

NUMBER AND WEIGHT OF SEEDS AND REPRODUCTIVE STRATEGIES OF HERBACEOUS PLANTS

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Abstract: The paper brings data set of seed reproduction of about 500 wild herbaceous species of Central Europe and presents a number of produced seeds in a new way. Number of seeds – reproductive capacity of population (RCP) was defined as a number of seeds produced by one species per 1 m² at its one-hundred-per-cent cover per one season. About 23% of seed weight variability and about 26% of variability in RCP were explainable on a family level. The trade-off between RCP and seed weight was confirmed both within families and also among families. Both characteristics had higher variability on a family level and on lower taxonomic levels than on subclass and class levels. Species with an annual life cycle have a larger number of seeds than perennials. Geophytes and species without lateral spread have a tendency to produce a large amount of relatively weighty seeds in comparison to other life forms, and to species with vegetative lateral spread. Species with seeds dispersed by wind usually have a large number of lightweight seeds. Multivariate analyses confirmed some tendencies of reproductive traits which correspond to the definition of C-, S-, R- strategies by Grime – “verification” of the RCP as ecological trait. The R- strategy was well distinguished from the C- and S- strategies by reproductive traits, whereas C- and S- strategies are very similar to each other. Species with insect pollination agent often correspond to C- strategy, wind agent to S- strategy, and species with self-pollination to R- strategy.

Keywords: Dispersal, Height, Life cycle, Lateral spread, Life form, Pollination

Electronic appendix (www.ibot.cas.cz/fofia): Appendix (the seed weight and RCP for all the species)

INTRODUCTION

The effectiveness of producing a few large seeds as opposed to many small seeds has been a focus of ecologists for a long time (SALISBURY 1942). Seed production is an evolutionary compromise between the size of seeds and their number. This trade-off has been assumed and proved by many authors (e.g. SALISBURY 1942, HARPER et al. 1970, SMITH & FRETWELL 1974, KAWANO 1981, LLOYD 1987, LALONDE & ROITBERG 1989). Generally, the size of seeds within a species is kept at the expense of their number (LLOYD 1987), so the number of produced seeds is more variable than their size.

Enormous interspecific variation in seed size and in the number of produced seeds indicates that the level on which this compromise is established must be strongly affected by other attributes of the species (LORD et al. 1995). The number and size of seeds vary both within and among the species, being influenced by many factors, most important are the abiotic and biotic characteristics of the localities (FRANKLAND 1975, THOMPSON 1984,

WARDLAW & DUNSTONE 1984). Within a species, reproductive traits depend on the plant fitness, height (HENDRIX 1984), specific leaf area (WESTOBY et al. 1996), pollination success (COLOSI & CAVERS 1984, BOYD et al. 1990), time of pollination (GALEN & STANTON 1991), season and plant age (DOWNS & MCQUILKIN 1944 sec. BEGON et al. 1990, CAVERS & STEELE 1984), position on plant (WALLER 1982, STANTON 1984, WULFF 1986), and position in the fruit (e.g. *Fabaceae*, SALISBURY 1942). Interspecific variation reflects the trade-offs shaping the species' life history strategies (GRIME 1977, BEGON et al. 1990). In this paper, we will address the variability among species and families.

Comparative studies of traits related to plant reproduction characteristics were carried out in different areas of the world (e. g. HARPER et al. 1970, KAWANO 1981, MAZER 1989, PEAT & FITTER 1994, JORDANO 1995, RENNER & RICKLEFS 1995, LORD et al. 1995, WESTOBY et al. 1996). Information about number, size or weight of seeds of Central European plants are scattered in a huge number of papers, but without a comparative synthesis. Mean values of the number of seeds per fruit, the number of fruits per plant, and number seeds per plant are usually available. Because the number of seeds can vary as many as 50,000 times within one species depending on environmental conditions (HARPER 1977), the standardization of seed production is difficult. To overcome this problem, we introduced a new variable, "reproductive capacity of a population" (RCP) characterized as the number of seeds produced by one species per 1 m² at its one-hundred-percent cover per one season.

The size and number of produced seeds has an important effect in species ecology: a high number of small seeds improves the species dispersal ability at the expense of the ability of the seedlings to get established successfully, particularly in a competitive environment. Consequently, the seed number/size trade-off is an important feature of the species strategy (GRIME 1977). It might also be expected that there could be a correlation with other generic ecological traits. The species' position in the seed number/size trade-off is, however, also constrained by the species' evolutionary history. The phylogenetic related species could be expected to share similar traits.

