

Species traits and plant performance: functional trade-offs in a large set of species in a botanical garden

Tomáš Herben^{1,2*}, Zuzana Nováková³, Jitka Klimešová⁴ and Lubomír Hrouda²

¹Institute of Botany, Academy of Science of the Czech Republic, CZ-252 43, Průhonice, Czech Republic; ²Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01, Praha 2, Czech Republic; ³Botanical Garden of the Charles University, Na Slupi 16, CZ-128 01, Praha 2, Czech Republic; and ⁴Institute of Botany, Academy of Sciences of the Czech Republic, CZ-379 82, Třeboň, Czech Republic

Summary

1. Earlier research has established a number of relationships between community structure and plant traits. However, these relationships are mediated by demographic processes that are constrained, but not determined, by the trait values, and involve responses of plants to their environments. In particular, life-history costs and associated trade-offs need to be examined at the level of demographic processes such as plant survival and reproduction, not only at the level of individual trait values.

2. We examined these demographic trade-offs using data on vegetative and seed reproduction from 951 species of the Central European flora kept in the Botanical Garden of Charles University in Prague. With each species grown under conditions close to its natural habitat, we view the data as information on vegetative and seed reproduction under favourable conditions. We used nonparametric tests and ordinal regressions to examine relationships of the vegetative and seed reproduction to each other, as well as to commonly used traits such as plant height, leaf size, specific leaf area, seed size and clonal traits.

3. There was an overall negative correlation between seed and vegetative reproduction, indicating trade-off between these two modes of reproduction. In contrast, there was no evidence of a trade-off between clonal and seed traits.

4. Traits of clonal growth were related to vegetative reproduction in the garden and seed trait to seed reproduction in the garden. Further, there were correlations between seed reproduction and clonal traits and vice versa. These results suggest that seed reproduction is associated with a wider array of traits than only seed traits, and vegetative reproduction with a wider array than clonal traits again indicating complex life-history relationships. These relationships did not change substantially after the incorporation of phylogenetic information.

5. Synthesis. The results suggest that trade-offs between vegetative and seed reproduction are not revealed by analysis of species traits, probably due to the fact that trade-offs often only arise due to life-history costs that are shaped by the local environment. This highlights the importance of examining life-history processes associated with trait values.

Key-words: life-history costs, ordinal regression, phylogenetic data, reproductive ecology, seed reproduction, vegetative reproduction

Introduction

The investigation of the role of species traits in structuring plant communities has become a major focus of research in plant ecology during the past decade. Functional trait values affect species performance, and employing them, rather than species, as a basic unit of ecological research has both conceptual and practical advantages. The distribution of traits at

the community level shows patterns that suggest their ecological importance. The community trait structure has been shown to respond in a consistent way to environmental gradients (Diaz *et al.* 2004; Messier, McGill & Lechowicz 2010), and trait structure within communities may also show a non-random pattern (Watkins & Wilson 2003; Pillar *et al.* 2009; Cornwell & Ackerly 2010).

As illustrated in Fig. 1, the relationships between organismal traits and community structure (in terms of both trait distribution and relative abundance of species) depend on a

*Correspondence author. E-mail: herben@site.cas.cz

chain of mediating processes (Suding, Goldberg & Hartman 2003; Gross *et al.* 2009; Mokany & Roxburgh 2010). Thus, species performance within communities, and ultimately, species abundance and distribution, are due to demographic responses of plant populations in such processes as growth, dispersal and multiplication (Suding, Goldberg & Hartman 2003; these processes largely corresponding to the ‘hard traits’; Weiher *et al.* 1999; Lavorel & Garnier 2002). While these responses are related to trait values of individual plants (‘easy’ or ‘soft’ traits; Weiher *et al.* 1999; Lavorel & Garnier 2002), they also involve responsive behaviour to environmental factors, both abiotic and biotic (Fig. 1; Suding, Goldberg & Hartman 2003; Vesk, Warton & Westoby 2004; McGill *et al.* 2006). Hence, the links between soft traits and its associated process do not yield one-to-one correspondence, as these processes are based on suites of traits acting together under variable conditions. Soft traits often constitute only constraints upon the plant’s response to its environment and thus should not be confused with the processes themselves (Eriksson 2011). For example, specific leaf area (SLA) is a good surrogate for relative growth rate of plants in optimal conditions (Reich, Walters & Ellsworth 1992; Wright & Westoby 1999; Shipley *et al.* 2005; Poorter *et al.* 2009; Donovan *et al.* 2011). The predictive power of SLA (a soft trait) in the field is limited, however, as actual growth rate (a hard trait) is shaped not only by growth rate potential, but also by the environmental conditions in which it occurs (Cornwell *et al.* 2008; Ordoñez *et al.* 2009) and other traits that the plant possesses.

The absence of good information on trait action in the field is particularly problematic when studying relationships among traits and trade-offs in the plant’s life. Some trade-offs are simple and occur at the level of traits; for example, seed size and seed number are constrained by energetic availability and thus can be detected using trait data from databases (Bruun & Ten Brink 2008). In contrast, a number of ecologically or evolutionarily important trade-offs arise through demographic processes (such as the trade-off between seed size and juvenile RGR) that involve plant responsive behaviour

(Silvertown & Gordon 1989; Gersani *et al.* 2001; Poorter *et al.* 2008; Novoplansky 2009). Such trade-offs are much less likely to be captured at the level of soft traits. Because current research typically uses simple correlation analysis of soft traits to detect trade-offs, it ignores the behavioural component of plant life, potentially overlooking the trade-offs that could arise through more complex ways that involve demographic responses (Gross *et al.* 2009; Bilton *et al.* 2010).

Obtaining data on demographic processes potentially related to species traits, which allows comparison across many species is a daunting task, with difficulty increasing not only with the number of species, but the different locales and habitats in which they occur. Here, we suggest that some of the data needed on these processes can be gathered from already existing growth records on plants in botanical gardens.

Botanical gardens have not only continued to serve as centres for taxonomic and systematic research (Dosmann 2006; Pautasso & Parmentier 2007; Stevens 2007), but have also been identified as valuable sources of plant ecology data for subjects such as phenological indication of climate change (Primack & Miller-Rushing 2009; Chambers & Keatley 2010; Ferenczy *et al.* 2010), physiology and growth patterns (Ebel & Kümmel 1985; Wang, Yakir & Avishai 1998; Gratani *et al.* 2008), and plant–herbivore interactions (Dawson, Burslem & Hulme 2009). For plant functional traits, botanical gardens could provide reasonable assessment of growth and multiplication processes for large sets of species, provided that proper, comparable records are kept on the growth and reproductive performance of each species, as well as the environment and management in which they are maintained. While there are a number of issues with these data (growth and multiplication records that are not necessarily fully quantitative; low sample sizes; plant growth typically not constrained by interspecific competition; lower control of environmental conditions and genetic composition) that render such data of lower quality than those from designed experiments, these disadvantages are easily outweighed by the large number of species that can be compared.

