

Plant rarity and the type of clonal growth

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The relationship between clonal growth types and plant rarity has been tested at local and regional scales. The participation of rare species in types of clonal growth differed from that of common plants. Plants with root tubers, shoot tubers and turions were over-represented among extinct and threatened taxa at the regional scales. In contrast, plants with short epigeogenous rhizomes were over-represented among rare plants at the local scale. Evolutionary aspects of this pattern are discussed.

Key words: Bílé Karpaty Mountains, Czech Republic, plant threat, red lists, spatial scales.

■ Introduction

A decline of previously common and abundant plants belongs to the serious consequences of human activities. Species are becoming rare, have restricted distributions and occur in small patches of preserved habitats. These plants are included into Red Lists, which are available throughout Europe (Schnittler & Gunther 1999), and show which plants are rare and which are vanishing. Red Lists have been routinely used for the evaluation of sites attractive from the point of view of nature conservation. However, they include hundreds of species, so that non-specialists may have difficulties to use them. Therefore, it would be useful to find out plant traits which correlate with rarity or plant decline, and which can easily be ascertained.

The relationship between rarity and distribution characteristics has been studied during the last decade all over the world (reviewed by Gaston 1994; Kunin & Gaston 1997). One of the basic findings is

that plant abundance is correlated over various scales so that a locally rare species is usually sparse also in the whole region (e.g. Hodgson 1986; Rapoport et al. 1986; Lahti et al. 1991).

In contrast, less attention has been paid to biological properties of plants associated with plant rarity. In spite of the effort the available results are still equivocal and often vary between habitats and taxonomic groups (Bevill & Louda 1999). However, there are a few generalisations which were proved repeatedly. For example, flowers of rare plants are often monomorphic, suggesting a breakdown of their incompatibility system, in contrast to their widespread congeners which are self-incompatible (Hamilton 1990; Orians 1997). Similarly, Gaston & Kunin (1997) claimed that common plants rely more often on outcrossing and sexual reproduction than their rare counterparts. Rare species are wind-pollinated less frequently than expected (Peat

& Fitter 1994) and zygomorphic flowers are over-represented among rare plants (Harper 1979). Dispersal ability of propagules produced by rare plants is rather restricted whereas widespread plants are armed with various structures promoting dispersal over longer distances. Seed size is also related to plant rarity. Rare species have often smaller seeds than common ones (Rabinowitz & Rapp 1981; Mitchley & Grubb 1986 but see Rees 1995 and Oakwood et al. 1993), and are competitively inferior (Mitchley & Grubb 1986; Miller & Werner 1987). Among prairie grasses Rabinowitz et al. (1989) found that common plants have temporally a more variable reproductive output than sparse plants. This reflects their ability to utilise limited precipitation more efficiently. Species of orchids which offer nectar to their pollinators tend to be common (Neiland & Wilcock 1998). In contrast, nectarless orchids are rare because their pollinators are not attracted by nectar rewards and their sexual reproduction therefore diminishes. Asexual vegetative multiplication cannot compensate for the unsuccessful generative reproduction in orchids because it is usually poor. These results show that several characters related to sexual reproduction correlate with plant rarity. Although some of the relationships were not supported in studies carried out in other regions or habitats, the observed pattern is in accord with predictions from population genetics of declining plants (Karron 1997).

All above findings are linked with sexual reproduction. Surprisingly little information is available about the relationship between rarity and vegetative plant traits. The idea that rare and threatened species rely on vegetative growth more than their commoner counterparts (Gaston & Kunin 1997) seems to be too gener-



Table 1. Definition of categories of threatened plants.

- A1. Extinct taxa. Taxa of which the occurrence in the area studied has not been confirmed for a very long period of time (sometimes for more than 100 years), further those not found in their well-known localities with unchanged biotopes at least for the past 50 years, and those with a narrow ecological amplitude extinct in their well-known localities due to a total environmental change even recently (new records of their native occurrence in the area studied are unlikely).
- A2. Missing taxa. Taxa probably extinct, as their occurrence in the area studied has not been confirmed during the past 25 years (in some cases a shorter period is considered), and those recorded a longer time ago, being particularly inconspicuous and therefore easily neglected (they might be found again).
- C1. Critically threatened taxa. Very rare and at the same time endangered plants occurring in only very few (1–5) localities in biotopes disappearing under the impact and sometimes also by natural causes; further taxa occurring in more than five localities, but with populations poor in individuals with a reduced vitality; finally taxa, the decline of which has reached to 10 (or less) per cent of the original state of their earlier presence, especially when the trend of their decline may be assumed to continue in the future.
- C2. Strongly threatened taxa: Taxa with an apparent and continued decline, demonstrated especially in recent time by a distinct decrease in number, extent and density of their local populations. The decline may reach up to 60% of the original state of their earlier presence or sometimes even more, but not necessarily in all populations. Also rare taxa (with 5–20 localities in the country) belong here.
- C3. Threatened taxa: Taxa with a somewhat weaker, but even demonstrable and continued decline in the whole country or at least in its part, appearing as a decrease of the extent of rich populations and extinction of poor ones. The decline may reach up to 20–50% of the original state of the earlier presence.
- D. Non-threatened plants (a category added for the purpose of this paper).