Our aim was to obtain a data set about the reproduction of a wide range of species, collected according to a standardized protocol. This extensive data set enabled us to compare the species' reproductive strategy with the selected traits of their life histories and to answer these questions: (1) What is the relation between the weight/number of seeds and the traits of life history? (2) Is RCP applicable as a characteristic of reproduction ecology? We aimed at examining the variability in seed reproduction on various levels of phylogeny (represented by various taxonomic levels – classes, subclasses, families), and at finding the correlation between reproductive and other ecological traits, both within and among families. Finally, we tried "to verify" the RCP with the species classification CSR (strategy by Grime) according to GRIME (1977).

MATERIALS AND METHODS

Data collection

Data for 492 herbaceous species, belonging to 294 genera and 65 families, were collected in 1993–1999 in various environmental conditions in the Czech Republic, and partly also in the Slovak Republic. Each species was investigated in at least three different localities

(various types of plant communities, elevations), where its population was very vigorous and fertile.

Cover of the population was recorded (visual estimation of a percentage per 1 m²), and all generative parts (full sample) were collected. This biomass was dried (80 °C, 48 hours) and weighed. Then it was crushed by hand into smaller parts, fruits opened, seeds released, and homogenized. A subsample of a minimum 0.5 g (for robust species much more) was selected, weighed, and all the seeds were counted. Each subsample contained a minimum of 100 seeds. Weighing was done on an analytical laboratory balance (SARTORIUS-B1 60P, precision 10⁻⁵ g). The number of seeds per population per 1 m² with theoretical 100% cover was counted from the weight of the whole sample, the weight of the subsample, the number of seeds in the subsample, and from the real percentage cover of the investigated population (1). All the information about the three populations of the same species were averaged, and the value was called “the reproductive capacity of a population”.

$$N = \frac{WF \cdot NS}{C \cdot WS} \quad (1)$$

where, *WF* – weight of all generative parts from 1 m² (full sample), *WS* – weight of subsample, *NS* – number of seeds from subsample, *C* – population cover per 1 m² (range of numbers from 0 to 1), *N* – number of seeds produced by the population per 1 m².

At least 20 mature seeds were chosen from the mixed biomass. A seed is understood here as a functional generative element (achene, caryopsis, and a seed with a flying apparatus – i.e., the diaspore). Seeds were weighed altogether; an average weight of a seed was calculated. The value of the average seed weight was obtained for 455 species.

Data on taxonomy and some parameters of reproductive strategies of plants were taken from literature: taxonomic classification, maximum height of species (DOSTÁL 1989, JUDD et al. 1999, HEJNÝ & SLAVÍK 1988, 1990, 1992, ROTHMALER et al. 1987, SLAVÍK 1995, 1997), types of life cycle (FRANK & KLOTZ 1988, ROTHMALER et al. 1987), growth life forms according to Raunkiaer, pollination and seed dispersal agents, and ability of lateral spread (DOSTÁL 1950, HEJNÝ & SLAVÍK 1988, 1990, 1992, SLAVÍK 1995, 1997). Plant species were related to seven types of life strategy by Grime (FRANK & KLOTZ 1988, GRIME et al. 1987). The seed weight and RCP for all the species are presented in the electronic Appendix.

Data analysis

Variability on a taxonomic level

Data were analyzed using a statistical program STATISTICA (STATISTICA 1999). The quantitative variables were log transformed prior to analysis to achieve their normal distribution. All statistical procedures were subsequently calculated from this transformed data set. Taxonomy was included into the comparative analysis using selected conventional taxonomic levels (family, subclass, class), based on HEJNÝ & SLAVÍK (1988, 1990, 1992), JUDD et al. (1999), and SLAVÍK (1995, 1997).

Nested ANOVA was used for partition variability to the selected taxonomic levels. Class, subclass, family, and genus/species were used for selected species (13 families that included more than 10 genera). Orders were not used, because 11 orders were formed by just one

family (of the 13 large ones), so it was practically impossible to differentiate between a family and order level. For the categorical variables, genus was used as a basic unit of observation. For each category, its representation in the genus was analyzed after applying the Freedman-Tukey transformation (2) (used as PEAT & FITTER 1994). Consequently, error variability (Table 1) corresponds to the variability in proportion of species, where the trait is present among genera within a family for categorical variables, and to the variability among species within a family for quantitative variables. The taxonomic levels for categorical and quantitative variables are drawn from the Freedman-Tukey transformation (2).

$$0.5 \left[\arcsin \left(\sqrt{\frac{x}{n+1}} \right) + \arcsin \left(\sqrt{\frac{x+1}{n+1}} \right) \right] \quad (2)$$

where, x = number of species in the genus with the trait present, n = number of all species in the genus.

Correlation patterns of seed weight and the reproductive capacity of a population

The differences among individual types of traits and selected families with regard to the number and weight of seeds were calculated using a multiple range analysis by the Tukey HSD test at the significance level $\alpha = 0.05$. Correlation among quantitative variables was calculated using standard methods.