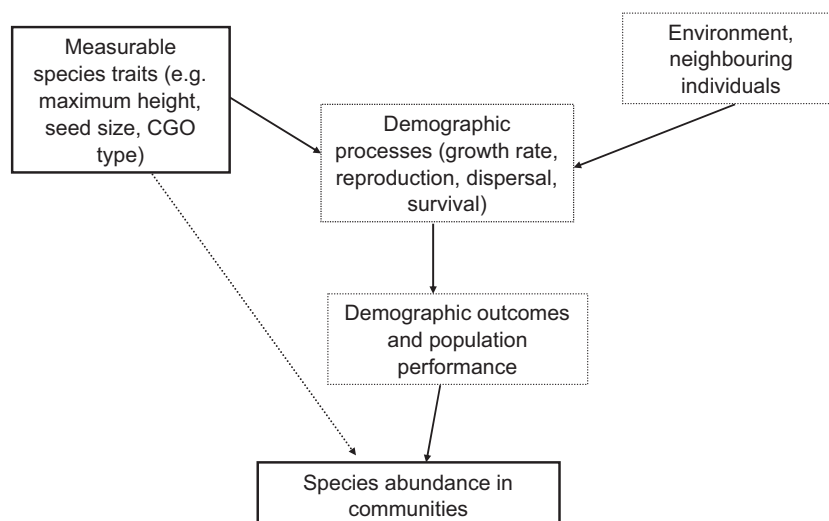


Fig. 1. Solid boxes indicate processes/patterns on which large amounts of data are available; dotted boxes indicate processes/patterns on which limited data are available and which involve plant responsive behaviour. The dotted line indicates the commonly tested relationship. Full lines indicate functional relationships.

In this study, we take data on spontaneous seed and vegetative reproduction in a botanical garden and examine their relationships with a number of soft traits that are available from species databases and have typically been used in the literature as proxies for specific demographic processes of plants. Further, we search for possible trade-offs between vegetative and seed reproduction in the garden and examine whether corresponding trade-offs can be found in the trait data. The traits we work with are plant height, leaf size and SLA, which are used as proxies for growth rate or competitive ability, and seed size as a proxy for seed dispersal and chance of seedling establishment. For clonally growing species, we also use a number of essentially morphological traits (Klimešová, Doležal & Sammul 2011a; Klimešová *et al.* 2011) to assess the potential for vegetative growth and also relate these traits to the garden's reproductive data.

We work with approximately one thousand central European species grown in the Botanical Garden of Charles University in Prague. The garden is rather environmentally heterogeneous, with each species maintained separately in conditions that can be reasonably assumed to be close to its natural habitat, but with competitive interactions (namely interspecific) largely reduced by weeding and thinning. Still the reproduction in the garden results from plants' responsive behaviour to their environment, which forms a key component of the species' demographic processes in nature. We hence view the data as information on vegetative and seed reproduction of individual species under favourable conditions.

Materials and methods

REPRODUCTION DATA FROM THE GARDEN

Our data were gathered from the collection of native plants of central European Flora, in the Botanical Garden of the Faculty of Science, Charles University in Prague (<http://www.bz-uk.cz>). The collection houses about 1200 central European plant species, mainly collected in the Czech Republic and Slovakia. Plants have been collected over an extensive period, beginning in the 1930s, although most of them were collected between 1960 and 2000.

Each of the species is kept under conditions that we assume to be as close to their natural conditions as possible within the garden. The habitats in the garden range in moisture from open, dry, sandy habitats and limestone, rocky habitats through mesic open habitats and shaded forest stands to moist (shaded and unshaded) places. Plants are grown in open soil, with weeding carried out, including the removal of individuals of the planted species, to keep stands of each species separate. The particular habitat in which each plant species is maintained has been chosen on the basis of field knowledge of the habitat in which it typically occurs, with the garden habitat matching this habitat as much as possible. If a particular plant does not grow well in the initial habitat, it is moved to other ecologically relevant habitat(s) in the garden until the greatest success in cultivation is attained. The majority of plant species are grown only in one habitat at a given time, although some are grown in several habitats.

For all plant species that have been growing in the garden for at least 10 years (Appendix 1), we assigned scores for vegetative and seed reproduction for that period, based on records that were contemporaneously kept. Seed and vegetative reproduction were scored

separately using the same ordinal scale by one person (Z.N.; Table 1). In most cases, seedlings could be distinguished from vegetative offspring. However, in some plants with vigorous vegetative reproduction, assessment of seed reproduction was impossible due to potential seedlings being mixed with the vegetative progeny. Seed reproduction in these plants is treated as a missing value (43 species). Plants that are maintained in several habitats (or plants that were moved from one habitat to the other to find suitable place for their maintenance) were scored based on growth in the habitat in which they performed best. Altogether, 1013 species were scored. This included 951 non-woody species, with 836 native to the Czech Republic. As the Czech flora contains *c.* 2500 species, including common aliens and woody species (depending on taxonomic treatment), this constitutes over 40% of the total flora. All further analyses are based on the set of all non-woody species (herbaceous species and dwarf shrubs), including species not native to the Czech Republic. Large woody plants were excluded because their reproduction processes may be driven by a different set of traits, and the sample size was too small to address them separately.

TRAIT DATA

Trait data were taken from the LEDA traitbase (Kleyer *et al.* 2008) and from the CLO-PLA3 database (Klimešová & de Bello 2009). We used the following traits from LEDA, with the number of species for which the trait data were available provided in parentheses: total leaf area (562 species), SLA (604 species), maximum height (722 species) and seed mass (574 species). If several records were available for one species, the simple (unweighted) arithmetic mean value was used. Plant height data missing from LEDA were taken from Kubát *et al.* (2001). Further, we used two general traits from the CLO-PLA3 database: shoot life span (1 or 1+ years; 832 species; called cyclicity by Klimešová & de Bello 2009) and life history (annual/perennial non-clonal/perennial clonal; 835 species).

For plants capable of clonal growth (by producing of potentially independent ramets, that is, having clonal growth organ (CGO) classified as necessary or additional in the database CLO-PLA), we used a set of additional traits from the CLO-PLA3 database: CGO type, further referred to as CGO type (for definitions of individual CGO types see Fig. 1 in Klimešová & de Bello 2009; available for 655 species), CGO role (necessary or additional; 653 species), persistence of connections between shoots (1, 2, > 2 years; 649 species), multiplication rate (number of offspring shoots per mother shoot per year: < 1, 1, > 1; 652 species), lateral spread (distance from the mother shoot at which offspring shoots are formed: (< 0.01,

Table 1. The scale used to score growth and reproduction in the botanical garden. Separate scoring using the same scale was used for vegetative and seed reproduction

Score	Definition
5	Multiplies spontaneously, must be thinned > 1 times a year
4	Multiplies spontaneously, must be thinned approximately once a year
3	Multiplies spontaneously to some extent, must be thinned once in several years
2	Does not multiply spontaneously, but it can be multiplied by simple outdoor gardening techniques (splitting tussocks, planting cuttings, sowing seed, etc.)
1	Does not multiply in the garden

0.01–0.25, > 0.25 m, dispersable; 652 species), depth of the below-ground bud bank (down to 10 cm, deeper than 10 cm; 795 species) and size of the below-ground bud bank (1–10 buds per shoot, > 10 buds per shoot; 795 species). For species with multiple entries in the database, the CGO leading to highest multiplication rate was selected, as was the most frequent value for shoot life span, while for each of the other traits, the category with the highest value was used. Following Johansson, Cousins & Eriksson (2011), we used the sum of ordinal values of multiplication rate and lateral spread as a synthetic measure of capacity for clonal growth (further referred to as clonal index). The index was given an arbitrary value of one for non-clonal perennials, and zero for annuals. Altogether, some trait data were available for 864 species.

