Perspectives in Plant Ecology, Evolution and Systematics 22 (2016) 55–62

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

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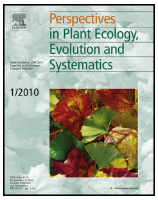

Links between shoot and plant longevity and plant economics spectrum: Environmental and demographic implications

Jitka Klimešová[a,*], Michael P. Nobis[b], Tomáš Herben[c,d]

[a] Department of Functional Ecology, Institute of Botany CAS, Třeboň, Czech Republic
[b] Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
[c] Department of Population Ecology, Institute of Botany CAS, Průhonice, Czech Republic
[d] Department of Botany, Charles University, Praha, Czech Republic

ARTICLE INFO

Article history:
Received 13 January 2016
Received in revised form 19 August 2016
Accepted 2 September 2016
Available online 4 September 2016

Keywords:
Clonality
Cyclicity
Demography
Ellenberg indicator values
Plant economic spectrum
Plant lifespan,

ABSTRACT

The tacit assumption of functional ecology is that traits affect plant fitness. However, this link is mediated by demography, e.g. specific leaf area is not affecting changes in abundance directly but through vegetative multiplication or generative reproduction of plants – it means via demographic processes. We propose that in herbaceous perennials, architectural traits that capture shoot development constitute simple morphological surrogates of a number of demographic functions (shoot lifespan, lateral spread, multiplication rate). A shoot is a reiterated basic unit of a plant body in herbs and is easily recognizable as an individual. We propose that potential shoot lifespan (shoot cyclicity) may serve as a simple character relevant to demographic processes of clonal herbs while whole plant longevity plays a similar role for non-clonal herbs. Therefore we examined relationships of shoot and whole-plant lifespans with a key trait of the plant economic spectrum (specific leaf area, SLA) for a large set of Central European temperate zone herbs. We also investigated whether shoot and whole-plant lifespan are non-randomly distributed along environmental gradients, using indicator values and their distribution among plant community types. Finally, we analysed whether shoot cyclicity underlies differences in temporal turnover of plants in species-rich meadows. Our analyses showed that fast-growing species had shorter shoot and/or plant lifespan and preferred more productive environmental conditions, but the relationship was not strong. In addition, the two lifespan measures were independent of each other, indicating that shoot lifespan captures a rather different aspect of plant demography than whole-plant longevity. Turnover of perennial plants with annual shoots in meadow community was much higher than that of plants with long-lived shoots. Whole-plant and shoot lifespan constitute promising proxy variables for a mechanistic link between functional traits and community ecology in the temperate zone and deserves further attention.

1. Introduction

In recent decades, plant ecology has undergone a deep change from a species-centred to a trait-centred approach (Weiher et al., 1999; Lavorel and Garnier 2002). Working with plant traits, instead of species, has much greater potential for generalized understanding of the distribution and dynamics of plant communities (refs. above). Comprehensive analyses of plant traits have identified major patterns or trait syndromes in the general structure of plant bodies, such as differences between slow-growing species with durable leaves and fast-growing species with high leaf turnover (leaf economic spectrum; Wright et al., 2004; Freschet et al., 2012, 2013).

The most commonly used plant traits are measured on leaves, stems or roots due to their clear physiological functions (Pérez-Harguindeguy et al., 2013). Similarly well understood is plant growth form because categories like tree, shrub or herb indicate a number of specific life-history functions (Weiher et al., 1999). On the other hand, traits based on plant architecture, i.e., on the placement and turnover of reiterated units like shoots (shoot is here defined as a product of an apical meristem, Hallé et al., 1978), are rarely used in functional analyses. Nevertheless, plant architecture can play a key role in determining and/or constraining plant demography (Fig. 1). Ignoring architectural traits is especially problematic in herbaceous plants where a shoot represents the basic functional

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[*] Corresponding author.
E-mail addresses: jitka.klimesova@ibot.cas.cz (J. Klimešová), michael.nobis@wsl.ch (M.P. Nobis), herben@site.cas.cz (T. Herben).

http://dx.doi.org/10.1016/j.ppees.2016.09.002
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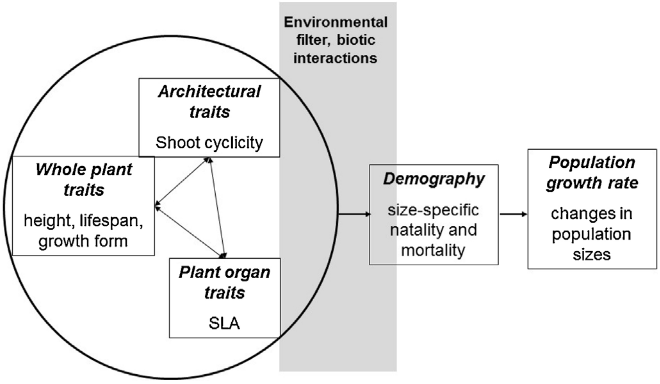

Fig. 1. Schema of relationships among plant traits and plant demographic functions. In the present study we examine interrelations of different types of plant traits, their environmental filtering and indirect effect on demographical process.

