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Root system variability in common legumes in Central Europe

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Abstract: The aim of this study was to provide an overview of field measured root systems of common legume species growing under different environmental conditions in the Czech Republic. The plants, 214 individuals of 21 selected legume species from the tribes *Galegeae* (*Astragalus glycyphyllos, Lupinus polyphyllus*), *Genisteae* (*Cytisus scoparius, Genista tinctoria*), *Loteae* (*Anthyllis vulneraria, Lotus corniculatus, Securigera varia*), *Trifolieae* (*Trifolium arvense, T. campestre, T. medium, T. pratense, T. repens*) and *Vicieae* (*Lathyrus pratensis, L. sylvestris, Vicia angustifolia, V. cracca, V. hirsuta*), were collected using the monolith method from 27 sites.
A rhizome was present in seven species and the maximum branching order was three for 15 species and five for five species. Recovery buds were recorded on the root system of eight species and woodiness was recorded in 11 species. Root diameter ranged from 1 to 12 mm – the minimum diameter was recorded in annuals and the maximum in perennials. The colour of the root system ranged from light to dark. In six species, young roots were light and older roots were dark. Globose, cylindrical, branched, fan-like and ruff-like nodules were recorded. Only one type of nodule shape was recorded in 11 species, two in seven species and three or four in three species. Nodules measured up to 2 mm in nine species, from 2 to 4 mm in three species and more than 4 mm in nine species. Legume root systems are highly variable and the variability was due to Raunkier's life forms rather than membership of a tribe.

Key words: annual and perennial species; environmental conditions; Fabaceae; nodules and nodulation; Raunkier's life form

Introduction

Legumes (family Fabaceae) comprise more than 650 genera and 18,000 species and are found almost worldwide (Doyle 2001). In Europe, the temperate herbaceous legumes are divided into eight tribes (Polhill 1981). Legumes are known for their symbiotic relationship with *Rhizobium* s.l. bacteria, enabling them to utilize aerial N_2, which is inaccessible to many other species (Garg & Geetanjali 2007; Novák 2010). Symbiotic nitrogen fixation makes legumes highly competitive especially in environments limited by mineral (NO_3^- and NH_4^+) nitrogen and with an adequate phosphorus and potassium supply (Honsová et al. 2007; Jackson et al. 2008). The presence of *Rhizobium* bacteria in the soil initiates nodulation – i.e. the creation of nodules of several shapes on the roots of legumes. Nodulation can be affected by soil salinity and pH, moisture, temperature and nutrient availability (Zahran 1999). In previous studies, the formation of nodules was recorded only when plants were grown in mineral nitrogen-deficient soils (Hirsch 1992), whereas high phosphorus together with high mineral nitrogen availability in the soil suppressed (Truongt & Brix 2009) or entirely inhibited nodulation (Roumet et al. 2008). According to Corby (1988), nodule shape is associated with legume taxonomy and can be species-specific (Zahran 1998) or tribe-specific (Rejili et al. 2007). In addition to nodulation, the response of the root system to soil conditions is believed to be life form (Johnson & Biondini 2001) or species-specific (Mia et al. 1996).

In this study, root systems were defined as the network of underground organs. As plants are sessile and therefore cannot select the best site for life, their root systems must be sufficiently plastic to cope with variable soil conditions, especially with water and nutrient availability (Briggs & Walters 1997; Hodge 2004; Sultan 2000; Šmilauerová & Šmilauer 2010).

The root systems of individual plants can be highly modified by root competition as the competition for nutrients provokes higher energy investment into roots in order to increase their density and length (Olde Venterink & Güsewell 2010). The presence of nutrient-rich patches in the soil profile may also modify the root system because roots are able to proliferate and grow preferentially into nutrient-rich patches (Robinson 1994; Forde & Lorenzo 2001; Hejcman et al. 2011).

Lucero et al. (1999) concluded that water deficit increases the rooting depth of *Trifolium repens.* According to Skinner & Comas (2010), drought stress increased not only the root depth of six legumes but also the length of their roots. On the other hand, waterlog-

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ging increased the root crown diameter of *Lotus glaber* in a study by Mendoza et al. (2005).

At the individual species level, some of the variability in root system morphology can be ascribed to life form and nutrient acquisition and conservation strategies. The root systems of perennials are more randomly branched and have larger diameter roots than annuals (Roumet et al. 2006, 2008). On the other hand, dichotomously branched root systems are more typical in annuals (Gross et al. 1993). This may explain the nutrient conservative strategy of perennials and the high nutrient uptake capacities of annuals recorded by Roumet et al. (2006). According to Antos & Halpern (1997), different annual species have a similar root morphology, differing from perennials especially in terms of rooting depth.

Root systems have been most frequently studied in grasses (Hodge et al. 1998; Janeček et al. 2007; Pecháčková et al. 2003; Šmilauerová & Šmilauer 2002; Van der Krift & Berendse 2002; Wahl et al. 2001; Wildová et al. 2007), field crops (Haberle & Svoboda 2000; Lamb et al. 2000; Merrill et al. 2002; Svoboda & Haberle 2006) and forage legumes (Braun et al. 2010; Hakl et al. 2007, 2011; Komárek et al. 2010), but there is a lack of detailed information about the root system morphology and variability of common legumes in Central Europe. Some results of plant excavations in the field were published by Kutschera (1960) and Kutschera & Lichtenegger (1992), but the root system variability of many common species such as *Vicia angustifolia*, *Vicia cracca*, *Lupinus polyphyllus*, *Lathyrus sylvestris*, *Astragalus glycyphyllos* and *Cytisus scoparius* has never been described.

The aim of this paper was therefore to provide an overview of field measured root systems of 21 common legume species growing under different environmental conditions in Central Europe. We asked the following research questions: (i) How does the morphology of the root systems plus nodules vary in the investigated species? (ii) Which root traits are characteristic for individual species?

