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Effect of root system morphology on root-sprouting and shoot-rooting abilities in 123 plant species from eroded lands in NE Spain

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Running heading: Effect of root morphology on root-sprouting

Abstract.

- *Background and aims.* The objective of this study was to test whether the mean values of several root morphological variables were related to the ability to develop root-borne shoots and/or shoot-borne roots in a wide range of vascular plants.
- *Methods.* A comparative study was carried out on the 123 most common plant species from eroded lands in NE Spain. After careful excavations in the field, we measured the maximum root depth, absolute and relative basal root diameter, specific root length (SRL), and the root depth/root lateral spread ratio on at least three individuals per species. Shoot-rooting and root-sprouting were observed in a large number of individuals in many eroded and sedimentary environments. The effect of life history and phylogeny on shoot-rooting and root-sprouting abilities was also analysed.
- *Key results.* The species with coarse and deep tap roots tended to be root-sprouting and those with fine, fasciculate and long main roots (which generally spread laterally), tended to be shoot-rooting. Phylogeny had an important influence on root system morphology and shoot-rooting and root-sprouting capacities. However, the above relations stood after applying analyses based on phylogenetically independent contrasts (PICs).
- *Conclusions.* The main morphological features of the root system of the study species are related to their ability to sprout from their roots and form roots from their shoots. According to our results, such abilities might only be functionally viable in restricted root system morphologies and ecological strategies.

Keywords. Root architecture, root morphology, root-borne shoots, shoot-borne roots, sprouting, soil erosion, functional strategies.

INTRODUCTION

One key morphological feature of plants is their sprouting ability, which is fundamental to understand their functional and evolutionary strategies (Bond and Midgley, 2001; Del Tredici, 2001; Bond and Midgley, 2003). Sprouting promotes a protraction of the life span of mature individuals following disturbance, while the development of shoot-borne roots or root-borne shoots facilitates vegetative reproduction (Jeník, 1994; Del Tredici, 2001). Sprouting requires the presence of surviving meristems and stored reserves. Allocation of resources to storage has an important cost on growth and reproduction, so sprouters generally show less seed production, less seedling survival, and slower growth rates than non-sprouters (Hansen *et al.*, 1991; Iwasa and Kubo, 1997; Verdú, 2000; Bond and Midgley, 2001; Bond and Midgley, 2003). Sprouting capacity depends on several factors, especially plant age and size, and the type and severity of disturbances (Bellingham and Sparrow, 2000; Bond and Midgley, 2001). Bellingham and Sparrow (2000) proposed a model based on the trade-off between allocation to re-sprouting vs. seeding. As the frequency of disturbance increases, re-sprouting rates in plant communities also increase (Midgley, 1996). When disturbance exceeds the tolerance threshold of sprouters, seeders have an advantage because of their higher growth rates and their greater colonization capacity. Following the predictions of Bellingham and Sparrow's model, regeneration responses must follow a continuum. However, in most studies only a few plant-response types are distinguished. For example, only two types (seeders and sprouters) are generally used to describe plant responses to intense fire events and other severe disturbances (Vesk and Westoby, 2004). Contrastingly, Groff and Kaplan (1988) differentiated four structural classes of rooted plants: class 1: bipolar plant; plants lacking shoot-borne roots and root-borne shoots; class 2: plants with only shoot-borne roots, i.e. plants able to root from layered branches, stems, or stem-derived structures: rhizomes, stolons, lignotubers, etc.; class 3: plants with only root-borne shoots, i.e. plants with root systems able to produce shoots, commonly know as root suckers; and class 4: plants with the ability to produce both shoot-borne roots and root-borne shoots. This approach has the advantage that takes into account both the ability of plants to sprout from its roots and the ability to form roots from its shoots.

The functionality of a root system is partially determined by its size and its morphological features (Fitter, 1991). It is generally assumed that deep roots help to avoid water stress in semi-arid and Mediterranean-type climates by reaching deep soil horizons which store water even in the driest periods (Levitt, 1980; Fitter and Hay, 1987; Canadell and Zedler, 1994; Canadell *et al.*, 1996). However, Schenk and Jackson (2002) found that plants of sub-humid climates had deeper maximum rooting depths than plants of dry climates, and that the below-ground/above-ground mass quotient increased with aridity only for herbaceous plants. Lateral spread enables roots to increase the explored soil surface (Rundel and Nobel, 1991). Extended lateral roots are advantageous for water and nutrient uptake after small rainfall events, or to survive in areas with shallow soils, with the highest nutrient concentration in the superficial soil horizons (Canadell and Zedler, 1994).

Plants of arid and semi-arid environments normally produce two types of roots: fine and coarse roots (Wilcox *et al.*, 2004). The former are more active in the absorption of water and nutrients and have higher rates of growth and turnover (Caldwell and Richards, 1986; Kummerow, 1989; Wilcox *et al.*, 2004). Root absorption capacity is related to total and specific root length (SRL, total root length/root dry weight) which in turn is enhanced by a higher fine-root density (Fitter, 1991). Plants with highly competitive root systems have high

fine-root densities (root length per soil volume) that explore soil intensively, while plants with less competitive root systems have low fine-root densities that can explore large volumes of soil but do not exploit it intensively (Caldwell and Richards, 1986). Less competitive root systems can be advantageous in infertile soils as they are better adapted to locate mobile or spatially uneven resources (Fitter and Hay, 1987; Fitter *et al.*, 1988; Fitter, 1991). Coarse roots can penetrate hard soils and reach deep horizons and water sources (Goss, 1977; Walker and Noy-Meir, 1982), allowing better anchorage than fine roots and the storage of carbon, nutrients and water (James, 1984; Boot and Mensink, 1990). Water storage in coarse roots can be advantageous for species that undergo long periods of drought (Kummerow, 1982).