As a source of phylogenetic data, we used data of Durka (2002) with dated branch lengths, updated by Stefan Michalski (unpubl. data). If no data were available for a given species in Durka (2002), data from congeneric species were taken; species for which no congeneric was available were excluded from the phylogenetic analysis. This yielded independent phylogenetic information for 628 species. Taking congeners into account, phylogenetic information was available for 752 species.

DATA ANALYSIS

As most of the data available were ordinal, we used nonparametric rank-based tests. Relationships between two ordinal variables were assessed using Kendall tau because of large numbers of ties in the data; approximate normal tests were carried out to assess significance of the relationship. The Kruskal–Wallis test was used to test any relationship between a categorical and an ordinal variable. The calculations were carried out using R ver. 2.15.2 (R Development Core Team 2012).

We further modelled statistical relationships between reproduction in the garden (as response variables) and trait variables (as predictors) by generalized ordinal regression. We used the cumulative proportional odds model for ordinal data with logit link (Christensen 2011). The predictor variables were factor, ordinal and continuous; all continuous predictors were log-transformed before the analysis. We modelled the effects of all predictor variables as location (additive) effects; all trait variables listed above were used as predictors with the exception of clonal index (which is a compound variable whose components were used as predictors). We searched for best models in a stepwise fashion (both forward and backward) until the model with the lowest Akaike Information Criterion was found. In the final model, significance of individual terms was tested using the log-likelihood ratio test. Only complete cases for all predictors used for selection were analysed.

Separate models were built for seed reproduction and vegetative reproduction. To account for potential interdependence of response variables, we also performed partial analyses (with the other response variable forced into the model as a covariate) to separate direct effects on these two response variables from indirect effects. We deleted plant species with rare CGO types (types 3, 8, 11, 16 and 17; Klimešová & de Bello 2009; altogether 13 plant species), leaving only seven basic CGO types. As not all trait data are available for all plants (both for technical and conceptual reasons), we performed three different analyses on three different subsets of the data: (i) all plants in the data set with a basic set of trait variables (height, SLA and seed size, life history, bud bank presence and shoot life span), (ii) only clonal, perennial plants with all available traits, including the clonal growth traits and (iii) only clonal, perennial plants with clonal

growth traits only. The last analysis was carried out because the number of species for which seed traits were available to permit analysis (ii) was rather low. The R package ordinal was used for the ordinal regression modelling (Christensen 2011). Coefficients of determination were calculated using the lrm function of the package rms.

To correct for phylogenetic relatedness in the ordinal regressions, we used the approach of Diniz-Filho, de Sant'Ana & Bini (1998; Desvignes *et al.* 2003). This can work with trees involving polytomies and makes possible to work with ordinal data. We calculated patristic distances from the source tree (Durka 2002) using function cophenetic.phylo from the R package ape (Paradis *et al.* 2012). The matrix of patristic distances was summarized using non-standardized principal coordinates analysis (PCoA) using the ade4 package for R (Dray & Dufour 2007). Scores at the first 17 PCoA axes (accounting for 90.0% of the total phylogenetic variation) were used as covariates in the ordinal regressions to capture phylogenetic relatedness of the taxa. Species with no phylogenetic information were treated as missing in all analyses that employed phylogenetic information.

Results

The values of seed and vegetative reproduction ranged widely, with all score levels well represented (Table 2). In the seed reproduction score, the distribution of values was rather unimodal, with score 3 maximum frequency; for vegetative reproduction, the lowest score, as well as scores 3 and 4 were common, with considerably fewer species in categories 2 and 5. Vegetative and seed reproduction were negatively correlated (Kendall $\tau = -0.230$, $n = 906$, $P < 0.001$; $\tau = -0.195$, $n = 825$, $P < 0.001$ for the subset of perennial plants only; $\tau = -0.161$, $n = 599$, $P < 0.001$ for the subset of clonal plants only). Only 11 species did not reproduce in the garden by either means, and 13 species showed the highest or second highest possible score for both seed and vegetative reproduction.

Bivariate analyses showed that both seed and vegetative reproduction were correlated with a number of traits (Table 3). The best single predictors of both reproduction types were seed mass, growth form, CGO type, lateral spread and clonal index (Figs 2–4). These variables were correlated with both seed and vegetative reproduction, although the

Table 2. Distribution of individual species values in the whole data set

	Vegetative reproduction						Total
	1	2	3	4	5	Unknown	
Seed reproduction							
1	11	14	42	56	30		153
2	46	39	36	26	4		151
3	111	36	80	80	20		327
4	102	21	57	44	4	1	229
5	31	2	5	8	1		47
Unknown		1	3	19	21		44
Total	301	113	223	233	80	1	951

For the score definitions, see Table 1. Correlation between variables is negative and highly significant (Kendall $\tau = -0.230$, $P < 0.001$).

Table 3. Tests of relationships between reproduction in the garden and plant traits

Trait	Test used	Seed reproduction	Vegetative reproduction
General plant traits			
Maximum plant height	Kendall tau	−0.001 n.s.	−0.038 n.s.
	<i>N</i>	687	725
Leaf area	Kendall tau	0.022 n.s.	−0.047 n.s.
	<i>N</i>	533	565
Specific leaf area	Kendall tau	0.109***	0.003 n.s.
	<i>N</i>	575	608
Seed mass	Kendall tau	0.076*	−0.078*
	<i>N</i>	544	576
Shoot life span	Kruskal–Wallis chi-square	1.3 n.s.	0.1 n.s.
	<i>N</i>	785	827
Life history	Kruskal–Wallis chi-square	48.5***	204.8***
	<i>N</i>	788	830
Clonal growth traits			
CGO type†	Kruskal–Wallis chi-square	33.1***	80.4***
	<i>N</i>	599	641
CGO role	Kruskal–Wallis chi-square	0.0 n.s.	0.2 n.s.
	<i>N</i>	605	648
CGO persistence	Kendall tau	−0.015 n.s.	−0.027 n.s.
	<i>N</i>	605	648
CGO multiplication	Kendall tau	0.046 n.s.	0.132***
	<i>N</i>	605	648
CGO lateral spread	Kendall tau	−0.205***	0.346***
	<i>N</i>	605	648
Bud bank depth	Kendall tau	−0.033 n.s.	−0.01 n.s.
	<i>N</i>	605	648
Bud bank size	Kendall tau	−0.085*	0.028 n.s.
	<i>N</i>	605	648
Clonal index	Kendall tau	−0.108**	0.308***
	<i>N</i>	605	648

N, number of species tested.

†Only clonal growth organ (CGO) 1, 9, 10, 12, 13, 14 and 15 (Klimešová & de Bello 2009) were used because of insufficient number of observations for the remaining CGO types.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$. Values in the table are observed test statistics (Kendall tau or chi-square).

magnitudes and signs of their effects varied (Table 3). SLA, multiplication and bud bank size were each correlated with only one of the response variables. In contrast, height, shoot life span, clonal connection persistence, bud bank depth and

CGO role (additive or necessary) showed no significant correlation with either reproduction type.

