goodman and Ennos 1997). These adaptations should improve the anchorage of plants. Finally, it should also be pointed out that other traits such as root stiffness (Crook and Ennos 1993; Goodman et al. 2001; Mickovski et al. 2007), changes in cell wall properties, i.e. lignin (Scippa et al. 2006) and cellulose (Genet et al. 2005), and root system asymmetry (Nicoll and Ray 1996; Mickovski and Ennos 2003) can also play a role in plant anchorage.

The objectives of most of the studies on plant anchorage carried out over the last 20 years (Table 1) were to gain information on the anchorage mechanics of a single species (Mickovski et al. 2005) or to investigate the influence of one specific factor such as branching pattern (Stokes et al. 1996), lateral roots, or root hairs (Bailey et al. 2001) on anchorage efficiency. To date, few studies have been conducted on large sets of species (Karrenberg et al. 2003; Nicoll et al. 2006; Toukura et al. 2006). Many of the factors related to anchorage, such as diameter, biomass, and root number, vary with regard to plant size and age. Consequently, the results available in the literature are often valid for one species and do not always enable relevant interspecific comparison. Moreover, a large number of studies investigated trees, herbaceous dicots, and grasses but very few studies have focused on shrubby species, which are dominant species in eroded marly lands and which are often used for restoration purposes.

To define the most efficient strategy for land management in the French Southern Alps, it is important to be able to evaluate and predict the resistance to uprooting of young plants and seedlings planted for restoration purposes or that develop naturally on eroded lands. Therefore, the aim of the present study was to relate uprooting resistance to plant traits at the early stages of plant development using a comparative approach. The following question was addressed: what is the trait, or combination of traits, that can best predict species resistance to lateral uprooting?

To test whether species differ in terms of resistance to uprooting, we performed *in situ* uprooting tests on 12 species growing in the French Southern Alps representing different growth forms. Ten traits related to plant morphology, the root biomass allocation pattern, root system topology, morphology, and architecture were examined for each of the 12 species studied. These traits were chosen because of their assumed or demonstrated role in plant anchorage (inspired and adapted from Table 1).

Analyses were performed on juvenile individuals in order to evaluate species survival when they are the most vulnerable to the effects of erosion. We chose to apply lateral traction force to mimic the external forces generated by concentrated flow and sediment loading. Plant morphological traits were then examined and we tested whether species with contrasting resistance to uprooting differed in terms of traits.

Materials and methods

Study site

The experiment was conducted in the Forêt Domaniale du Grand Vallon (site 1) and in the Forêt Domaniale de la Haute Bléone (site 2) in the French Southern Alps. These two areas, approximately 50 km apart, are situated, respectively, near Sisteron and Digne in the Alpes-de-Haute-Provence, France. At both sites, the climate is mountainous sub-Mediterranean with summer droughts interspersed with intense storms. The annual total precipitation is 787 mm and 822 mm at site 1 and 2, respectively, and the average annual temperature is 10.2°C at both sites with four to five cold months (temperature < 7°C; Rey 2002). At both sites, vegetation has developed on partly eroded black marls and the slopes are covered with a loose regolith layer made of disintegrated black marl fragments within a silty matrix (Oostwoud Wijdenes and Ergenzinger 1998).

The dominant tree species on the two sites is *Pinus nigra* Arn. s*sp. nigra* from massive reforestation operations for erosion control dating from the beginning of the last century (Vallauri et al. 2002). The other dominant tree species are *Acer opalus* Mill., *Quercus pubescens* Wild., and *Robinia pseudoacacia* L. introduced in the 19th century. *Ononis fruticosa* L., *Sorbus aria* L., and *Genista cinerea* Vill. mainly compose the shrub layer and *Achnatherum calamagrostis* L. the grass layer.