Material and methods

Study area

The plants, 214 individuals of 21 selected legume species, were collected from 27 sites in the Czech Republic at an altitude ranging from 350 to 580 m. a.s.l. (see Table 1 for a list of investigated species and the number of sites from which each species was collected). The species belonged to five tribes (*Galegeae*, *Genisteae*, *Loteae*, *Trifolieae* and *Vicieae*). The names of the tribes follow Allen & Allen (1981). The average annual precipitation and temperature ranged from 600 mm and 8 °C at 350 m a.s.l. up to 700 mm and 6.5 °C at 580 m a.s.l. The sampling sites were described as dry or humid, field, forest, ruderal or meadow, sun exposed or shaded, stony or without stones in the upper 30 cm soil layer, and with low (up to 40%) or high (above 40%) cover of herbaceous vegetation in a 1-m diameter circle.

Plant collection

The plants were collected from June to August in the years 2007, 2008 and 2009. Collection of all species at all sampling sites was impossible as the investigated species had different environmental requirements, and therefore it was impossible to strictly separate the variability in root systems due to the species effect and that due to environmental conditions. The monolith method was used to collect individual plants (Böhm 1979). The soil monolith measuring 30 × 30 × 30 cm beneath the plant was dug up and washed with water to extract the underground organs of the studied plants from the soil. The plant species nomenclature follows Kubát et al. (2002).

Traits of root systems

The traits of root systems and nodules that were investigated are summarized in Table 1. Eight traits were evaluated for root systems: type of root system, presence of rhizomes, depth, special diameter, maximal branching order, colour and woodiness; and two traits for root nodules: shape and size. The type of root system was classified according to the database of clonal and bud bank traits of Central European flora (Klimešová & de Bello 2009). The life forms of the investigated species follow Raunkiaer (1934). The measured rooting depth was limited to 30 cm by the use of the monolith method. The special diameter is the mean value of taproot diameter under the crown and the maximum diameter within the root system. The root colour ranged from light to dark (light, near white, light/dark (young roots light and old dark) and dark). The maximum order of branching indicated the maximum position of a root within the branched hierarchy of the root system (Eissenstat et al. 2000; Wells & Eissenstat 2003).

The shape of the root nodules was classified according to Corby (1971, 1988). The nodules were classified according to their size as more than 4 mm, 2–4 mm, or less than 2 mm in diameter (Patreze & Cordeiro 2005).

Data analysis

Intraspecific variability in root morphology was evaluated using cluster analysis in the STATISTICA 8.0 program (Statsoft, Tulsa). This analysis was based on the mean values of all measured root traits for individual species. Individual categorical variables were coded in the form of dummy variables. The ordination approach was used to evaluate interspecific as well as intraspecific variability together. Detrended Correspondence Analysis (DCA) was used to evaluate total variability and the results were visualized in the form of an ordination diagram. Redundancy Analysis (RDA) was used to evaluate the proportion of root system variability explained by environmental variables and by species effect. Standardization by species (dependent variables) was used because the analysed data were of various types and units. The statistical significance of the first and all constrained canonical axes was determined by the Monte Carlo permutation test. In all analyses, 999 unrestricted permutations were used. All ordination analyses were performed in the CANOCO for Windows 4.5 program (ter Braak & Šmilauer 2002).

Results

Over three years, 214 plants of 21 legume species were excavated and measured. The mean values of the investigated root traits for all studied species are given in Table 1. The investigated species belonged to five

Table 1. Summary of root morphology and nodule traits.

Species	Abbreviation	Tribus	Number of plants	Number of sites	Life forms	Type of root system	Depth [cm]	Rhizome	Maximum order of branching	Recovery buds	Special diameter [mm]	Woodiness	Colour	Shape of nodules	Size of nodules [mm]
Anthyllis vulneraria	AntVul	*Loteae*	5	1	H	RS	>30	0	3	no	3–4	yes	dark	a	<2
Astragalus glycyphyllos	AstGly	*Galegeae*	7	2	H	RS	>30	0	5	yes	3–4	no	near–white	b, c, e	> 4
Cytisus scoparius	CytSco	*Genisteae*	6	3	N	RS	>30	0	5	yes	7–8	yes	dark	b, c	> 4
Genista tinctoria	GenTin	*Genisteae*	11	1	N	HR	10–20	1	5	yes	5–6	yes	dark	a, b, c, e	> 4
Lathyrus pratensis	LatPra	*Viciaea*	11	6	H	HR	20–30	1	3	no	3–4	yes	light/dark	c	< 2
Lathyrus sylvestris	LatSyl	*Viciaea*	13	2	H	HR	20–30	1	3	yes	11–12	yes	light/dark	c	2–4
Lotus corniculatus	LotCor	*Loteae*	16	5	H	RS	>30	1	3	yes	5–6	yes	dark	a	<2
Lupinus polyphyllus	LupPol	*Galegeae*	11	3	H	RS	>30	0	3	yes	10–11	no	light/dark	d	> 4
Medicago lupulina	MedLup	*Trifolieae*	10	2	H	RS	>30	0	3	no	3–4	yes	light/dark	c, e	> 4
Medicago sativa	MedSat	*Trifolieae*	10	2	H	RS	>30	0	3	yes	5–6	yes	dark	c, e	> 4
Melilotus albus	MelAlb	*Trifolieae*	5	1	H	RS	20–30	0	5	no	8–9	no	light	c, e	> 4
Melilotus officinalis	MelOff	*Trifolieae*	5	1	H	RS	20–30	0	5	no	8–9	no	light	c, e	> 4
Securigera varia	SecVar	*Loteae*	12	3	H	RS, HR	>30	0	3	yes	3–4	yes	dark	c, e	2–4
Trifolium arvense	TriArv	*Trifolieae*	29	3	T/H	RS	0–10	0	3	no	1–2	no	near–white	c, e	<2
Trifolium campestre	TriCam	*Trifolieae*	6	3	T/H	RS	0–10	0	3	no	1–2	no	near–white	c	<2
Trifolium medium	TriMed	*Trifolieae*	6	3	H	RS	20–30	1	4	no	3–4	yes	light/dark	c	<2
Trifolium pratense	TriPra	*Trifolieae*	21	3	H	RS	20–30	0	3	no	3–4	no	near–white	c	<2
Trifolium repens	TriRep	*Trifolieae*	6	3	H/Ch	HRS	10–20	1	3	no	1–2	no	near–white	c	<2
Vicia angustifolia	VicAng	*Viciaea*	7	3	T/H	RS	10–20	0	3	no	1–2	no	near–white	c	<2
Vicia cracca	VicCra	*Viciaea*	12	3	H	HR	20–30	1	3	no	3–4	yes	dark/white	c, e	> 4
Vicia hirsuta	VicHir	*Viciaea*	5	4	T/H	RS	0–10	0	3	no	1–2	no	near–white	c, b, e	2–4