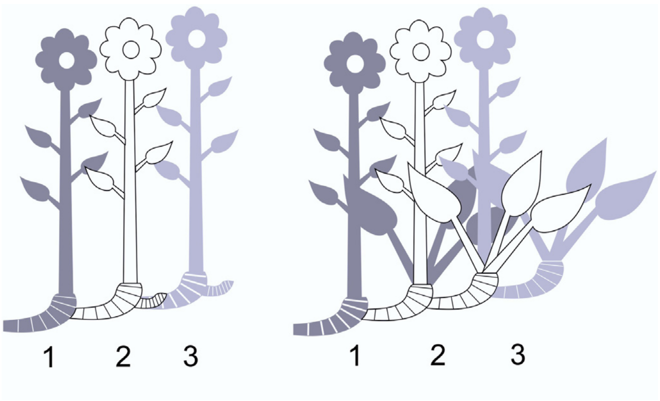

Fig. 2. Alternation of shoot generations (1, 2, 3) in a clonal plant with monocyclic shoots (left) and dicyclic shoots (right). Shoot(s) occurring on plant in one growing season are marked by one shade of grey.

entity, which is also easily recognizable in the field. While there are a couple of architectural/developmental constraints on shoot demography (i.e. lifespan, multiplication rate, and lateral spread), we propose here that one of the most important and so far unexplored constraints is due to the difference in potential lifespan of the aboveground part of shoots and associated morphological differences (hereafter called shoot cyclicity; following Serebryakov, 1952).

In annuals and monocarpic herbs, which have only one shoot per whole plant lifespan, shoot cyclicity is equal to the lifespan of the whole genet (defined as a plant established from a seed, see Krumbiegel, 1999) whereas in polycarpic herbs we can distinguish shoot and whole plant lifespan. Shoots living for only one year (monocyclic shoots) typically lack a rosette stage and directly form a leafy shoot that dies at the end of the growing season (regardless of whether they produce flowers). In contrast, herbaceous shoots living more than one year (di- and polycyclic shoots) spend one or more growing seasons as a leaf rosette and only afterwards does their apical meristem turn into a flowering state. Such shoots often have leaf rosettes and/or remnants of old leaves from the previous growing season and thus cyclicity is easily determined from simple morphological observations in the field or from a herbarium specimen and seems to be a species-specific trait (Fig. 2, see also Tamm et al., 2001; Sammul et al., 2003; Klimešová and de Bello 2009).

Differences in shoot cyclicity in herbs have three possible implications:

(i) shoot cyclicity inevitably has demographic consequences as it determines shoot turnover in a community, i.e. how long shoots of perennial plants persist in one spot and how often they can potentially produce seeds. Plants with monocyclic shoots must be able to complete shoot development from bud sprouting to flowering and fruiting in one growing season while plants with dicyclic and polycyclic shoots postpone reproduction to subsequent years. Consequently, while species with monocyclic shoots form homogeneous populations of shoots of one cohort only, species with di- and polycyclic shoots form populations in which juvenile non-flowering shoots co-occur with flowering shoots, showing considerable overlap of shoot generations.

(ii) It is likely that shoot cyclicity is related to plant economic spectrum (Reich, 2014), as shoot cyclicity describes the pace of life in plants at the level of single shoots. We can expect, therefore, that plants with monocyclic shoots will have characteristics of short lived and photosynthetically effective leaves (e.g. with high specific leaf area) and will preferentially inhabit favourable environmental conditions enabling fast growth. Under such conditions their leafy shoots able to flower first year of life will be superior in competition for light with shoots of polycyclic plants. Plants with polycyclic shoots, on the other hand, will have long lived leaves and will be restricted to more stressful conditions where flowering may be postponed several years and they can benefit from their ability to accumulate resources over longer period as they stay for several years as a rosette.

(iii) In spite of this differential preference of monocyclic and polycyclic plants for different parts of productivity gradient, plants with different shoot cyclicity typically coexist in one community (e.g. Sammul et al., 2003). It may be assumed that co-occurrence of species differing in cyclicity may help them to avoid competition by using the time axis, i.e. by different persistence on a spot or in vertical space due to different placements of leaves (Schmid and Harper, 1985).

While there is no information about the relationship of shoot cyclicity and environmental gradients, such relationships have been reported for the whole plant lifespan. It has been shown to affect both plant demography (Salguero-Gómez et al., 2016) and distribution of plants along environmental gradients (Nobis and Schweingruber 2013). We can therefore expect a correlation between whole plant lifespan and shoot cyclicity. However, we propose that shoot cyclicity will differ in functional meaning for clonal versus non-clonal herbs (plants retaining a main root for the whole lifespan are usually non-clonal, they represent one rooting unit whereas plants that replace the main root by adventitious roots have the potential to grow clonally, i,e, to produce several rooting units *sensu* Aarssen 2008). In a clonal plant each shoot usually possess its own roots and is potentially independent of the rest of the clone (and denoted as a ramet); thus shoot cyclicity (i.e., shoot longevity) will be functionally more important than whole plant longevity. On the other hand, in non-clonal plants, a shoot is not likely to behave as an independent entity as all shoots are connected to the same main root. Thus whole plant longevity will be functionally more important than shoot cyclicity.