In this study the approach of Groff and Kaplan (1988) was followed, considering both shoot-rooting and root-sprouting abilities of vascular plant species. Few studies have considered the morphological implications of root systems with regard to plants root-sprouting and shoot-rooting abilities. Several authors have reported that species with thick and/or very deep roots tend to sprout after fire (Hellmers *et al.*, 1955; James, 1984; Canadell and Zedler, 1994), but most of these studies are based on general field observations without detailed analyses and measurements (but see Bell *et al.*, 1996). It is generally accepted that sprouters in fire-prone ecosystems usually allocate more reserves to roots, as compared to shoots, than non-sprouters (Pate *et al.*, 1990; Hansen *et al.*, 1991; Bell *et al.*, 1996). However, studies about sprouting after fire do not discriminate if sprouts are produced from roots, stems or stem-derived structures (e.g., stolons or rhizomes). Furthermore, literature dealing with sprouting responses under edaphic disturbances is very scarce (but see Sakai *et al.*, 1995) as most studies on plant sprouting responses have dealt with responses to fire (López-Soria and Castell, 1992; Trabaud, 1992), hurricanes, wind throws (Bellingham *et al.*, 1994; Zimmerman *et al.*, 1994) and tree cuttings (Flinn and Wein, 1977; Mazzoleni and Esposito, 1993).

Several studies have demonstrated the functional relevance of the morphological variables: maximum root depth (Canadell and Zedler, 1994; Canadell *et al.*, 1996); lateral root spread (Rundel and Nobel, 1991); specific root length (SRL), which is related to fine-root density (Fitter, 1991); and main-root diameter (James, 1984; Boot and Mensink, 1990). In the present study, we formulate the hypothesis that plants with different abilities to develop root-borne shoots and shoot-borne roots might show different values of these four variables. To test this hypothesis a comparative analysis was performed including the aforementioned root morphological features and the capacity to develop shoot-borne roots and/or root-borne shoots of the most common 123 species of vascular plants growing in eroded lands from the NE Iberian Peninsula. The effect of life history and phylogeny on root-sprouting and shoot-rooting abilities was also explored.

MATERIAL AND METHODS

Species and study area

A survey of 734 vegetation relevés was performed on scrub pastures and badlands affected by different degrees of soil erosion. The 123 most frequent phanerogams, i. e. those that appeared in at least 5 % of the relevés, were selected. This large species set included most of the growth forms found in the territory, from shrubs to annual plants. The area surveyed was located between the middle Ebro Valley and the Pre-Pyrenees (NE Spain), and comprised the following substrates: almost pure gypsum (350 mm average annual rainfall), gypsum

mixtures with clays or marls (400-500 mm), Miocene clays from the Somontanos (500 mm), Eocene Pre-Pyrenean marls (800 mm) and Eocene Pyrenean flysch (1000 mm). For more details about the study area and field survey see Guerrero-Campo (1998) and Guerrero-Campo and Montserrat-Martí (2000 and 2004).

Root morphological features

To estimate the different types of rooting or sprouting characteristics, we surveyed several eroded sites in detail, particularly highly eroded surfaces, talus slopes and sedimentary sites. Data were pooled with previous observations to build a large data base. For each species we recorded the cases of observed root-borne shoots and shoot-borne roots. There was a continuous variation between the species that produced large amounts of shoot-borne roots and those that produced no shoot-borne roots. A similar variation pattern was observed with regard to root-borne shoots. However, in order to simplify the interpretation of results, and due to the great number of species analyzed, we only considered the presence/absence of each ability in the study species set.

At least three well developed specimens of each species were carefully excavated in natural populations growing in sites with few stones and rocks to ensure a free development of root systems. To facilitate excavation, we selected plants growing near the faces of road through-cuts or gullies. When large differences were found between the root systems of the three specimens, additional individuals were excavated. Selected specimens were well developed adults, except for the few large shrubs studied which were young individuals. In each root system we measured the maximum depth, maximum lateral spread, absolute diameter (basal diameter of the main root axis at 10 cm depth, or at 5 cm in the shallow-rooted annual plants) and the relative basal root diameter. The relative basal root diameter is an index that relates absolute basal root diameter (mm) with the average general dimensions of the root system, i. e. root depth (cm) and root lateral spread (cm). It was calculated according to the following formula:

$$\text{Relative basal root diameter} = 1000 \times [(\text{absolute basal root diameter}) / (\text{maximum root depth} \times \text{maximum root lateral spread})^{1/2}]$$

If the root system had more than one root axis we measured the thickest one. We considered the specific root length (SRL: total root length / root weight) as a variable related to the absorption capacity and the intensity of exploration of the soil volume (Caldwell and Richards, 1986; Fitter, 1991). The large species set compromised the measurement of the SRL of all sampled species in detail. Accordingly, SRL was measured in the whole root system of 14 representative species which were ranked according to their SRL values. Four categories of SRL were then recognized within the gradient of variation displayed by the 14 reference species. Finally, unmeasured species were assigned to one of the four SRL categories by visual comparison with measured plants, which had been pressed and preserved in a herbarium. To enable the comparison between SRL data and the rest of variables, we grouped the root variables in categories. Accordingly, species maximum root depth, species depth / lateral spread ratio, and average relative basal root diameter were included in four categories, while average absolute basal root diameters were included in three categories. Continuous data for these variables for the study species can be found in Appendix 1.

Statistical analyses

Log-likelihood ratio analyses (G) were used to assess the relationships between shoot-rooting and root-sprouting abilities and root morphological features; to compare the former abilities and plant life history; and to explore the differences between these relationships in each of the main families studied. A taxonomic analysis was performed to test whether the results were affected by relations above the species level (Felsenstein, 1985; Harvey and Pagel, 1991). Provided we had discrete variables and little phylogenetic information on the taxa used, we chose the paired comparison method combined with a sign test (Ackerly, 2000; Harvey and Pagel, 1991). This method provides a very robust and conservative approach to significance testing for independent contrasts, maintaining very low Type I error rates, but greatly reducing statistical power for detecting non-zero correlations (Ackerly, 2000). For each set of two subtaxa belonging to the same taxa (e.g. species within genera) and differing in shoot-rooting capacity or root-sprouting, the trend of the relationship was either positive, negative or neutral. If more than two taxa were available (for example if there were three genera in a family), we chose the taxon to be included in the pair randomly. Always different taxa were then used for a similar comparison at the next taxonomic level (e.g. families within orders) always following parsimony rules and using the Angiosperm phylogeny of Soltis and co-workers (2000). After combining the results at different taxonomic levels, several one tailed binomial tests were performed to verify whether there were more positive or negative relationships than expected or if there were no underlying relationships (relationships were significant when $P \leq 0.05$). All statistical analyses were conducted with SPSS 11.0 (SPSS Inc, Chicago, USA).