Life forms according to Raunkiaer (1934): H – hemicryptophyte; N – nanophanerophyte; T – terophyte; Ch – chamaephyte; type of root system: RS – root splitters, HR – hypogeogenous rhizomes, HRS –horizontal rooting stems or above the soil surface; special diameter – mean value of taproot diameter under the crown and maximum diameter within the root system; shape of nodules: a – globose, b – branched, c – cylindrical, d – ruff-like, e – fan-like.

tribes (*Galegeae*, *Genisteae*, *Loteae*, *Trifolieae* and *Vicieae*), four life forms (hemicryptophyte, chamaephyte, nanophanerophyte and therophyte), and three types of root system (root splitter – Fig. 1; hypogeogenous rhizomes – Figs 2a,b; horizontal rooting stems on or above the soil surface – Figs 2c,d). The depth of the root systems ranged from 0 to 10 cm in three annual species, from 10 to 20 cm in one annual and five perennial species, from 20 to 30 cm in four perennial species, and was more than 30 cm in seven perennial species. A rhizome was present in seven species and the maximum order of branching was three for 15 species, four for one species, and five for five species. Recovery buds were recorded on the root system of eight species and woodiness was recorded in 11 species. Root diameter ranged from 1 to 12 mm – the minimum diameter was recorded in annuals and the maximum in the perennials *Lathyrus sylvestris* and *Lupinus polyphylus.* The colour of the root systems ranged from light to dark. In six species, young roots were light whereas older roots were dark (see Fig. 2a). Globose (Figs 3a,b), cylindrical (Figs 3c,d), branched (Figs 4a,b), fan-like (Figs 4c,d), and ruff-like (Figs 4e,f) nodules were recorded. One type of nodule shape was recorded in 11 species, two types in seven species, and three or four types in three species. Nodules of up to 2 mm in size were recorded in nine species, from 2 to 4 mm in three species, and more than 4 mm in nine species.

The results of the cluster analysis are shown in Fig. 5. The root system of *L. polyphyllus* differed the most from the other investigated species, being separated from the other species in the first division. The main reason for the separation of *L. polyphyllus* was the large size of its root system and nodules in comparison to other species. In addition, roof-like shaped nodules were only recorded in this species (see Figs 4e,f).

Two large groups of species were distinguished in the second division. The main cause of the second division was the light *versus* dark colour of the root systems. The large group on the left was divided into four smaller groups. *Trifolium repens,* the only species in Group 1, had horizontal rooting stems on the soil surface (Fig. 2c). Group 2 included species with rhizomes, such as *Vicia cracca*, *L. sylvestris*, *Trifolium medium* and *Lathyrus pratensis* (Fig. 2a). All these species had light then dark root systems. Group 3 was divided into two sub-groups: *Trifolium pratense* (Fig. 1c) on one side and the annual species *Vicia hirsuta*, *Trifolium campestre*, *Vicia angustifolia* and *Trifolium arvense* (Fig. 1a) on the other. The overall structure of the root systems was similar, but the annuals differed from *T. pratense* by having a flat fibril root system