Species selection

Twelve species from the local vegetation were chosen (Table 2). These species were selected according to different criteria: i) they are prevalent on marly lands of the French Southern Alps and include different growth forms and families to obtain contrasted responses to uprooting and to measure a large range of plant trait values; ii) they all have tap-like root systems, i.e. with an identifiable main vertical root and smaller lateral roots growing horizontally and vertically, to simplify the analysis and species comparison; iii) species already used by practitioners for land management were favored; iv) species are available at the development stage investigated, i.e. juvenile individuals (stem basal diameter < 20 mm) in a relatively isolated position to avoid root system interaction between plants and modifications of anchorage strength; and v) species are available on flat areas since slope angle influences root system

architecture and anchorage mechanics (Di Iorio et al. 2005).

We sampled two trees (*P. nigra* and *Q. pubescens*), nine shrub species (*B. sempervirens*, *D. pentaphyllum*, *G. cinerea*, *J. communis*, *L. angustifolia*, *O. fruticosa*, *O. natrix*, *S. dubia* and *T. serpyllum*) and one herbaceous dicotyledonous species (*A. vulneraria*). Because of variations in local vegetation composition, all species were not present or very abundant at both sites. Eight species were tested in the Forêt Domaniale du Grand Vallon (site 1) while the other species were tested in the Forêt Domaniale de la Haute Bléone (site 2). Moreover, the species selected represented different families and successional status. Some species, such as *Robinia pseudo acacia* and *Hippophae rhamnoides*, despite their abundance in local vegetation, could not be included in the selection because they were not available at the juvenile stage at the sites investigated. Uprooting tests and trait measurements were carried out between May and June in 2007 and 2008 at the peak of vegetative growth. During the experiment, individuals were selected to represent different stem basal diameters and thus to represent species anchorage strength and species morphology throughout the range of diameters studied (0–20 mm).

Uprooting tests

Soil moisture content and soil mechanical properties strongly influence anchorage strength. Since uproot-

Table 2 Ecological characteristics and sampling site of the 12 species studied

Species	Family	Growth form	Successional status	Sampling site
Pinus nigra Arn. *ssp. nigra*	Pinaceae	T	Pioneer	1
Quercus pubescens Wild.	Fagaceae	T	Dryad	1
Buxus sempervirens L.	Buxaceae	S	Post-pioneer	2
Dorycnium pentaphyllum Scop.	Fabaceae	S	Post-pioneer	2
Genista cinerea Vill.	Fabaceae	S	Post-pioneer	1
Juniperus communis L.	Cupressaaceae	S	Pioneer	1
Lavandula angustifolia Mill.	Lamiaceae	S	Post-pioneer	2
Ononis fruticosa L.	Fabaceae	S	Pioneer	1
Ononis natrix L.	Fabaceae	S	Post-pioneer	1
Staehelina dubia L.	Asteraceae	S	Pioneer	2
Thymus serpyllum L.	Lamiaceae	S	Post-pioneer	1
Anthyllis vulneraria L.	Fabaceae	H	Post-pioneer	1

T = Tree; S = Shrub; H = Herbaceous

Table 3 Soil shear strength (kPa) at 5-and 10-cm depths at site 1 and 2

Depth		Site 1	Site 2
5 cm	Mean	58.8	47.1
	SE	3.6	3.6
10 cm	Mean	121.4	150.8
	SE	9.2	10.9

ing tests were carried out on different sites and different dates, particular precautions were taken to be sure tests were valid. To prevent soil moisture content differences, the tests were carried out in the morning, at least 2 days after an intensive rainfall event. Soil shear strength at 5-and 10-cm depths was measured with a shear vane (Geonor H-60, Geonor Inc., Oslo, Norway) to determine the soil's mechanical properties at sites 1 and 2 (15 tests at each site and depth). A repeated measures analysis of variance showed that soil cohesion increased with soil depth (Effect of depth: $F = 151.4$, $p = 0.000$) but that there were no significant differences in soil shear strength between sites (Effect of site: $F = 1.1$, $p = 0.29$; Interaction Depth x Site: $F = 9.2$, $p = 0.005$–Table 3).

