Evolutionary and organismic constraints on the relationship between spacer length and environmental conditions in clonal plants

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The rate of lateral spread of clonal plants is considered a plastic trait that responds directly to environmental conditions. However, this response is likely constrained by evolutionary history and other species attributes. Here we ask how the relationships between lateral spread and the distribution of herbaceous plant species in different environments are influenced by the type of spacer (epigeogenous versus hypogeogenous rhizome), its persistence (integrator versus splitter), and the height and phylogeny of the plant. Analysis of spacer length of 367 species from temperate to arctic Europe revealed that other plant characteristics modulate the relationship between spacer length and environmental conditions. While plants with epigeogenous rhizomes, which have usually shorter spacers than hypogeogenous rhizomes, were associated with illuminated habitats, plants with hypogeogenous rhizomes were associated with warm habitats. These relationships were also shown within the specific rhizome type, as within the group of species with epigeogenous rhizomes, those having short spacers were associated with more light. The trend toward long spacers in warm environment was detected within both epigeogenous and hypogeogenous rhizome bearing species. Splitters were found to be associated with wet, nutrient rich habitats irrespective of rhizome type. When plant height was accounted for by using the ratio of spacer length to plant height (L:H) instead of absolute spacer length, no relationship with environmental variables was found until phylogenetic relationships among the species were taken into account. This implies that overall variability in L:H ratio in the dataset masked trends common for different taxonomic groups. Future comparative studies relating particular clonal growth forms or individual traits to environmental conditions should consider the constraints arising from other growth characteristics and evolutionary history of the subject species.

Lateral spread rate – along with the rate at which offspring ramets are produced, ramet longevity, and persistence of connection between ramets – is a crucial trait of clonal plant growth (Herben 1995, Sammul et al. 2003, Klimešová and Klimeš 2008). It ranges from less than 1 cm per year in tussock sedge *Carex curvula* (Steinger et al. 1996) up to more than 100 cm in *Petasites hybridus* (Klimešová and Klimeš 2006). On the community level, rapid lateral spread provides species mobility considered important for species coexistence in meadows (Schmid and Harper 1985, Klimeš 1999, Sammul et al. 2003, Zobel et al. 2010), while comparisons on the level of regional floras show that a high lateral spread rate is associated with environmental conditions (van Groenendael et al. 1996, Song et al. 2002, Sammul et al. 2004). On the individual level, plasticity in lateral spread rate is important for foraging in heterogeneous environments (Hutchings and deKroon 1994).

Early comparative studies based on analysis of the central European flora found plants with extensive lateral spread to have short-lived connections among ramets (i.e. to be splitters), and to occupy moist, shaded, nutrient rich habitat, whereas plants with tightly packed ramets tend to have long-lived connections among ramets (i.e to be integrators) and to occupy dry, well-lit, nutrient poor habitats (van Groenendael et al. 1996). Covariation in the environmental conditions was hypothesized to be one of the factors driving the covariation of the clonal traits (van Groenendael et al 1996, Stuefer et al. 1996, Jónsdóttir and Watson 1997). However, this relationship could be complicated by phylogenetic inertia, as integration within a clone is an ancestral trait (Kelly 1995) of whole taxonomic groups that share other plant traits (Klimeš 2008).

Alternatively, the covariation of these clonal traits might be explained by a tradeoff between investments in lateral spread rate and ramet connection durability (van Groenendael et al. 1996). Both producing and maintaining spacers (the structures by which clonal plants can laterally spread) presumably incur costs (Pitelka and Ashmun 1985, Hutchings and Wijesinghe 1997) that include investment into growth, respiratory costs of maintaining a structure, dilution of internal resources due to sharing, and higher risk of genet mortality from systemic disease spreading through interconnected

ramets (Eriksson and Jerling 1990). Therefore, long spacers are commonly possible at the expense of their durability.

Plant height could also limit the length of spacers. Nevertheless, the possibility that spacer length varies allometrically with plant height has thus far been considered only rarely (Ye et al. 2006). A plant can afford to invest into belowground parts only a portion of its assimilates (Müller et al. 2000), and a general allocation model (Enquist and Niklas 2002) predicts that bigger plants should invest relatively more in supporting structures (stems) and below-ground parts (roots and rhizomes) than small plants do. Therefore, one could expect that in smaller plants, rhizomes would be either shorter or less persistent than in larger ones.

The fact that comparative studies and analyses of functional traits use absolute measures of spacer length (or lateral spread) across communities potentially differing substantially in plant height could yield erroneous conclusions if they are examining responses to environmental factors that actually select for overall plant height rather than spacer length. This problem could be avoided by using the ratio of spacer length to plant height (L:H). The low L:H ratio is characteristic of plants that spread as a tightly packed advancing front of ramets, maximizing intraspecific contacts i.e. in plants with phalanx strategy (Lovett Doust 1981), while high L:H ratio, the guerilla end of the continuum, comprises plants that infiltrate surrounding vegetation, maximizing interspecific contacts. Guerilla and phalanx strategies represent different ways to cope with the environment (Lovett Doust 1981), although comparative studies examining the consequences of this difference are scarce. It has been postulated, however, that phalanx plants usually are competitively superior, whereas guerilla plants do better in disturbed conditions (Eriksson and Jerling 1990, Fahrig et al. 1994, Stuefer et al. 2002). Additionally, according to a comparative study of wetlands across China, guerilla plants tend to be more common in wetlands of cold and dry environments in comparison with wetlands of wet and warm environments (Song and Dong 2002), and they tend to occur later rather than early in succession as evidenced from various man-made habitats in central Europe (Prach and Pyšek 1994), or from the course of revegetation following deglaciation in Kamchatka (Doležal et al. 2008). On the other hand, phalanx plants are more abundant in high elevation, dry and nutrient poor

regions of China (Song et al. 2002) than in habitats with opposite conditions.

The costs and benefits of lateral growth likely depend upon the type of spacer. Most important, the cost of aboveground leaf-bearing spacers should differ from those of belowground spacers that depend on the translocation of assimilates. Analogously, the production costs should differ between the two origination-based types of rhizomes: hypogeogenous and epigeogenous (Fig. 1) (Serebriakov and Serebriakova 1965, Klimeš et al. 1997). Hypogeogenous rhizomes originate belowground, grow horizontally at a species-specific depth and then turn upwards, producing a vertical aboveground shoot. Their growth is fully dependent on translocation of assimilates. Epigeogenous rhizomes, on the other hand, initially form on the soil surface and bear green leaves and only later descend into the soil. Thus, the production of epigeogenous rhizomes should be less demanding for plants.