There were many correlations at the level of traits (Table 4). Plant height was positively correlated with leaf area and seed

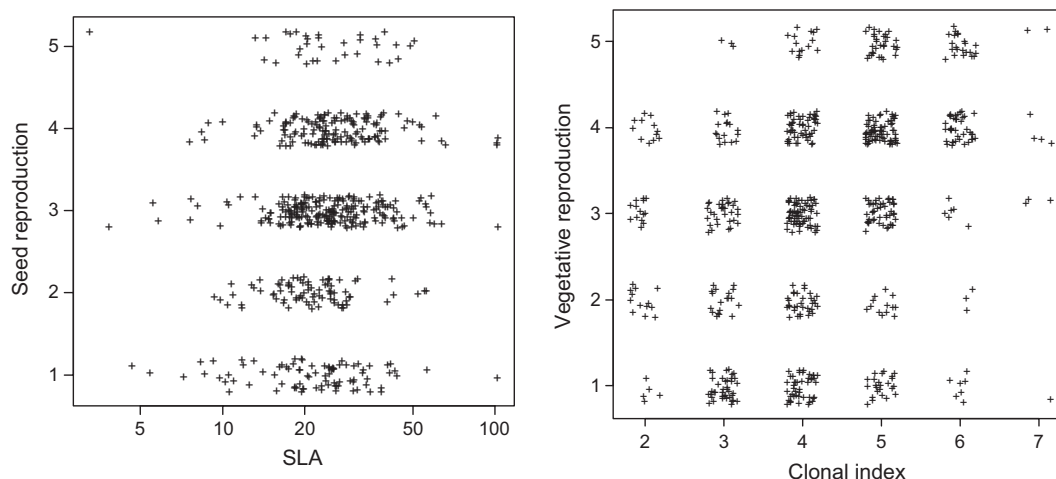


Fig. 2. Examples of relationships between plant traits and reproduction in the garden. Reproduction scores and clonal index are jittered to display the structure in the data more clearly. Both relationships are highly significant using Kendall tau. For the tests, see Table 3.

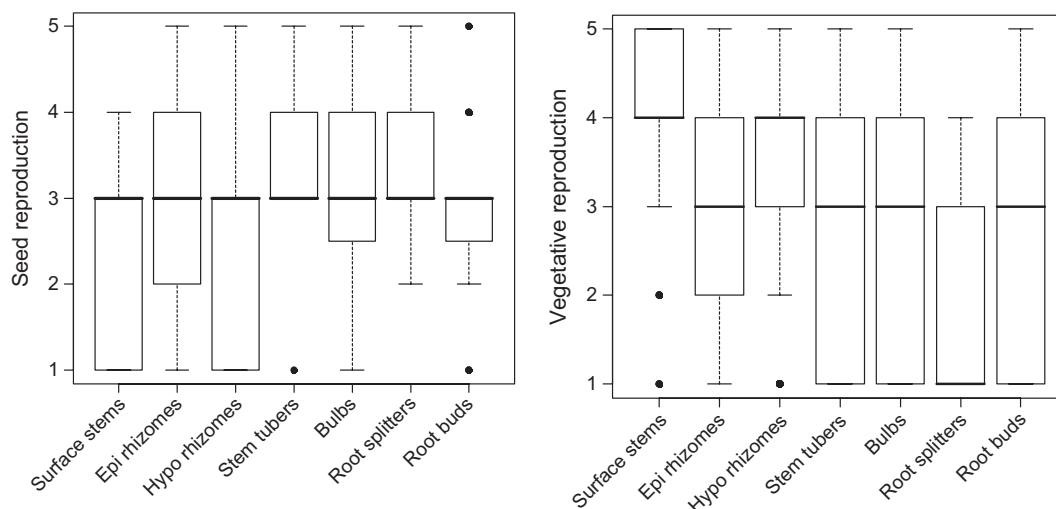


Fig. 3. Relationships between clonal growth organ type and reproduction in the garden. Thick lines are medians; boxes indicate interquartile range. Both relationships are highly significant using Kruskal–Wallis chi-square. For the tests see Table 3.

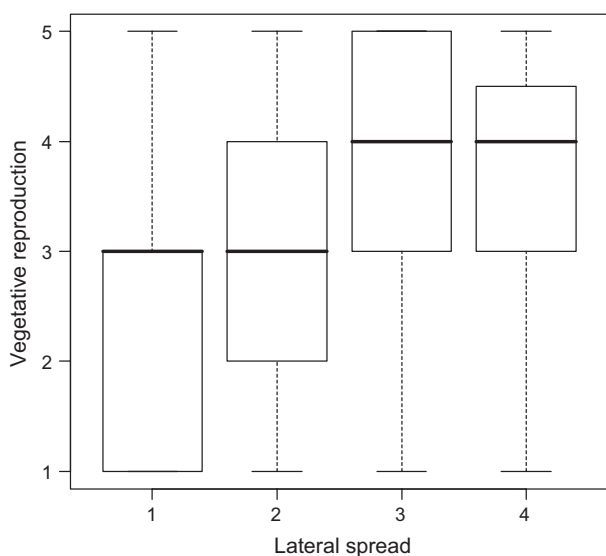


Fig. 4. Effects of lateral spread (in clonal plants only) on vegetative reproduction. Thick lines are medians; boxes indicate interquartile range. The relationship is highly significant using Kruskal–Wallis chi-square (Table 3).

size. There were a number of positive correlations between clonal growth traits, and persistence was negatively correlated with many other clonal traits. Further, there were some correlations between clonal traits and height/leaf/seed traits, but none of them very strong. Clonal multiplication was correlated negatively with leaf area and positively with shoot life span, and persistence negatively with SLA. Shoot life span was also positively correlated with clonal multiplication and negatively with lateral spread. There were only very weak correlations of seed mass with clonal trait variables; namely, seed mass was weakly negatively correlated with clonal multiplication. Although significance values in the data set are of limited importance due to large sample sizes, effect magnitudes were often big enough to represent real signals in the data.

Regression modelling of the LEDA traits (i.e. without using clonal traits) showed that growth form and SLA were the key predictors of seed reproduction and growth form; seed mass, while significant in the pairwise analysis, does not enter the model that already includes growth form and SLA (Table 5). Growth form and leaf area were the predictors of vegetative reproduction; vegetative reproduction was predicted by none of the key LEDA traits (seed mass, height and SLA). In analyses that also consider clonal trait variables, seed reproduction was predicted mainly by SLA and lateral spread (both in simple and partial analyses); if only clonal traits were used, there was an additional effect of clonal multiplication. All these effects remained significant in partial analyses. Vegetative reproduction was predicted mainly by lateral spread, CGO type and seed traits. All of these traits remained significant in partial analyses.

Phylogenetically independent analysis did not show major differences to species-based analysis (Table 6.). Effect of bud bank variables (size and depth) and CGO type on vegetative reproduction became much more important in phylogenetic analysis.