RESULTS

Root systems and root/shoot relationships

Shoot-rooting species

Shoot-rooting species were quite abundant among the studied species. There was not a clear relation between shoot-rooting capacity and maximum root depth, relative root depth and absolute basal root diameter (Fig. 1). Shoot-rooting capacity was significantly associated with high or intermediate SRL (Fig. 1)., In addition, shoot-rooting was related to the relative basal root diameter, being significantly more frequent in species with fine than in species with coarse relative root diameters (Fig. 1).

When annuals and grass-like species were excluded from the analyses, the above relations stood with the exception of relative basal root diameter. The above relationships also stood after applying analyses based on phylogenetically independent contrasts (PICs) (Table 1). Accordingly, the SRL and the relative basal root diameter are related to the shoot-rooting capacity, but not the relative root depth, the maximum root depth and the absolute basal root diameter are related (Table 1).

Root-sprouting species

Root-sprouting species had significantly deeper root systems than non root-sprouting species (Fig. 2). There were no significant differences in the relative root depth of root-sprouting and non root-sprouting species, though there were no root-sprouting species with low values of this ratio (Fig. 2). Root-sprouters had significantly lower SRL than non root-sprouters, root-sprouting ability being absent in species with high SRL (Fig. 2). Root-sprouting was significantly associated to coarse or medium relative basal root diameters, but never to very

low values (Fig. 2). This tendency was also evident in the case of absolute diameter (Fig. 2). Accordingly, plants with root-borne shoots never had fine main roots (Fig. 2). *Coris monspeliensis* and *Euphorbia minuta* were the species which could form root-borne shoots and had the finest main roots (around 2 mm at 10 cm depth, see Appendix 1).

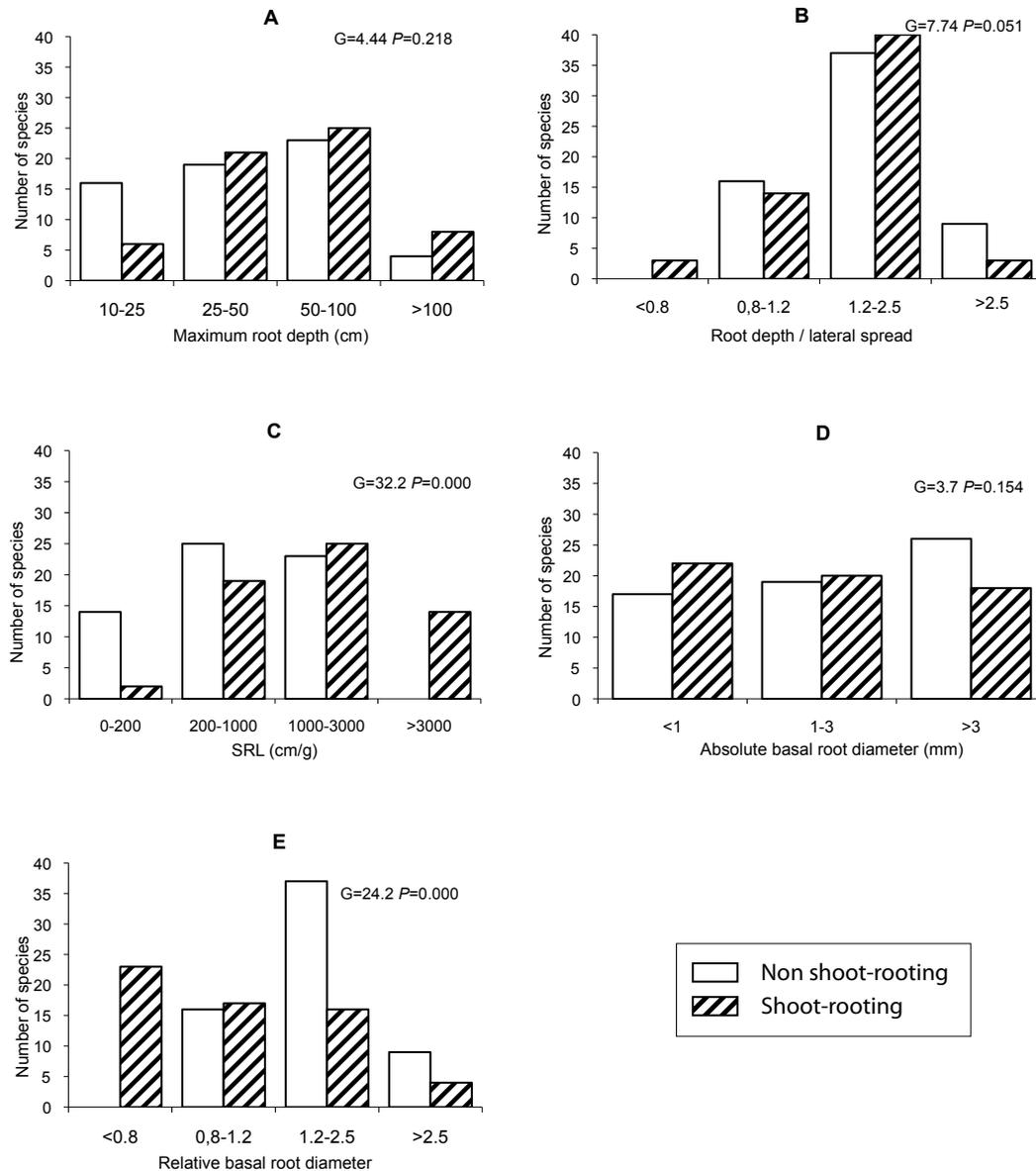


Fig. 1. Number of shoot-rooting and non shoot-rooting species as related to (A) maximum depth, (B) root depth/ root lateral spread ratio, (C) fine-root density (SRL), (D) absolute basal root diameter and (E) relative basal root diameter. G-statistics and P-values are provided after a log-likelihood ratio analysis ($\alpha = 0.05$).

When analyses based on phylogenetic independent contrast (PICs) were applied, the above relationships stood. All root system features analyzed, except the root depth/root lateral spread ratio, were significantly related with root-sprouting (Table 2). However, when annuals

and grass-like species were excluded from the analysis, all significant relationships disappeared .

Table 1. Taxonomic relatedness analysis of the relationship between shoot-rooting capacity and the studied morphological features of roots.