Building on our earlier studies (Klimešová et al., 2008), we aim to show that shoot cyclicity is an important trait in functional plant ecology which has so far been widely unrecognized. We test four simple hypotheses:

1 Herbs with monocyclic shoots are placed on the fast end of the plant economic spectrum, i.e., they are characterized by high

specific leaf area (SLA) and plant height, whereas plants with polycyclic shoots will have low SLA and plant height.

2 Monocyclic perennial herbs are found preferentially under productive conditions while polycyclic plants are found in more unproductive environments. We use two approaches to assess this hypothesis. First, we perform species-based analyses to test whether monocyclic and polycyclic species differ in mean optima along ecological gradients using Ellenberg indicator values (Schaffers and Sýkora 2000). Second, we perform habitat-based analyses to test whether community types differ in proportion of monocyclic vs. polycyclic species. In all species-based analyses, we use phylogenetic regressions to take account of species non-independence.
3 Shoot cyclicity will show a similar relationship to leaf traits and environmental gradients as whole plant lifespan (further called plant age, see explanation methods), with plant age being more important for non-clonal species and shoot lifespan for clonal species.
4 Shoot cyclicity affects temporal turnover of shoots in the field. We use data on time series of fine-scale shoot densities in two herbaceous communities, and test the hypothesis that monocyclic plants will show much faster turnover of density due to shorter lifespan of their shoots indicating mechanism for their coexistence.

2. Methods

2.1. Data on shoot cyclicity and plant age

We used morphological analysis to determine cyclicity for 1469 perennial herbaceous species of Central European flora (data stored in CLO-PLA database, Klimešová and de Bello 2009). Shoot cyclicity is assessed for the aboveground parts of shoots (i.e. stems bearing leaves and inflorescences) as the number of growing seasons it takes from its sprouting to flowering. We consider aboveground branches to be parts of a shoot and not shoots themselves. We worked on the assumption that plants with monocyclic shoots have no leaf rosette and/or no remains of leaves from the previous growing season and that all shoots in the population are in the same developmental stage. In contrast, plants with leaf rosettes, and remains of leaves that had formed the leaf rosette the previous year and with shoots of different developmental stages (e.g. vegetative leaf rosettes and flowering semi-rosette shoots) in one population were assumed to be polycyclic (see also Klimeš and Klimešová 2005). For practical reasons, we also included as polycyclic those polycarpic perennial herbs with monopodial growth which form both vegetative shoots (consisting of leaf rosette) with indeterminate growth and flowering shoots that are initiated in leaf axils of that vegetative shoot (e.g. *Betonica officinalis*). Plants with this architecture are functionally polycyclic plants as they have in their population leaf rosettes and flowering shoot at the same time. Finally, we get two categories of shoot cyclicity: plants with shoots living for one year (monocyclic) and plants with shoots growing for two or more years (polycyclic); both groups have dicotyledonous as well as monocotyledonous representatives, including grasses and graminoids).

As a minimum estimate of whole plant lifespan, we used plant age data (in years), which refer to typical, mature, full-grown plants collected under natural conditions (Nobis and Schweingruber 2013). We used data estimated from the root collar or oldest part of the rhizome by growth ring counting (Buentgen et al., 2014). These data are available for 302 of the 879 perennial herbaceous species with cyclicity information. With very few exceptions, the plant age data are available only for dicotyledonous species. Note that for non-clonal plants, age denotes the whole plant individual derived from a seed (genet) whereas in clonal plants it is associated with only a given clonal fragment (physically interconnected parts of the clone).

2.2. Additional plant traits

Data on clonality (yes/no) and cyclicity were taken from CLO-PLA version 3.3 (Klimešová unpubl.; see also Klimešová and De Bello 2009). Data on plant height (average) were primarily taken from Kubát et al. (2002), and for species with no information there, we used data from Biopop (Poschlod et al., 2003) and LEDA traitbases (Kleyer et al., 2008). Plant height was available for 875 of the 879 species with cyclicity information. Data on SLA (average) were taken from the LEDA traitbase (Kleyer et al., 2008; available for 675 of the 879 species with cyclicity information). In herbs, shoot height is correlated more with productivity (e.g. Klimešová et al., 2008) than with time since disturbance as has been suggested for trees (Westoby, 1998); therefore plant height is here used as a trait relevant to the plant economic spectrum.