al and not valid in all environments. This does not necessarily mean that all sexually reproducing plants are common and clonal plants are rare.

Vegetative organs possess numerous traits which may potentially contribute to plant multiplication and spreading, whereby rarity can be avoided. For example, vegetative propagules are utilised for long-distance dispersal (turions and plant fragments in hydrophytes), clonal growth may play a significant role in competition and may promote long persistence in a spot (dense turf of some grasses). The negative effects of disturbance can be avoided by some clonal plants as their extensive clonal growth ensures that some ramets of a genet escape from the disturbed area. Thus, we may expect a relationship between clonal growth and plant rarity (Fiedler 1986) and it is of interest to search for plant traits shared by threatened plants. Out of the numerous potentially important vegetative traits we will concentrate on clonality of vascular plants. We restricted our analysis to the flora of Central Europe (Czech Republic and eastern part of Germany), an area with a predominantly temperate and moderately rich flora. Our aim was to find out whether unitary plants belong to threatened taxa more often than expected on a ran-

dom basis, in contrast to clonal plants, and whether any type of clonal growth includes an unexpectedly high number of rare plants. We may expect that the relationship between clonal growth and rarity is scale-dependent. Therefore, we used in our analysis three spatial scales, ranging from a local to two regional ones.

In this paper we first introduce our database of clonal growth of plants. Secondly, we describe our hierarchical classification of clonal growth of plants and thirdly, we focus on the scale-dependent relationship between plant rarity and clonal growth of vascular plants occurring in Central Europe.

■ Biological floras and plant databases

At present there are numerous biological and ecological floras and databases covering various aspects of plant life. Most of them have been published in the form of biological floras. However, only three of them are relatively comprehensive and include more than 200 species. The best known one is probably the Biological Flora of the British Isles, published since 1941 and currently including more than 250 species (see http://www.open.ac.uk/OU/Academic/Biology/J_Ecol/

JEBflora.htm for the list of species published until 1997; see also Poschod et al. 1996). The uncompleted monumental work by Kirchner et al. (1908–1936) covers more than 300 species and is more morphologically oriented than its English counterpart. The Biological Flora of the Moscow Region has been published since 1974 and includes at present 13 volumes with 213 species (Rabotnov 1974–; last volume 1997). It covers numerous species to a considerable depth, comparable to the Biological Flora of the British Isles. Other biological floras deal with considerably smaller number of species. The Biological Flora of Canadian Weeds includes about 100 species and is still being published (see Cavers & Mulligan 1972 for the first issue). The Comparative Plant Ecology by Grime et al. (1988) summarises extensive observational and experimental data on 281 species of herbaceous plants occurring in Great Britain (another 221 species are included in a "Tables of attributes"). The Biological Flora of Coastal Dunes and Wetlands has recently been initialised (Lonard & Judd 1997), similarly as a series on growth forms and life history of plants from the Hercynian region (Jäger et al. 1997; Jäger & Reckardt 1998; Hollaender & Jäger 1998). Finally, the Biological Flora of Central

Europe has been introduced by a bibliography of biological floras (Poschod et al. 1996) and first two issues have been published (Prati & Peintinger 2000; Weber 2000; see also Matthies & Poschod 2000). A wealth of information is available in the form of illustrations included in the third volume of Rothmaler's

"Exkursionsflora" (Rothmaler 1995) showing also underground structures of the plants, in general poorly covered by any biological flora, except for the monumental "Wurzelatlas" (Kutschera 1960; Kutschera & Lichtenegger 1982, 1992; Kutschera & Sobotik 1992, 1997; Lichtenegger et al. 1997).

