

# CLONAL PLANT ARCHITECTURE: A COMPARATIVE ANALYSIS OF FORM AND FUNCTION

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## Introduction

One of the tacit assumptions in many ecological theories about vascular plants is that plants are non-clonal organisms, separated both physiologically and physically from their conspecific neighbours. However, in most environments plants with inter-connected modules play an important role in community and ecosystem processes (Schmid 1990; Oborny and Bartha 1995). For example, large tundra areas are dominated by clonally propagating graminoids like *Eriophorum* spp. (Callaghan *et al.* 1992a), the ten most abundant plant species covering 19% of Britain are clonal (Bunce and Barr 1988). Mangroves consist of several shrub species with extensive vegetative growth and grasslands over the world are formed mainly by species that form tussocks of numerous inter-connected shoots and by rhizomatous species with long below-ground stems (Walter and Breckle 1986-1991). Thus, to understand the dynamics of many plant populations and most plant communities the clonal nature of species should be considered.

Clonal growth (vegetative multiplication) results in the production of new, genetically identical descendants (ramets) with the potential to become independent of the mother organism. It has been repeatedly documented that clonal growth brings about benefits (resource acquisition, successful establishment of offspring in new environments, risk aversion for the genet) as well as costs (transmission of diseases, a decrease of resources available for sexual reproduction) to the plant (Jackson *et al.* 1985; van Groenendael and de Kroon 1990a; Callaghan *et al.* 1992b; Soukupová *et al.* 1994; Oborny and Podani 1996). The costs and benefits of clonal growth have been related to a number of clonal growth strategies, but a straightforward analysis of the relationship between growth form and its function is hampered by the fact that homologous clonal organs may have different functions, and that different organs often have a similar function in the clonal growth of different species (analogous organs) (Foster and Clifford 1959; Huber 1996). Roots with adventitious buds in *Rumex acetosella* agg. and root tubers of *Ranunculus ficaria* are examples of homologous organs with different functions, long



below-ground spacers of stem origin in *Aegopodium podagraria* and of root origin in *Epilobium angustifolium* are analogous organs that have a similar function.

During the evolution of vascular plants there is an apparent trend of diversification and increasing specialisation of clonal growth forms following geographical isolation of taxa and climatic changes on all continents since the late tertiary (Tiffney and Niklas 1985; Mogie and Hutchings 1990; Kremer and van Andel 1995). Species belonging to different phylogenetic lineages had to adapt to 'abrupt' environmental changes which either induced or suppressed clonality. Presumably, numerous changes between non-clonal and clonal growth have occurred during the evolution of the Angiosperms (van Groenendael *et al.* 1996). As a result, plants using similar modes of clonal growth can be found in different habitats but also plants with different modes of clonal growth can be found together in the same habitat. The pertinent ecological question is whether the observed distribution of the trait-environment relationship reflects an ecological adaptation to individual habitats that can help us interpret the evolution of clonality.

The evolutionary process can rarely be described as a radiation resulting in the simultaneous splitting of one taxon into several or many descendant taxa. Instead, cladogenesis or successive splitting from a mother taxon is a model to which the contemporary knowledge fits the best (Donoghue and Doyle 1989). Therefore, any pattern of species characteristics like patterns in clonal growth in a group of species can be the result of selective forces operating against maladapted individuals in these species but also of a shared phylogenetic history of a particular taxon which constrains the evolutionary development. Thus, species used in comparative studies should not be considered as independent items but their phylogenetic relations should be taken into account (Felsenstein 1985; Harvey *et al.* 1995).

Our aims are (1) to present an overview of the diversity of clonal growth forms in the central European flora and (2) to relate these growth forms to other plant traits, such as dispersal mechanism and pollination type, (3) to quantify their distribution over habitat types and plant communities and (4) to contrast the pattern found at the family level with the level of the species using a species-rich genus of *Rumex* as an example. These comparisons have been made within the frame of contemporary knowledge of phylogenetic relationships between the individual taxa in the database that we used. The resulting patterns will be discussed in the light of existing expectations about the distribution of clonal growth forms. Given the importance of the phylogenetic heritage for the relations between clonal traits and the environment, the discussion of the results will be preceded by a brief review of the possible avenues of the evolution of clonality in vascular plants.

### The database

To have a homophyletic and species-rich group we have chosen vascular plants. For this purpose we selected the well-known flora of central Europe.

We built up a database containing about 2760 species. We included all species occurring in former East Germany (Frank and Klotz 1990–2208 species) and added the species found in our database of vegetation units (see below) and the species occurring in central Europe which the first two authors have experience with from the field. The database contains plant names, Ellenberg indicator values (Ellenberg 1979), data on dispersal, pollination and degree of human disturbance (Frank and Klotz 1990). The data on clonal growth are based on our own experience and on an extensive literature survey. These data include the origin of the clonal connection, the distance between ramets, the longevity of the connection, the frequency of clonal growth events, as well information on the function of clonal organs, such as storage, anchorage, together forming a classification system for clonal growth forms (Fig. 1 and Appendix). The basic reference sources were Velenovský (1905–1913), Kirchner *et al.* (1908–1936), Rauh (1937), Troll (1937–1942), Lukaszewicz (1962), Rabotnov (1974–), Rothmaler (1987), Kutcher and Lichtenegger (1982–1992), Sculthorpe (1985), Smirnova (1987) and Rysin and Rysina (1987). All species which may show clonal growth are considered as clonal species. From our analysis we excluded all types of agamospermy, *i.e.*, production of fertile seeds in the absence of sexual fusion between gametes (Richards 1990). Thus, we restrict our presentation to species with vegetative multiplication. The database of vegetation types is based on comprehensive 4-volume work by Oberdorfer *et al.* (1977–1992) where a description of vegetation types based on floristic criteria is presented for Southern Germany. To reduce the amount of data we selected a single, most common vegetation type to represent each 'alliance', which comprises a group of vegetation types occurring in similar habitats. The selection consists of 112 vegetation types roughly covering the diversity in the vegetation of south Germany. Most of them are distributed over large areas of temperate Europe. Each type is characterised by frequencies of plant species. These frequencies are based on the occurrence of 1726 species in 20761 plots used for the description of the 112 vegetation types.