We can therefore expect that the relationship between spacer length and environmental conditions should be affected by several allometric and functional constraints, such as plant height, persistence of connection between ramets, and the architecture of clonal growth organs. As such, constraints could represent trait attributes that have been conserved during evolution and shared by related species with other co-occurring trait attributes. The phylogenetic relatedness of the species should also be taken into account. To test this general hypothesis, we first asked whether environmental preferences of species (sensu Ellenberg 1991) showed covariation within our dataset covering 367 herbaceous species from temperate to arctic Europe. Second, we asked whether plants with hypogeogenous and epigeogenous rhizomes differ in their clonal growth characteristics (plant height, spacer length and spacer length/plant height ratio) and environmental preferences. Third, we asked how spacer length, rhizome type and persistence of connection between ramets are related to environmental preferences. Finally, we asked how spacer length/plant height ratio (L:H) is related to environmental preferences of plants. The analyses for answering the last three questions were done both with and without phylogenetic correction so that we could detect effects of phylogenetic inertia in the observed patterns. In the case where a relationship disappears after taking phylogeny into account,
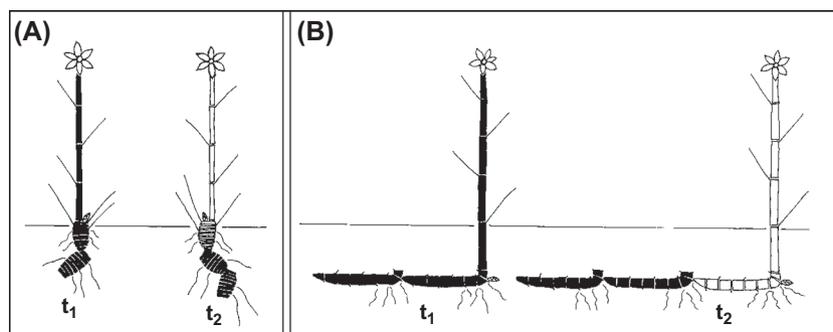
Figure 1. The two rhizome types examined in the present study. (A) an epigeogenous rhizome grows initially on the soil surface, with its internodes bearing green leaves, and is only later covered by litter or pulled by contractile roots into the soil so that it is belowground, with possible orientation ranging from horizontal to vertical. (B) a hypogeogenous rhizome begins by growing belowground, with scale leaves, but after a period of belowground horizontal growth its tip turns upwards and an aboveground shoot is initiated. (t₁), (t₂) time steps with most recent growth highlighted, with its length corresponding to the spacer length examined in the present study.

we can expect that the association of a certain morphological character with some specific environmental conditions occured early in phylogeny; in the case where a relationship appears only after taking phylogeny into account, we can expect that specialization for a certain environment to have occured repeatedly later in phylogeny.

Methods

To answer our questions, we compiled relevant data from two sources. The information on spacer length came from the morphological studies performed on plants collected in field in order to fill CLO-PLA 3, the database of clonal growth of plants from Europe outside of the Mediterranean (Klimešová and Klimeš 2006), as well as a database of clonal plants of Estonian meadows (Sammul et al. 2003). Plants from their natural habitats were excavated with care to obtain at least two interconnected shoots or whole belowground organs bearing the bud bank (organ of clonal growth, rhizome). Plants were cleaned and decaying parts of old rhizomes, leaf bases etc, as well as fine roots were removed. Plants were measured and drawn on the paper in scale. A more detailed description of measuring plant clonal growth traits for Estonian database is given by Tamm et al. (2001). The European flora was represented from the Alps in the south to Svalbard in the north and from the western coast of the Netherlands to Estonia, the most represented community types were meadows, but forests, alpine grasslands and arctic tundra were also represented. Assessed plants were mainly herbaceous perennials, less often small shrubs. We selected only those species that possess epigeogenous (204 species) or hypogeogenous (163 species) rhizomes (Fig. 1, Klimeš et al. 1997), and for which exact spacer length measurements were available. In cases of multiple measurements for one species, the longest spacer length value was selected. Spacer length was measured as the nearest distance between this year's and last year's shoot along the rhizome. This method of measurement was also used when an epigeogenous rhizome was growing more or less vertically rather than horizontally. Long, curved hypogeogenous rhizomes were straightened for measuring purposes. In cases of multiple generations of shoots per year, the distance between the youngest shoot from the preceding year and the youngest shoot from this year was considered.

Persistence of connection among ramets was assessed using the CLO-PLA 3 database. Rhizomes with connection persistence of two years or less were considered splitters and rhizomes with connection persistent for more than two years were considered integrators. The delimation of spacer persistence longevity was based on morphological characters (whether or not spacers older than two years occured on the plant).

For each species, shoot height was taken from widely accepted floras of the regions (Czech republic: Kubát et al. 2002, Svalbard: Rønning 1996, Estonia: Anon. 1959–1984) and its median value was used in analyses.

Environmental preferences of the species were assessed indirectly using Ellenberg indicator values (EIV), which are empirically determined based on occurrence of the species of the central Europe in plant communities along various environmental gradients. EIV-s generally range from 1 (lowest preference) to 9 (highest preference), and in the case of moisture the values range from 1 to 12, in an ordinal scale. These gradients span habitats with low to high availability of light, nitrogen, and water, and low to high mean annual temperatures or estimated continentality of climate. Ellenberg indicator values were extracted from Ellenberg (1991) and were not available for species not occurring in central Europe (e.g. from Svalbard). Moreover, some species have no preferences recorded for certain environmental characteristics and therefore do not have indicator values for these characteristics. Therefore, there are different numbers of replicates in our analyses, depending upon the characteristics (Table 2, 3).

Data analysis

The assembled dataset included 367 plant species. Ellenberg indicator values (EIV) were available for 323 species. We first used principal component analysis (PCA) to detect patterns of similarity between species according to their environmental preferences as expressed by EIV. PCA was calculated using Canoco for Windows (ter Braak and Šmilauer 1998). The relationships of the species EIV to examined plant traits (spacer length, plant height) and four categories of rhizomes (hypogeogenous integrator, hypogeogenous splitter, epigeogenous integrator and epigeogenous splitter) and plant phylogeny (family affiliation) were visualized by passive projection on the PCA ordination plane.

Differences in mean values of traits (spacer length, plant height) and EIVs among plants with two types of rhizomes (epigeogenous and hypogeogenous) and two kinds of connection persistence (splitters and integrators) and their interaction were tested using a factorial ANOVA. If the main effect was significant, the unequal N HSD test was used for post-hoc comparisons as a reasonable compromise between control of type I error inflation and power of the test. Data on spacer length and plant height was log-transformed to improve normality and homoscedascity.

Relationships between spacer length and predictor variables (shoot height, EIV) were first examined using linear regression analyses. Second, due to the possibility that phylogenetic relatedness could affect both the values of lateral spread and the explanatory variables implied in the tested hypotheses, the tests were also done with phylogenetic correction, using phylogenetically independent contrasts (PIC, see Webb et al. 2002 for a broad discussion of phylogenetic correction approaches) using the ape package in R, ver. 2.10.1 (R Development Core Team 2009). Independent contrasts are widely used to incorporate phylogenetic information into studies of trait relationships (Ackerly 2000, with each PIC providing a replicate for assessing the correlation between taxon attributes (Westoby 1999). Removing the effects of phylogenetic relatedness should enable us to see the taxa's unconstrained response to natural selection. The computed phylogenetic contrasts of all variables were analyzed using linear regression. Finally, we sought to control the comparison wise type I error rate by using the false discovery rate approach (Benjamini and Hochberg 1995) for both phylogenetically uncorrected and corrected analyses, considering all the variables as equivalent.