Various multivariate analyses by the program CANOCO (TER BRAAK & ŠMILAUER 1998) were used to test the mentioned questions. At first, the principal components analysis (PCA), as exploratory data analysis, was carried out with the primary data set (i.e., types of life cycle, growth life forms, pollination, seed dispersal agents and ability of lateral spread, together with RCP, seed weight, and also maximum plant height). Then, partial PCA analysis with families as covariables was carried out to see the correlation structure within families (i.e., with the phylogenetic dependencies partially removed). Plant strategy classification according to Grime was then passively projected into the ordination diagrams.

Then, stepwise discriminant analysis was carried out to see which of the measured traits were the best predictors of species strategy. The discriminant analysis was calculated as canonical correspondence analysis (CCA), where “species” (i.e., the response data in CANOCO) were a fuzzy classification of the real species into the strategies according to Grime, and the “environmental data” (i.e., predictors) were the measured traits. The stepwise selection was stopped when no variable improved the fit significantly at $\alpha = 0.05$.

Results of the previous analyses showed, that RCP and seed weight had a phylogenetic component, and were affected by the species ecology. Using several redundancy analyses (RDA) (with various combinations of explanatory variables and covariables), we performed the variance partitioning of the response (consisting of the two traits, seed weight and RCP) explained by two sets of explanatory variables: families (the phylogenetic component) and ecological traits (see TER BRAAK & ŠMILAUER 1998 for technical details of variance partitioning). This method is able to separate variability in a response that could be ascribed to various (potentially correlated) subsets of predictors.

Table 1. The percentage variability of investigated traits on different taxonomic levels. Nested ANOVA and Friedman-Tukey transformation were used. Error variability corresponds to variability among genera within a family for a qualitative trait, and to variability among species within a family for a quantitative trait (see Data analysis).

Traits		Classes	Subclasses	Families	Error	
Quantitative	Maximum height	0	0	17	83	
	Seed weight	0	4	23	73	
	Reproductive capacity of population	0	4	25	71	
Qualitative	Life cycle	Annual	13	12	15	60
		Biennial	9	1	12	78
		Monocarpic perennial	10	0	28	62
		Perennial	25	5	15	55
	Life form	Therophyte	14	10	15	61
		Hemicryptophyte	10	13	8	69
		Chamaephyte	11	0	19	69
		Geophyte	0	0	14	86
	Lateral spread	Without	30	4	13	53
		< 0.30 m per year	2	7	8	83
		>= 0.30 m per year	16	0	15	68
	Pollination agents	Wind	72	4	12	12
		Insect	14	0	35	51
		Self	17	13	21	49
	Seed dispersal	Wind	0	0	38	62
		Gravitation	0	0	14	86
		Ant	0	0	25	75
On animal's hair		0	5	24	71	
In animal's digestive tract		7	4	11	78	
Water		3	0	18	79	
	Self	17	13	21	49	

RESULTS

Variability on various taxonomic levels

Most variability of RCP and seed weight can be attributed to families and lower taxonomic levels. The majority of variability of the quantitative traits occurred also on the lowest level. Only one trait (wind pollination) is connected with higher taxonomic levels. The distribution of variability is often spread across several taxonomic levels (Table 1).

Negative correlation between seed weight and RCP was found on various levels: for every single family out of all 13 selected families, for mean values of these families, and in the full data set (Table 2). As expected, the seed weight and number were negatively correlated both among and within families. With some caution we could say that the trade-off was not only ecological, but had also a phylogenetic component.

Seed weight and reproductive capacity of population

The largest RCP was found for *Typha latifolia* (almost 19 000 000 seeds/m²) and the least for *Potamogeton pectinatus* (< 300 seeds/m²). The range of RCP was five orders of magnitude. Counting the family averages, the *Orchidaceae* family exhibited the highest RCP

Table 2. Parameters in the linear regression between seed weight [g] and reproductive capacity of population [$1/m^2$]. Logarithmic transformation of data, r – correlation coefficient, k – slope, q – intercept. Significant regressions ($P < 0.05$) are displayed in bold.

Groups	n	r	k	q	P
<i>Apiaceae</i>	24	-0.193	-0.184	4.379	0.367
<i>Asteraceae</i>	62	-0.726	-0.753	2.445	0.000
<i>Boraginaceae</i>	11	-0.659	-0.277	3.807	0.027
<i>Brassicaceae</i>	26	-0.883	-0.716	2.875	0.000
<i>Caryophyllaceae</i>	18	-0.762	-0.713	2.892	0.000
<i>Cyperaceae</i>	20	-0.523	-0.513	2.887	0.018
<i>Fabaceae</i>	23	-0.896	-1.032	1.944	0.000
<i>Chenopodiaceae</i>	11	-0.421	-0.285	4.133	0.194
<i>Juncaceae</i>	11	-0.960	-1.080	1.356	0.000
<i>Lamiaceae</i>	24	-0.394	-0.297	3.960	0.057
<i>Poaceae</i>	48	-0.494	-0.399	3.607	0.000
<i>Rosaceae</i>	15	-0.580	-0.555	2.936	0.023
<i>Scrophulariaceae</i>	32	-0.879	-0.865	2.186	0.000
Means of families	13	-0.868	-0.765	2.527	0.000
Full data set	455	-0.732	-0.653	2.874	0.000