Uprooting tests were performed on six to twelve individuals per species (Table 5) using the method described in Mickovski et al. (2005). Before each test, the superficial litter layer was removed to clear the stem base; plant height and stem basal diameter were then measured. A non-stretch rope was bound to the stem base at one end and to a portable force gauge (Alluris FMI-300) at the other end. A horizontal traction force was then applied manually until the plant was uprooted. Whenever the sample area was not completely flat, the force was applied parallel to the downslope direction. The main drawback of this method is that speed of pulling, which influences anchorage resistance, cannot be controlled, as it can be when using a winch. Consequently, the traction force was applied slowly, as regularly as possible, to avoid altering the results. Many uprooting tests failed because of rope or stem breakage or the rope slipping around the stem. During the valid tests, as the plants began to fail, roots could be heard breaking until complete root breakage and root system dislodgement from the sediment. The maximum force reached before uprooting (F_{max} in N) was noted and the critical stress

(σ in MPa), i.e. the force per unit area necessary to induce uprooting, was calculated as F_{max} divided by plant stem basal cross-sectional area (mm^2).

Trait measurement

On the basis of the existing literature on anchorage mechanics and root traits (Table 1), ten morphological traits were selected (Table 4). For each species, at least six juvenile individuals were carefully excavated with hand tools to avoid damaging the roots and were preserved at 5°C. The week following harvest, the plants were cleaned using a fine stream of water to remove soil particles. After cleaning, plant height (H) and stem basal diameter (D) were measured.

Root samples were separated into tap root (R_1) and lateral roots and were conserved in ethanol 50% (v:v) until analysis. The tap roots and laterals were scanned and analyzed using WinRHIZO Pro (version 2003b, Regent Instrument, Quebec, Canada), following the scanning protocol proposed by 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, a root density less than 0.5 mm root/mm^2 surface and with the automatic threshold option. WinRHIZO was used to determine root length

Table 4 Morphological traits measured on 12 species growing on marly lands

Traits	Abbreviations (units)	Measurement
Plant slenderness ratio	H/D (cm.cm^{-1})	H/D
Root slenderness ratio	L$_{R1}$/D (cm.cm^{-1})	L$_{R1}$/D
Relative root volume	V/D (cm^3.cm^{-1})	V/D
Relative root dry weight	DW$_R$/D (g.cm^{-1})	DW$_R$/D
Relative external root surface area	Surf/D (cm.cm^{-1})	Surf/D
Percentage of root system dry weight accounted for by the tap root	%DW$_{R1}$ (%)	DW$_{R1}$/DW$_R$
Root Tissue Density	RTD (g.cm^{-3})	DW$_R$/V
Specific Root Length	SRL (m.g^{-1})	L/DW$_R$
Topological index	a/E(a) (−)	a/E(a)
Proportion of root length with diameter < 0.5 mm	%FR (%)	Fine root length (< 0.5 mm)/total root length

(L), surface (Surf), volume (V), and the percentage of fine root (%FR). After scanning, samples were dried at 60°C for 72 h and weighed.

Root Tissue Density (RTD), Specific Root Length (SRL), and the percentage of tap root biomass to total root biomass (%DW$_{R1}$) were calculated. The branching intensity of root systems was analyzed using Fitter's terminology (Fitter, 1985). The magnitude (μ) and altitude (a) were determined manually from the scanned images. The expected altitude [E(a)] was calculated and was then used to determine a root topological index [a/E(a)]. Values of a/E(a) < 1 indicate a largely dichotomous root system, while values > 1 indicate a herringbone-like root system where branching is largely confined to the tap root. Values of 1 indicate a random branching structure. Finally, we calculated the plant slenderness ratio (H/D) and the root slenderness ratio (L$_{R1}$/D). To compare differences between plant traits, all traits that were plant size-dependent (DW$_R$, V, Surf) were standardized by stem basal diameter (DW$_R$/D, V/D, Surf/D).