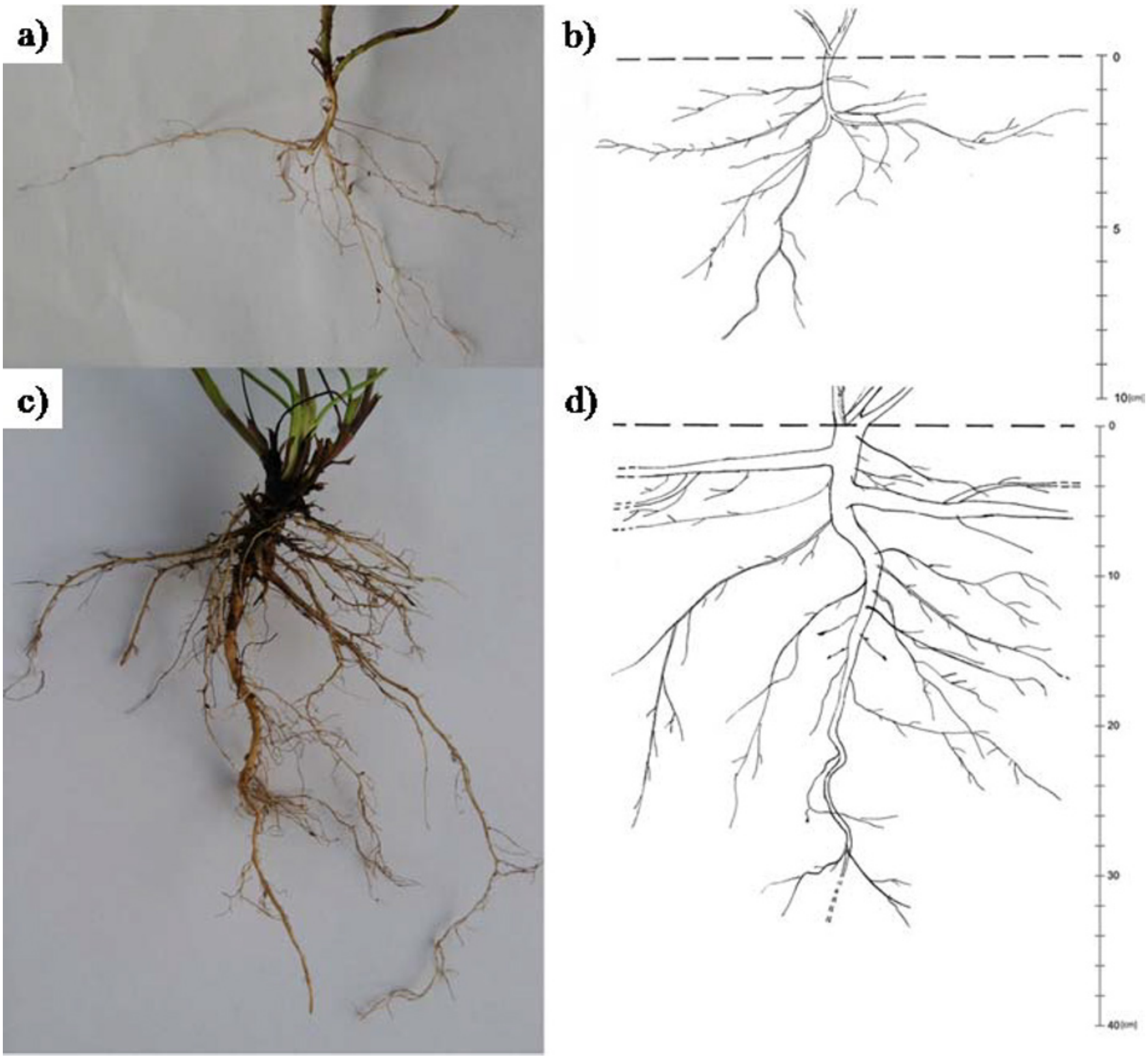

Fig. 1. a – root system of *Trifolium arvense*; b – schematized typical root system of studied annual legumes with "root splitter" root type; c – root system of *Trifolium pratense* and d – schematized typical root system of studied perennial legumes with "root splitter" root type.

spread under the soil surface. The root systems of annuals were more branched than in *T. pratense* and lacked regenerating buds or rhizomes. The clearly visible taproot of *T. pratense* indicated its perennial character. Group 4 was composed of species with a taproot and larger nodules than in the previous groups. Another typical feature of legumes in Group 4 was the presence of more shapes of nodules in each species. The righthand group following division number two included perennial species with a well-developed taproot. Species in Group 5 differed from species in Group 6 (division number 4) by the shape of their nodules (globose, fan-like, cylindrical and branched *versus* globose) and by their larger size. In Group 5, *Securigera varia* and *Medicago sativa* were strictly separated from nanophanerophytes *Genista tinctoria* and *Cytisus scoparius*. Group 6 contained species from the tribe *Loteae* (*Lotus corniculatus* and *Anthyllis vulneraria*). A typical feature of these species was nodules of up to 2 mm in size.

The results of DCA (Fig. 6) corresponded well with the results of the cluster analysis as the same groups of species were distinguished. As in the cluster analysis, *L. polyphyllus* was separated from all other species. Intraspecific variability in this species was high, mainly due to the different sized root systems in the measured plants.

L. corniculatus and *A. vulneraria* (Group 6) had the lowest intraspecific variation in root systems as all investigated plants were close together in the ordination diagram. On the other hand, *S. varia* had the highest interspecific variability in the root system. This was because individuals with root splitter (55% cases) and hypogeogenous rhizome (45% cases) root types were recorded in this species. Further variability in the root systems was due to the presence of more than one shape of nodule on one plant (cylindrical and fan-like) and their variable size (2–4 mm). The transition between perennial species with rhizomes (Group 2) and annual species with a taproot (Group 3) was shown by *T. repens*, which has horizontal rooting stems (Group 1).