(more than 2 000 000 seeds/ m^2). Families of *Juncaceae* and *Caryophyllaceae* also produced high numbers of seeds ($> 1\,000\,000$ seeds/ m^2). On the contrary, families of *Apiaceae*, *Boraginaceae*, *Cyperaceae*, and *Fabaceae* had a small number of seeds ($< 100\,000$ seeds/ m^2).

An RCP larger than 1 000 000 seeds/ m^2 was found for anemochorous species, SR-strategists, and S-strategists. A lower number of produced seeds ($< 200\,000$ seeds/ m^2) was recorded for monocarpic perennials, species with gravitation dispersal of seeds, endozoochorous, and myrmecochorous species.

The lightest seeds were recorded in the *Pyrolaceae* family, *Moneses uniflora* and *Pyrola minor* (0.000 8 mg). The *Orchidaceae* family and the genus *Juncus* belonged to the groups with light seeds, too (< 0.010 mg). *Lilium martagon* (> 100 mg), *Pulmonaria obscura*, and *Iris pseudacorus* (ca. 40 mg) had the heaviest seeds. The weight range of the recorded species was six orders. Species with heavy seeds (> 8 mg) were often from the *Boraginaceae* and *Fabaceae* families, and those with light seeds (< 0.05 mg) from the *Caryophyllaceae* and *Juncaceae* families.

Seed weight average bigger than 5 mg was recorded for geophytes, autochorous, and myrmecochorous species. On the contrary, the lightest seeds (< 1 mg) had anemophilous and anemochorous species. R-, SR-, and S-strategists had quite light seeds, too.

Trends among the traits of reproductive strategy of plants

The PCA and partial PCA analyses (Fig. 1) provided similar structures, revealing that the within-family correlation was similar to that in the whole data set. Interestingly, based on the studied traits, the ruderal strategy was well separated from the remaining two, whereas the competitive and stress-tolerant strategies were rather similar to each other. This was not so surprising, because the distinction between S- and C- strategies is probably based more on physiological traits not used in this study (growth rate, resistance to environmental extremes).

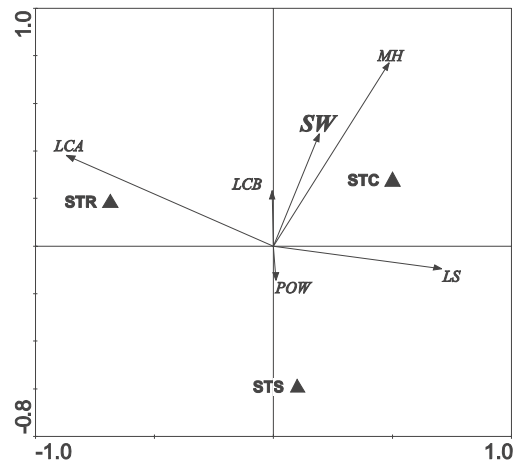


Fig. 2. Results of the stepwise discriminant analysis, calculated as CCA (canonical correspondence analysis). The selected explanatory variables are: SW – log(seed weight), MH – log(maximum height), LS – lateral spread. Triangel of CSR strategy according to Grime is signed as STC, STS, and STR. LCA – annual life cycle, LCB – biennial life cycle, POW – wind pollination.

higher than we expected according to the seed weight), whereas families with a positive score on the second axis invested less. Ecological traits (life form, pollination agents, etc.) explain 29.8%. Of those, however, the shared effect was 19.6%, so the two reproductive traits explained 62.2% altogether. Although it seems that phylogeny explains more, we should take into account the higher degrees of freedom for families (61 families in comparison with 20 “ecological variables” – including all the dummy variables for individual categories). Both effects were,

however, highly statistically significant, which corresponded to the results obtained from the univariate analyses (Table 3).

DISCUSSION

Seed weight and reproductive capacity of population

Many authors (e.g., CAVERS & STEELE 1984, FRANKLAND 1975, HENDRIX 1984, STANTON 1984, THOMPSON 1984, WALLER 1982, WARDLAW & DUNSTONE 1984, WULFF 1986) present large phenotypic variability in seed weight within a species, population, individual, or even fruit. Our results showed that the variability in seed weight among and in RCP was roughly the same. Also, the distribution of variability among the taxonomic levels was similar as far as number of seeds and seed weight is concerned. About 23% of seed weight variability was explainable on a family level; this is slightly less than the value by MAZER (1989), who found 30% of variability.