Statistical analysis

An analysis of covariance (ANCOVA) with D as a covariate and an analysis of variance (ANOVA) were used to test for differences between species in uprooting resistance and traits (Tukey HSD tests). The assumption of normal distribution was checked before analysis (Shapiro-Wilk's test). Duncan's multiple range test was used to classify species into four resistance groups; a discriminant analysis was then performed to determine which traits best discriminate between the groups. Trait differences between groups were investigated with ANOVA and Tukey HSD tests. We used correlation analysis to investigate relationships between resistance to uprooting and plant traits. All the analyses were carried out with STATISTICA (version 7.1 for Windows, Statsoft 1984).

Results

Uprooting resistance

Plant height, stem basal diameter and maximum uprooting force showed large inter-and intra-specific variability. For example, the plant height (H) of *Q. pubescens* ranged form 6 to 24 cm, its stem basal

diameter (D) from 1.8 to 14.8 mm, and its maximum uprooting force (F$_{max}$) from 29 to 430 N (Table 5). This large variability in F$_{max}$ is mainly explained by the variation in D. Indeed, we found a linear positive relationship between F$_{max}$ and D (F$_{max}$ = 25.1D + 12; r = 0.66, p<0.001). Root breakage generally occurred between 10 and 20 cm below the soil surface and the root system section dislodged from the soil consisted of the tap root, main lateral roots, and a few fine roots without soil particles. However, for *L. angustifolia*, 'root balls', i.e. root-soil aggregates containing many fine roots were observed around the main root branches.

When F$_{max}$ was normalized by stem basal cross-sectional area (σ: critical stress), the intraspecific variability was lower (Fig. 1).

The ANCOVA analysis showed that σ differed between species (Fig. 1). The highest values were found in *O. natrix* (9.08 MPa), and the lowest in *L. angustifolia* (2.77 MPa). Species were classified into four resistance groups using Duncan's multiple range test:

– Group 1: *O. natrix*, *G. cinerea*, *O. fruticosa* and *B. sempervirens*
– Group 2: *A. vulneraria* and *Q. pubescens*
– Group 3: *J. communis*, *T. serpyllum* and *D. pentaphyllum*
– Group 4: *P. nigra*, *S. dubia* and *L. angustifolia*

Species classification according to resistance to uprooting did not highlight a particular influence of growth form or successional status. The four most resistant species and the least resistant one, were shrubby species. Tree species were found in Groups 2 and 4.

Plant traits and relationship with resistance to uprooting

All traits differed significantly between species and between resistance groups (Table 6). For example, the root slenderness ratio (L$_{R1}$/D) ranged from 54.2 (*S. dubia*) to 190.9 (*D. pentaphyllum*) and the percentage of root biomass allocated to the tap root (%DW$_{R1}$) from 0.45 (*B. sempervirens*) to 0.96 (*Q. pubescens*). Group 1, with high critical stress, is characterized by high L$_{R1}$/D and plant slenderness ratio (H/D), a low topological index (a/E(a)), and a low relative root dry weight (DW$_R$/D). Species from group 4, which were less resistant, invested less length and biomass in the