In 1920s the phytosociological school was established in Europe. The detailed classification of plant communities, based on species composition, required a deep knowledge of the distribution of hundreds of plants along basic environmental gradients. This knowledge, based on field observations,

Table 2. The 31 types of clonal growth in vascular plants growing in Central Europe (modified from Klimeš et al. 1997: the 21 types of "CLO-PLA1" were kept, "special adaptations" (no. 21) were divided into seven types (21–27), newly added types are labelled "a"). We avoided vague terms, such as stolon, corm, layer and rootstock, which have very different meaning with individual authors. Rhizome means a stem growing below-ground or eventually growing at the soil surface and buried by litter, or pulled into the soil by contractile roots. Long-lived organs show senescence after more than 2 years, short-lived ones earlier.

- A. Root-derived organs of clonal growth (1–4)
 1. "*Trifolium pratense*" type. Main (tap) root of the primary root system without adventitious roots and buds. Clonal fragmentation possible in old plants only. Vegetative spreading is poor.
 2. "*Alliaria petiolata*" type. Main root of the primary root system with adventitious buds.
 3. "*Rumex acetosella*" type. Lateral roots of the primary root system or adventitious roots with adventitious buds.
 4. "*Ranunculus ficaria*" type. Root tubers (bearing buds of stem origin).
- B. Stem-derived organs of clonal growth (5–20a)
 - Ba. Long-lived stems (5–10)
 - Ba1. Stems growing above-ground (5)
 5. "*Lycopodium annotinum*" type. Creeping stems.
 - Ba2. Stems growing below-ground (6–10)
 6. "*Festuca ovina*" type. Epigeogenous rhizomes (= formed above-ground – Serebryakov & Serebryakova 1965). Turf graminoids.
 7. "*Rumex obtusifolius*" type. Epigeogenous rhizomes < 10 cm in length.
 8. "*Rumex alpinus*" type. Epigeogenous rhizomes > 10 cm in length.
 9. "*Dactylis glomerata*" type. Hypogeogenous rhizomes (= formed below-ground – Serebryakov & Serebryakova 1965) < 10 cm in length.
 10. "*Aegopodium podagraria*" type. Hypogeogenous rhizomes > 10 cm in length.
 - Bb. Short-lived stems (11–13)
 11. "*Fragaria vesca*" type. Plagiotropic above-ground stems specialised in spreading.
 12. "*Caltha palustris*" type. Epigeogenous rhizomes.
 13. "*Galium odoratum*" type. Hypogeogenous rhizomes.
 - Bc. Below-ground tubers (14–17a)
 14. "*Calystegia sepium*" type. Annual below-ground tubers on distal part of plagiotropic above-ground stems.
 15. "*Lycopus europaeus*" type. Annual below-ground tubers on distal part of rhizomes.
 - 15a. "*Adoxa moschatellina*" type. Annual below-ground tubers on distal part of rhizomes with thickened scale leaves or leaf bases.
 16. "*Corydalis solida*" type. Mother and daughter below-ground tubers annual and attached.
 - 16a. "*Colchicum autumnale*" type. Daughter tuber attached to the mother tuber; daughter tuber much smaller than the mother tuber.
 17. "*Corydalis cava*" type. A single perennial below-ground stem tuber. Clonal fragmentation possible in old plants only.
 - 17a. "*Bolboschoenus maritimus*" type. Perennial tubers on hypogeogenous rhizomes.
- Bd. Bulbs (18–20a)
 18. "*Galanthus nivalis*" type. Daughter bulb formed inside the mother bulb; daughter bulb of the same size as the mother bulb.
 19. "*Ornithogalum gussonei*" type. Daughter bulb formed inside the mother bulb; daughter bulb much smaller than the mother bulb.
 20. "*Tulipa sylvestris*" type. Bulb formed on distal part of a rhizome.
 - 20a. "*Allium montanum*" type. A rhizome preserved behind the bulb.
- C. Special adaptations (21–27)
 21. "*Polygonum viviparum*" type. Pseudovivipary.
 22. "*Cardamine pratensis*" type. Gemmipary (adventitious buds on leaves).
 23. "*Saxifraga bulbifera*" type. Axillary buds.
 24. "*Aldrovanda vesiculosa*" type. Turions.
 25. "*Lemna gibba*" type. Budding plants.
 26. "*Elodea canadensis*" type. Plant fragments.
 27. "*Butomus umbellatus*" type. Buds formed on rhizomes which may be detached.

has been summarised in numerous monographs with tabulated plant demands, using ordinal scales in most cases. The following list gives selected examples of tables with indicator values published for European countries and regions. Hungary: Borhidi (1995) and Zólyomi (1966), Russia: Tsyganov (1983) and Ramenskij (1956), the Netherlands: de Vries et al. (1957), Romania: Donita (1977) and Sanda (1983), Germany: Ellenberg et al. (1992) and Frank & Klotz (1988, 1990), Slovakia: Jurko (1990), Switzerland: Landolt (1977), Central Europe: Lindacher (1995; a compilation). Most of these tables include data on plant distribution along moisture, pH, and altitudinal gradients. However, the recent database by Frank & Klotz (1988, 1990) covers many more aspects of plant biology.