Life cycle

Our study confirmed that monocarpic species produced more seeds per year than polycarpic species. For a plant that invests into reproduction only once in its life (annual, biennial, monocarpic perennial) it is strategic to produce more seeds than a plant with repeated flowering (SALISBURY 1942), even at the expense of seed weight. Monocarpic species invest all their energy into reproduction before the end of their life (FENNER 1985). As the persistence of population is vitally dependent on seedling settlement, only a high number of seeds ensures a successful survival. Monocarpic populations are typical for temporary

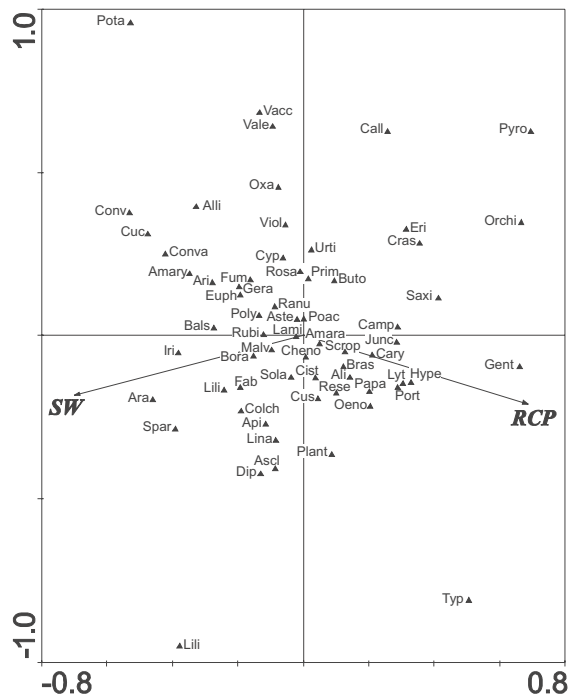


Fig. 3. Results of RDA (redundancy analysis) on family level with families as explanatory variables, and seed weight/number as explained variables. SW – log(seed weight), RCP – log(reproductive capacity of population).

seeds than annuals or perennials. Similarly to BAKER (1972) and SILVERTOWN (1981), we found that annuals and monocarpic perennials have in average lighter seeds than polycarpic plants, but the differences were not significant, despite the large number of compared species. Variability in species was huge, and, on the contrary to the theoretical predictions, some annuals had relatively large seeds (e.g. *Melampyrum*, annual species of *Vicia*), and many perennials had extremely small seeds (e.g. *Pyrolaceae*, *Orchideaceae*).

Vegetative spread

The ability of vegetative propagation is frequent and its rate differs among species (SALISBURY 1942, KLIMEŠ & KLIMEŠOVÁ 1999a,b). The trade-off between vegetative propagation and generative reproduction is expected both as a flexible adaptation to the habitat conditions within a species (CASWELL 1985, ERIKSSON 1997, MOGIE & HUTCHINGS 1990), and also as an evolutionary trade-off among species (HARPER 1977, FENNER 1985). Interestingly, plants without lateral vegetative spread produce not only a significantly higher number of seeds, but even have a higher average seed weight (even when the difference in seed weight is not significant, Table 3). This confirms the interspecific trade-off, plants without vegetative spread can (and must) invest more energy into seeds (e.g. SUTHERLAND &

habitats, and consequently, a high number of small seeds is their adaptation to the dispersal in space and time (SOUTHWOOD 1988). This characteristic well corresponds to the R-strategy by GRIME (1977). The repeated flowering means division of energy between somatic growth and survival, and reproduction. Theoretically the number of seeds produced per year decreases with the length of the plant's life (HARPER 1977).

The expected trends were confirmed on this data set: annuals produce more seeds than perennials, and the number of seeds produced by biennials and monocarpic perennials is comparable. We did not confirm the suggestion of LOVETT DOUST (1980) and THOMPSON (1984) that biennials should have heavier

Table 3. Comparison of reproductive capacity of population [$1\ 000/m^2$] and seed weight [mg] for reproductive traits of investigated herbaceous species. Types of traits followed by the same letters were not significantly different in multiple range analysis (Tukey HSD test, log transformation, $P < 0.05$, see columns HSD).