2.3. Data on environmental gradients and habitats

Species environmental occurrences (habitat preferences) were assessed using Ellenberg indicator values (EIVs) for light, moisture and nutrients. The EIVs are based on empirical assessment of distribution of species along environmental gradients (see e.g. Schaffers and Sýkora 2000). The scales for EIVs are ordinal, and generally range from 1 (low end of the gradient) to 9 (high end; in the case of moisture 12) (Ellenberg, 1992). Ellenberg indicator values were taken from Ellenberg (1992) through Czech National Phytosociological Database (Chytrý and Rafajová 2003; available for 840 of the 879 species with cyclicity information). Phylogenetic data were obtained from Durka and Michalski (2012) with dated branch lengths. If no data were available for a given species in Durka and Michalski (2012), the species were excluded from phylogenetic analyses. Phylogenetic information was available for 864 species with cyclicity data, and for 310 species with whole plant lifespan.

Data on habitat distribution of species were taken from a stratified subset of the Czech National Phytosociological Database (Chytrý and Rafajová 2003) containing 20,468 vegetation plots sampled after 1970 (see Chytrý et al., 2005 for the stratification procedure). Plots from this set were assigned to 32 EUNIS habitat types (see Chytrý et al., 2005) representing major vegetation types of Central European vegetation. The numbers of vegetation plots in individual EUNIS habitat types varied widely, from wet grasslands, dry grasslands and littoral zone habitats with more than 2000 samples each, down to riverine willow stands, alpine and subalpine scrub and brackish marshes, with 20–32 samples each.

2.4. Temporal turnover of shoots in plant communities: field data

Data on shoot-level temporal dynamics were taken from fine-scale permanent plots in grasslands. Two data sets were used. First, we considered data from species-rich mountain grasslands in the Krkonoše Mts. (Czech Republic). This is a time series of rooted shoots per species counts from four 0.5 m × 0.5 m plots divided into 15 × 15 cells (i.e. each cell is 0.033 m × 0.033 m in size), recorded over the period 1985–2012. For further details on the plot location, grassland type and environmental conditions, see Herben et al. (1993). Second, we used data from highly species-rich calcareous grasslands in the Bílé Karpaty Mts. (Czech Republic). This is a time series of rooted shoots per species counts from one 1.5 × 1.5 m plot divided into 900 cells (30 × 30 cells, each 0.05 × 0.05 m), recorded over the period 1993–2001. For further details on the plot location, grassland type and environmental conditions see Klimeš (1999).

2.5. Data analysis

2.5.1. Relationship with plant traits and species environmental optima

Relationships of cyclicity and plant age with plant traits and Ellenberg indicator values were assessed using phylogenetic analyses to estimate R^2 (Orme et al., 2012). We fitted models with plant age and cyclicity as predictors and estimated R^2 of their relationship with plant traits (SLA, height at maturity) and plant niche parameters (EIVs). As many traits we work with show weak phylogenetic signals (Herben & Klimešová unpubl. data), we estimated phylogenetic dependence (parameter λ; Freckleton et al., 2002) for each analysis separately using a maximum likelihood approach (see Orme et al., 2012). We log-transformed SLA, plant age and height at maturity. All models were fitted by phylogenetic generalized least squares using function pgls from the package caper for R (Orme et al., 2012). All calculations were done with R ver. 3.2.3 (R Core Team, 2012).

2.5.2. Habitat distribution data

To compare habitat types, we calculated the proportions of polycyclic plants in individual vegetation plots from the Czech National Phytosociological Database and averaged these values for all vegetation plots belonging to the same EUNIS habitat type. Vegetation plots in which data on cyclicity of constituent plants were available for fewer than 80% of the species present were discarded; we also discarded habitat types for which such information was available for fewer than 15% of the total number of plots belonging to that habitat type, or for fewer than 20 vegetation plots to avoid chance effects due to small sample size. Consequently, sufficient information was available only for 18 EUNIS habitat types based on 9657 vegetation plots. Difference among habitat types was tested using logistic regression with EUNIS habitat types as a predictor and proportion of polycyclic plants as the response variable, with number of cases in each EUNIS category as weights.

2.5.3. Temporal turnover of shoots in plant communities

We used the data on temporal dynamics of fine scale shoot density to assess differences in turnover between monocyclic and polycyclic species occurring in the meadow plots. To determine turnover of species that differ in cyclicity we used a species-level measure (Moran's I). Moran's I was calculated as temporal autocorrelation of shoot densities of individual species at the level of grid cells over time and with a temporal lag of one to four or five years (Upton and Fingleton 1985). Only species with a sufficiently high frequency (occurrences in at least 10 grid cells and found in at least half of the years of investigation) were used for the analysis, yielding 43 species in the mountain grasslands and 60 species in the calcareous grasslands. Clonal plants prevail at both localities. These species were classified as monocyclic or polycyclic, and differences in their autocorrelation values were tested using split-plot ANOVA with cyclicity as a factor tested at the level of individual species and time-lag nested within species.