Discussion

VEGETATIVE VS. SEED REPRODUCTION: EVIDENCE FOR FUNCTIONAL TRADE-OFFS

Data from the garden clearly show a negative correlation between vegetative and seed reproduction. This is not surprising, as the trade-off between biomass investment into generative and vegetative plant structures is one of the fundamental constraints plants face (Cohen 1967; Kozłowski 1992; Obeso 2002), although not necessarily easily demonstrable by trait data. However, the negative correlation between vegetative and seed reproduction contrasts with the analysis of the trait data, where seed mass does not show a strong relationship to

Table 4. Pairwise correlations of traits

	Maximum plant height	Leaf area	Specific leaf area	Seed mass	Shoot life span	Clonal growth organ (CGO) role	CGO persistence	CGO multiplication	CGO lateral spread	Bud bank depth	Bud bank size
Maximum plant height	Corr. N	0.424*** 541	0.049 n.s. 580	0.19*** 551							
Leaf area	Corr. N	0.336*** 541	0.132** 561	0.336*** 485							
SLA	Corr. N	0.041 n.s. 580	0.093*** 561	0.082 n.s. 513							
Seed mass	Corr. N	0.099*** 551	0.23*** 513	0.043 n.s. 513							
Shoot life span	Corr. N	-0.084** 693	0.061 n.s. 574	0.161*** 553	0.053 n.s. 574						
CGO type	Chisq. d.f., N	52.1*** 6, 524	24.0*** 6, 411	11.0 n.s. 6, 441	34.8*** 6, 426						
CGO role	Corr. N	0.003 n.s. 529	-0.008 n.s. 416	-0.006 n.s. 446	0.009 n.s. 430	0.048 n.s. 650					
CGO persistence	Corr. N	0.033 n.s. 528	-0.033 n.s. 415	-0.146*** 445	-0.022 n.s. 430	0.049 n.s. 649	-0.121** 649				
CGO multiplication	Corr. N	0 n.s. 528	-0.171*** 415	0.014 n.s. 445	-0.079* 430	0.185*** 649	0.101** 649	-0.102** 649			
CGO lateral spread	Corr. N	0.056 n.s. 528	-0.005 n.s. 415	0.091* 445	-0.032 n.s. 430	0.045 n.s. 649	0.106** 649	0.202*** 649			
Bud bank depth	Corr. N	0.068* 658	0.047 n.s. 504	0.051 n.s. 540	-0.04 n.s. 527	0.24*** 650	0.028 n.s. 649	0.066 n.s. 649	0.159*** 649		
Bud bank size	Corr. N	0.086** 658	0.094** 504	-0.042 n.s. 540	0.007 n.s. 527	-0.052 n.s. 650	0.387*** 649	-0.088* 649	0.009 n.s. 649	0.135*** 792	
Clonal index	Corr. N	0.043 n.s. 528	-0.085* 415	0.069 n.s. 445	-0.068 n.s. 430	0.031 n.s. 649	-0.129*** 649	NA 649	NA 649	0.151*** 649	-0.038 n.s. 649

Lower triangle: nonparametric tests: Kendall tau (Corr.) or Kruskal–Wallis chi-square (Chisq.); upper triangle: Pearson correlation coefficients of log-transformed values.

N, number of species tested; NA, correlation not calculated as variables are dependent by definition.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$.

Table 5. Best models of seed and vegetative reproduction

Predictor variable	Variable notes	Data and trait subset					
		All plants		Clonal plants only, all traits		Clonal plants only, clonal traits only	
		Simple	Partial	Simple	Partial	Simple	Partial
Seed reproduction							
<i>N</i>		426	425	317	317	594	594
<i>R</i> ²		0.122	0.046	0.083	0.047		
Growth form	Factor, 3 levels	(×)***	(×)**	NA	NA	NA	NA
Maximum plant height	Log transformation					NA	NA
Leaf area	Log transformation					NA	NA
Specific leaf area	Log transformation	(+)**	(+)**	(+)**	(+)**	NA	NA
Seed mass	Log transformation					NA	NA
Shoot life span	Ordinal, 2 values						
CGO type	Factor, 7 levels	NA	NA			(×)**	(×)*
CGO persistence	Ordinal, 3 values	NA	NA				
CGO multiplication	Ordinal, 3 values	NA	NA		(+)	(+)**	(+)**
Lateral spread	Ordinal, 3 values	NA	NA	(-)**	(-)**	(-)**	(-)**
Bud bank depth	Ordinal, 2 values	NA	NA				
Bud bank size	Ordinal, 3 values	NA	NA			(-)*	(-)*
Vegetative reproduction							
<i>N</i>		454	425	345	317	636	594
<i>R</i> ²		0.356	0.246	0.263	0.183		
Growth form	Factor, 3 levels	(×)***	(×)***	NA	NA	NA	NA
Maximum plant height	Log transformation					NA	NA
Leaf area	Log transformation	(-)*		(-)*	(-)*	NA	NA
Specific leaf area	Log transformation					NA	NA
Seed mass	Log transformation					NA	NA
Shoot life span	Ordinal, 2 values			(+)	(+)		
CGO type	Factor, 7 levels	NA	NA	(×)***	(×)**	(×)***	(×)***
CGO persistence	Ordinal, 3 values	NA	NA				
CGO multiplication	Ordinal, 3 values	NA	NA				
Lateral spread	Ordinal, 3 values	NA	NA	(+)**	(+)**	(+)**	(+)**
Bud bank depth	Ordinal, 2 values	NA	NA				
Bud bank size	Ordinal, 3 values	NA	NA	(+)**	(+)*	(+)*	(+)*

Results from models with the lowest Akaike Information Criterion are shown. (+) indicates positive effect of a continuous or ordinal predictor, (-) indicates negative effect of a continuous or ordinal predictor, (×) indicates an effect of an unordered factor predictor. Significance of individual terms in the final model using log-likelihood ratio test is shown. Partial – vegetative reproduction used as covariate for tests of seed reproduction, seed reproduction used as covariate for tests of vegetative reproduction.

N, number of species used; NA, not used for selection in the model building; CGO, clonal growth organ.

****P* < 0.001, ***P* < 0.01, **P* < 0.05, +*P* < 0.1.

any of the clonal growth traits (with the exception of CGO type, see below). While this could be partly due to the fact that trait values were taken from databases and not measured directly in the field, it means that (database) seed and clonal traits cannot be equated with seed and clonal reproduction, respectively, in spite of strong correlations between seed traits and seed reproduction, and clonal traits and vegetative reproduction. Instead, these traits constitute the potential of an individual to reproduce in these ways, which might not be realized in the field (or, in this case, garden) depending on the growth/environmental constraints that the plants face and that determine the actual choice of the options provided (Arendt 1997).

While the trade-off between biomass investment into generative and vegetative plant structures at the individual level is due to energetic or resource constraints (Obeso 2002), such constraints are not necessarily the key drivers of the trade-offs

in actual reproduction in the garden. Namely, seed reproduction also includes seedling establishment and survival, which pose no energetic costs on the mother plant; and vegetative growth/multiplication may be somewhat self-sustaining due to the photosynthesis of the resultant additional plant tissue (Reekie & Bazzaz 1987). Instead, an important role in the trade-off between seed and vegetative reproduction in the garden is likely to be played by life-history or other costs related to the abiotic or biotic environment, and not from direct resource limitations.