Traits		<i>n</i>	Reproductive capacity of population			
			median	mean	SD	HSD
Life cycle	Annual	131	120	595	1640	a
	Biennial	40	106	400	805	ab
	Monocarpic perennial	4	75	147	186	ab
	Perennial	317	60	500	1870	b
Life form	Therophyte	130	118	599	1640	a
	Hemicryptophyte	252	65	306	903	b
	Chamaephyte	30	91	782	2010	ab
	Geophyte	80	51	947	3140	b
Lateral spread	Without	224	109	665	1940	a
	< 0.30 m per year	176	68	384	1230	b
	\geq 0.30 m per year	92	54	408	2010	b
Pollination agents	Wind	119	68	517	2090	a
	Insect	232	57	472	1780	a
	Self	141	126	590	1280	b
Seed dispersal	Wind	137	178	1250	2870	a
	Gravitation	123	68	131	181	b
	Ant	44	44	124	222	b
	On animal's hair	76	55	232	878	b
	In animal's digestive tract	17	31	168	295	b
	Water	25	125	360	660	ab
	Self	70	53	451	1600	b

Traits		<i>n</i>	Seed weight			
			median	mean	SD	HSD
Life cycle	Annual	126	0.58	1.79	4.13	a
	Biennial	39	1.05	2.88	5.41	a
	Monocarpic perennial	4	1.09	1.30	0.85	a
	Perennial	284	0.64	2.75	8.80	a
Life form	Therophyte	126	0.58	1.86	4.20	ab
	Hemicryptophyte	230	0.62	1.93	4.63	ab
	Chamaephyte	26	0.17	2.68	7.03	b
	Geophyte	71	1.00	5.27	15.23	a
Lateral spread	Without	217	0.66	2.92	9.59	a
	< 0.30 m per year	157	0.70	2.21	4.95	a
	\geq 0.30 m per year	79	0.58	1.79	4.36	a
Pollination agents	Wind	105	0.56	0.92	1.11	b
	Insect	215	0.84	3.81	10.43	a
	Self	133	0.55	1.56	2.90	b
Seed dispersal	Wind	127	0.14	0.64	1.42	b
	Gravitation	115	0.92	1.72	2.76	c
	Ant	43	0.96	2.88	7.36	ac
	On animal's hair	71	1.15	2.73	4.38	ac
	In animal's digestive tract	15	1.18	6.41	9.45	ac
	Water	23	0.20	3.47	9.81	bc
	Self	59	1.07	5.93	16.44	ac

VICKERY 1988); the reserves allocated into vegetative propagation hinder or delay flowering (SILVERTOWN & LOVETT DOUST 1993).

Pollination

Individual investigated types of pollination approximately corresponded to apices of the C-S-R Grime's triangle (Figs 1, 2). Species tending to pollination by insects approximately corresponded to C-strategy, self-pollinated species to SR-strategy, and species pollinated by wind to S-strategy. Competitive plants developed the ability to succeed in productive, relatively undisturbed conditions (GRIME 1977), therefore maximum species height and pollination by insects may be an advantage. Ruderal selection is associated with a short lifespan (GRIME 1977) and self-pollination is the way to increase the probability of the reproduction success in disturbed habitats. Finally, plants with a stress-tolerant strategy, which allows a survival in continuously unproductive environments (GRIME 1977), may use wind as the best pollination agent in predictably unfavourable habitats.

Insect pollinated species tended to produce a low number of large seeds (Figs. 1, 2), whereas self pollinated species had a high number of small seeds (Table 3). Self pollination is connected with the syndrome of adaptation to an unpredictable environment. A plant needs to produce a large number of seeds in the shortest possible time, and the necessity of out crossing might be a constraining factor (GRIME 2001). On the contrary, an investment into conspicuous flowers that attract (often highly specific) insects presupposes a predictable presence of insects that could be guaranteed only in a relatively stable and predictable environment. Allocation to reproduction may depend on pollination effectiveness, too (COLOSI & CAVERS 1984, GALEN & STANTON 1991, ÅRGEN & WILLSON 1992, 1994, PROCTOR & HARDER 1994).

Seed dispersal

Seeds of various plant species are phylogenetically adapted to buoyancy in the air by a number of various morphological features on seeds and fruits. Some seeds dispersed by wind do not need a special modification; their small size is sufficient (HENDRY & GRIME 1993). Anemochorous species, with seeds dispersed by wind, produced the smallest and the most numerous seeds of the six plant groups with a different type of seed dispersal (Table 3). The higher number of tiny seeds increases the probability of dispersal to long distances from the maternal plant, and seedling development in the required environments (PIJL 1982).

Life history strategy

We compared our results with the life history strategies by GRIME (1977). Principal component analyses (PCA) with the centroids of strategies projected into the ordination diagram *ex post* corresponds to the measured traits only. The results have shown that the R-strategy is well distinguished from the C- and S- in the data set, both in reproductive traits, but also in other ecological traits, whereas C- and S- are rather similar to each other on the first two PCA axes. This conclusion is rather robust to the use of families as covariables, i.e., it could be seen as a major trend also within the families. However, using the discriminant analysis, we found traits that distinguished the C- and S-strategy quite well; as expected,

C-strategists were higher on average, and had heavier seeds. The basic difference between PCA and discriminant analysis is that PCA could be seen as an independent confirmation of the major trends, whereas discriminant analysis just showed that there indeed was a difference among the compared groups. Consequently, we could say that we indeed confirmed the major axis of variation between R-strategists and the others; further we confirmed that there were differences between C- and S-strategies, but they did not appear as the major variation axis. This conclusion is, however, partially dependent on the selection of variables in the analysis.