Taxonomic level	Maximum depth	Relative depth	SRL	Absolute diameter	Relative diameter
Species within genera					
<i>Centaurea</i>	-	-	+	-	-
<i>Convolvulus</i>	-	-	=	-	-
<i>Ononis</i>	=	=	+	=	=
<i>Hippocrepis</i>	+	=	-	+	+
<i>Linum</i>	+	-	=	+	=
Genera within families					
Rosaceae	-	-	+	=	-
Rubiaceae	+	-	+	-	-
Apiaceae	+	+	+	+	-
Families within orders					
Lamiales	+	-	+	-	-
Euphorbiales	+	-	+	-	-
Orders within subclasses					
Cariophyllidae	+	+	+	-	-
Rosiflorae	-	-	+	+	-
Total	6+, 5-	2+, 8-	9+, 1-	4+, 6-	1+, 9-
<i>P</i> (one-tailed binomial test)	0.500	0.054	0.011	0.377	0.011

+, indicates that the relationship for the set of subtaxa belonging to the same taxon was *positive*, i.e. shoot-rooting species had greater values of the measure variables than non shoot-rooting species; - indicates that the relationship was *negative*; = indicates no significant differences. P-values smaller than 0.05 are in bold.

Life history and root-shoot relationships

Life history had a strong effect on the ability to form roots from shoots; shoot-rooting species being more frequent among perennial plants (Fig. 3). Life history had also a significant effect of on root sprouting ability . Thus, annual plants were unable to form shoots from their roots (Fig. 3).

Phylogeny and root-shoot relationships

Phylogeny had a significant effect on the shoot-rooting ($G = 47.5$, $P < 0.001$) and root-sprouting ($G = 13.1$, $P = 0.004$) abilities of study species. Cistaceae were unable both to root-sprout and to form roots from its shoots; Poaceae were only able to form roots from its shoots but not to sprout from its roots; while Asteraceae and Fabaceae had all sort of combinations between both abilities. The percentage of variation of root/shoot relationships in the main taxonomic families is summarised in Fig. 4.

DISCUSSION

In general, our results agree with the hypothesis that the ability to produce shoot-borne roots and root-borne shoots is related to basic morphological characteristics of the root system. Nevertheless, other linked aspects like phylogeny and life history had some effect on these relationships, although they did not change the main tendencies found in the study.

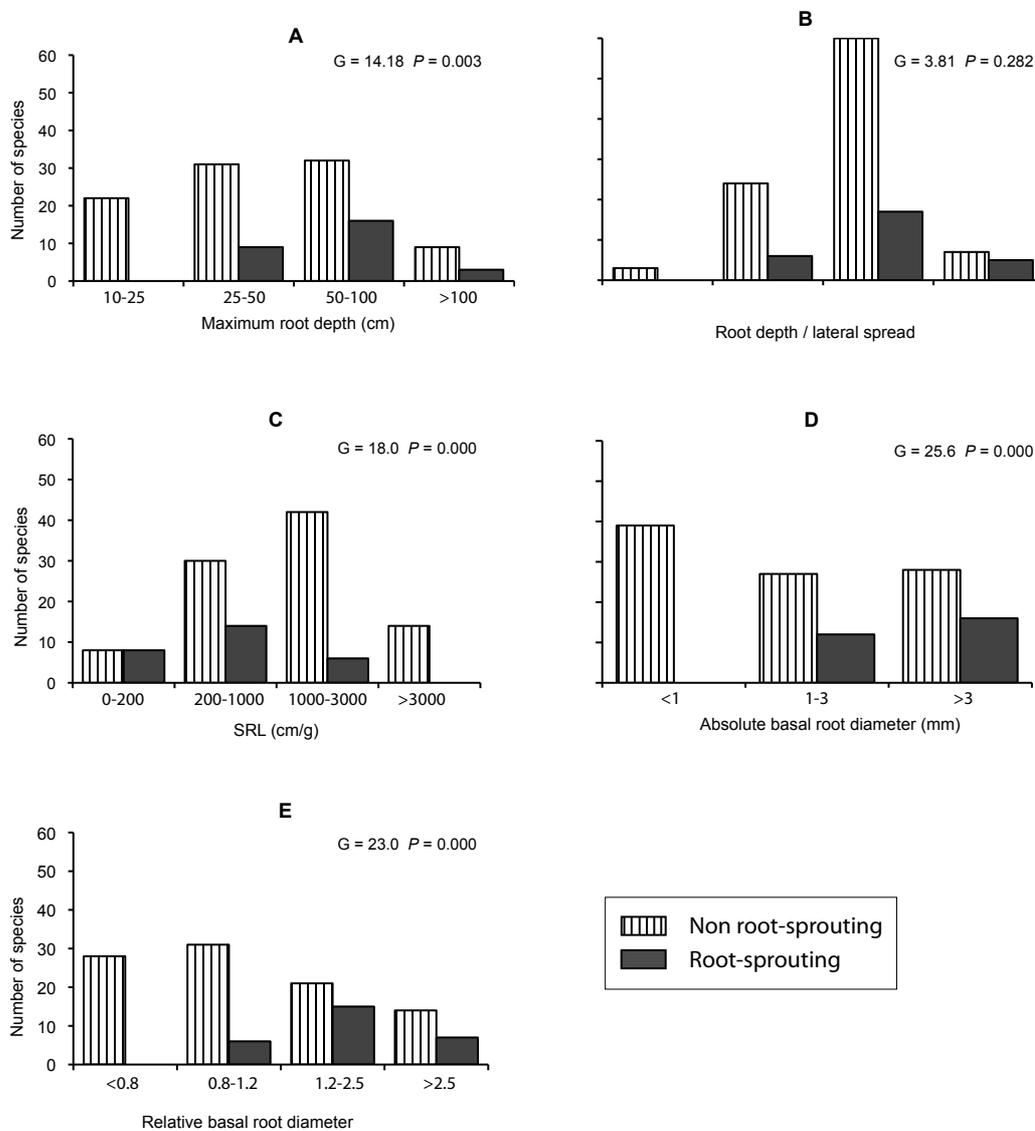


Fig. 2. Number of root-sprouting and non root-sprouting species as related to (A) maximum depth, (B) root depth/ root lateral spread ratio, (C) fine-root density (SRL), (D) absolute basal root diameter, and (E) relative basal root diameter. G-statistics and P-values are provided after a log-likelihood ratio analysis ($\alpha = 0.05$).