3. Results

Polycyclic herbs, with longer-lived shoots, tend to have lower SLA and shoot height than do monocyclic herbs and this difference does not differ significantly between clonal and nonclonal plants (Table 1, Fig. 3). Plants with higher age also tend to have lower SLA and shoot height than plants with lower age (Table 1). In this case, the relationships are similar for clonal and non-clonal plants for SLA (Fig. 4), whereas differ significantly between clonal and non-clonal species for plant height (Table 1). Cyclicity does not show any simple relationship to clonality (Kendall correlation coefficient −0.006, n = 302, n.s.).

Table 1
Relationships of cyclicity and plant age to SLA and height at maturity. Values in the table are R^2 from phylogenetic regressions. * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$. Sign of the relationship in parentheses. d.f. – residual degrees of freedom. Monocyclic plants are coded as zero and polycyclic plants as one.

	Response variable	
Effect	SLA	Height
Lambda	0.645	0.851
d.f.	664	855
Cyclicity	0.010^{**} (−)	0.055^{***} (−)
Clonality	0.015^{**} (+)	0.001
Cyclicity *Clonality	0.000	0.002
Lambda	0.141	0.625
d.f.	249	301
Plant age	0.087^{***} (−)	0.027^{*} (−)
Clonality	0.030	0.012
Plant age*Clonality	0.004	0.013^{*} (+)

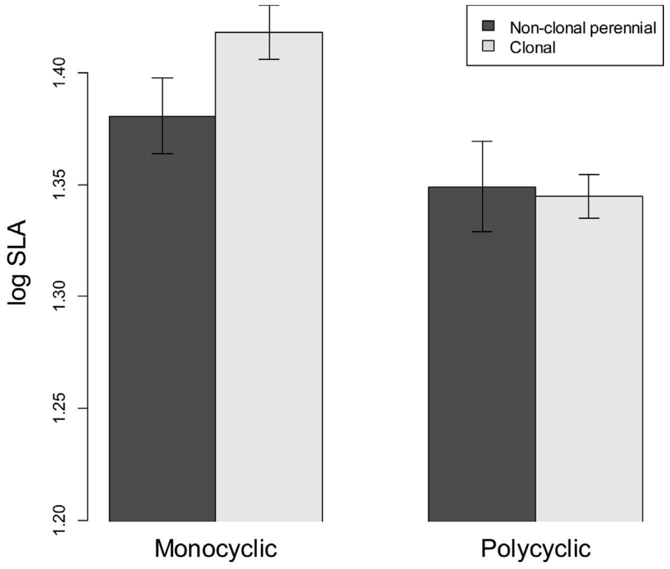

Fig. 3. Differences in SLA between monocyclic and polycyclic plants. For the statistical test, see Table 1.

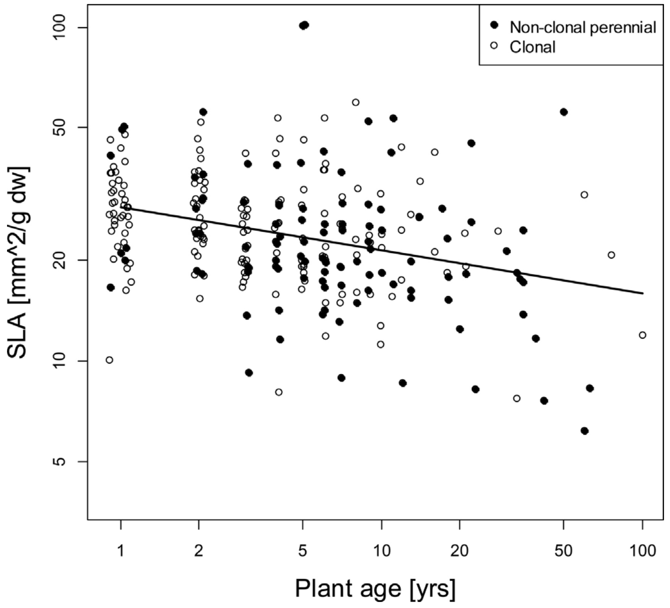

Fig. 4. Relationship between plant age and specific leaf area. The line is a least squares regression model on log-transformed variables (for the test see Table 1). Because the interaction between cyclicity and clonality is not significant, non-clonal and clonal perennials were merged.

Table 2

Relationships between cyclicity of shoots or whole-plant age, clonality and species environmental optima defined by Ellenberg indicator values for light, moisture and nutrients. Values in the table are adjusted R^2 from phylogenetic regressions.+– P < 0.1, * – P < 0.05, ** – P < 0.01, *** – P < 0.001. N ~ 828–837 for the tests of cyclicity, N ~ 294-296 for the tests of plant age. Range of numbers of observations is due to different numbers of missing values in individual response variables. In the tests of the set of all species, effects of clonality were tested in a model that included the other tested variable (cyclicity and plant age respectively). Sign of the relationship in parentheses. Monocyclic plants are coded as zero and polycyclic plants as one.