In our study, the branching structure of the phylogenetic tree was based on the BIOLFLOR database (Klotz et al.

2002, <www.ufz.de/biolflor/index.jsp>). Time of divergence from common ancestor branch length estimates were taken from the Angiosperm Phylogeny Group website (Stevens 2001) and from Kellog (2001), Bremer et al. (2002) and Janssen and Bremer (2004).

Results

Covariation of environmental characteristics

PCA revealed strong correlations among various indicator values of species environmental preferences (Fig. 2). EIVs of pH and temperature were positively correlated (r = 0.20, p < 0.0001, n = 322). The temperature EIV was negatively correlated with with the light EIV (r = –0.24, p < 0.0001), whereas EIVs of pH and moisture were negatively correlated (r = –0.14, p < 0.012). The EIV of continentality was negatively correlated with with the EIV of soil fertility (r = –0.17, p < 0.002), and positively with the EIV of light (r = 0.16, p = 0.003).

Environmental preferences and growth characteristics of rhizomes

The PCA (Fig. 2) revealed that plants with splitting hypogeogenous rhizomes were associated with high soil fertility, and plants with splitting epigeogenous rhizomes were associated with high moisture. On the other hand, integrators tended to occur in dry, nutrient poor conditions. Some plant families were specialized for certain environmental conditions, e.g. Brassicaceae for high fertility, and Fabaceae and Rubiaceae for high temperature and pH (Fig. 2).

When examining environmental preferences of plants with different rhizome type (epigeogenous or hypogeogenous) without taking phylogenetic relationships into account, we found that plants with hypogeogenous rhizomes were associated with warmer environments than plants with epigeogenous rhizomes (Fig. 3). On the other hand, plants with epigeogenous rhizomes were associated with more illuminated environments than plants with hypogeogenous rhizomes. Neither rhizome types showed association with particular levels of continentality, pH, moisture, or soil fertility.

Association of plants with hypogeogenous rhizomes with warmer environments became nonsignificant after phylogenetic relationships were taken into account while their association with continentality became significant only after phylogenetic corrections.

Splitters of both rhizome types were associated with habitats with higher moisture and soil fertility (Fig. 2, 3, Table 1). These correlations persisted after correcting for the relatedness of the species. Positive relationship between integration of rhizome and the EIV of continentality was lost after phylogenic corrections.

Plants with hypogeogenous rhizomes had longer spacers, greater height, and higher ratios between spacer length and plant height (Table 1, Fig. 4). When analyzing relationships between spacer length and plant height (Fig. 5, Table 2) within individual rhizome types a positive relationship was found only for epigeogenous rhizomes, and in the comparison of all four rhizome categories this relationship was found only for integrators with epigeogenous rhizomes. After applying phylogenetically independent contrasts, the relationship between spacer length and plant height remained significant and positive only for the broad category of plants with epigeogenous rhizomes and became significant and negative for plants with hypogeogenous rhizomes.

Correlation between spacer length and environmental preferences

Analysis of whole dataset by PCA (Fig. 2) showed that plant height and spacer length were positively correlated with the
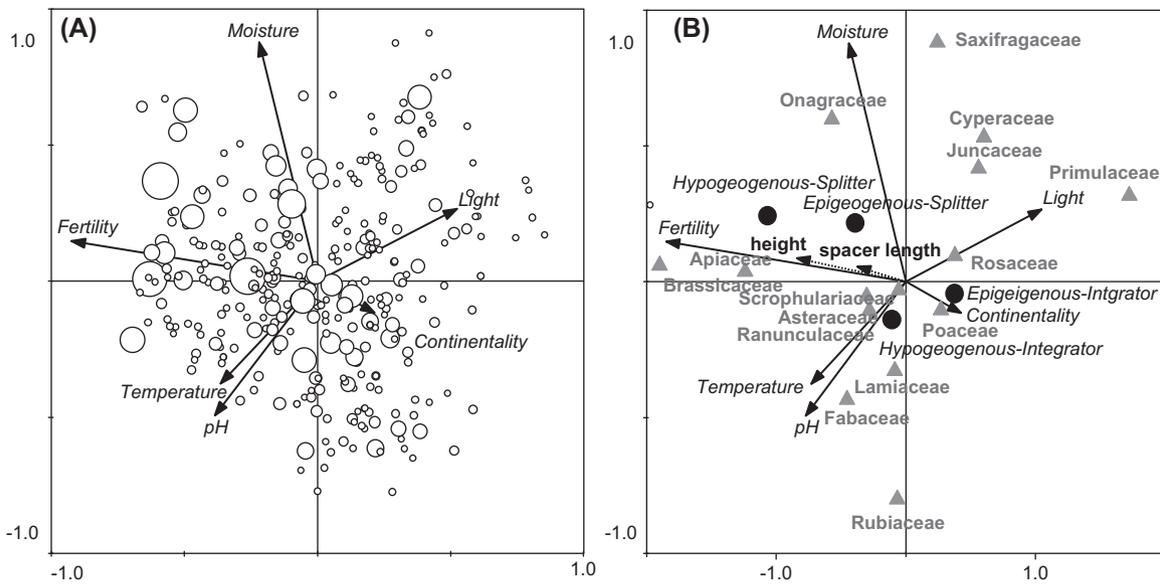
Figure 2. PCA diagrams showing (A) the habitat associations (expressed as Ellenberg indicator values) of 323 plant species (symbol size corresponds to spacer length, with maximum values around 67 cm), with (B) the family affiliation (only those families with more than 5 species are shown), plant traits (spacer length, plant height), and for categories of rhizomes (based on type and persistence) passively projected onto the resulting ordination space.

EIV of soil fertility. Analysis of plants with epigeogenous rhizomes showed that there is a negative correlation between spacer length and light, and a positive correlation between spacer length and temperature (Table 2) with only the former remaining significant after phylogenetic correction. Moreover, after phylogenetic correction, negative relationships with pH and a positive correlation with soil fertility emerge.

Spacer length of epigeogenous integrators was negatively correlated with light and positively correlated with temperature. However, after taking phylogeny into account, the only significant positive relationship found was with moisture. For epigeogenous splitters, none of the correlations was confirmed after applying a false discovery rate approach (Table 2). For hypogeogenous rhizomes, we found only one significant result – a positive correlation between spacer length and temperature when the data were corrected for phylogeny.

Correlation between spacer length/plant height ratio and environmental preferences

We found no correlation between the ratio of spacer length and plant height (L:H) and any of the EIVs in our dataset. After taking phylogeny into account, the L:H ratio turned out to be positively correlated with light, negatively correlated with soil fertility in plants with splitting epigeogenous rhizomes, and negatively correlated with moisture in all plants with hypogeogenous rhizomes (Table 3).