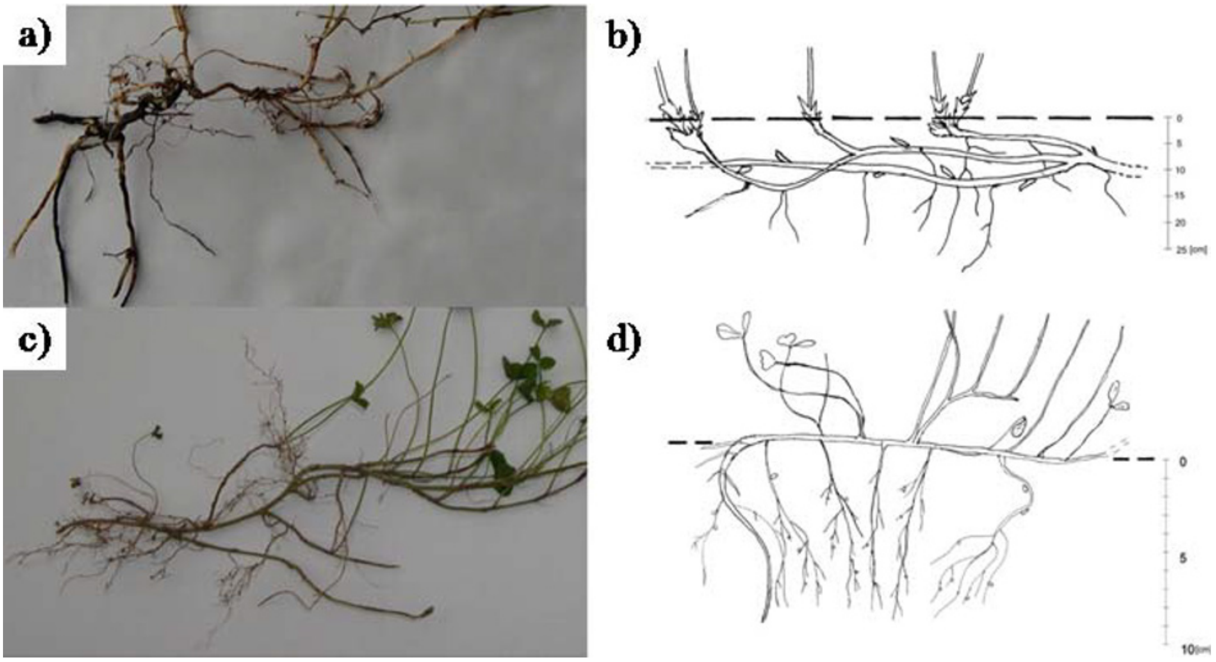

Fig. 2. a – root system of *Lathyrus pratensis* with light/dark colour; b – schematized typical root system of legumes with rhizomes – “hypogeogenous rhizomes”; c – root systems of *Trifolium repens*;and d – schematized horizontal rooting stems on or above the soil surface.

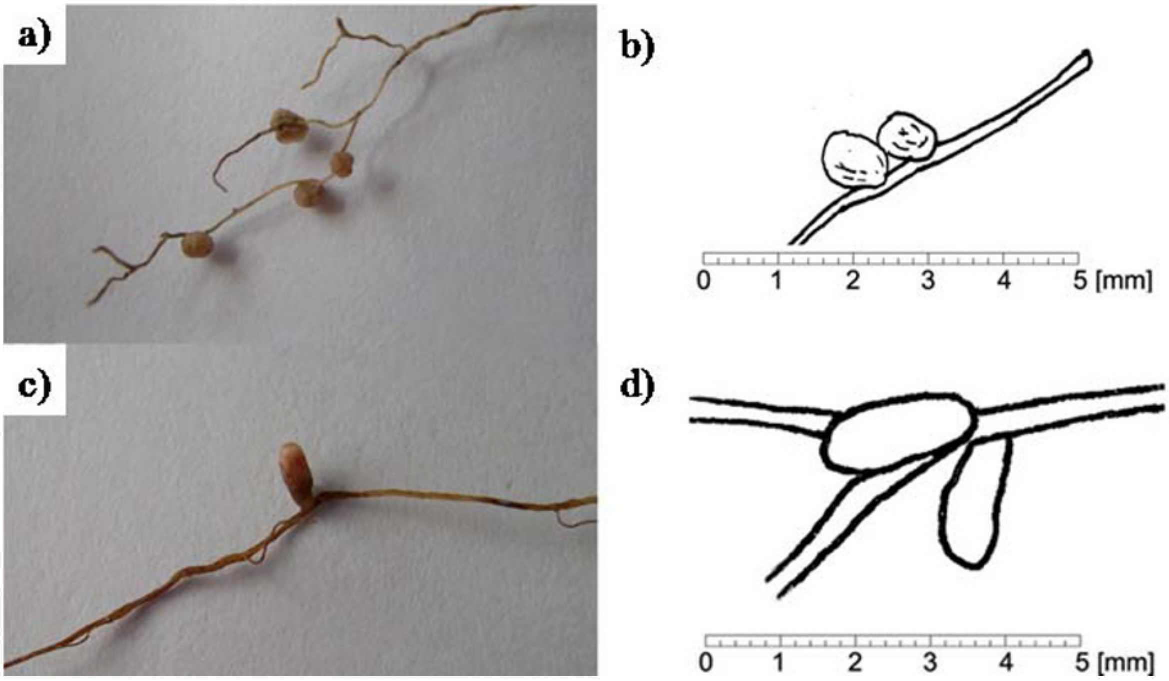

Fig. 3. a – nodule shape of *Lotus corniculatus*; b – schematized globose nodules; c – nodule shape of *Lathyrus pratensis*; d – schematized cylindrical nodules.

Interspecific variability in the root systems of *T. repens* was low.

With the exception of two individuals, root system variability was low in *T. arvense.* The typical shape of nodules for all investigated *Trifolium* species was cylindrical, but the two most distinct individuals of *T. arvense* had fan-shaped nodules. In species with more than one shape of nodule, not all recorded shapes were found on all individuals. This substantially increased the intraspecific variability of the root systems in *Astragalus glycyphyllos*, *C. scoparius*, *G. tinctoria*, *Medicago lupulina*, *M. sativa*, *Melilotus albus*, *Melilotus officinalis*, *S. varia*, *T. arvense*, *V. cracca* and *V. hirsuta.*

The intraspecific variability in annual species (*T. arvense*, *T. campestre*, *V. angustifolia* and *V. hirsuta*) and *T. repens* was due primarily to the depth of the root systems. The special diameter was highly variable in *A. vulneraria*, *C. scoparius*, *L. pratensis*, *M. albus*, *M. of-*