Well-developed tap roots were generally associated with deep root systems and with species developing root-borne shoots, while fasciculate roots with numerous fine roots were usually associated with species forming shoot-borne roots but never root-borne shoots. In the studied species, shoot-rooting was related to laterally spreading root systems reaching

moderate depths, high fine-root densities (SRL) and fine main root axes. These features are clearly adaptive for those species which tend to spread horizontally. Decumbent shoots or shoot-derived structures, like stolons and rhizomes, allow plants to explore the horizons close to the soil surface. Such features favour wide-spread clonal growth which in turn is favoured in fertile sites (Shumway, 1995; Jónsdóttir and Watson, 1997). In shoot-rooting species, shoots and shoot-derived structures can work as storage organs (de Kroon and van Groenendael, 1990), while roots mainly function as absorbing organs. To maximise the absorbing capacity, roots allocate most of their resources to develop numerous fine roots, achieving a high fine-root density and a high SRL (Kummerow, 1981; Caldwell and Richards, 1986). Grass-like species might be an extreme case within shoot-rooting species, as they present a very high fine-root density (SRL) and a massive production of shoot-borne roots. However, some shoot-rooting species, like *Gypsophila hispanica*, *Santolina chamaecyparissus*, *Rosmarinus officinalis* and *Thymus vulgaris*, lacked several of the characteristic features of shoot-rooting plants, like a high fine-root density (SRL), important lateral root spread, or shallow rooting depths. These species might use their ability to develop shoot-borne roots to maintain a dense fine root layer near the soil surface, which might enable them to take advantage of small and moderate rainfall events and to exploit the high fertility of the upper soil layer. In addition, some of these species have deep main roots which can reach water stored in deep soil horizons. This architecture is called a mixed or dual root system (Dawson and Pate, 1996) and seems to be favoured by the seasonal Mediterranean climate (Canadell and Zedler, 1994; Dawson and Pate, 1996). We found clear examples of this root type in *Salsola vermiculata*, *Gypsophila hispanica*, *Atriplex halimus* and *Rosmarinus officinalis*. All of these species are woody plants, and hence they fit the predictions of the two-layer model of soil partitioning between woody and herbaceous plants (Walker and Noy-Meir, 1982). According to this model, only woody species can obtain resources from the deepest part of the soil, while both woody and herbaceous species compete for resources in the upper soil layers (Walker and Noy-Meir, 1982; but see Schenk and Jackson, 2002).

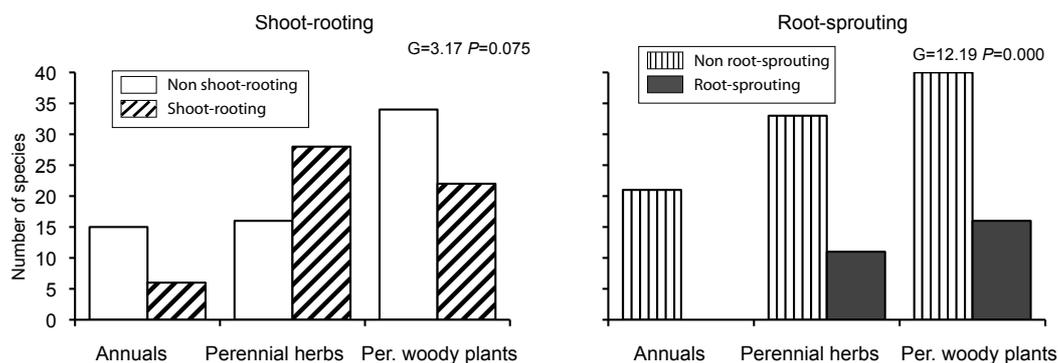


Fig. 3. Number of species with different root/shoot relationships within the main life history types considered. G-statistics and P-values are provided after a log-likelihood ratio analysis ($\alpha = 0.05$).

A different trend is followed by species bearing root-borne shoots, which might be a highly adaptive feature when roots perform important functions other than absorption. These roots tend to grow deeper with low lateral spread and to be thicker in order to penetrate tough soil horizons (Goss, 1977; Fitter, 1991). Accordingly, in this study the basal diameter of the main root was always greater than 2 mm in root-sprouting species. The need to store water and nutrient reserves to supply root sprouting might also lead to greater main root diameters (Kummerow, 1982; Bell *et al.*, 1996). In Mediterranean plants, root swelling is frequently used to provide a place for resource storage to survive fire, defoliation and drought (James, 1984; Kummerow, 1989; Canadell and Zedler, 1994). Non-structural carbohydrates and particularly starch are necessary to start sprouting, so the amount of stored starch in roots, stumps or stems is a good indicator of the species sprouting ability (Rundel and Parsons, 1980; Baker *et al.*, 1982; Bell *et al.*, 1996). According to Bellingham and Sparrow (2000) and Iwasa and Kubo (1997), the ability to sprout depends on the presence of storage organs. For example, in graminoid and shrub species of the Australian areas where fire is an important factor, sprouters present at least four times higher root starch concentrations and root:shoot ratios than seeders (Pate *et al.*, 1990; Bell and Pate, 1996). These root systems can therefore explore deep horizons and store water and nutrients. The high amount of resources invested in the construction of such large and expensive roots might be compensated by the species faculty to survive, producing root-borne shoots when the above-ground biomass is destroyed by disturbances (Iwasa and Kubo, 1997).

Table 2. Taxonomic relatedness analysis of the relationship between root-sprouting capacity and the studied morphological features of roots.

Taxonomic level	Maximum depth	Relative depth	SRL	Absolute diameter	Relative diameter
Species within genera					
<i>Centaurea</i>	+	-	-	-	-
<i>Euphorbia</i>	+	=	+	+	+
<i>Teucrium</i>	+	=	=	+	+
<i>Linum</i>	+	-	=	+	+
Genera within families					
Boraginaceae	+	+	-	+	+
Cariophyllaceae	=	-	-	+	+
Fabaceae	+	-	-	+	-
Primulaceae	+	+	-	+	+
Rosaceae	+	-	-	=	+
Apiaceae	-	+	-	+	+
Families within orders					
Dipsacales	+	-	-	+	+
Orders within subclasses					
Asteriflorae	+	+	-	+	+
Cariophyllidae	-	+	-	-	=
Total	10+, 2-	5+, 6-	1+, 10-	10+, 2-	10+, 2-
<i>P</i> (one-tailed binomial test)	0.019	0.500	0.005	0.019	0.019

+, indicates that the relationship for the set of subtaxa belonging to the same taxon was *positive*, i.e. root-sprouting species had greater values of the measure variables than non root-sprouting species; - indicates that the relationship was *negative*; = indicates no significant differences. P-values smaller than 0.05 are in bold.