Table 5 Results of aboveground traits and uprooting tests

Species	Plant Height (H, cm)			Stem basal diameter (D, mm)			Maximum uprooting force F_{max} (N)			Number of valid tests
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	
P. nigra	39	23	53	6.5	4.9	8.1	126.4	32	245	11
Q. pubescens	15.9	6	24	4.8	1.8	14.8	108.7	29	430	10
B. sempervirens	21.2	10	32	4.9	3.2	5.8	158.5	66	294	10
D. pentaphyllum	4.8	11	27	6.5	3.9	9.9	164.9	79	387	12
G. cinerea	35.1	17	44	6.7	4.8	12.2	266.6	134	358	10
J. communis	29.8	17	43	5.7	3.7	7.7	158.5	63	266	12
L. angustifolia	29.6	23	45	10.1	4.4	17.5	203.8	74	379	11
O. fruticosa	28.8	19	42	7.1	4.9	8.1	333.3	182	402	6
O. natrix	19.4	11	25	5.1	3.2	8.4	174	65	347	9
S. dubia	21.9	16	30	6.6	4.3	9.9	126.3	37	279	10
T. serpyllum	5	8	24	7.8	2.9	12.4	211.4	71	369	11
A. vulneraria	6.6	5	10	4.2	1.7	7.2	102.7	33	185	10

tap root (low L_{R1}/D and $\%DW_{R1}$) and were characterized by coarse roots (low Specific Root Length (SRL) and percentage of fine roots (%FR) and high relative root volume (V/D)).

Discriminant analysis showed that among traits, %FR, L_{R1}/D and a/E(a) best discriminated the groups (Table 7). To a lesser extent, $\%DW_{R1}$ also significantly influenced plant anchorage as well as H/D, Root Tissue Density (RTD), and relative root surface (Surf/D). Species with high %FR and L_{R1}/D values and low a/E(a) values were the most resistant (e.g. *B. sempervirens* from group 1 with %FR=88, L_{R1}/D=113.2, and a/E(a)=0.56), while the opposite traits characterized the least resistant species from group 4 (e.g. *S. dubia* with %FR=54.6, L_{R1}/D=54.2, and a/E(a)=1.47). Species with a low %FR or L_{R1}/D value, or a high a/E(a) value were found in the intermediate groups (group 2 or 3). Despite having the highest L_{R1}/D value (190.9), *D. pentaphyllum* was one of the least resistant species (σ = 5.2 MPa) because of a high a/E(a) value (1.62) and a low %FR value (46.4). Similarly, the rank of *Q. pubescens* (group 2) can be explained by its high topological index (a/E(a)=1.93). Despite equivalent or even better values than species from group 1, *L.*

Fig. 1 Uprooting resistance (σ) of the 12 species studied (means ± SE). Letters indicate significant differences between species (ANCOVA D: F = 41.3, p<0.001; species: F = 6.97, p<0.001– Duncan's multiple range test, α = 0.05)
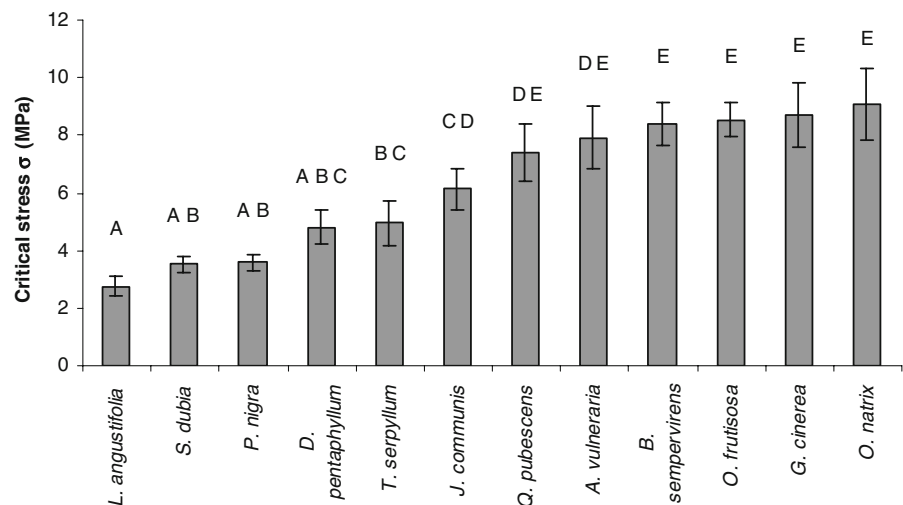
Table 6 Plant traits of the 12 species studied, individually and when classed into four groups depending on resistance to lateral uprooting, and results of the ANOVA. Species are classified according to their resistance to uprooting. When letters differ, differences are significant between groups using a Tukey HSD test ($p < 0.05$). Significance levels: ns nonsignificant, *$p < 0.05$, **$p < 0.001$, ***$p < 0.0001$