Besides there are several computerised databases accessible on the Web. The Botanical Database of the Netherlands includes 1781 species of vascular plants with > 40 variables concerning morphology, life history, reproduction and distribution in particular habitats (http://neon.vb.cbs.nl/sec_lmi_e/flofaufloveg/f44bbr00.htm). The Ecological Flora of the British Isles database (Fitter & Peat 1994) covers 1777 species of gymnosperms and angiosperms; 131 morphological and ecological features are included there (<http://www.bids.ac.uk/eco/flora.html>). Another database, containing 491 species and an extensive set of plant traits, has been compiled by Kleyer (1995; <http://www.agr.uni-rostock.de/landpl/landeco/biot.htm>).

Finally there are several databases on special aspects of plant biology, such as seed banks, diaspores, DNA contents, RGR, etc., which are beyond the scope of this paper (see also the contributions by Bakker et al., Jäger, and Bonn et al. in this volume).

However, not all aspects of plant biology are equally well represented in the biological floras and databases. Clonality, defined as plant growth resulting in potentially independent units, is one of the aspects treated rather marginally in the large plant databases mentioned above. So far three databases have been developed specifically for

clonal plants. "CLO-PLA1" (van Groenendael et al. 1996; Klimeš et al. 1997) is a database of types of clonal growth and includes 3079 species occurring in Central Europe. This database is now available on the Web (<http://www.butbn.cas.cz/klimes>). The second database is based on data from Estonian wooded meadows (Kull 1997) and contains quantitative data on clonal growth of 130 grassland species. The third database – "CLO-PLA2" – extends our previous database "CLO-PLA1" by including several more features of plant growth, extensive literature and figures (Klimeš & Klimešová 1999) (Table 2).

Plant rarity belongs to the variables often included into plant databases. Moreover, as geographical distribution and population size are usually well-known for threatened plants numerous red lists have been compiled which include virtually all rare plants in particular regions (see Köppel et al., this volume). These red lists use categories of threatened plants which usually combine several criteria: plant rarity (estimated as the number of localities in a region), population size and plant vitality, and observed or expected changes in the number of occupied localities. It would be useful to separate these variables but, unfortunately, the raw data from which plant threat was derived are usually not available. Moreover, threat and rarity are vague terms which have been defined by individual authors in various ways (e.g. Harper 1981; Rabinowitz 1981; Kunin & Gaston 1993; Gaston 1997; Vanauken 1997; Izco 1998) and are often even interchangeable. In this paper we follow the definitions of rarity given in the Red List of Plants of the Czech Republic (Holub 1999; Table 3), which were derived from the widely used

IUCN definitions (IUCN 1994). Rarity, as used in this paper, always refers to categories of threatened plants.

■ Clonal growth types

In Central Europe more than 70% of plants are capable of clonal growth (Klimeš et al. 1997). Generative reproduction plays a minor role in the short-term dynamics in many of them. However, the enormous diversity of clonal growth makes many ecological generalisations concerning clonal plants oversimplified because the contrasted morphology of growth forms necessarily results in very different functioning. For example, bulbils of *Saxifraga cernua* (plant names follow Ehrendorfer 1973) and stolons of *Potentilla anserina*, or root-suckers of *Robinia pseudoacacia* and tubers of *Ranunculus ficaria*, represent very different structures utilised for different purposes and in different situations. Therefore it is useful and desirable to consider plants using different types of clonal growth separately. To do this we need a classification of growth types of clonal plants.

Several attempts have been made to develop such a classification (e.g. Hartmann 1957; Lukaszewicz 1962; Leakey 1981). A common way of discriminating between types of clonal growth is based on a combination of criteria using morphology of organs related to plant and population growth. In our database the origin of the organ of clonal growth is considered first (stem, root, other). Secondly, the above- vs. below-ground position of growing tips producing daughter ramets at the time of their initiation (epi- vs. hypogeogenous origin) and the resulting position of the daughter

Table 3. Number of species included in the analyses. Percentage of species present in CLO-PLA is in brackets.