Life history might affect root system features and root/shoot relationships, as it is a very important attribute of plant functional strategy (Grime 2001). Annual species were unable to produce shoot-borne roots or root-borne shoots, with the exception of annual grass-like species (class 2; Groff and Kaplan, 1988). This is an inherent characteristic of the ecological strategy of annual plants, which are commonly ruderal species with short-lived organs and high reproductive and growth rates (Grime 2001). This strategy is incompatible with sprouting ability, as it requires allocation to storage organs with detriment to resource investment to growth and reproduction (Bellingham and Sparrow, 2000; Bond and Midgley, 2001). Consequently, annual species share many root system characteristics, including shallow maximum depths, fine main roots and intermediate or high SRL. The species that can produce shoot-borne roots and/or root-borne shoots might have a very different functional strategy, since their goal is long-term survival. Accordingly, such species comprised perennial herbs and woody plants in our study.

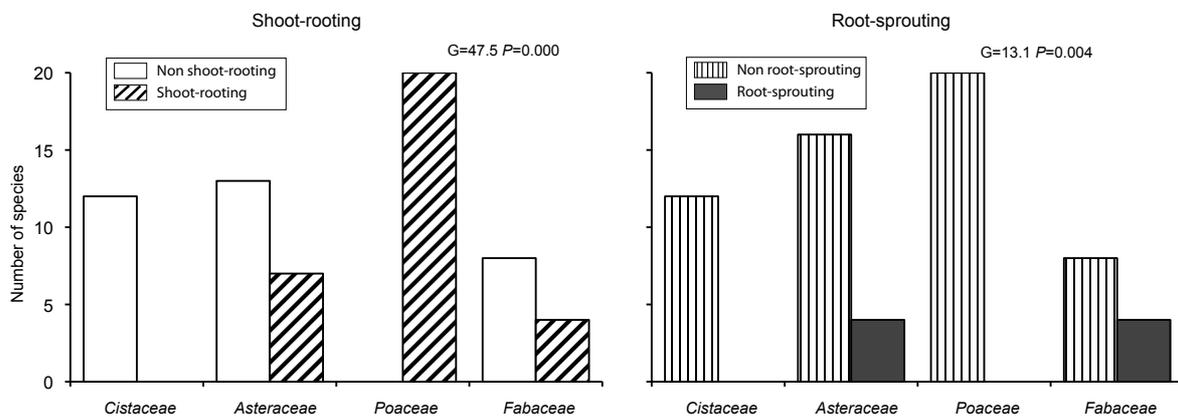


Fig. 4. Number of species with different root/shoot relationships within the main families considered. G-statistics and P-values are provided after a log-likelihood ratio analysis ($\alpha = 0.05$).

Functional strategies and life histories were not the only factors that explained the observed relationships between root system morphology and the capacity of plants to root-sprout and form roots from shoots. Phylogeny also has an important influence as it shapes many root system features (Klepper, 1987; de Kroon and van Groenendael, 1990) such as the main-root diameter (Fitter, 1991). However, other root features such as root depth and lateral root spread are less influenced by phylogeny (Guerrero-Campo, 1998). Phylogeny explained some differences in the observed shoot-root relations through the study species at a family level: all the studied Cistaceae were unable both to root sprout and to produce shoots from their roots; and Poaceae were all shoot-rooting plants. However, Fabaceae, Asteraceae, Lamniaceae and a single genus like *Centaurea* all included different classes of root/shoot relationships. Furthermore, most relationships found in this study between the features of root system and the types of root/shoot relationship stood after applying phylogenetical independent contrast. Such results agree with the hypothesis that sprouting and clonality are not conservative, but quite labile traits (Klimes *et al.*, 1997, Bond and Midgley 2003).

Accordingly, clonality has appeared several times during evolution, so clonal species might constitute a phylogenetically heterogeneous group (Klimes *et al.*, 1997). Nevertheless, a recent study shows that sprouters of the Mediterranean flora correspond to older lineages than non-sprouters or seeders (Pausas and Verdú, 2005).

In conclusion, our results demonstrate that the main morphological features of the root system of the 123 study species are clearly related to their faculty to produce root-borne shoots and/or shoot-borne roots. These relations are not only mediated by phylogeny, as the life history and the ecological strategy of each species are also crucial. According to our results, the ability to develop shoot-borne roots and root-borne shoots might only be possible and functionally viable in restricted root morphologies.

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Appendix 1. Features of the 123 most frequent vascular species in the studied eroded lands. Abbreviations: **R-S:** classes of shoot-root relationships following Groff and Kaplan (1988): 1, “bipolar” plants; 2, shoot-rooting plants; 3, root-sprouting plants; 4, shoot-rooting and root sprouting plants. **Mx. d.:** maximum root depth. **D/L:** root depth / lateral root spread. **SRL:** specific root length. **A. d.:** Absolute basal root diameter. **R. d.:** Relative basal root diameter. The first columns contain data in the categories used in the analyses, in the last four columns continuous original data are shown.