Species/ resistance group	H/D (cm/cm)	L_{RI}/D (cm/cm)	V/D (cm³/D)	DW_R/D (g/D)	Surf/D (cm/D)	%DW_{RI}	RTD (g.cm⁻³)	SRL (m.g⁻¹)	a/E(a)	%FR (<0.5 mm)
ANOVA between species	F=11.7***	F=6.8***	F=10.5***	F=11.4***	F=9.6 ***	F=12.9***	F=31.7***	F=12***	F=30.1***	F=35.1***
ANOVA between groups	F=11.1***	F=4.8**	F=3.2*	F=3.6*	F=2.9*	F=4.9***	F=7.8***	F=1.2 ns	F=11.2***	F=14.6***
Ononis natrix	51.9	158.1	0.21	0.08	84.1	0.88	0.36	6.37	0.75	88.6
Genista cinerea	65.7	103.1	0.32	0.21	170.9	0.57	0.63	5.61	0.71	73.2
Ononis fruticosa	49.2	100.8	0.43	0.16	147.3	0.7	0.37	6.87	0.69	77.6
Buxus sempervirens	53.1	113.2	0.5	0.23	329.5	0.45	0.46	11.7	0.56	88
Group 1	54.8 A	115.9 A	0.38 AB	0.18 A	189.6 A	0.63 AB	0.46 A	7.76 ABC	0.67 A	81.4 A
Anthyllis vulneraria	31.7	99	0.22	0.07	124.9	0.51	0.29	15.1	0.82	80.9
Quercus pubescens	28.1	100.7	0.33	0.26	82.3	0.96	0.79	1.4	1.93	91.5
Group 2	29.8 B	99.9 AB	0.28 A	0.17 AB	102.2 B	0.74 A	0.56 AB	7.77 ABC	1.41 C	86.5 A
Juniperus communis	65.6	77	0.21	0.13	103.1	0.59	0.6	5.55	0.87	79.6
Thymus serpyllum	20.2	94.9	0.20	0.14	136.3	0.57	0.70	11.2	0.59	88.8
Dorycnium pentaphyllum	34.4	190.9	0.79	0.44	344.9	0.47	0.56	3.83	1.62	46.4
Group 3	43.6 B	110.1 A	0.35 AB	0.21 AB	171.8 AB	0.56 B	0.62 B	6.95 ABC	0.96 B	74.6 A
Pinus nigra	39.2	77	0.56	0.32	176.9	0.57	0.57	2.25	0.77	42.2
Staehelina dubia	34	54.2	0.38	0.21	180.2	0.5	0.57	4.8	1.47	54.6
Lavandula angustifolia	38.7	91.6	0.44	0.24	263.3	0.56	0.55	11.3	0.37	88.6
Group 4	37.5 B	73.9 B	0.47 B	0.27 B	201.2 A	0.55 B	0.56 B	5.46 ABC	0.88 AB	58.5 B

Table 7 Results of the discriminant analysis on ten plant traits (Wilks lambda = 0.19, $p<0.001$). Wilks lambda values reflect the discriminant power: the lower the Wilks lambda, the higher the discriminant power

Trait	Wilks lambda	p
%FR	0.75	<0.001
L_{R1}/D	0.77	<0.001
a/E(a)	0.79	<0.001
$\%DW_{R1}$	0.85	0.0013
Surf/D	0.88	0.006
RTD	0.88	0.007
H/D	0.88	0.008
SRL	0.90	0.018
DW_R	0.94	0.11
V	0.94	0.13

angustifolia was found to be the least resistant species (σ = 2.77 MPa; L_{R1}/D=91.6; a/E(a)=0.37; %FR=88.6).