	No. of species
CLO-PLA	
Red list of vascular plants of the Czech Republic	3079 (100.0)
Flora of the Bílé Karpaty Mountains	1199 (90.8)
Red list of vascular plants of the Bílé Karpaty Mountains	1223 (99.3)
Species-rich meadows in the National Reserve of "Čertoryje"	152 (98.0)
	143 (100.0)

ramets with respect to the soil surface (above- vs. below-ground) are taken into account. Thirdly, thickening of the organs of clonal growth is used, as the structures often serve as storage organs (tubers, bulbs). Finally, the length and longevity of spacers between ramets is important as it determines how far the daughters may be dispersed, how much energy is required for this and how fast fragmentation of clones is.

Based on these characteristics a robust morphological classification of clonal plants has been obtained consisting of 31 hierarchically related types named after a typical representative and covering the clonal diversity in vascular plants of Central Europe (Klimeš & Klimešová 1999; Table 4). In the analysis presented here a single preferentially utilised type of clonal growth is considered for each species. In Central Europe the most abundant are the "*Rumex obtusifolius*" type (short epigeogenous rhizomes) representing 17.4% of vascular plants and the "*Aegopodium podagraria*" type (long hypogeogenous rhizomes) with 9.9%. All other types include less than 6% of plants of the central European flora. The rarest types of clonal growth are found among plants with some types of tubers ("*Calystegia sepium*" type) and bulbs ("*Tulipa sylvestris*" type), represented each by less than 10 species in Central Europe (Klimeš et al. 1997; Klimešová & Klimeš 1997).

■ Plant rarity and clonal growth

We studied the relationship between plant rarity and clonal growth at three spatial scales - one local and two regional. For the largest scale we used all plants of the database CLO-PLA1 and the Red List of Vascular Plants of the Czech Republic (Holub 1999) as an estimate of plant rarity in Central Europe. At the medium scale we utilised the Check-list of Vascular Plants of the Bílé Karpaty Mts. (Jongepier & Jongepierová 1999a) and the Red List of Vascular Plants of the Bílé Karpaty Mts. (Jongepier & Jongepierová 1999b). For the

small (local) scale we used data from the National Nature Reserve of "Čertoryje" in the Bílé Karpaty Mts. We restricted our analysis to species-rich grasslands, where 143 plant species have been recorded (Klimes et al. 2000). Instead of a red list we used cover estimates from 75 plots, 1 m² in size each as a measure of plant rarity (unpublished data). Plant rarity was estimated using frequency in 75 plots, 1 m² each. Species present in ≤10 plots were considered rare (A), in >20 plots common (D) and the remaining species were placed into category C. As results from analyses based on plant cover gave very similar results, we present here only the results based on species frequency. The total number of species used in the analyses are given in Tables 3 and 4.

The first hypothesis to be tested was that the ratio between the number of species belonging to individual growth types is the same for rare and common plants. This would indicate that rare plants are not under- nor over-represented in any of the types of clonal growth. For extinct plants (A1) and critically

threatened plants (C1) the hypothesis was rejected at both regional scales (Table 5). Similarly, for strongly threatened plants of the Czech Republic (C2) and strongly threatened plants lumped with threatened plants in the Bílé Karpaty Mts. (C2+C3) the difference between observed and the expected ratio was significant. However, at the largest scale threatened plants were represented in individual clonal growth types in the same ratio as expected, and for unclear cases ("missing" - A2) we failed to reject the null hypothesis at both scales (Table 5). At the smallest scale the ratio between the number of plants belonging to individual growth types was the same for rare and common plants ($P > 0.1$; χ^2 -test).

These results show that (1) plant rarity depends to some extent on the type of clonal growth, and (2) the relationship between clonality and rarity is scale-dependent. Therefore, it is of interest which clonal growth types are over-represented among threatened plants. For this analysis we lumped categories A1 and A2, and C1 to C3. The

Table 4. Number of species in the Red Lists of the Czech Republic and the Bílé Karpaty Mts., and percentage of these species represented in CLO-PLA (in brackets).

Category	Czech Republic	Bílé Karpaty Mountains
A1	64 (98.4)	26 (100.0)
A2	41 (80.5)	37 (94.6)
C1	427 (84.1)	49 (95.9)
C2	354 (95.2)	41 (100.0)
C3	313 (94.9)	
Totals	1199 (90.8)	151 (98.7)

Table 5. Representation of plants in individual types of growth types calculated for individual categories of plant threat. The observed ratio was compared with the expected one, based on all species not belonging to the category for which the test was calculated. A significant result indicates that plants belonging to a particular category of threat are not represented among types of clonal growth in the same ratio as plants belonging to other categories of threat. Tested by χ^2 .