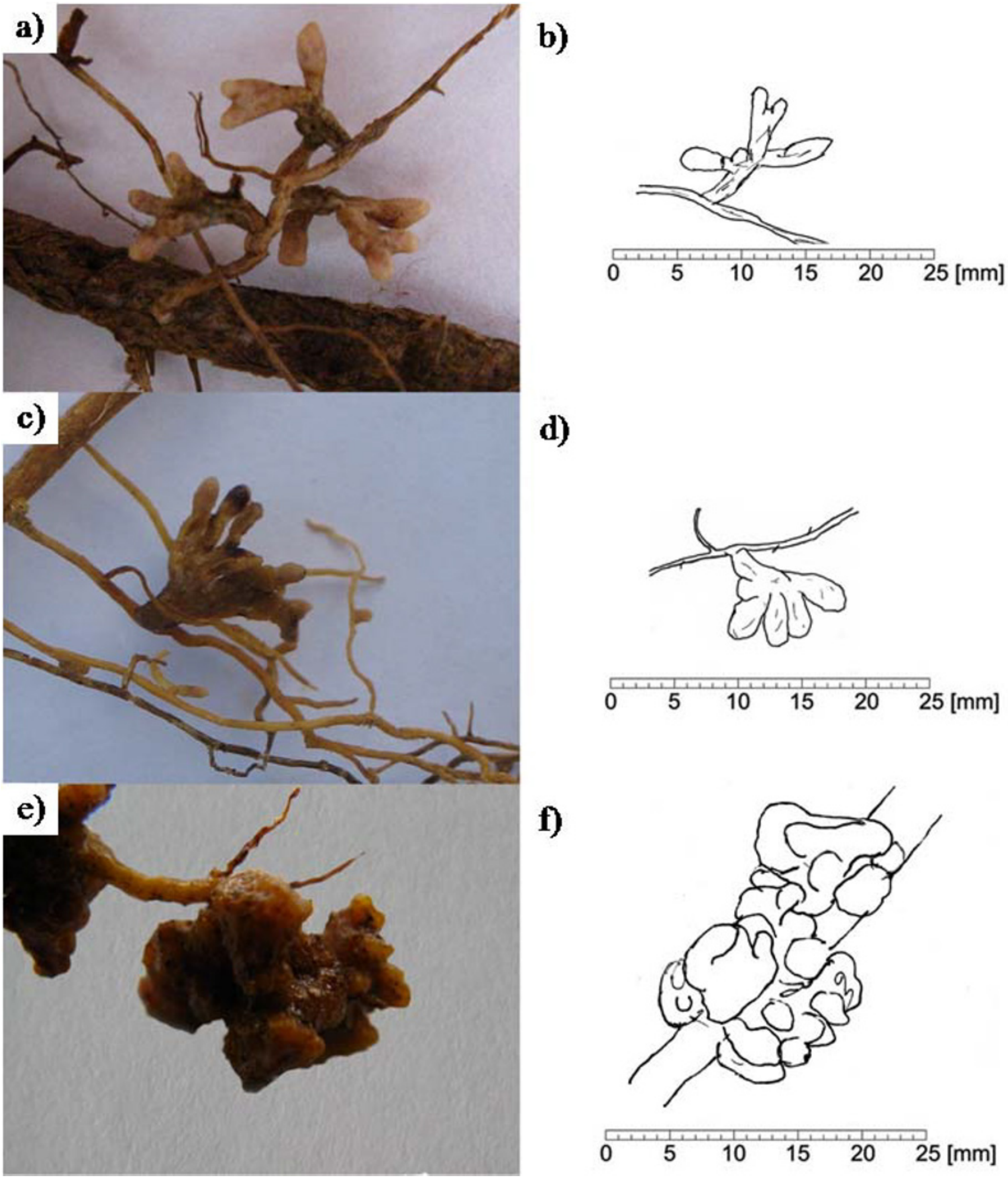

Fig. 4. a – nodule shape of *Lathyrus sylvestris*; b – schematized branched nodule; c – nodule shape of *Vicia cracca*; d – schematized fan-like nodule; e – nodule shape of *Lupinus polyphyllus*; f – schematized ruff-like nodule.

ficinalis and *T. medium*. The special diameter together with the maximum order of branching was variable in *L. pratensis*, *L. polyphyllus*, *M. lupulina*, *M. sativa*, *S. varia* and *T. pratense*.

The results of the redundancy analyses are shown in Table 2. The environmental variables (dry or humid site, field, forest, ruderal or meadow, shaded or sun exposed, stony or without stones in the upper 30 cm soil layer, with low or high cover of herbaceous vegetation) together explained 48.9% (analysis a1) of the variability in root systems.

Forward selection was employed to select only the environmental variables that significantly improved the model. The total number of 11 environmental variables was reduced to three, i.e. field, shade and drought, which together explained 47.1% of the variability (analysis a2). The variability explained by field, shade and drought was only 17.4% after the effect of species was removed from the analysis (analysis a3).

The highest proportion of root system variability was explained by the effect of species – species alone