Discussion

Our results indicated that the relationship between spacer length and environmental conditions is subject to morphological, functional and evolutionary constraints. In our dataset, the main relationship between spacer length and EIV (light and temperature) was influenced by the rhizome type of the plant (hypogeogenous and epigeogenous rhizomes). In the case of temperature, this difference was phylogenetically old, with related plants tending to share rhizome type. On the other hand, the difference in rhizome persistence (integrators versus splitters), represents a specialized strategy for different environmental factors (moisture and soil fertility, respectively), with this specialization having evolved repeatedly across different groups.

Spacer length was correlated with environmental preference in only a few cases, and most often with EIV of temperature and light, as there was a tendency for plants with
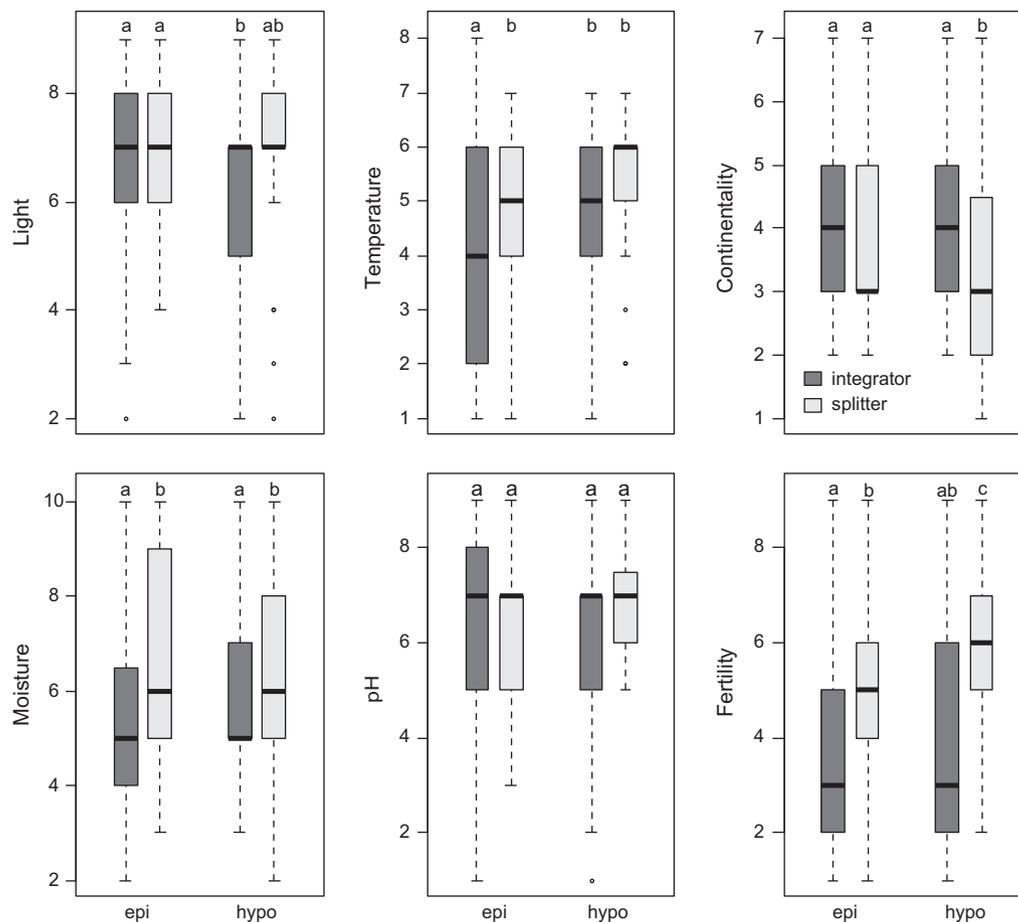
Figure 3. Pairwise comparisons of environmental associations (expressed as Ellenberg indicator values) among clonal plant categories based on rhizome type (epigeogenous or hypogeogenous) and the longevity of their connections (integrators: connection > 2 years; splitters: connection 1–2 years). Differing letters above the boxes indicate significant differences between categories (post - hoc test - unequal N HSD test).

Table 1. Comparison of traits and habitat associations among clonal plant categories based on rhizome type (epigeogenous or hypogeogenous) and the longevity of their connections (integrators: connection > 2 years; splitters: connection 1–2 years). Average trait values are presented next to the summary of ANOVA analyses (F values and corresponding type I error estimate – p) for plant size characteristics and Ellenberg indicator values, with (PIC) and without (uncorrected) phylogenetic correction. Asterisk indicates a statistically significant difference after controlling for familywise error rate by using a false discovery rate approach.

	Epigeogenous rhizomes		Hypogeogenous rhizomes		Differences between rhizomes		Differences between persistence		Interaction rhizome × persistence	
	integ	split	integ	split	$p_{uncorrected}$	p_{PIC}	$p_{uncorrected}$	p_{PIC}	$p_{uncorrected}$	p_{PIC}
Spacer length (mm)	25.7	40.5	109.8	127.8	0.0001*	0.024	0.229	0.985	0.907	0.012
Height (cm)	37.9	46.3	50.4	65.2	0.0001*	0.0001*	0.015*	0.892	0.491	0.891
Spacer/height ratio	0.09	0.32	0.31	0.34	0.0001*	0.730	0.192	0.600	0.513	0.063
Light	7.02	7	6.26	6.71	0.0002*	0.016*	0.458	0.099	0.330	0.111
Temperature	4.12	4.88	4.85	5.17	0.0039*	0.485	0.046	0.772	0.463	0.001*
Continentality	4.1	3.72	4.13	3.45	0.882	0.001*	0.015*	0.028	0.483	0.348
Moisture	5.45	6.39	5.69	6.6	0.321	0.350	0.0007*	0.0000*	0.951	0.119
pH	6.24	6.28	6.17	6.78	0.931	0.217	0.363	0.210	0.370	0.291
Fertility	3.69	4.87	4.12	5.82	0.036	0.306	0.0000*	0.0000*	0.389	0.134

longer spacers to be found in warm conditions and shorter spacers in illuminated environments (note that EIV were available only for central-European species in our dataset). Analysis of different rhizome types revealed a similar pattern: plants with hypogeogenous rhizomes (which tend to be longer) were associated with warm environments whereas plants with epigeogenous rhizomes (usually shorter) were associated with illuminated habitats.

After relating spacer length to plant height (L:H ratio) the few significant results imply that spacer length to plant height ratio is not selected for in different habitats. Thus, contrary to our expectation, the phalanx–guerilla continuum could not represent adaptation to certain environmental conditions, at least in terrestrial communities of temperate Europe.