	Response variable		
Effect	Light	Moisture	Nutrients
Cyclicity	0.002	0.002	**0.017***** (−)
Clonality	**0.027***** (−)	**0.054***** (+)	**0.022***** (+)
Cyclicity*Clonality	0.002	0.000	0.000
Plant age	**0.035**** (+)	**0.167***** (−)	**0.106***** (−)
Clonality	**0.037***** (−)	**0.061***** (+)	**0.023*** (+)
Plant age*Clonality	0.001	**0.006+**	**0.010+**

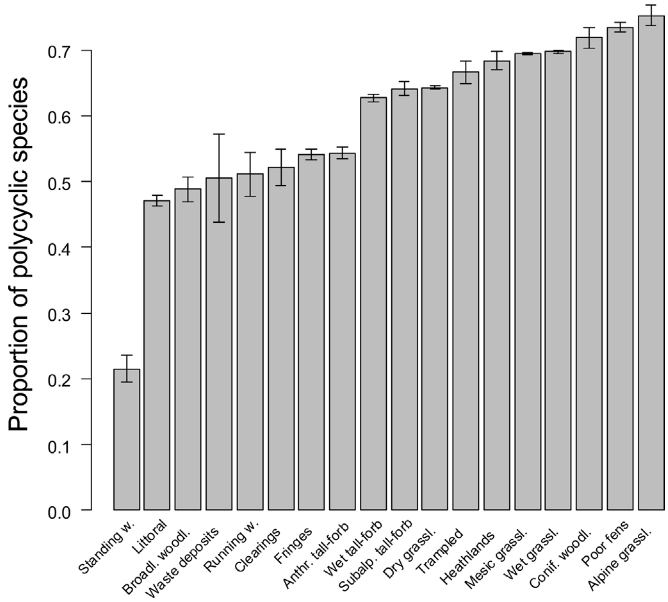

Fig. 5. Distribution of monocyclic and polycyclic plants in major EUNIS habitat types ordered by increasing proportion of polycyclic plants. Bars indicate standard errors. Differences among habitat types are highly significant even after removing standing water (see the text).

Monocyclic plants tend to have higher optimum values for nutrients than polycyclic plants (Table 2) and this relationship did not significantly differ between clonal and non-clonal plants (it is stronger in clonal plants, Table 2). No relationship of cyclicity and optima for light or moisture was found. Plants with higher plant age had higher optimum values for light and lower optimum values for moisture and nutrients than plants with lower age (Table 2); these relationships (except of light) are marginally significantly different between clonal and non-clonal plants. The age of non-clonal species had stronger relationship to light (positive) and nutrients (negative) while the age of clonal species had stronger relationship to moisture (negative).

The distribution of monocyclic and polycyclic plants is highly non-random among EUNIS habitat types (Fig. 5). Monocyclic plants prevail in standing water, broadleaved woodland and littoral, whereas polycyclic plants dominate especially in fens, alpine grasslands, heathlands and coniferous forests. Interestingly, while the mean proportions of polycyclic plants differed strongly among habitat types, in most vegetation plots monocyclic and polycyclic plants co-occur. The notable exception to this rule are standing water habitats, which in many cases host only monocyclic plants (in 76 out of 225 records with sufficient cyclicity data, compare also Fig. 5). The effect of habitat types on the proportion of monocyclic plants is highly significant using logistic regression (effect deviance = 765.7, d.f. effect = 20, residual deviance = 2040.0, P < 0.001; effect deviance = 623.3, d.f. effect = 19, residual deviance = 1881.7, P < 0.001 when standing water habitats are excluded).