The correlation analysis showed no significant correlations between critical stress and any one plant trait (Table 8).

Discussion

In all species, the maximum uprooting force increased linearly with stem basal diameter, a surrogate for plant size: the larger the plant, the higher its anchorage strength. This result is not surprising and confirms, for small plants and seedlings, the relationship between plant size and resistance to uprooting already found for other types of plants in previous studies (Mickovski et al. 2005; Schutten et al. 2005). Moreover, F_{max} values, which ranged from 29 to 430 N, are similar to those reported in other studies (Karrenberg et al. 2003; Mickovski et al. 2005). Standardized by the basal cross-sectional area (σ), the values differed significantly between species, suggesting that anchorage strength may be dependent on other plant traits.

The results did not show any particular influence of growth forms or successional status on uprooting resistance of species at the early stages of development. Indeed, tests were carried out on small plants with comparable tap-like root systems whose rooting depth did not exceed 50 cm and did not reach the bedrock. This conclusion might be different on mature plants for which root system size, morphology, and biomechanical properties may show greater differences between trees, shrubs, and grasses.

The correlation analyses showed that anchorage strength cannot be related to one particular plant trait. As expected, it depends on a combination of several traits. In this study, we found that resistance to lateral uprooting is mainly determined by three traits: the root slenderness ratio (L_{R1}/D), the percentage of fine roots (%FR), and the topological index (a/E(a)). L_{R1}/D is related to anchorage in depth. High L_{R1}/D values correspond to a greater growth of the tap root in length than in width and thus result in a long and thin tap root. The major mechanical role of the tap root in providing resistance to lateral uprooting by external forces has already been highlighted (Ennos 1993; Ennos 2000). In juvenile individuals, this main rigid axis acts as a stake in the ground with lateral roots acting as guy ropes to withstand lateral loading (Ennos 1994; Fourcaud et al. 2008). The two other traits, a/E(a) and %FR, are related to horizontal anchorage and lateral roots. In particular, a low topological index indicates a highly branched root system per unit volume of soil with branches on second-and third-order lateral roots, while high values indicate a herringbone-like root system with branches on the tap root only. Low a/E(a) values and high %FR values result in more root-soil contact and in a quicker transfer of the external forces into the soil. The results for *L. angustifolia* suggest that a combination of high L_{R1}/D and %FR values and a low a/E(a) value does not always result in a strong anchorage. In this case, there were too many roots. Soil failure, rather than root failure, occurred around the root balls which were then removed from the soil at very low forces

Table 8 Correlations between critical stress σ and ten plant traits. The parameters presented are correlation coefficients (r) and the significance of the relationship (p)

Trait	r	p
%FR	0.48	0.11
H/D	0.47	0.12
DW_R/D	−0.43	0.16
$\%DW_{R1}$	0.40	0.19
L_{R1}/D	0.37	0.24
V/D	−0.33	0.3
RTD	−0.33	0.3
Surf/D	−0.28	0.38
SRL	0.1	0.76
a/E(a)	−0.08	0.81

(Ennos 2000). Consequently, there is an optimal number of roots to efficiently anchor the plant to the soil, which could be described by threshold a/E(a) and %FR values.

Two other traits, %DW_{R1} and H/D, may have an influence on anchorage strength. %DW_{R1}, like L_{R1}/D, refers to rooting depth and vertical anchorage. H/D can be considered the aboveground analog of L_{R1}/D. Insofar as anchorage is most often related to belowground traits, the measurement of which is destructive, a routine and immediate application of results by practitioners is not easy. Therefore, the efficiency of this trait (H/D), simple and easy to measure, in evaluating uprooting resistance should be further investigated in future studies.