Plant species	R-S	Mx. d.	D/L	SRL	A. d.	R. d.	Mx.d	D/L	A.d.	R.d.
<i>Aegilops geniculata</i>	2	1	1	3	1	1	22	0,58	0,13	0,84
<i>Agropyron cristatum</i>	2	3	3	3	2	1	75	1,46	1,06	2,05
<i>Aphyllanthes monspeliensis</i>	2	3	3	3	1	1	80	1,00	0,84	2,09
<i>Argyrobium zanonii</i>	2	3	3	2	3	3	72	2,03	3,09	9,02
<i>Artemisia herba-alba</i>	2	3	3	3	3	3	92	0,78	3,33	8,96
<i>Asperula aristata</i>	1	2	2	3	1	1	51	0,67	0,92	2,50
<i>Asperula cynanchica</i>	1	2	3	3	2	2	48	1,28	1,48	4,50
<i>Aster sedifolius</i>	2	3	3	2	2	2	66	2,19	1,20	4,76
<i>Asterolinon linum-stellatum</i>	1	1	3	3	1	1	14	1,96	0,17	2,71
<i>Astragalus incanus</i>	3	3	3	1	3	4	102	1,76	5,71	16,35
<i>Atractylis humilis</i>	3	3	4	1	3	4	96	2,75	6,19	15,19
<i>Atriplex halimus</i>	2	4	3	2	3	4	155	2,13	4,95	12,61
<i>Avenula bromoides</i>	2	2	3	4	1	1	42	1,63	0,27	1,04
<i>Avenula pratensis</i> subsp. <i>iberica</i>	2	3	3	4	1	1	71	1,72	0,53	2,12
<i>Bombycilaena erecta</i>	1	1	3	3	1	2	11	1,75	0,24	3,84
<i>Brachypodium distachyon</i>	2	1	2	4	1	1	12	0,58	0,30	2,71
<i>Brachypodium ramosum</i>	2	3	3	3	1	1	63	1,20	0,55	2,00
<i>Bromus erectus</i>	2	3	3	4	1	1	75	0,77	0,38	1,31
<i>Bromus rubens</i>	2	1	2	4	1	1	12	0,69	0,28	2,43
<i>Bupleurum fruticoscens</i>	1	3	3	1	3	4	88	2,05	5,43	12,76
<i>Bupleurum rigidum</i>	1	3	4	1	3	4	70	3,72	6,08	27,76
<i>Buxus sempervirens</i>	2	4	2	3	3	3	110	1,00	4,25	10,21
<i>Camphorosma monspeliaca</i>	2	3	3	2	2	2	55	1,51	2,55	6,64
<i>Carduncellus monspeliensis</i>	2	3	4	1	3	3	73	4,17	3,84	11,09
<i>Carex flacca</i>	2	2	2	4	2	2	48	1,00	1,10	5,50
<i>Carex hallerana</i>	2	2	2	4	1	1	53	0,75	0,85	2,45
<i>Carex humilis</i>	2	3	2	4	1	1	78	1,00	0,81	2,70
<i>Centaurea linifolia</i>	4	2	3	2	2	2	60	1,39	1,81	5,57
<i>Centaurea melitensis</i>	1	1	3	3	2	2	30	1,86	1,03	5,69
<i>Centaurea ornata</i>	1	3	4	1	3	4	104	3,83	8,42	23,50
<i>Centranthus calcitrapae</i>	1	1	3	3	1	2	13	1,61	0,63	7,37
<i>Cephalaria leucantha</i>	3	3	4	1	3	4	102	4,83	5,31	19,37
<i>Convolvulus arvensis</i>	4	2	2	2	2	2	46	1,45	1,76	6,49
<i>Convolvulus lineatus</i>	3	3	3	2	3	3	102	2,23	3,28	10,62
<i>Coris monspeliensis</i>	3	2	2	2	2	3	52	1,06	2,04	7,74
<i>Coronilla minima</i> subsp. <i>minima</i>	4	3	3	2	2	2	96	2,08	2,42	6,43
<i>Crepis albida</i>	1	3	4	1	3	4	68	3,42	6,32	27,44
<i>Crepis vesicaria</i> subsp. <i>haenseleri</i>	1	2	3	3	2	3	24	2,59	1,38	9,22
<i>Dactylis glomerata</i>	2	2	3	4	1	1	37	0,88	0,50	1,93
<i>Desmazeria rigida</i>	2	1	1	4	1	1	10	0,82	0,12	1,27
<i>Dorycnium pentaphyllum</i>	4	4	3	2	3	3	117	2,32	5,12	8,93
<i>Echinops ritro</i>	3	3	4	1	3	3	97	3,61	3,65	11,53

Appendix 1. (Continuation).