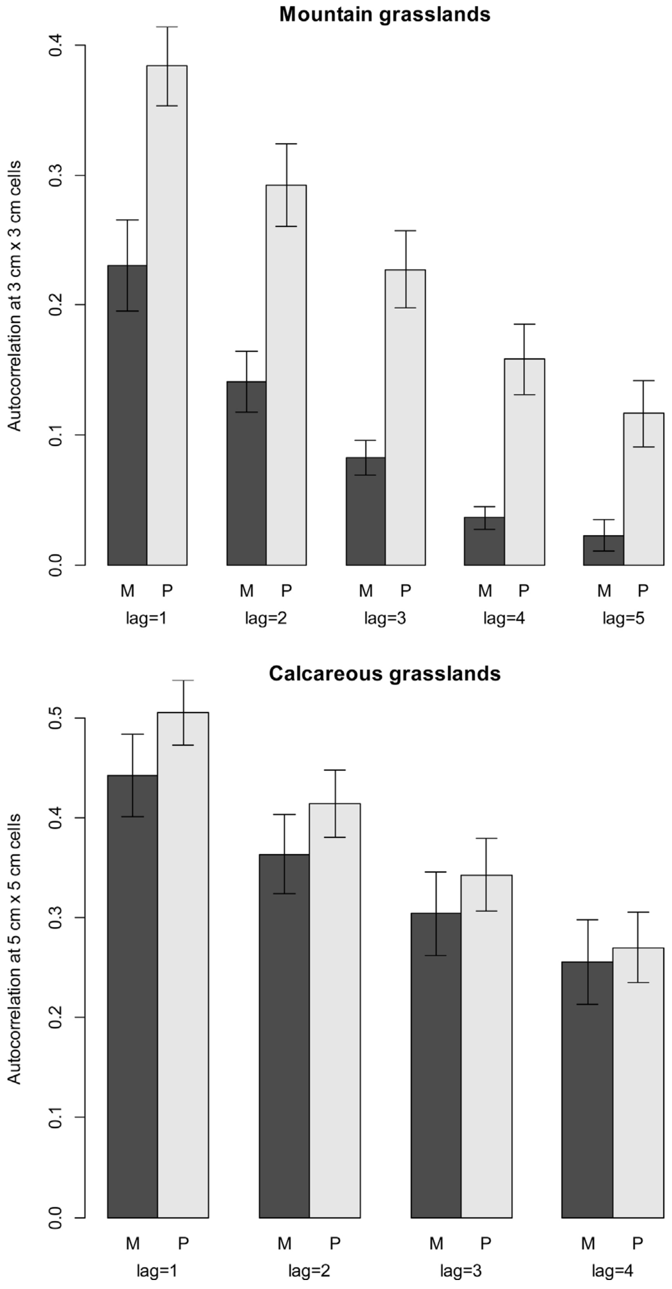

Fig. 6. Turnover of grassland species measured by Moran's *I* over time within of individual cells (3.3 cm × 3.3 cm in the mountain grasslands, 5 cm × 5 cm in the calcareous grasslands). M—monocyclic, P—polycyclic, lag—temporal lag (i.e., the number of years over which autocorrelation is calculated). Higher autocorrelations imply lower turnover. Bars indicate standard errors. N = 43 species in the mountain grasslands; N = 60 species in the calcareous grasslands. Clonal plants prevail at both localities.

In both data sets on temporal dynamics of shoots in meadows, monocyclic plants tended to have higher turnover than polycyclic plants (Fig. 6), but the difference over the whole observation period was significant only in mountain grasslands (ANOVA; F = 8.29, P < 0.01, d.f. = 1, 38) and not in calcareous grasslands (F = 2.48, P = 0.12, d.f. = 1, 57). For calcareous grasslands, the difference between monocyclic and polycyclic is high and significant when compared over one year (F = 4.27, P = 0.043, d.f. = 1, 57 using one-way ANOVA), but disappeared over longer time intervals resulting in the overall nonsignificant result.

4. Discussion

We confirmed that shoot cyclicity, i.e. plant architectural trait defined on shoot level, is related with a number of traits based on whole plant or organ characters (Fig. 1), changes along key environmental gradients, and plays a role in determining and/or constraining plant demography. Cyclicity is more closely tied to plant traits than plant age in clonal plants, whereas it is just the opposite in non-clonal plants. Relationships of cyclicity to environmental gradients was weaker than relationship of plant age to environmental gradients and was more important in clonal than non-clonal plants. Although plant age was more important in non-clonal than clonal species as expected, still age of clonal plant (age of its clonal fragment) varied significantly along studied environmental gradients. We showed that shoot cyclicity has economic and demographic implications for functioning of plant populations in communities and may play a role in species coexistence.

4.1. Shoot cyclicity and plant age

The distinction between monocyclic shoots of polycarpic perennial plants that flower in their first year and die and those that postpone flowering to obtain more resources while in a vegetative state (polycyclic shoots) parallels the dichotomy between annuals and monocarpic perennials. In contrast to annual and monocarpic plants, where the individual dies after flowering investing all its resources into its generative reproduction, perennial plants, no matter whether both mono- and polycyclic, invest also in survival and do not depend on a single reproductive event. Nevertheless, the selective forces should be similar between plant age in monocarpic plants and cyclicity in polycarpic plants: namely, a longer lifespan is favoured when adult mortality is low and higher fitness can be attained by delayed reproduction (Gadgil and Bossert 1970; Metcalf et al., 2003). This is the case in low-productivity habitats, where competition takes place mainly belowground and therefore is more symmetric and hence less likely to lead to mortality (Weiner, 1990). In contrast, in highly productive habitats, asymmetric competition aboveground favours plants with monocyclic shoots. Delayed reproduction in polycyclic shoots and the capacity to remain in the rosette stage can also help plants to avoid disturbance (biomass removal) that takes place in grazed and mown habitats (Klimešová et al., 2008, 2011).