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REFERENCES

- ÅRGEN J. & WILLSON M.F. (1992): Determination of seed production in *Geranium maculatum*. *Oecologia* 92: 177–182.
- ÅRGEN J. & WILLSON M.F. (1994): Cost of seed production in the herbs *Geranium maculatum* and *G. sylvaticum*: an experimental field study. *Oikos* 70: 35–42.
- BAKER H.G. (1972): Seed weight in relation to environmental conditions in California. *Ecology* 53: 997–1010.
- BEGON M., HARPER J.L. & TOWNSEND C.R. (1990): *Ecology: individuals, populations and communities*. Blackwell Scientific Publications, London.
- BOYD M., SILVERTOWN J. & TUCKER C. (1990): Population ecology of heterostyle and homostyle *Primula vulgaris*: growth, survival and reproduction in field populations. *J. Ecol.* 78: 799–813.
- CASWELL H. (1985): The evolutionary demography of clonal reproduction. In: JACKSON J.B.C., BUSS L.W. & COOK R.E. (eds.), *Population biology and evolution of clonal organisms*, Yale University Press, New Haven, pp. 187–224.
- CAVERS P.B. & STEELE M.G. (1984): Patterns of change in seed weight over time on individual plants. *Amer. Naturalist* 124: 324–335.
- COLOSI J.C. & CAVERS P.B. (1984): Pollination affects percent biomass allocated to reproduction in *Silene vulgaris* (bladder champion). *Amer. Naturalist* 124: 299–306.
- DOSTÁL J. (1989): *Nová květena ČSSR 1, 2 (Ne flora of the CSSR)*. Academia, Praha.
- DOWNS C. & MCQUILKIN W.E. (1944): Seed production of Southern Appalachian oaks. *J. Forest.* 42: 786–790.
- ERIKSSON O. (1997): Clonal life histories and evolution of seed recruitment. In: DE KROON H. & VAN GROENENDAEL J. (eds.), *The ecology and evolution of clonal plants*, Backhuys Publishers, Leiden, pp. 211–226.
- FENNER M. (1985): *Seed ecology*. Chapman and Hall, London.
- FRANK D. & KLOTZ S. (1988): *Biologisch-ökologische Daten zur Flora der DDR*. MLU, Halle-Wittenberg.
- FRANKLAND B. (1975): Phytochrome control of seed germination in relation to the light environment. In: SMITH H. (ed.), *Light and plant development*, Butterworth, London, pp. 477–502.
- GALEN C. & STANTON M.L. (1991): Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (*Ranunculaceae*). *Amer. J. Bot.* 78: 978–988.
- GRIME J.P. (1977): Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer. Naturalist* 111: 1169–1194.
- GRIME J.P. (2001): *Plant strategies, vegetation processes, and ecosystem properties*. Wiley & Sons, Chichester.
- GRIME J.P., HODGSON J.G. & HUNT R. (1987): *Comparative plant ecology. A functional approach to common British species*. Unwin Hyman, London.
- HARPER J.L. (1977): *Population biology of plants*. Academic Press, London.
- HARPER J.L., LOVELL P.H. & MOORE K.G. (1970): The shapes and sizes of seeds. *Annual Rev. Ecol. Syst.* 1: 327–356.
- HENDRIX S.D. (1984): Variation in seed weight and its effects on germination in *Pastinaca sativa* L. (*Umbeliferae*). *Amer. J. Bot.* 71: 795–802.