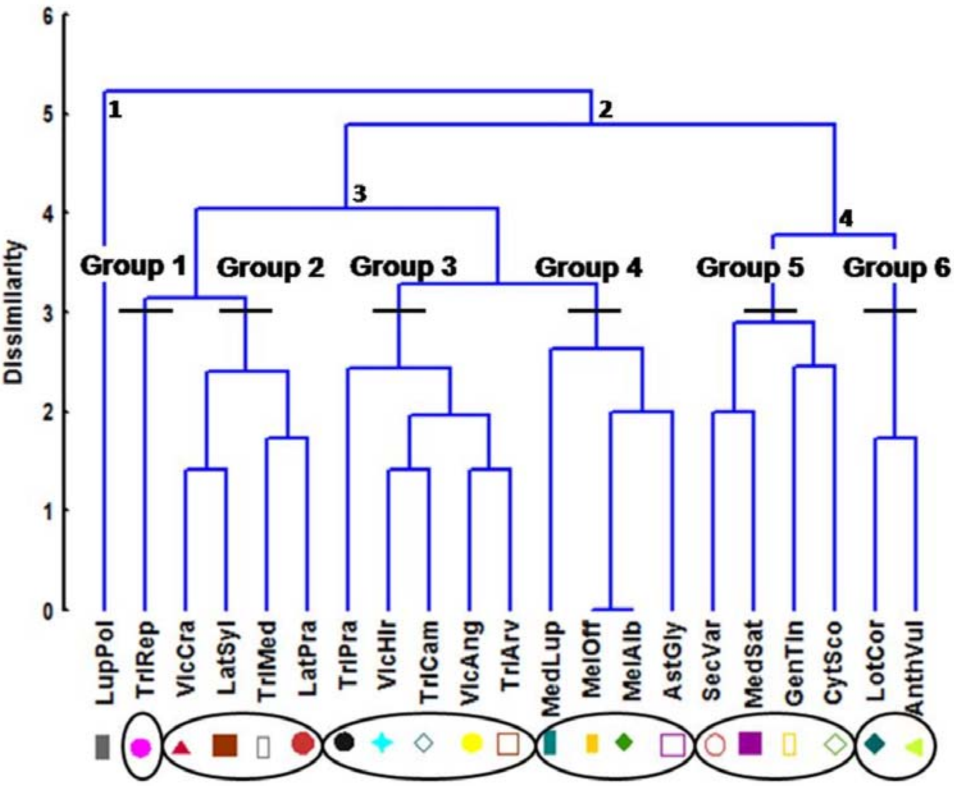

Fig. 5. Dendrogram based on cluster analysis representing interspecies variability between 21 investigated legume species. The numbers refer to divisions described in the text. Species abbreviations are given in Table 1. The labels for individual species are consistent with Fig. 6.

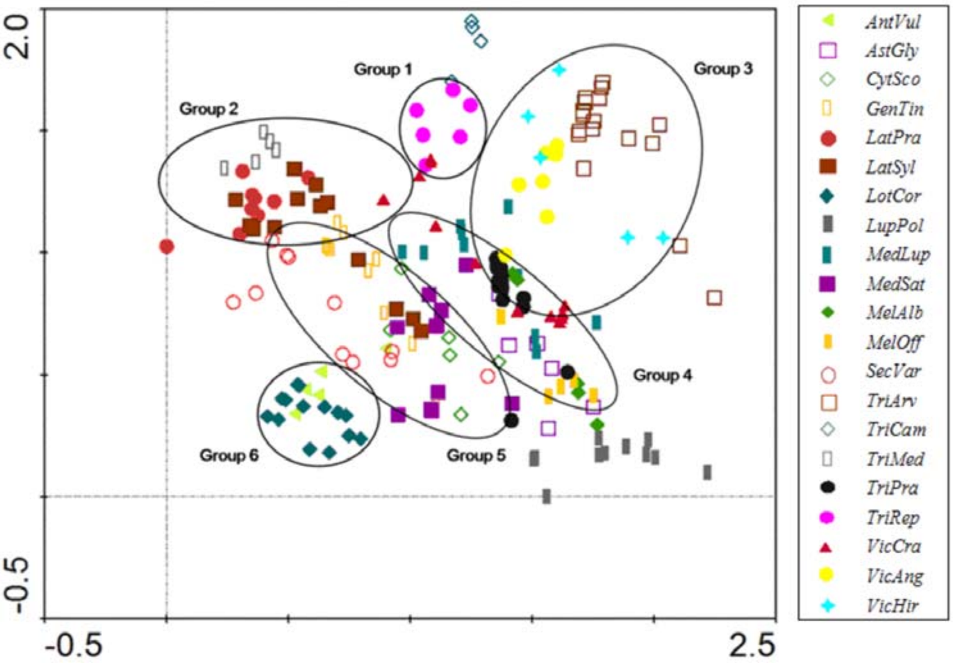

Fig. 6. Ordination diagram of the Detrended Correspondence Analysis (DCA) reflecting the intraspecific and interspecific variability in the root systems of 21 investigated legume species. Species abbreviations are given in Table 1. The labels for individual species are consistent with Fig. 5.

explained 44.9% of the root system variability (analysis a5), and this decreased only marginally when variability caused by drought, field and shade was removed from the model (analysis a6).

Discussion

Although the root systems of legumes have frequently been studied in laboratory and field conditions, there is

Table 2. Results of redundancy analyses of root systems data.

	Expl. Var.	Covariables	% ax 1 (all)	F 1 (all)	P 1 (all)
a1	C, D, F, Fo, Mo, R, S, St, H, Species		21.5 (48.9)	49.81 (16.12)	0.001 (0.001)
a2	D, F, S		20.0 (47.1)	47.55 (19.55)	0.001 (0.001)
a3	C, D, F, Fo, Mo, R, S, St, H	Species	13.0 (17.4)	27.23 (3.74)	0.001 (0.001)
a4	D, F, S	Species	7.9 (22.0)	16.28 (6.49)	0.001 (0.001)
a5	Species		18.4 (44.9)	43.41 (19.82)	0.001 (0.001)
a6	Species	D, F, S	16.7 (43.8)	38.08 (19.29)	0.001 (0.001)

An. – analysis code; Expl. var. – explanatory (environmental in Canoco terminology) variables; % ax 1 (all) – species variability explained by canonical axis 1 or by all axes in brackets (measure of explanatory power of the environmental variables); F 1 (all) – F statistics for the test of axis 1 or all axes in brackets; P 1 (all) – corresponding probability value obtained by the Monte Carlo permutation test for the test of axis 1 or all axes in brackets. Environmental variables and covariables: C– cover of vegetation above 40%; D – dry site; F – site with field conditions; Fo – forest; H – humid site; M – meadow; R – ruderal site; S – shaded site; St – stony site in upper 30 cm of the soil profile. Species were coded in the form of 21 dummy variables.

a lack of studies covering a wide range of species in natural conditions. Therefore a unique feature of this study is the wide range of investigated species collected from different environmental conditions, thus demonstrating the natural variability of leguminous root systems.

The effect of species and environment on root system variability was not fully separated in this study performed at the landscape level because not all investigated species were present at all localities. Therefore there was much overlap between the root system variability explained by the effect of species and by environmental conditions. This was clear from the large reduction in variability explained by the environment when the variability caused by effect of species was removed from the redundancy analysis by covariables. Despite being unable to strictly separate the variability caused by species and by the effects of the environment, large differences in root systems were recorded between particular species. This was supported by the fact that species recorded together at one locality frequently had different root systems. The variability in root systems within each species was substantially lower than that of the whole data set, as indicated by clusters of points for individual species in the ordination diagram (Fig. 6). The restricted variability of the root system for individual species compared to all species together is consistent with the results of Galloway & Fenster (2000).