The role of cyclicity is more important in clonal plants than in non-clonal perennials while plant age is important in both groups. This is a direct consequence of different morphological constraints in these two plant types as pointed out by Harper and White (1974). Demography of clonal plants is primarily driven by demography of their ramets, ideally defined as shoots (White, 1979), and cyclicity acts as an important constraint for them. In clonal plants, cyclicity is related to clonal traits such as lateral spread and persistence of connection between ramets; monocyclic plants tend to have more extensive lateral spread and less persistent rhizomes than polycyclic plants (Herben et al., 2012). A similar result may be found in other studies. Tamm et al. (2001) and Sammul et al. (2003) found negative correlation among site productivity and community weighted mean for shoot cyclicity. Similarly, Craine et al. (2001) found that with increasing availability of nutrients dominance changed from rosette plants (presumably polycyclic) to erosulate plants (presumably monocyclic), although cyclicity or shoot lifespan is not explicitly mentioned in this study.

The matter is different for non-clonal herbaceous perennials. Their demography is driven by long-lived parts belowground or close to the soil surface (where plant age can be estimated), whose lifespan is not necessarily related to the lifespan of individual shoots. The major demographic constraint in non-clonal plants is hence whole-plant longevity (i.e., longevity of the genetic individual), which plays a role similar to that of cyclicity in clonal plants, for which the ramet (shoot) is the demographic unit. The absence of correlation between cyclicity and plant age (at least in dicot plants, where whole-plant age can be determined) means that cyclicity indeed captures a different aspect of plant demography than the age of the whole plant (see also White, 1979). These differences are due to different selective forces on cyclicity and overall plant longevity, and different action of these forces in clonal and non-clonal plants.

4.2. Relationships to the plant economic spectrum

While cyclicity and plant age in clonal plants seems to be connected with preference for high availability of soil nutrients, in non-clonal plants nutrient availability correlates only with plant longevity, but is not related to cyclicity. These patterns correspond to different niches occupied by monocyclic and polycyclic clonal species. Ellenberg indicator values and analysis of ratio between polycyclic and monocyclic plants in community types show that monocyclic plants tend to have their maximum occurrence in relatively nutrient-rich habitats such as aquatic and littoral habitats, broadleaved forests and synanthropic habitats. In contrast, polycyclic plants are more likely to have their optima in open, nutrient-poor habitats, and are common in grasslands, fens, heathlands, and coniferous forests. These differences correspond to differences in traits of the leaf economics spectrum (such as SLA) in temperate herbs (Wright et al., 2004), providing evidence of demographic differences between slow and fast growing plants (see also Nobis and Schweingruber 2013; Adler et al., 2014). The fact that they correlate also with plant potential height support an idea that plant height in temperate herbs is a trait relevant more to plant economy than to the time since disturbance as proposed by Westoby (1998).

Interestingly, there are almost no community types from which one type of plant cyclicity is generally absent, with the exception of submerged vegetation, from which polycyclic plants are as a rule missing. In the other community types, the proportion of polycyclic plants ranges from 0.3 to 0.7, indicating that both demographic types usually co-occur and might potentially contribute to species coexistence. Prevalence of monocyclic shoots in aquatic habitats may be attributed to high turnover of plant tissues in water habitats, and lower danger of frost damage under water column than in terrestrial habitats.

4.3. Cyclicity and community dynamics

Cyclicity is fairly easy to determine by morphological analysis, and data on it can be collected for large sets of species. This contrasts with true demographic parameters such as natality and mortality, which are time-consuming to collect and for a large number of species likely will never be available across all the habitats in which these species occur. Nevertheless, demographic data are extremely useful for comparative analyses either across species (see e.g. Baudisch et al., 2013; Adler et al., 2014) or across communities (Herben et al., 2014). Our data on small scale species turnover show that cyclicity is strongly associated with the degree of species persistence in one spot over time: monocyclic plants are more mobile on a small scale (i.e., they have higher natality and mortality of shoots) while polycyclic plants form a matrix of less mobile shoots. These effects themselves, without a contribution of clonality or seedling establishment, may contribute to coexistence of species (in the sense of the carousel model of van der Maarel and Sykes, 1993) and the observed co-occurrence of both main cyclicity types may support to this observation. This is also supported by the findings of Tamm et al. (2001), who showed that there was no correlation of community weighted mean of cyclicity with species diversity when compared across communities. In contrast, average cyclicity of community decreased with decreasing species richness with time after fertilization (Sammul et al., 2003). This implies that not high mobility itself, but combination of slow and fast plants may be responsible for observed patterns.

As discussed above, for comparative analyses of plant abundance across environmental gradients cyclicity might be a link between traits of the economic spectrum (SLA and shoot height in our case) and population/community dynamics. Finding a good proxy variable for species demography is thus an important task. Cyclicity clearly only partly reflects species demography and can, therefore, fill this gap only to some extent, however, it likely varies less within species than do actual demographic rates (e.g. Horvitz and Schemske 1995; Oostermeijer et al., 1996). It therefore can be used in functional analyses as an easy-to-collect, soft-trait proxy for the demography of perennial herbs.

Acknowledgements

We thank Fritz Schweingruber for providing the data on plant age and Deborah Goldberg for comments on an earlier version of the manuscript. The research was partly supported by the Czech Science Foundation (GA 16-19245S, Centre of Excellence 14-36079G, PLADIAS).

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