		Czech Republic	Bílé Karpaty Mountains
Extinct	A1	***	*
Missing	A2	n.s.	n.s.
Critically threatened	C1	***	***
Strongly threatened	C2	***	***
Threatened	C3	(*)	

(*) - $0.05 < P < 0.1$, * - $P < 0.05$, *** - $P < 0.001$

Table 6. Representation of plants belonging to individual categories of threatened plants and non-threatened plants in plants with particular clonal growth types. obs – observed number of species, exp – expected number of species, based on the proportion calculated from all species except those belonging to the tested category. A – “extinct” (A1) and “missing” (A2) plants, C – threatened plants (C1+C2+C3), D – non-threatened plants, see Table 1 for definitions. Types of clonal growth are explained in Table 2.

No.	Type of clonal growth	obs			exp			
		A	C	D	A	C	D	P

A. Czech Republic. Results for types of clonal growth represented by <10 species are not shown.

1	" <i>Trifolium pratense</i> "	4	70	116	6	61	123	n.s.
2	" <i>Alliaria petiolata</i> "	1	9	12	1	7	14	n.s.
3	" <i>Rumex acetosella</i> "	1	18	37	2	18	36	n.s.
4	" <i>Ranunculus ficaria</i> "	5	32	9	1	15	30	***
5	" <i>Lycopodium annotinum</i> "	2	19	39	2	19	39	n.s.
6	" <i>Festuca ovina</i> "	0	42	94	4	44	88	(*)
7	" <i>Rumex obtusifolius</i> "	9	160	331	17	161	322	n.s.
8	" <i>Rumex alpinus</i> "	3	25	70	3	32	63	n.s.
9	" <i>Dactylis glomerata</i> "	2	60	85	5	47	96	*
10	" <i>Aegopodium podagraria</i> "	7	89	188	9	92	183	n.s.
11	" <i>Fragaria vesca</i> "	4	33	61	3	31	64	n.s.
12	" <i>Caltha palustris</i> "	3	18	52	2	24	47	n.s.
13	" <i>Galium odoratum</i> "	2	30	66	3	32	63	n.s.
15	" <i>Lycopus europaeus</i> "	0	1	14	0	5	10	(*)
16	" <i>Corydalis solida</i> "	0	14	11	1	8	16	*
18	" <i>Galanthus nivalis</i> "	1	26	30	2	18	37	(*)
20a	" <i>Allium montanum</i> "	0	6	7	0	4	8	n.s.
24	" <i>Aldrovanda vesiculosa</i> "	3	11	9	1	7	15	**
	Annuals, biennials	46	232	545	18	277	528	***
	Trees	0	17	74	3	30	58	**
	Shrubs	2	74	119	6	62	127	(*)

(*) – 0.05 < P < 0.1, * – P < 0.05, ** – P < 0.01, *** – P < 0.001

B. Bílé Karpaty Mts. Results for types of clonal growth represented by <10 species are not shown.

1	<i>Trifolium pratense</i>	4	1	57	3	4	55	n.s.
2	<i>Alliaria petiolata</i>	2	2	9	1	1	12	(*)
3	<i>Rumex acetosella</i>	0	4	34	2	2	34	n.s.
4	<i>Ranunculus ficaria</i>	5	10	27	2	2	38	***
5	<i>Lycopodium annotinum</i>	0	0	12	1	1	11	n.s.
6	<i>Festuca ovina</i>	4	2	46	2	3	46	n.s.
7	<i>Rumex obtusifolius</i>	9	10	167	8	12	165	n.s.
8	<i>Rumex alpinus</i>	2	1	42	2	3	40	n.s.
9	<i>Dactylis glomerata</i>	1	3	63	3	4	59	n.s.
10	<i>Aegopodium podagraria</i>	7	6	138	7	10	134	n.s.
11	<i>Fragaria vesca</i>	2	1	31	2	2	30	n.s.
12	<i>Caltha palustris</i>	2	3	35	2	3	36	n.s.
13	<i>Galium odoratum</i>	4	3	53	3	4	53	n.s.
16	<i>Corydalis solida</i>	1	1	9	0	1	10	n.s.
18	<i>Galanthus nivalis</i>	0	1	19	1	1	18	n.s.
	Annuals, biennials	18	37	351	18	22	366	**
	Trees	0	1	51	2	3	46	(*)
	Shrubs	0	2	45	2	3	42	n.s.