Such costs could be incurred through at least two mechanisms. Firstly, if the spatial extent of clonal spread overlaps with the distance to which the majority of seeds disperse (Tackenberg 2003; Klimešová & Klimeš 2008), then vegetative reproduction will prevail over seed reproduction in clonally spreading species. This would be due to competitive superiority of vegetative offspring, as seedlings are likely to

Table 6. Best models of seed and vegetative reproduction after partialling out the phylogenetic information

Predictor variable	Variable notes	Data and trait subset					
		All plants		Clonal plants only, all traits		Clonal plants only, clonal traits only	
		Simple	Partial	Simple	Partial	Simple	Partial
Seed reproduction							
<i>N</i>		339	338	262	262	483	483
<i>R</i> ²		0.081	0.039	0.068	0.033	0.079	0.036
Growth form	Factor, 3 levels	(×)***	(×)**	NA	NA	NA	NA
Maximum plant height	Log transformation					NA	NA
Leaf area	Log transformation					NA	NA
Specific leaf area	Log transformation	(+)**	(+)**	(+)**	(+)*	NA	NA
Seed mass	Log transformation					NA	NA
Shoot life span	Ordinal, 2 values						
Clonal growth organ (CGO) type	Factor, 7 levels	NA	NA			(×)*	
CGO persistence	Ordinal, 3 values	NA	NA				
CGO multiplication	Ordinal, 3 values	NA	NA				
Lateral spread	Ordinal, 3 values	NA	NA	(-)**		(-)**	(-)**
Bud bank depth	Ordinal, 2 values	NA	NA				
Bud bank size	Ordinal, 3 values	NA	NA	(-)*	(-) ⁺	(-)*	(-)**
Vegetative reproduction							
<i>N</i>		361	338	262	262	519	483
<i>R</i> ²		0.197	0.141	0.271	0.232	0.240	0.188
Growth form	Factor, 3 levels	(×)***	(×)***	NA	NA	NA	NA
Maximum plant height	Log transformation			(+) ⁺	(+)*	NA	NA
Leaf area	Log transformation					NA	NA
Specific leaf area	Log transformation					NA	NA
Seed mass	Log transformation					NA	NA
Shoot life span	Ordinal, 2 values						
CGO type	Factor, 7 levels	NA	NA	(×)***	(×)***	(×)***	(×)***
CGO persistence	Ordinal, 3 values	NA	NA				
CGO multiplication	Ordinal, 3 values	NA	NA				
Lateral spread	Ordinal, 3 values	NA	NA	(+)**	(+)**	(+)**	(+)**
Bud bank depth	Ordinal, 2 values	NA	NA	(-)*	(-)*	(-)**	(-)**
Bud bank size	Ordinal, 3 values	NA	NA	(+)**	(+)**	(+)*	(+)*

Results from models with the lowest Akaike Information Criterion are shown. ‘+’ indicates positive effect of a continuous or ordinal predictor, ‘-’ indicates negative effect of a continuous or ordinal predictor, ‘×’ indicates an effect of an unordered factor predictor. Significance of individual terms in the final model using log-likelihood ratio test is shown. Partial – vegetative reproduction used as covariate for tests of seed reproduction, seed reproduction used as covariate for tests of vegetative reproduction.

NA, not used for selection in the model building; *R*², proportion of total variation explained by the factors listed in the table; *N*, number of species used.

****P* < 0.001, ***P* < 0.01, **P* < 0.05, +*P* < 0.1.

experience longer juvenile periods and be shorter in stature than vegetative offspring. On the other hand, seed reproduction would be unhindered in species with less extensive clonal growth, thus yielding a life-history trade-off between the two reproduction modes. This phenomenon could be exaggerated in the garden data, as only short-distance-dispersed seedlings were recorded and open space is maintained around plants by weeding/thinning, but is likely to act in the wild as well. Secondly, there may be a strong effect of habitat productivity. Extensive lateral spread by rhizomes is found in plants in more productive and wetter habitats and also correlates with plant height (Klimešová, Doležal & Sammul 2011a). This means that extensive lateral spread is typical for habitats with high above-ground competition where seedling establishment could be difficult. Seed dispersal would then serve less for local regeneration than for new habitat coloni-

zation (Eriksson 2011). In the garden, where plants are weeded and thinned, the effect of habitat productivity is weaker than it can be in the field, but higher stature (and hence shading effects) of these plants makes this phenomenon likely to act also here. Finally, building underground structures necessary for clonal growth at the seedling stage is often costly and may constrain growth and competitive ability of seedlings that need to build extensive CGOs early at their life (Suzuki & Hara 2001).

As a result of the costs encountered at a given site, plants will preferentially use one prevailing mode of reproduction depending on the typical conditions there (including, e.g. competitor density, which affects clonal reproduction, Chaloupecká & Lepš 2004) in spite of the fact that they can (and typically do) possess means for the other one as well. Such a generative-vegetative trade-off has been suggested to be due

to 'reproductive economy' by Aarssen (2008), who assumed that clonality evolved as a reproductive insurance in plants that had problems with generative reproduction. This would mean that seed reproduction would be the prime driver of the trade-off. While this can be true on the evolutionary time-scale, at the ecological time-scale, clonal reproduction may be the driver of the trade-off as well.

MEASURABLE TRAITS AS PREDICTORS OF GARDEN REPRODUCTION

The analyses show that garden reproduction data, that is, population growth rates under favourable conditions, are highly correlated with a number of plant traits. Apart from unsurprising correlations between vegetative growth traits and vegetative reproduction, and between seed mass and seed reproduction, there are a number of less obvious correlations. These correlations often appear also in partial analyses, meaning that they are not an outcome of the relationships through a third variable. They show that population level seed and vegetative reproduction reflect wider arrays of traits than those that would be conventionally linked with them. This is indicative of trade-offs between realized vegetative and seed reproduction at the population level.

Interestingly, SLA contributed only to seed reproduction and had no effect on vegetative reproduction. This indicates that fast-growing plants are more successful at seed reproduction (SLA could be a proxy for individual growth rate, particularly at the seedling stage; Wright & Westoby 1999; Poorter & Garnier 2007). Again, this signal is not present in the analysis of the soft trait data, where SLA shows no correlation with seed size; this variable represents (together with seed number per ramet) potential for seed reproduction, while the realized seed reproduction is constrained also by additional factors (Eriksson 2011).

Westoby (1998; Westoby *et al.* 2002) proposed a life-history scheme that uses three traits, namely seed size, plant maximum height and SLA. Although the system was primarily intended to identify differences among all plants from *Arabidopsis* to dipterocarps, these three traits (height only after growth form is taken into account) predict rather well both seed reproduction (all three traits) and vegetative reproduction (only height and seed mass, but not SLA) in the narrower data set of species in the garden (Wright & Westoby 1999; Poorter & Garnier 2007; Rees & Venable 2007). However, these variables miss an important dimension of vegetative reproduction as they do not account for potential for clonal growth (Weiher *et al.* 1999; Aarssen 2008). This is shown by very high and independent predictive power of growth form (annual/perennial non-clonal/perennial clonal) for vegetative reproduction for the set of all species and by clonal lateral spread in the set of clonal species.