Covariation of environmental preferences and clonal growth traits

Our findings differed from the pattern of covariation of EIVs of clonal plants reported for the central European flora by van Groenendael et al. (1996) that clonal plants are associated either with moist, shaded, nutrient rich conditions or dry, illuminated and nutrient poor conditions. We found, instead, two separate main gradients: from nutrient-rich, shaded habitat to nutrient-poor sites and from moist, cold conditions to dry, warm environments. The specialization of plants we detected along the temperature gradient was evolutionarily older than specialization along light, moisture and soil fertility gradient. This result too is contrary to previous work (van Groenendael et al. 1996), in which moisture was the most influential environmental characteristic in habitat specialization. However, differences between the two studies in the examined sets of plant species and in the used methods might explain the different findings. van Groenendael et al. (1996) included all the clonal plants of central Europe in their analysis, whereas the present study encompassed only plants having either hypogeogenous or epigeogenous rhizomes. The earlier study used clonal growth type as a proxy for both spacer persistence and lateral spread, whereas the present study evaluated actual measurements of individual plants. Additionally, van Groenendael et al. (1996) analyzed trait–environment relationships at the family level
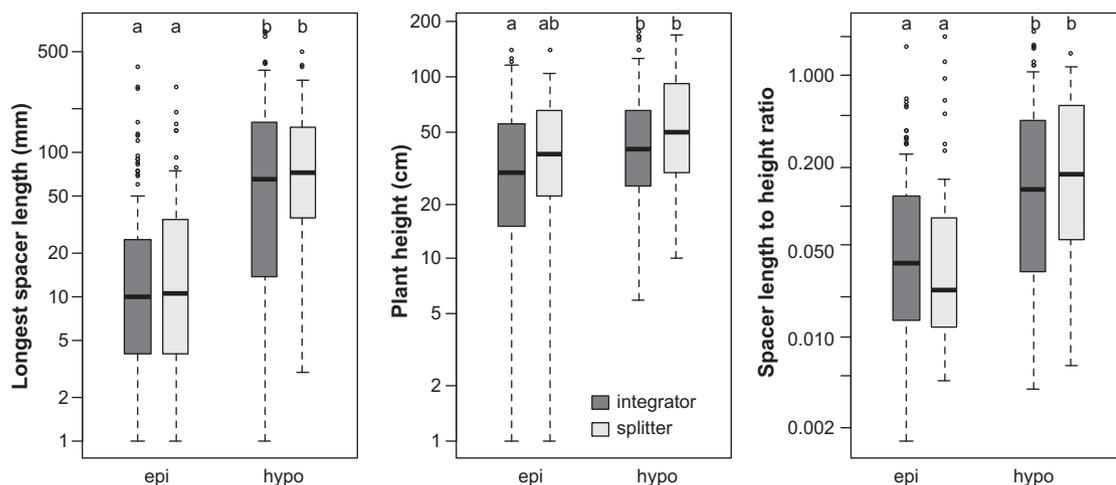
Figure 4. Pairwise comparisons of size characteristics among clonal plant categories based on rhizome type (epigeogenous or hypogeogenous) and the longevity of their connections (integrators: connection > 2 years; splitters: connection 1–2 years). Axes are logarithmic. Differing letters above the boxes indicate significant differences between categories (post - hoc test - unequal N HSD test).
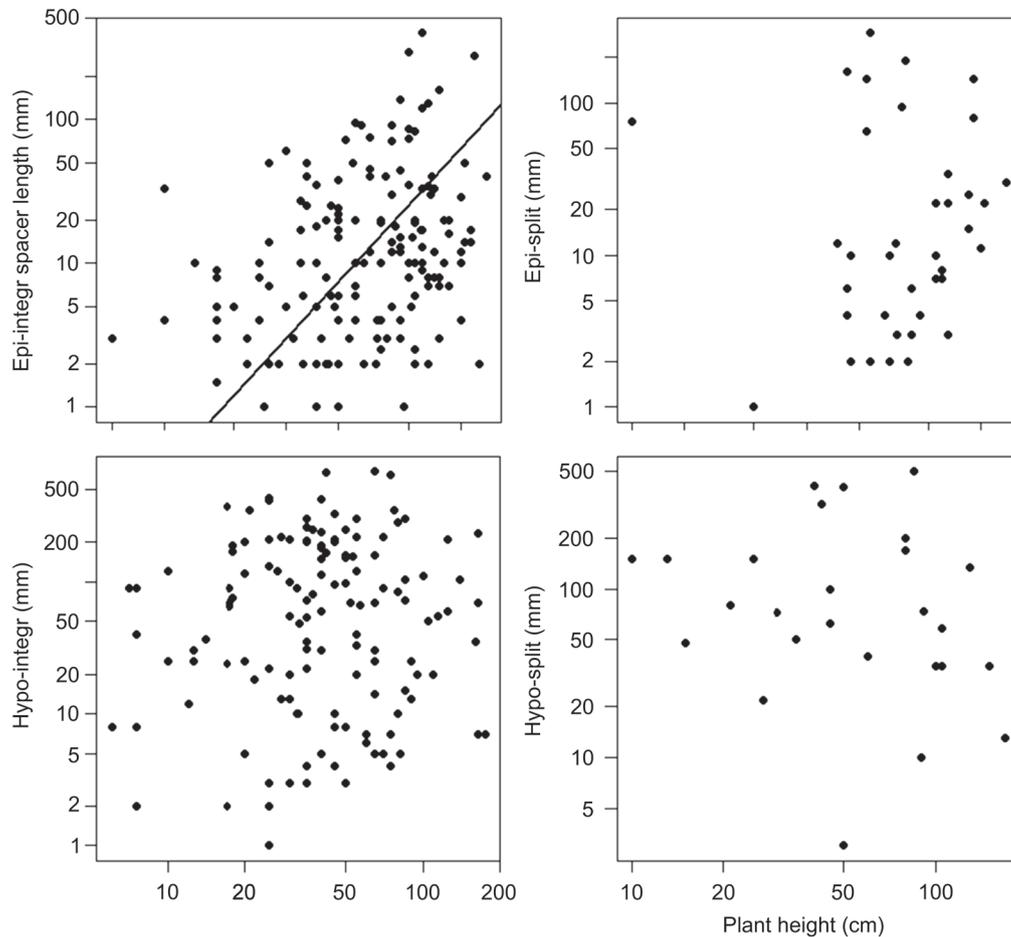
Figure 5. Relationship between spacer length and plant height for clonal plants categories based on rhizome type (epigeogenous or hypogeogenous) and the longevity of their connections (integrators: connection > 2 years; splitters: connection 1–2 years). Axes are logarithmic. The only significant relationship found was for the epigeogenous integrators ($R^2 = 10.1\%$, $p < 0.001$).

to correct for phylogeny, while we used more detailed data on species relatedness down to the species level. Finally, our investigation omitted true aquatic plants (submerged and free floating), with the range in moisture consequently being smaller than in the earlier study.