(*) – 0.05 < P < 0.1, ** – P < 0.01, *** – P < 0.001

C. Čertoryje National Nature Reserve – species-rich meadows. Results for types of clonal growth represented by <5 species are not shown.

1	<i>Trifolium pratense</i>	8	4	1	7	3	4	n.s.
6	<i>Festuca ovina</i>	2	5	3	5	2	3	(*)
7	<i>Rumex obtusifolius</i>	11	7	19	20	9	8	***
8	<i>Rumex alpinus</i>	3	1	1	3	1	1	n.s.
9	<i>Dactylis glomerata</i>	4	3	4	5	3	3	n.s.
10	<i>Aegopodium podagraria</i>	12	6	6	11	5	7	n.s.
	Annuals, biennials	9	2	1	5	3	4	(*)

(*) – 0.05 < P < 0.1, * – P < 0.05, *** – P < 0.001

results show that at the largest scale the ratio between the number of plants belonging to individual categories of threat did not differ from expected ones for most clonal growth types (Table 6A). Only three clonal growth types were significantly over-represented among rare plants. These were plants with root tubers ("*Ranunculus ficaria*" type), plants with attached annual mother and daughter tubers ("*Corydalis solida*" type) and plants producing turions ("*Aldrovanda vesiculosa*" type). In contrast, plants with short hypogaeous rhizomes ("*Dactylis glomerata*" type) and trees were over-represented among widespread plants (category D). Annuals showed an interesting pattern - they were over-represented among extinct and "missing" plants (A) and under-represented among threatened species (C).

At the medium scale the above result for plants with root tubers ("*Ranunculus ficaria*" type) was confirmed (Table 6B), whereas annuals were over-represented among threatened species, in contrast to the large scale results. All other ratios corresponded to the expected ones. Due to the low number of species the results were less significant also at the small scale (Table 6C). Interestingly, one strongly significant result was obtained at the small scale for a growth type different from those for which the relationship was significant at larger scales - plants with short epigeogenous rhizomes ("*Rumex obtusifolius*" type) were over-represented among widespread species (category D).

■ Discussion

We found that plant rarity is associated with certain clonal growth types more often than expected on a random basis. However, this relationship was not too strong in most cases and was scale-dependent to some extent. For example, plants with short epigeogenous rhizomes ("*Rumex obtusifolius*" type) were over-represented among common plants growing at a local scale (Table 6C) but at the two larger scales this relationship was not

confirmed. The differences between the results obtained for the two larger scales were small and can be explained by the differences in the power of the tests due to the different number of species. The contrasted results between small and larger scales indicate that processes determining plant rarity may differ at different scales. At larger scales the plants which are endangered may suffer from changes in their habitats which are becoming fragmented, small, isolated and often eutrophicated. This results in a continuous decline of some species and spreading of other ones, pre-adapted to the new prevailing conditions. For the local scale we selected an area which is relatively well preserved and not under serious impact of airborne or water pollution. Moreover, the abiotic conditions are relatively homogeneous there. Rarity in this area could partly be a natural phenomenon (not all plants can be equally abundant), partly it may result from a long-term pressure of mowing which selectively suppresses some plants, together with complicated biotic interactions which include both facilitation and competition among individual plants. While rarity at regional scales correlates with categories of threat in most cases, at the local scale these two variables need not be associated. Some plants are more rare than others but they need not decline or become extinct. Therefore, the observed differences between the local and regional scales is not surprising and could be expected.

Clonal growth types are categories defined by a number of correlated plant traits. Morphological peculiarities of plants are always associated with developmental ones and also with physiological characteristics determining plant behaviour under very different conditions (Klimeš et al. 1997). Plant traits determining clonal growth types form a complex syndrome of covarying characteristics. One or several of them can affect plant rarity. Thus, not the clonal type itself, but some of the characteristics defining it or associated with it could be important and determine plant rarity. Moreover, under different conditions the cru-

cial decisive trait may differ. The significant over-representation of plants with root tubers among rare and threatened plants at regional scales may serve as an example. Most plants belonging to clonal plants with root tubers are orchids. These were over-represented among rare plants at regional scales. Orchids share a number of characteristics which are unique to this family or uncommon in other plants (Wells 1981). For example, most genera of orchids belonging to this type have their centre of diversity in the Mediterranean and are adapted to a different climate. They grow vigorously in spring and finish their reproductive period rather early. After mowing, most of them remain suppressed or even do not re-appear above the soil surface. Therefore, they do not utilise the whole vegetation season efficiently and can be suppressed by plants utilising the available resources better.