Of all the recorded environmental variables, root system traits were the most affected by moisture and light availability and by field conditions. This is consistent with studies dealing with the effect of environmental conditions on root systems (Koukoura et al. 2009; Salako et al. 2002; Šmilauerová & Šmilauer 2002; Wahl et al. 2001). Further, it must be noted that the species present at dry sites frequently differed from species recorded at wet sites, and therefore it is impossible to discuss the effect of environmental conditions on the root system variability of individual species in more detail.

Although the variability caused by site and species effect cannot be strictly separated, the intraspecific variability of legume root systems was substantially lower than the variability within all species. However, the root systems of many legume species may differ even when growing in the same environmental conditions, and this difference is genetic. It must be noted that, to compare the intra- and interspecific variability of all studied species exactly, all investigated species must be present at all studied localities, and this can only be achieved via transplantation.

The intraspecific variability in root systems was due to Raunkier's life forms rather than tribes, since in several cases species with different life forms were recorded in the same tribe. For example, annual and perennial species with highly different root systems were both recorded in the tribes *Trifolieae* and *Viciaea.* On the other hand, species in the tribes *Loteae*, *Galegeae* and *Genisteae* were all perennial and therefore had relatively low root system variability. The differences between root systems of annuals and perennial species were also recorded by Fitter et al. (1988), Gross et al. (1992) and Roumet et al. (2008).

Annual root systems were intermediate between perennial rhizomatic and perennial species with a taproot. This is clearly visible in Fig. 5, in which annuals (*T. arvense*, *T. campestre*, *V. angustifolia* and *V. hirsuta*) are located in the middle of the dendrogram between rhizomatic and taproot perennials. The relation between differences among species and life form is consistent with the results of Gross et al. (1992).

The intraspecific variability in root systems probably enables better survival of individual plants in different environmental conditions. The individual traits of root systems differed in terms of their plasticity under various environmental conditions, e.g. branching was more plastic than special root diameter. The same result was recorded by Forde & Lorenzo (2001), indicating that root diameter may be highly species-specific and therefore highly heritable, while branching may depend more on soil conditions at the level of the individual plant. We concluded that some root traits are determined more by environmental conditions and others by heritability. This conclusion is in accordance with the results of Johnson et al. (1996). In *A. vulneraria*, *A. glycyphyllos*, *L. corniculatus*, *M. sativa* and *S. varia*, differences in branching contributed the most to the large differences among individual plants within the species. The colour of the root systems depended on the life form: most of the root systems were pale brown and this colour was recorded in all annuals and in the young roots of perennials. According to Corby (1971), pale brown is the most frequent root colour. Rejili et al. (2007) suggested that the colour of the roots is dependent on the nodules and the leghaemoglobin content. The latter was not investigated in our study, nor was the dependence of colour on nodulation recorded.

The most frequently recorded shape of nodules was cylindrical. Small globose nodules were considered juvenile and thus were ignored by Corby (1971), but not in our study. We recorded all shapes of nodules, because small nodules can be wrongly considered as juvenile, especially in species with small nodules. For example, small globose nodules were typical in *L. corniculatus* and *A. vulneraria*, and small cylindrical nodules were found in all *Trifolium* species. According to Corby (1988), one shape of nodule may be typical for a particular tribe or there may be tribes in which more nodule shapes are possible, but only several of these are dominant. Our results indicate that more than one shape of nodule is present in some tribes (*Galegeae*, *Genisteae* and *Viciaea*), but that often only one shape is dominant. In our study, most nodules were located on the lateral roots, which is consistent with the results of Capoen et al. (2010). The shapes of the nodules were highly species-specific, as reported previously by Rejili et al. (2007). The exceptions were two plants of *T. arvense*, which had fan-like nodules of a different size than all other *T. arvense* specimens. A possible explanation is that different species of bacteria had created these nodules, but this requires further investigation. It is possible that these two plants were infected by bacteria from *S. varia* growing in their vicinity, because the nodules of *S. varia* were fan-like. The differences in root systems may be related to plant taxonomy, but the taxonomy of *S. varia* is not entirely clear. According to Allen & Allen (1981), *S. varia* belongs to the tribe *Loteae*. In our study, nodules other than those that are typical for this tribe were recorded in *S. varia*, indicating that *S. varia* could be included in the tribe *Coronilleae* rather than *Loteae*. The transitional character of *S. varia* on the border between these two tribes was also discussed by Allan & Porter (2000).

The nodules of *L. polyphyllus* were the most different from all other species, which is consistent with the classification suggested by Corby (1988).

Eight of studied perennial root splitters (*A. vulneraria*, *A. glycyphyllos*, *C. scoparius*, *L. corniculatus*, *L. polyphyllus*, *M. lupulina*, *M. sativa* and *S. varia*) reached a rooting depth of more than 30 cm. This is consistent with the description of these species in plant trait databases, as all these species are described as deep rooting (Fitter & Peat 1994). On the other hand, all annuals (*T. arvense*, *T. campestre*, *V. angustifolia* and *V. hirsuta*), rhizomatous perennials (*G. tinctoria*, *L. pratensis*, *L. sylvestris*, *S. varia* and *V. cracca*) and some root splitter perennials (*L. polyphyllus*, *M. albus*, *M. officinalis*, *T. medium* and *T. pratense*) were shallow rooting, reaching depths of up to 30 cm. During plant excavation, we recorded most of the fine roots of all investigated legumes in the shallow-rooted species. This is probably an adaptation to drought, as described by Merrill et al. (2002).

We can conclude that the root systems of common European legumes are highly variable. The variability of root systems was attributed to Raunkier's life forms rather than the membership of species in tribes.

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