Implications of rhizome type

In accordance with our expectation, the differences in rhizome type coincided with differences in morphological properties as well as with environmental preferences. In our dataset, species with epigeogenous rhizomes, as expected, were associated with habitats with high light availability, whereas within this group of species there was a trend towards short spacers in highly illuminated habitats. Species with hypogeogenous rhizomes, however, were associated with warm habitats. Moreover, the trend towards long spacers in warm environments was detected for both epigeogenous and hypogeogenous rhizome-bearing species. These environmental associations have not previously been recognized, as the two types of rhizomes are not usually distinguished in comparative studies of clonal growth in various environments (but see Sosnová et al. 2010). The relationships between spacer length and other environmental variables, however, were less consistent.

The fact that plants with short epigeogenous rhizomes were associated with illuminated habitats might also be interpreted as a direct effect of light, as it is well known that in ample illumination, stem elongation is reduced (Larcher 1995). However, this process is more important in within-species comparisons. Thus, the effect we detected could instead be due to small plant stature, as in our dataset the species that prefer well lit habitats were those from places with low soil fertility. Similarly, the association of plants with hypogeogenous rhizomes to warmer habitats might be interpreted as either a direct, detrimental effect of solifluction and frost heave on long and usually slender hypogeogenous rhizomes in cold regions (Jonasson and Callaghan 1992, Klimeš 2008) or as a side-effect of relatively impermeable, sterile, and stony substrates in cold regions (Klimešová et al. 2011). Additionally, the fact that high altitude ecosystems are devoid of nutrient rich or wet habitats which usually support plants with long rhizomes might also have influenced the observed patterns.

As expected, splitters of both rhizome types tend to have longer spacers in absolute terms. In hypogeogenous rhizomes this was also true in relation to plant height (i.e. the L:H ratio). This shows support for a tradeoff between spacer length and persistence, and moreover, the splitters with long spacers had taller shoots than the integrators with short spacers. The maintenance cost of a perennial rhizome

Table 2. Relationships between lateral spread rate and plant height and habitat preferences (expressed by Ellenberg indicator values) for species having epigeogenous or hypogeogenous rhizomes, showing ANOVA outcomes from analyses with both categories of ramet connection persistence (splitter: connection 1–2 years, integrator: connection > 2 years) pooled (all) or with each of these persistence categories considered separately. ANOVA results are presented for analyses with (PIC) and without (uncorrected) phylogenetic correction. Effects of individual predictors (rows) were examined for each response variable (columns) with linear regression. The first three entries in each cell comprise the number of tested species (n), F statistic value and corresponding type I error estimate (p). The symbol next to F values (present only for predictors with p < 0.1) summarizes the direction of the effect: ↑ means a positive correlation between the predictor and response values, ↓ means a negative correlation. Asterisk after p-value indicates a statistically significant relationship after applying a false discovery rate approach.

		Epigeogenous, all		Epigeogenous, integ		Epigeogenous, split		Hypogeogenous, all		Hypogeogenous, integ		Hypogeogenous, split	
		uncorrected	PIC	uncorrected	PIC	uncorrected	PIC	uncorrected	PIC	uncorrected	PIC	uncorrected	PIC
Height	n	204		166		38		163		134		29	
	F	15.79 ↑	5.74	18.35 ↑	0.35	0.13	2.89 ↓	0.26	6.49 ↓	0.4	3.57 ↓	1.13	1.23
	p	0.0001*	0.0175*	0.0001*	0.557	0.717	0.097	0.607	0.012	0.528	0.061	0.297	0.278
Light	n	174		140		34		145		117		25	
	F	7.33 ↓	14.04 ↓	6.24 ↓	1.07	1.17	0.11	0.15	1.00	0.62	0.04	1.31	0.2
	p	0.007*	0.0002*	0.013*	0.303	0.286	0.742	0.695	0.318	0.43	0.832	0.264	0.658
Temperature	n	136		111		25		105		88		17	
	F	8.53 ↑	2.735	8.24 ↑	7.86 ↑	0.38	0.65	1.68	11.94 ↑	1.42	2.86 ↓	0.054	0.23
	p	0.004*	0.1005	0.004*	0.058	0.541	0.426	0.197	0.0007*	0.237	0.094	0.82	0.639
Continentality	n	157		128		29		130		106		24	
	F	0.009	0.0796	0.088	1.827	4.68 ↑	8.97 ↑	0.001	0.025	0.39	3.72 ↑	1.47	3.75 ↓
	p	0.92	0.7782	0.766	0.179	0.039	0.006	0.994	0.874	0.534	0.065	0.238	0.065
Moisture	n	164		131		33		138		113		25	
	F	0.33	1.145	2.35	7.03 ↑	0.1	5.71 ↓	1.26	3.62 ↑	0.28	1.58	3.92	0.04
	p	0.564	0.2862	0.127	0.009*	0.754	0.023	0.263	0.0589	0.597	0.211	0.059	0.849
pH	n	141		116		25		119		100		19	
	F	0.506	16.14 ↓	0.103	0.27	1.35	0.56	2.94 ↑	2.67	3.94 ↑	0.06	3.71	8.33 ↓
	p	0.478	0.0001*	0.747	0.602	0.257	0.458	0.0891	0.105	0.049	0.798	0.071	0.011
Fertility	n	164		133		31		139		116		23	
	F	1.48	14.84 ↑	1.557	0.67	0.04	0.09	2.90 ↑	0.27	4.43 ↑	0.88	0.99	3.85 ↓
	p	0.225	0.0001*	0.2143	0.413	0.843	0.762	0.031	0.602	0.037	0.349	0.329	0.062

Table 3. Relationship between spacer length to shoot height ratio and plant habitat preferences (expressed by Ellenberg indicator values) for species having epigeogenous or hypogeogenous rhizomes, showing ANOVA outcomes from analyses with both categories of ramet connection persistence (splitter: connection 1–2 years, integrator: connection > 2 years) pooled (all) or with each of these persistence categories considered separately. ANOVA results are presented for analyses with (PIC) and without (uncorrected) phylogenetic correction. Effects of individual predictors (rows) were examined for each response variable (columns) with linear regression. The first three entries in each cell comprise the number of tested species (n), F statistic value and corresponding type I error estimate (p). The symbol next to F values (present only for predictors with $p < 0.1$) summarizes the direction of the effect: ↑ means a positive correlation between the predictor and response values, ↓ means a negative correlation. Asterisk after p-value indicates a statistically significant relationship after applying a false discovery rate approach.