Another interesting feature of this group of orchids concerns their clonal growth. Their tuber is annual and in contrast to most other clonal plants one plant rarely vegetatively produces more than one descendant. This is a consequence of the very limited bud bank. At the shoot base two to four axillary buds are formed, one of which is enlarged and predetermined for spring growth. The other ones die at the end of the vegetation season together with the mother shoot and its tuber. Exceptionally two buds are utilised (Ziegenspeck 1936), but in any case the limited bud bank and poor vegetative multiplication are risky because any disturbance or enemy may kill the whole genet if a single or two small buds are damaged. Similarly, even if a not so seriously limited by bud bank, plants belonging to the "*Corydalis solida*" type were also significantly over-represented among threatened plants. The third group of clonal plants over-represented among threatened plants includes species which multiply by turions ("*Aldrovanda vesiculosa*" type). The decline of many plants belonging to this type is likely caused by their exclusive demands for oligotrophic watersheds which are becoming rare in the whole of Central

Europe due to eutrophication. Therefore, a lack of suitable habitats rather than an inefficient clonal multiplication seems to be responsible for the decline of plants belonging to this type.

The above results indicate that not the type of clonal growth itself but other traits associated with it may be responsible for the decline of plants belonging to plants with root tubers, shoot tubers and turions. Moreover, there is another alternative explanation which is more parsimonious and should be considered first. As a result of phylogenetic constraints the plants belonging to a monophyletic clade share more traits than expected on a random basis. Consequently, their traits may be inherited from their common ancestor rather than represent an adaptation to certain environmental conditions. Therefore, the traits correlated across species and not corrected for phylogeny should not be interpreted as adaptive (Harvey & Pagel 1991; Harvey et al. 1995). Before testing for adaptiveness of particular combinations of plant traits the phylogenetic effects should be removed. The patterns presented by us are real but their evolutionary interpretation is insecure. Unfortunately, there are very few examples of analyses of the relationship between plant traits and rarity which account for phylogenetic relationships among plants (but see Kelly & Woodward 1996). On the other hand, the phylogenetic constraints do not change the fact that special attention should be paid to certain groups of clonal plants because they have a tendency to disappear from our landscapes.

■ Summary

The traits so far reported as associated with plant rarity or categories of plant threat are usually linked with sexual reproduction. However, the functioning of vegetative traits suggests that some of them may also be associated with plant rarity. We studied this idea at three spatial scales, ranging from local to regional. The hypothesis that rare plants are distributed among types of clonal growth types in the same way as

common plants was rejected. Plants with root tubers were over-represented among extinct and threatened taxa at the regional scales. At the largest scale plants with short hypogaeous rhizomes were under-represented among extinct and over-represented among threatened plants. Plants with shoot tubers and turions were over-represented among them. Results obtained at the local scale were different. Plants with short epigeous rhizomes were over-represented among rare plants. It is suggested that the type of clonal growth itself need not be responsible for plant rarity because it includes a number of covarying traits.

■ Zusammenfassung

Seltenheit von Pflanzen und Art des klonalen Wachstum – die biologischen Merkmale, die bisher mit der Seltenheit oder den Gefährdungskategorien von Pflanzen in Verbindung gebracht wurden, beziehen sich gewöhnlich auf die sexuelle Reproduktion. Es liegt jedoch nahe, daß auch die Funktion einiger Merkmale der vegetativen Reproduktion Einfluß auf die Seltenheit hat. Wir untersuchten diesen Gedanken in drei räumlichen Maßstäben (lokal bis regional). Die Hypothese, daß seltene Pflanzen in der gleichen Weise auf die Typen des klonalen Wachstums verteilt sind wie häufige, wurde abgelehnt. Im regionalen Maßstab sind Pflanzen mit Wurzelknollen unter den ausgestorbenen und gefährdeten Taxa überrepräsentiert. Pflanzen mit kurzen unterirdischen Rhizomen sind innerhalb der gefährdeten Arten überrepräsentiert und innerhalb der ausgestorbenen Arten unterrepräsentiert. Pflanzen mit Sproßknollen und Turionen sind innerhalb der gefährdeten Arten überrepräsentiert. Die Ergebnisse im lokalen Maßstab weichen davon ab. Pflanzen mit kurzen epigeogenen Rhizomen sind unter den seltenen Pflanzen überrepräsentiert. Die Art des klonalen Wachstums muß nicht selbst für die Seltenheit der Pflanzen verantwortlich sein, da die Varianz einiger anderer Merkmale damit verbunden ist.

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