Indeed, one of the key traits that correlate with both vegetative and seed reproduction is CGO type. This is essentially a morphological trait that constrains how the plant can grow clonally, but is correlated with many specific plant traits forming a general growth syndrome. It therefore shows strong

links to many other elements of life-history strategy. It is partly phylogenetically conserved (namely its rare types, such as bulbs, Sosnová, van Diggelen & Klimešová 2010), but the common types occur in all major plant groups. Its effect becomes also much clearer in the phylogenetically corrected analysis.

Some CGO types (hypogeous rhizomes, above-ground creeping stems and roots with adventitious buds) consist of organs that allow for long-distance spreading, underlying the link between CGO type and vegetative reproduction. However, while all three of these CGO types make long spacers possible, there is variation along the whole spectrum of spacer lengths among the species that employ them. In contrast, the range of spacer lengths among the species having the other CGO types is much narrower. Such inherent limitations on clonal reproduction could be compensated for by larger seed reproduction. Further, the length of the juvenile period is determined by the time needed to develop the morphological structures of the particular CGO type (Serebryakova 1971; Šmilauerová & Šmilauer 2007), thus potentially affecting the rate of seed reproduction. This constitutes a further link between CGO type and generative reproduction and, via the constraint of CGO on clonal growth, is likely to contribute to the negative relationship between vegetative and seed reproduction.

CAVEATS

While we believe that the garden reproduction data give us reasonable information on the actual plant growth under favourable circumstances, and the trade-offs observed represent genuine ecological effects, there are a number of caveats that must be kept in mind. Firstly, we cannot be sure that the assumption of favourable circumstances is fully valid. This is exemplified by the species in which no reproduction in the garden is observed, but is known from the field. Apart from the fact that the soil conditions might not match those in the field for some of the plants, there may be climatic differences, mainly for high-altitude plants. The exclusion from the botanical garden of certain potential sources of disruption of plant growth (big herbivores, flooding, litter or sediment deposition, fire, etc.) might enhance survival of individual plants but, on the other hand, might also restrict seed reproduction dependent on special regenerative niches. However, there is no reason to assume that these effects would be non-randomly distributed over the species; they are likely to add noise, but not systematic error.

Further, it must be kept in mind that weeding largely removed interspecific competition and occasional thinning reduced intraspecific competition. The processes observed in the garden necessarily reflect these conditions; in the field, plants will, in addition to the processes occurring in the garden, face additional challenges leading to differences in life-history costs and associated trade-offs. These need not be fully independent of the traits examined here, as some of the traits (e.g. height) are correlated with competitive ability. Namely, the absence of interspecific competition would have

a different effect on a species that is typically competitively dominant than on an inferior species. The set of species kept in the garden is also not a random sample of the total flora (namely, annuals are rather underrepresented). In addition, it must be noted that garden collections typically consist of an unknown number of genotypes. This may reduce the potential for seed reproduction in species that have low selfing rates.

Finally, the data set is potentially limited by the fact that trait values have been taken from databases, which span larger range of values than found within one population and are not necessarily measured according to fully standardized protocols. This might have contributed to low correlations between such traits.

Conclusions

Our study demonstrates that records on plant growth from a botanical garden can help fill the gap in our knowledge of the relationships between seed, growth and clonal traits and processes at the population level. Although seed and clonal traits do represent prerequisites for seed and vegetative reproduction, respectively, the actual seed and vegetative reproduction arises by more complex behavioural relationships that are not captured by the values of these traits. An important consequence of this is that even if the functional trade-off between seed and vegetative reproduction is not detected at the level of easily measurable traits, it can be revealed in population level outcomes.

Acknowledgements

The research reported here would not be possible without the vision and long-term generous support of the garden collections by the Faculty of Science, Charles University. Members of the Plant Ecology Discussion Group at the University of Michigan greatly helped to shape the ideas presented here. Ingolf Kühn kindly provided us the updated BiolFlor phylogenetic tree. We thank Kenneth Elgersma, Deborah Goldberg, Jonathan Rosenthal, Mark Rees and two anonymous referees for comments, and Jonathan Rosenthal for linguistic revision. The research was partially supported by the Grant Agency of the Czech Republic (P505/12/1007, GA 206/09/1471, GA 526/09/0963), and by the long-term research development project no. RVO 67985939.