- HEJNÝ S. & SLAVÍK B. (eds.) (1988): *Květena České socialistické republiky (Flora of the Czech Republic) 1*. Academia, Praha.
- HEJNÝ S. & SLAVÍK B. (eds.) (1990): *Květena České republiky (Flora of the Czech Republic) 2*. Academia, Praha.
- HEJNÝ S. & SLAVÍK B. (eds.) (1992): *Květena České republiky (Flora of the Czech Republic) 3*. Academia, Praha.
- HENDRY G.A.F. & GRIME J.P. (eds.) (1993): *Methods in comparative plant ecology. A laboratory manual*. Chapman and Hall, London.
- JORDANO P. (1995): Frugivore-mediated selection on fruit and seed size: birds and St. Lucieff's cherry, *Prunus mahaleb*. *Ecology* 76: 2627–2639.
- JUDD W.S., CAMPBELL C.H., KELLOG E.A. & STEVENS P.F. (1999): *Plant systematics – a phylogenetic approach*. Sinauer Associates, Sunderland.
- KAWANO S. (1981): Trade-off relationships between some reproductive characteristics in plants with special reference to life history strategy. *Bot. Mag. Tokyo* 94: 285–294.
- KLIMEŠ L. & KLIMEŠOVÁ J. (1999a): CLO-PLA2 – a database of clonal plants in central Europe. *Pl. Ecol.* 141: 9–19.
- KLIMEŠ L. & KLIMEŠOVÁ J. (1999b): *Database of clonal plants*. <http://www.butbn.cas.cz/klimes> (March 2002).
- LALONDE R.G. & ROITBERG B.D. (1989): Resource limitation and offspring size and number trade-offs in *Cirsium arvense* (Asteraceae). *Amer. J. Bot.* 76: 1107–1113.
- LLOYD D.G. (1987): Selection of offspring size at independence and other size-versus-number strategies. *Amer. Naturalist* 129: 800–817.
- LORD J., WESTOBY M. & LEISHMAN M.R. (1995): Seed size and phylogeny in six temperate floras: constraints, niche conservatism and adaptation. *Amer. Naturalist* 146: 349–364.
- LOVETT DOUST J. (1980): A comparative study of life history and resource allocation in selected *Umbelliferae*. *Biol. J. Linn. Soc.* 13: 189–154.
- MAZER S.J. (1989): Ecological, taxonomic and life history correlates of seed mass among Indiana dune angiosperms. *Ecol. Monogr.* 59: 153–175.
- MOGIE M. & HUTCHINGS M.J. (1990): Phylogeny, ontogeny and clonal growth in vascular plants. In: GROENENDAEL J. & DE KROON H. (eds.), *Clonal growth in plants*, SPB Academic Publishing, Hague, pp. 3–22.
- PEAT H.J. & FITTER A.H. (1994): Comparative analysis of ecological characteristics of British angiosperms. *Biol. Rev.* 69: 95–115.
- PIJL L. (1982): *Principles of dispersal in higher plants*. Berlin Heidelberg, New York.
- PROCTOR H.C. & HARDER L.D. (1994): Pollen load, capsule weight, and seed production in three orchid species. *Canad. J. Bot.* 72: 249–255.
- RENNER S.S. & RICKLEFS R.E. (1995): Dioecy and its correlates in the flowering plants. *Amer. J. Bot.* 82(5): 596–606.
- ROTHMALER W., JÄGER E., SCHUBERT R. & WERNER K. (1987): *Exkursionsflora für die Gebiete der DDR und der BRD. Atlas der Gefäßpflanzen*. Volk und Wissen Volkseigener Verlag, Berlin.
- SALISBURY E.J. (1942): *The reproductive capacity per plants*. Bell and Sons, London.
- SILVERTOWN J.W. (1981): Seed size, lifespan and germination date as co-adapted features of plant life history. *Amer. Naturalist* 118: 860–864.
- SILVERTOWN J.W. & LOVETT DOUST J.L. (1993): *Introduction to plant population biology*. Blackwell Scientific Publications, Oxford.
- SLAVÍK B. (ed.) (1995): *Květena České republiky (Flora of the Czech Republic) 4*. Academia, Praha.
- SLAVÍK B. (ed.) (1997): *Květena České republiky (Flora of the Czech Republic) 5*. Academia, Praha.
- SMITH C.H. & FRETWELL S.D. (1974): The optimal balance between size and number of offspring. *Amer. Naturalist* 108: 499–506.
- SOUTHWOOD T.R.E. (1988): Tactics, strategies and templates. *Oikos* 52:3-18.
- STANTON M.L. (1984): Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). *Amer. J. Bot.* 71: 1090–1098.
- STATISTICA (1999): A comprehensive system for statistics, graphics, and application development.

- SUTHERLAND S. & VICKERY R.K. (1988): Trade-offs between sexual and asexual reproduction in the genus *Mimulus*. *Oecologia* 76: 330–335.
- TER BRAAK C.F.J. & ŠMILAUER P. (1998): *CANOCO reference manual and user's guide to Canoco for Windows: Software for canonical community ordination*. Microcomputer power, Ithaca.
- THOMPSON J.N. (1984): Variation among individual seed masses in *Lomatium grayi* (*Umbelliferae*) under controlled conditions: magnitude and partitioning of variance. *Ecology* 65: 626–631.
- WALLER D.M. (1982): Factors influencing seed weight in *Impatiens capensis* (*Balsaminaceae*). *Amer. J. Bot.* 69: 1470–1475.
- WARDLAW I.F. & DUNSTONE R.L. (1984): Effect of temperature on seed development in jujube (*Simmondsia chinensis* (LINK) SCHNEIDER). 1. Dry matter changes. *Austral. J. Agric. Res.* 35: 685–691.
- WESTOBY M., LEISCHMAN M. & JANICE L. (1996): Comparative ecology of seed size and dispersal. *Philos. Trans. Ser. B* 351: 1309–318.
- WULFF R.D. (1986): Seed size variation in *Desmodium paniculatum*. I. Factors affecting seed size. *J. Ecol.* 74: 87–97.

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