Plant species	R-S	Mx. d.	D/L	SRL	A. d.	R.d.	Mx.d.	D/L	A.d.	R.d.
<i>Elymus pungens</i>	2	2	3	3	1	1	46	1,30	0,67	2,00
<i>Erodium cicutarium</i>	1	1	3	3	1	2	34	1,84	0,80	4,53
<i>Erucastrum nasturtiifolium</i>	3	2	3	3	2	3	52	1,95	2,89	8,59
<i>Eryngium campestre</i>	3	3	4	1	3	4	86	3,50	5,02	17,87
<i>Euphorbia flavicoma</i> subsp. <i>mariolensis</i>	3	3	3	1	3	4	94	2,44	5,30	16,69
<i>Euphorbia minuta</i>	3	2	3	2	2	3	34	1,80	2,30	10,64
<i>Euphorbia sulcata</i>	1	1	3	3	1	2	14	2,30	0,33	4,13
<i>Festuca</i> gr. <i>indigesta</i>	2	2	3	3	1	1	59	0,80	0,30	1,32
<i>Festuca rubra</i>	2	2	3	4	1	1	48	1,10	0,47	2,10
<i>Filago pyramidata</i>	1	1	3	3	1	2	14	1,31	0,37	4,05
<i>Fumana ericifolia</i>	1	2	2	2	3	3	49	0,89	3,25	10,59
<i>Fumana ericoides</i>	1	3	3	2	2	3	40	1,83	1,57	11,75
<i>Fumana procumbens</i>	1	2	2	2	2	2	46	1,01	2,20	5,75
<i>Fumana thymifolia</i>	1	2	2	2	2	2	57	0,88	2,80	8,66
<i>Galium lucidum</i>	2	2	3	3	2	1	67	1,27	1,41	2,93
<i>Galium parisiense</i>	1	1	3	3	1	1	25	2,24	0,27	2,28
<i>Genista scorpius</i>	3	4	3	2	3	3	84	1,67	4,37	9,69
<i>Globularia vulgaris</i>	4	2	3	2	3	3	47	1,39	3,09	11,38
<i>Gypsophila hispanica</i>	2	4	3	2	3	3	186	1,55	9,05	7,14
<i>Hedysarum humile</i>	1	3	3	2	3	4	62	1,43	8,38	15,74
<i>Helianthemum apenninum</i>	1	2	2	2	2	2	31	0,72	1,21	4,81
<i>Helianthemum hirtum</i>	1	2	3	2	3	2	77	1,38	3,59	6,47
<i>Helianthemum marifolium</i>	1	2	2	2	2	2	28	0,96	1,12	4,65
<i>Helianthemum oelandicum</i> subsp. <i>italicum</i>	1	2	2	2	2	2	42	1,05	1,03	3,41
<i>Helianthemum pilosum</i>	1	3	3	2	2	2	95	1,50	1,78	4,36
<i>Helianthemum salicifolium</i>	1	1	3	3	1	3	14	1,95	0,62	9,12
<i>Helianthemum squamatum</i>	1	3	2	2	2	3	65	1,07	2,98	9,05
<i>Helianthemum syriacum</i>	1	3	2	2	3	3	67	0,91	3,64	7,20
<i>Helichrysum stoechas</i>	2	3	2	3	2	3	52	0,96	2,81	7,42
<i>Herniaria fruticosa</i>	4	3	3	2	3	3	62	1,72	3,39	7,43
<i>Hippocrepis conmutata</i>	2	2	3	2	3	3	64	1,08	4,04	10,58
<i>Hippocrepis multisiliquosa</i> subsp. <i>ciliata</i>	1	1	3	3	1	2	15	1,86	0,52	6,34
<i>Jasonia tuberosa</i>	2	2	3	2	2	2	62	1,25	1,47	4,64
<i>Juniperus oxycedrus</i>	3	4	2	3	3	3	168	0,60	9,05	23,37
<i>Koeleria vallesiana</i>	2	2	3	4	1	1	51	1,00	0,34	1,36
<i>Laserpitium gallicum</i>	3	3	2	1	3	4	72	0,62	17,07	23,65
<i>Launaea pumila</i>	3	3	4	1	3	4	84	3,56	4,65	17,18
<i>Lavandula latifolia</i>	2	3	2	3	3	3	87	1,05	6,90	24,16
<i>Lepidium subulatum</i>	2	3	3	2	3	3	74	1,30	4,64	8,14
<i>Leuzea conifera</i>	1	3	4	1	3	4	61	4,00	4,40	14,67
<i>Limonium</i> sp.	3	2	3	2	2	3	33	1,38	2,53	9,63
<i>Linum apperessum</i>	4	3	3	3	2	2	98	1,80	2,97	4,43
<i>Linum narbonense</i>	4	2	2	3	2	2	41	1,06	1,44	4,54
<i>Linum strictum</i>	1	1	3	3	1	2	10	2,00	0,25	3,89
<i>Linum suffruticosum</i> var. <i>milleti</i>	4	3	2	3	3	3	123	1,11	3,22	10,21
<i>Lithodora fruticosa</i>	3	3	3	2	3	3	68	0,92	5,24	9,12
<i>Lolium rigidum</i>	2	1	3	4	1	2	17	1,41	0,40	3,28
<i>Lygeum spartum</i>	2	4	3	3	2	1	84	2,10	1,65	2,70
<i>Matthiola fruticulosa</i> subsp. <i>fruticulosa</i>	1	2	3	2	2	3	46	2,08	1,29	7,19
<i>Medicago minima</i>	1	1	3	3	1	2	25	1,53	0,54	3,14
<i>Neatostema apulum</i>	1	1	3	3	1	2	14	2,40	0,43	6,27
<i>Onobrychis argentea</i> subsp. <i>hispanica</i>	1	3	3	2	3	4	69	1,67	4,80	13,30
<i>Ononis fruticosa</i>	2	4	3	2	3	4	156	0,64	12,84	22,87
<i>Ononis tridentata</i>	1	4	3	1	3	4	156	2,32	11,16	21,43
<i>Paronychia kapela</i> subsp. <i>serpyllifolia</i>	2	2	2	3	2	2	32	0,82	1,80	6,10

<i>Phlomis lychnitis</i>	2	3	3	2	3	3	65	1,67	3,10	8,00
<i>Plantago albicans</i>	4	3	3	2	2	2	66	1,96	1,45	5,49

Appendix 1. (Continuation).

Plant species	R-S	Mx. d.	D/L	SRL	A.d.	R. d.	Mx.d.	D/L	A.d.	R.d.
<i>Polygala rupestris</i>	1	2	2	2	2	2	37	0,86	1,28	3,81
<i>Potentilla neumanniana</i>	2	2	2	2	2	2	52	1,12	2,11	6,28
<i>Reseda stricta</i>	1	2	3	3	1	2	45	1,73	0,93	4,91
<i>Rosmarinus officinalis</i>	2	4	3	3	3	3	136	1,20	7,25	13,80
<i>Salsola vermiculata</i>	2	4	4	1	3	4	324	2,75	5,09	12,86
<i>Sanguisorba minor</i>	3	3	3	2	2	3	75	1,91	2,97	7,84
<i>Santolina chamaecyparissus</i>	2	3	2	3	3	3	67	1,14	3,40	8,81
<i>Scorzonera graminifolia</i>	1	3	4	1	3	4	67	4,17	4,93	16,09
<i>Sedum sediforme</i>	2	2	1	3	1	2	28	0,69	0,57	3,97
<i>Senecio vulgaris</i>	1	1	3	3	1	1	19	1,89	0,26	2,43
<i>Seseli montanum</i>	2	3	4	2	3	4	95	2,96	3,39	12,58
<i>Sherardia arvensis</i>	1	1	3	3	1	1	12	1,78	0,19	2,48
<i>Sonchus oleraceus</i>	1	1	3	3	1	2	31	1,81	0,90	5,49
<i>Staehelina dubia</i>	1	2	2	2	3	4	47	0,73	4,00	13,55
<i>Stipa lagascae</i>	2	3	3	3	1	1	64	0,70	0,98	2,59
<i>Stipa offneri</i>	2	3	3	3	1	1	71	0,90	0,69	2,08
<i>Stipa parviflora</i>	2	3	3	3	1	1	85	1,17	0,95	1,85
<i>Teucrium chamaedrys</i>	2	2	3	3	2	2	37	0,97	1,46	6,10
<i>Teucrium polium</i> subsp. <i>polium</i>	4	2	3	3	2	3	43	1,21	2,30	7,28
<i>Thesium divaricatum</i>	1	2	2	2	2	3	29	0,46	1,95	8,82
<i>Thymelaea tinctoria</i>	1	4	3	2	3	4	146	1,38	7,16	12,73
<i>Thymus fontqueri</i>	2	2	3	3	2	2	65	1,29	1,12	3,26
<i>Thymus vulgaris</i>	2	3	2	3	2	2	59	0,92	2,39	6,53
<i>Vulpia unilateralis</i>	2	1	3	4	1	1	15	2,50	0,11	1,46