References

- Aarssen, L.W. (2008) Death without sex – the ‘problem of the small’ and selection for reproductive economy in flowering plants. *Evolutionary Ecology*, **22**, 279–298.
- Arendt, J.D. (1997) Adaptive intrinsic growth rates: an integration across taxa. *The Quarterly Review of Biology*, **72**, 1–29.
- Bilton, M.C., Whitlock, R., Grime, J.P., Marion, G. & Pakeman, R.J. (2010) Intraspecific trait variation in grassland plant species reveals fine-scale strategy trade-offs and size differentiation that underpins performance in ecological communities. *Botany-Botanique*, **88**, 939–952.
- Bruun, H.H. & Ten Brink, D.-J. (2008) Recruitment advantage of large seeds is greater in shaded habitats. *Ecoscience*, **15**, 498–507.
- Chaloupecká, E. & Lepš, J. (2004) Equivalence of competitor effects and trade-off between vegetative multiplication and generative reproduction: case study with *Lychnis flos-cuculi* and *Myosotis nemorosa*. *Flora*, **199**, 157–167.
- Chambers, L.E. & Keatley, M.R. (2010) Phenology and climate – early Australian botanical records. *Australian Journal of Botany*, **58**, 473–484.
- Christensen, R.H.B. (2011) Ordinal regression models for ordinal data. R package version 2010.10–22. Available at: <http://www.cran.r-project.org/package=ordinal/>.
- Cohen, D. (1967) Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has been made and the subsequent outcome. *Journal of Theoretical Biology*, **16**, 1–14.
- Cornwell, W.K. & Ackerly, D.D. (2010) A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology*, **98**, 814–821.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E.E. & Valerie, T. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.
- Dawson, W., Burslem, D.F.R.P. & Hulme, P.E. (2009) Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions*, **15**, 141–147.
- Desdés, Y., Legendre, P., Azouzi, L. & Morand, S. (2003) Quantifying phylogenetically structured environmental variation. *Evolution*, **57**, 2647–2652.
- Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. et al. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.
- Diniz-Filho, J.A.F., de Sant’Ana, C.E.R. & Bini, L.M. (1998) An eigenvector method for estimating phylogenetic inertia. *Evolution*, **52**, 1247–1262.
- Donovan, L.A., Maherali, H., Caruso, C.M., Huber, H. & de Kroon, H. (2011) The evolution of the worldwide leaf economics spectrum. *Trends in Ecology and Evolution*, **26**, 88–95.
- Dosmann, M.S. (2006) Research in the garden: averting the collections crisis. *The Botanical Review*, **72**, 207–234.
- Dray, S. & Dufour, A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.
- Durka, W. (2002) Phylogenie der Farn- und Bluetenpflanzen Deutschlands. (eds S. Klotz, I. Kuehn & W. Durka) BIOLFLOR - Eine Datenbank zu biologisch-oekologischen Merkmalen der Gefaesspflanzen in Deutschland. *Schriftenreihe fuer Vegetationskunde* **38**, 75–91.
- Ebel, F. & Kimmel, F. (1985) Beobachtungen über die Frostempfindlichkeit einiger makronesischer und mediterraner Pflanzensippen im Botanischen Garten Halle (Saale). *Flora*, **176**, 411–429.
- Eriksson, O. (2011) Niche shifts and seed limitation as mechanisms behind seedling recruitment patterns in clonal plants. *Preslia*, **83**, 301–314.
- Ferenczy, A., Eppich, B., Varga, R.D., Bíró, I., Kovács, A., Petrányi, G. et al. (2010) Comparative analysis of the relationship between phenological phenomena and meteorological indicators based on insect and plant monitoring. *Applied Ecology And Environmental Research*, **8**, 367–376.
- Gersani, M., Brown, J.S., O’Brien, E.E., Maina, G.M. & Abramsky, Z. (2001) Tragedy of the commons as a result of root competition. *Journal of Ecology*, **89**, 660–669.
- Gratani, L., Crescente, M.F., Varone, L., Fabriani, G. & Digulio, E. (2008) Growth pattern and photosynthetic activity of different bamboo species growing in the Botanical Garden of Rome. *Flora*, **203**, 77–84.
- Gross, N., Kunstler, G., Liancourt, P., de Bello, F., Suding, K.N. & Lavorel, S. (2009) Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology*, **23**, 1167–1178.
- Johansson, V.A., Cousins, S.A.O. & Eriksson, O. (2011) Remnant populations and plant functional traits in abandoned semi-natural grasslands. *Folia Geobotanica*, **46**, 165–179.
- Kleyer, M., Bekker, R.M., Bakker, J., Knevel, I.C., Thompson, K., Sonnenschein, M. et al. (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.
- Klimešová, J. & de Bello, F. (2009) CLO-PLA: the database of clonal and bud bank traits of Central European flora. *Journal of Vegetation Science*, **20**, 511–516.
- Klimešová, J., Doležal, J. & Sammul, M. (2011a) Evolutionary and organismic constraints on the relationship between spacer length and environmental conditions in clonal plants. *Oikos*, **120**, 1110–1120.
- Klimešová, J. & Klimeš, L. (2008) Clonal growth diversity and bud banks of plants in the Czech flora: an evaluation using the CLO-PLA3 database. *Preslia*, **80**, 255–275.
- Klimešová, J., Doležal, J., Dvorský, M., de Bello, F. & Klimeš, L. (2011b) Clonal growth forms in eastern Ladakh, western Himalayas: classification and habitat preferences. *Folia Geobotanica*, **46**, 191–217.
- Kozłowski, J. (1992) Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology and Evolution*, **7**, 15–19.
- Kubát, K., Hrouda, L., Chrtek, J., Jun Kaplan, Z., Kirschner, J. & Štěpánek, J. (2002) Klíč ke Květeně České republiky [Key to the Flora of the Czech Republic]. *Functional Plant Ecology*. Academia, Praha, Czech Republic.
- Lavorel, S. & Garnier, E. (2002) Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838–848.
- Mokany, K. & Roxburgh, S.H. (2010) The importance of spatial scale for trait-abundance relations. *Oikos*, **119**, 1504–1514.
- Novoplansky, A. (2009) Picking battles wisely: plant behaviour under competition. *Plant Cell and Environment*, **32**, 726–741.
- Obeso, J.R. (2002) The costs of reproduction in plants. *New Phytologist*, **155**, 321–348.
- Ordoñez, J.C., van Bodegom, P.M., Witte, J.-P.M., Wright, I.J., Reich, P.B. & Aerts, R. (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, **18**, 137–149.
- Paradis, E. *et al.* (2012) Package ape. Analyses of phylogenetics and evolution. R package version 2012.04.04. <http://www.cran.r-project.org/package=ape/>.
- Pautasso, M. & Parmentier, I. (2007) Are the living collections of the world's botanical gardens following species-richness patterns observed in natural ecosystems? *Botanica Helvetica*, **117**, 15–28.
- Pillar, V.D., Duarte, L.d.S., Sosinski, E.E. & Joner, F. (2009) Discriminating trait-convergence and trait-divergence assembly patterns in ecological community gradients. *Journal of Vegetation Science*, **20**, 334–348.
- Poorter, H. & Garnier, E. (2007) The ecological significance of variation in relative growth rate and its components. *Functional Plant Ecology*, 2nd edn (eds F.I. Pugnaire & F. Valladares), pp. 67–100. CRC Press, Boca Raton.
- Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G. *et al.* (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, **89**, 1908–1920.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.
- Primack, R.B. & Miller-Rushing, A.J. (2009) The role of botanical gardens in climate change research. *New Phytologist*, **182**, 303–313.
- R Development Core Team. (2012) *R – A Language and Environment for Statistical Computing*. R foundation for statistical computing, Vienna, Austria. Available at: <http://www.R-project.org>.
- Reekie, E.G. & Bazzaz, F.A. (1987) Reproductive effort in plants. 3. Effect of reproduction on vegetative activity. *American Naturalist*, **129**, 907–919.
- Rees, M. & Venable, D.L. (2007) Why do big plants make big seeds? *Journal of Ecology*, **95**, 926–936.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365–392.
- Serebryakova, T.I. (1971) *Morphological Development of Tillers and Evolution of Life-Forms of Grasses*, 359 pp. Nauka, Moskva. [in Russian].
- Shipley, B., Vile, D., Garnier, E., Wright, I.J. & Poorter, H. (2005) Functional linkages between leaf traits and net photosynthetic rate: reconciling empirical and mechanistic models. *Functional Ecology*, **19**, 602–615.
- Silvertown, J. & Gordon, D.M. (1989) A framework for plant behavior. *Annual Review of Ecology and Systematics*, **20**, 349–366.
- Šmilauerová, M. & Šmilauer, P. (2007) What youngsters say about adults: seedling roots reflect clonal traits of adult plants. *Journal of Ecology*, **95**, 406–413.
- Sosnová, M., van Diggelen, R. & Klimešová, J. (2010) Distribution of clonal growth forms in wetlands. *Aquatic Botany*, **92**, 33–39.
- Stevens, A.D. (2007) Botanical gardens and their role in ex situ conservation and research. *Phyton-Annales Rei Botanicae*, **46**, 211–214.
- Suding, K.N., Goldberg, D.E. & Hartman, K.M. (2003) Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology*, **84**, 1–16.
- Suzuki, J.I. & Hara, T. (2001) Partitioning of stored resources between shoots in a clone, and its effects on shoot size hierarchy. *Annals of Botany*, **87**, 655–659.
- Tackenberg, O. (2003) Modeling long distance dispersal of plant diaspores by wind. *Ecological Monographs*, **73**, 173–189.
- Vesk, P.A., Warton, D.I. & Westoby, M. (2004) Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos*, **107**, 72–89.
- Wang, X.F., Yakir, D. & Avishai, M. (1998) Non-climatic variations in the oxygen isotopic compositions of plants. *Global Change Biology*, **4**, 835–849.
- Watkins, A.J. & Wilson, J.B. (2003) Local texture convergence: a new approach to seeking assembly rules. *Oikos*, **102**, 525–532.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science*, **10**, 609–620.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Wright, I.J. & Westoby, M. (1999) Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology*, **87**, 85–97.

Received 25 May 2012; accepted 14 August 2012

Handling Editor: Mark Rees

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix. List of plant species for which reproduction scores are available.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.