		Epigeogenous, all		Epigeogenous, integ		Epigeogenous, split		Hypogeogenous, all		Hypogeogenous, integ		Hypogeogenous, split	
		uncorrected	PIC	uncorrected	PIC	uncorrected	PIC	uncorrected	PIC	uncorrected	PIC	uncorrected	PIC
Light	n	172		140		34		145		117		25	
	F	0.04	0.02	0.08	6.73↑	0.65	12.35↑	3.69↓	0.71	1.68	0.89	2.29	0.66
	p	0.843	0.894	0.78	0.01	0.424	0.0013*	0.056	0.399	0.076	0.348	0.143	0.425
Temperature	n	136		111		25		105		88		17	
	F	0.66	1.44	0.16	0.16	1.1	1.82	0.004	0.01	0.04	0.86	0.06	6.24↑
	p	0.417	0.231	0.685	1.968	0.304	0.191	0.946	0.912	0.838	0.354	0.804	0.024
Continentality	n	157		128		29		130		106		24	
	F	0.06	2.25	0.19	0.47	1.23	1.32	0.011	0.87	0.011	0.43	4.34↓	0.25
	p	0.81	0.136	0.664	0.496	0.276	0.261	0.917	0.352	0.917	0.51	0.048	0.619
Moisture	n	164		131		33		138		113		25	
	F	0.21	2.14	1.02	0.28	0.03	6.53	0.88	10.03↓	0.15	2.27	1.46	1.14
	p	0.654	0.145	0.316	0.593	0.858	0.015	0.347	0.001*	0.695	0.134	0.239	0.295
pH	n	141		116		25		119		100		19	
	F	0.15	1.62	0.05	0.49	0.19	0.63	0.01	0.87	0.01	2.04	4.99↓	0.92
	p	0.701	0.206	0.823	0.484	0.667	0.434	0.986	0.351	0.656	0.155	0.039	0.35
Fertility	n	164		133		31		139		116		23	
	F	1.33	4.71↑	1.55	3.04↓	0.27	19.48↓	0.06	1.06	0.12	1.75	0.08	0.06
	p	0.251	0.031	0.216	0.083	0.603	0.0001*	0.811	0.304	0.723	0.188	0.776	0.798

system could reduce current plant growth and competitive ability. However, extensive lateral spread in competitive species was reported by Svensson et al. (2005) on the basis of classification of 255 herbs from the British flora into Grime's strategy scheme (Hodgson et al. 1995). As plant height is very important in nutrient-rich, competitive environments, we consider plant height as the main trait which is selected for under these conditions and spacer length and its persistence as co-occurring traits.

The tendency of plants with hypogeogenous rhizomes to be taller and presumably more competitive in competition for light than plants with epigeogenous rhizomes could be due to the different shoot architecture associated with each of these two types of rhizomes. Species with epigeogenous rhizomes often have leaves in a basal rosette and dicyclic (or polycyclic) shoots (86% of them according to CLO-PLA 3 database, Klimešová and Klimeš 2006). With dicyclic shoots, a plant produces shortened basal internodes, for some time (typically the first season of shoot life) and then grows one or several long internodes that bear inflorescences and finish shoot growth (typically in the second season or later). This growth habit makes such plants sensitive to the presence of large and shadowing neighbours, but more tolerant to disturbances such as grazing or mowing (Klimeš and Klimešová 2000, Klimešová et al. 2008, Moora et al. 2009).

Plants with hypogeogenous rhizomes, on the other hand, are characterized by monocyclic (emerging, flowering and dying in one growing season) and erosulate shoots (92% of them according to CLO-PLA 3 database, Klimešová and Klimeš 2006) and consequently tend to be tall and have high competitive ability (Klimešová et al. 2008, Moora et al. 2009).

Our results supported the hypothesis that larger plants have longer spacers only if they have epigeogenous rhizomes, where formation of the spacer is not so strongly dependent on translocation of assimilates. For hypogeogenous rhizomes, a negative correlation between spacer length and plant height was found after phylogenetic correction. This might be a sign of allocation limitations for large plants, which must invest assimilates in supporting structures. This discrepancy with the hypothesis, based on scaling theory, is attributable to the fact that – although acknowledged only rarely (Niklas 2003) – scaling theory is based only on unitary plants (namely trees), and therefore it cannot yet generate valid predictions for herbaceous plants having assimilating stems in addition to their leaves.

Surprisingly, significant relationships among spacer length/plant height ratios (L:H) and environmental characteristics were rare, and were only found after phylogenetic correction. This can be due to selection effect, with big variation masking tendencies that are typical of individual taxonomic groups. In published comparative studies, guerilla and phalanx growth forms are not exactly defined and are mostly based solely on spacer length (Song et al. 2002). However, as we have shown here, instead of a simple relationship between a single trait and environmental conditions, the combination of different attributes (including rhizome type and phylogenetic relatedness), as well as allometric effects on plant height and rhizome length, could all influence observed patterns.

Conclusions

Our analysis of plants growing from temperate to arctic Europe revealed the effects of different morphological types of rhizomes and different degrees of persistence of rhizome connections on the relationship between their lateral spread (spacer length) and environmental conditions. We also believe that nutrient rich habitats select for tall, competitive species, and, because larger statue correlates with long and splitting hypogeogenous rhizomes, these clonal traits are favored in this type of environment. Some of the examined relationships were significant only after taking phylogenetic relationship into account, implying that the relationship was masked by large differences among individual taxonomical groups while the tendency within many groups was similar. It is imperative that further comparative studies relating clonal growth forms or clonal growth traits to environmental conditions consider the constraints originating from evolutionary history and the architecture of the subject species.

References

Ackerly, D. D. 2000. Taxon sampling, correlated evolution, and independent contrasts. – Evolution 54: 1480–1492.

Anon. 1959–1984. Flora of the Estonian SSR I-XI Eesti Riiklik Kirjastus, Tallinn, in Estonian.

Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. – J. R. Stat. Soc. B 57: 289–300.

Bremer, B. et al. 2002. Phylogenetics of asterids based on 3 coding and 3 non-coding chloroplast DNA markers and the utility of non-coding DNA at higher taxonomic levels. – Mol. Phyl. Evol. 24: 274–301.

Doležal, J. et al. 2008. Primary succession following deglaciation at Koryto Glacier Valley, Kamchatka. – Arct. Antarct. Alp. Res. 40: 309–322.

Ellenberg, H. 1991. Zeigerwerte von Pflanzen in Mitteleuropas, 1 ed. – Scripta, Geobotanica. 18.

Enquist, B. J. and Niklas, K. J. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. – Science 295: 1517–1520.

Eriksson, O. and Jerling, L. 1990. Hierarchical selection and risk spreading in clonal plants. – In: van Groenendael, J. M. and de Kroon, H. (eds), Clonal growth in plants: regulation and function. SPB Academic Publishing, pp. 79–94.

Fahrig, L. et al. 1994. The advantage of long-distance clonal spreading in highly disturbed habitats. – Evol. Ecol. 8: 172–187.

Herben, T. 1995. Founder and dominance control: neglected concepts in the community dynamics of clonal plants. – Abstr. Bot. 19: 3–10.

Hodgson, J. G. et al. 1995. The electronic comparative plant ecology. – Chapman and Hall.

Hutchings, M. J. and de Kroon, H. 1994. Foraging in plants – the role of morphological plasticity in resource acquisition. – Adv. Ecol. Res. 25: 159–238.