For juvenile plants growing on marly soils, our results suggest that the best root system design to resist lateral loading on marls is a long and thin tap root with fine lateral ramifications. This conclusion is in agreement with Khuder et al. (2007), who highlighted the role of a deep tap root in young trees in preventing toppling, and with previous results on lateral roots (Stokes et al. 1996; Bailey et al. 2001).

The present study focused on morphological traits inspired from Table 1. Of course, traits related to root biomechanical properties, such as root tensile strength or root stiffness also influence plant anchorage. Several authors have studied root tensile strength and have found significant differences between species (Bischetti et al. 2005; Mattia et al. 2005). Mickovski et al. (2007) showed that more rigid root models had greater resistance to uprooting than more flexible root models. Neither our experiment, nor the data available in the literature allow us to specify the role of root strength in uprooting resistance, but further investigations on that area would provide useful information.

Given the restrictions of field research, the number of samples per species was sometimes low in our study, especially for the two *Ononis* species for which only six and nine valid uprooting tests could be retained. Moreover, our results only concern Mediterranean vegetation growing on black marls. Further investigations are needed to determine whether root traits involved in juvenile plant anchorage are the same for different soil types and different plant species.

The results of our study provide new elements that can help explain and predict uprooting resistance of small plants that colonize eroded lands after restoration. These findings can have important applications in land management of eroded marly lands of the French Southern Alps. Firstly, these results can be used to evaluate, the resistance of species used by practitioners for erosion control or the efficiency of the existing vegetation cover to withstand erosive pressures, based on plant traits. Secondly, the results can be used for prediction purposes. However, they have to be discussed with regard to species ecology (Barrouillet 1982; Rameau et al. 1993). Parameters such as germination and growth rates, vegetative multiplication ability, and invasion risk can balance the conclusions on species efficiency in resisting uprooting. *B. sempervirens* and *G. cinerea* were found to be among the most resistant species but their slow growth rates do not make them the best species for rapid colonization. On the other hand, *O. fruticosa* and *O. natrix* are pioneer species that have much higher seed production, germination, and growth rates and can colonize large surface areas in a few years. In addition, *O. fruticosa*, already used for land rehabilitation, is known to spread widely by vegetative multiplication. *J. communis* and *S. dubia* are pioneer species and therefore would be suitable for the colonization of the most degraded soils. Nevertheless, *S. dubia* would be more vulnerable to intense erosion than *J. communis* since it was found to be one of the least resistant species. The other shrubby species, *T. serpyllum*, *D. pentaphyllum*, and *L. angustifolia*, all post-pioneer woody species, had quite low anchorage strength and present slow growth in the field compared to *A. vulneraria*, a herbaceous post-pioneer species, which anchored well in the soil. This result suggests that self-supporting herbaceous species (forbs and legumes) could resist erosive constraints and could allow faster soil restoration (humus layer, soil structuring, depth). Among tree species, *P. nigra*, a pioneer species, is very efficient for degraded soil colonization, as evidenced by old reforestation operations and the large surface areas it covers. However, its anchorage strength is low and adults have a high mortality due to mistletoe infestation (*Viscum album* L.). Forest regeneration with late succession species such as *Q. pubescens*, which is much more resistant to uprooting than *P. nigra*, would therefore be useful.

To carry out a global diagnosis, results on species efficiency for soil protection, e.g. soil fixation by roots and sediment trapping, should also be taken into account. Flume experiments on species efficiency in

preventing marly topsoil erosion during concentrated flow are in preparation and should provide useful additional information. Long-term predictions could be made by combining the results of the present study with knowledge of vegetation colonization and succession on marly lands (Vallauri 1997; Rey et al. 2005; Burylo et al. 2007). This knowledge would improve existing ecological tools so that the evolution of vegetation cover after rehabilitation could be modeled. Therefore, plant community efficiency for erosion control could be better predicted when diagnosing how vulnerable marly lands are to erosion.

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