Hutchings, M. J. and Wijesinghe, D. K. 1997. Patchy habitats, division of labour and growth dividends in clonal plants. – Trends Ecol. Evol. 12: 390–394.

Janssen, T. and Bremer, K. 2004. The age of major monocot groups inferred from 800+*rbcL* sequences. – Bot. J. Linn. Soc. 146: 385–398.

Jonasson, S. and Callaghan, T. V. 1992. Root mechanical properties related to disturbed and stressed habitats in the Arctic. – New Phytol. 122: 179–186.

Jónsdóttir, I. S. and Watson, M. 1997. Extensive physiological integration: an adaptive trait in resource-poor environments? – In: de Kroon, H. and van Groenendael, J. (eds), The ecology and evolution of clonal plants. Backhuys Publishers, pp. 109–136.

Kellog, E. A. 2001. Evolutionary history of the grasses. – Plant Physiol. 125: 1198–1205.

Kelly, C. K. 1995. Thoughts on clonal integration: facing the evolutionary context. – Evol. Ecol. 9: 575–585.

Klimeš, L. 1999. Small-scale plant mobility in a species-rich grassland. – J. Veg. Sci. 10: 209–218.

Klimeš, L. 2008. Clonal splitters and integrators in harsh environments of the Trans-Himalaya. – Evol. Ecol. 22: 351–367.

Klimeš, L. and Klimešová, J. 2000. Plant rarity and the type of clonal growth. – Zeitschr. Ökol. Natursch. 9: 43–52.

Klimeš, L. et al. 1997. Clonal plant architectures: a comparative analysis of form and function. – In: de Kroon, H. and van Groenendael, J. (eds), The ecology and evolution of clonal plants. Backhuys Publishers, pp. 1–29.

Klimešová, J. and Klimeš, L. 2006. CLO-PLA3: a database of clonal growth architecture of central-European plants. – http://clopla.butbn.cas.cz.

Klimešová, J. and Klimeš, L. 2008. Clonal growth diversity and bud banks in the Czech flora: an evaluation using the CLO-PLA3 database. – Preslia 80: 255–275.

Klimešová, J. et al. 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. – Preslia 80: 245–253.

Klimešová, J. et al. 2011. Clonal growth forms in eastern Ladakh, western Himalayas: classification and habitat preferences. – Folia Geobot. in press.

Kubát, K. et al. (eds) 2002. Klíč ke květeně České republiky. (Key to the Flora of the Czech Republic). – Academia, Praha.

Klotz, F. et al. 2002. BIOLFLOR – Eine Datenbank mit biologisch–ökologischen Merkmalen zur Flora von Deutschland. – Bundesamt für Naturschutz, Bonn, Bad Godesberg.

Larcher, W. 1995. Physiological plant ecology. – Springer.

Lovett Doust, L. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*) I. The dynamics of ramets in contrasting habitats. – J. Ecol. 69: 743–755.

Moora, M. et al. 2009. Understory plant diversity is related to higher variability of vegetative mobility of coexisting species. – Oecologia 159: 355–361.

Müller, I. et al. 2000. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. – Persp. Plant Ecol. Evol. 3: 115–127.

Niklas, K. J. 2003. Reexamination of a canonical model for plant organ biomass partitioning. – Am. J. Bot. 90: 250–254.

Pitelka, L. F. and Ashmun, J. W. 1985. Physiology and integration of ramets in clonal plants. – In: Jackson, J. B. C. et al. (eds), Population biology and evolution of clonal organisms. Yale Univ. Press, pp. 399–435.

Prach, K. and Pyšek, P. 1994. Clonal plants – what is their role in succession. – Folia Geobot. Phytotax. 29: 307–320.

Rønning, O. I. 1996. The flora of Svalbard. – Norsk Polar Institutt.

Sammul, M. et al. 2003. Clonal growth in species-rich grassland: the results of a 20-year fertilization experiment. – Folia Geobot. 38: 1–20.

Sammul, M. et al. 2004. A comparison of plant communities on the basis of their clonal growth patterns. – Evol. Ecol. 18: 443–467.

Schmid, B. and Harper, J. L. 1985. Clonal growth in grassland perennials I. Density and pattern dependent competition between plants with different growth forms. – J. Ecol. 73: 793–808.

Serebriakov, I. G. and Serebriakova, T. I. 1965. On the two types of the rhizome formed by perennial plants. – Biulletin Moskovskogo Obshchestva Ispitatelei Prirody, Biologia, 70: 67–81, in Russian.

Song, M. and Dong, M. 2002. Clonal plants and plant species diversity in wetland ecosystems in China. – J. Veg. Sci. 13: 237–244.

Song, M. H. et al. 2002. Importance of clonal plants and plant species diversity in the northeast China Transect. – Ecol. Res. 17: 705–716.

Sosnová, M. et al. 2010. Distribution of clonal growth forms in wetlands. – Aquat. Bot. 92: 33–39.

Steinger, T. et al. 1996. Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. – Oecologia 105: 94–99.

Stevens, P. F. 2001. Angiosperm Phylogeny Website, ver. 7.0, May 2006. – http://www.mobot.org/MOBOT/research/APweb/.

Stuefer, J. F. et al. 1996. Exploitation of environmental heterogeneity by spatial division of labour in a clonal plant. – Funct. Ecol. 10: 328–334.

Stuefer, J. F. et al. 2002. A genotypic trade-off between the number and size of clonal offspring in the stoloniferous herb *Potentilla reptans*. – J. Evol. Biol. 15: 880–884.

Svensson, B. M. et al. 2005. Clonal plants in the community. – In: van der Maarel, E. (ed), Vegetation ecology. Blackwell, pp. 129–146.

Tamm, A. et al. 2001. Classifying clonal growth forms based on vegetative mobility and ramet longevity: a whole community analysis. – Evol. Ecol. 15: 383–401.

ter Braak, C. J. F. and Šmilauer, P. 1998. CANOCO reference manual and user's guide to Canoco for Windows. Software for canonical ordination (ver. 4). – Centre for Biometry, Wageningen.

van Groenendael, J. M. et al. 1996. Comparative ecology of clonal plants. – Phil. Trans. R. Soc. B 351: 1331–1339.

Webb, C. O. et al. 2002. Phylogenies and community ecology. – Ann. Rev. Ecol. Syst. 33: 475–505.

Westoby, M. 1999. Generalization in functional plant ecology: the species-sampling problem, plant ecology strategy schemes, and phylogeny. – In: Pugnaire, F. I. and Vallandares, F. (eds), Handbook of functional plant ecology. M. Dekker, pp. 847–872.

Ye, X. H. et al. 2006. A trade-off between guerrilla and phalanx growth forms in *Leymus secalinus* under different nutrient supplies. – Ann. Bot. 98: 187–191.

Zobel, M. et al. 2010. Clonal mobility and its implications for spatio-temporal patterns of plant communities: what do we need to know next? – Oikos 119: 802–806.

Supplementary material (available online as Appendix O19332 at www.oikosoffice.lu.se). Appendix 1.