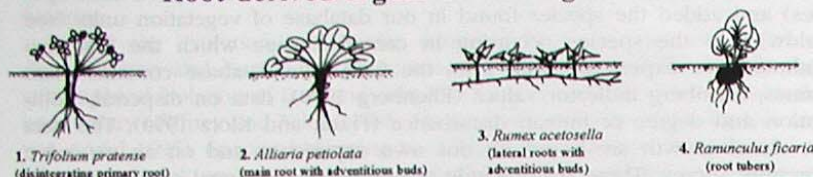
The overall pattern present in the species of the central European flora, belonging to a great number of families, is contrasted with a global pattern at the level of species belonging to one genus. We chose the genus of *Rumex*. Its species inhabit various environments on all continents except Antarctica. The genus of *Rumex* includes nearly 200 species and is represented by 21 species in central Europe. Using our field data, literature and herbarium sheets (Lund, Sweden) we assessed clonal growth in about 140 species of the genus.

### How common is clonal growth?

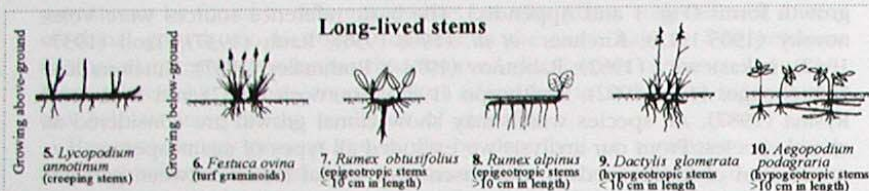
There are only few estimates of how common clonal species really are, both in terms of frequency in flora's as in terms of cover-abundance in the field. Clegg (1978, cited in Leakey 1981) estimated that 28% of the dicotyledonous species have some form of vegetative regeneration. Söyrinki (1938) found



### Root-derived organs of clonal growth



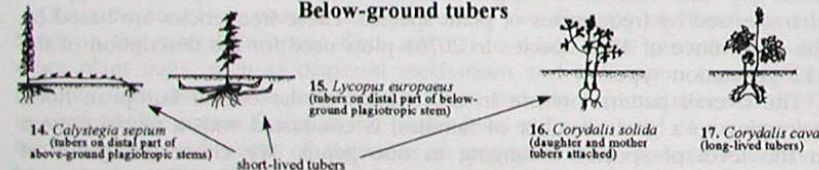
### Stem-derived organs of clonal growth



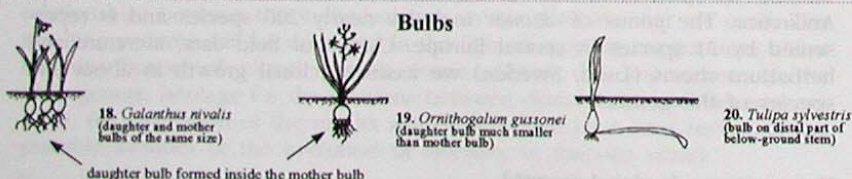
#### Short-lived stems



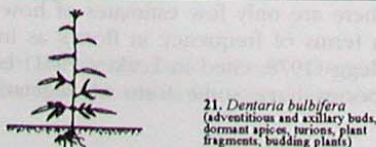
#### Below-ground tubers



#### Bulbs



### Special adaptations



that 45 % of the species possessed means for vegetative multiplication in a Finnish birch tundra. Perttunen (1941) estimated the proportion of clonal plants in the boreal taiga at 80% and Salisbury (1942) gives an estimate of 46 % of all angiosperms in temperate Great Britain as being clonal. Prach and Pyšek (1994) calculated the mean cover of clonal plants in 15 successional series starting on bare soil and found values from 67 % cover for clonal plants up to maximum values close to 100 %. Unfortunately, these estimates of the commonness of clonal growth are difficult to compare as the definition of clonality differs widely among individual authors. Moreover, some estimates are based on frequencies of species, others on percentage of plant cover.

To evaluate the role of clonal growth in the flora of central Europe we further analysed the data from our database. Out of the 2760 species included into the database nearly 2000 (66.5%) may form potentially independent daughter plants (Table 1). This estimate is close to that by van Groenendael and de Kroon (1990b) for the temperate zone (70%). Considering species frequency in the 112 plant communities, based on presence/absence data, we get at an even higher estimate (79.3%). It means that in central Europe at a scale of ca. 1 to 200 m<sup>2</sup>, the scale at which species composition of plant communities is described, the frequency of clonal plants in plant communities exceeds the frequency of non-clonals. If we consider even smaller scales, the proportion of clonal plant species further increases. In species-rich meadows in the Biele Karpaty Mountains there are 70 species of vascular plants per 2.25 m<sup>2</sup> (Klimeš 1995). Of these 80% are clonal. At a scale of 0.0025 m<sup>2</sup>, the proportion of clonal plant species further increases to 94.0 % and at the level of individual plant shoots it reaches 97.0 % in these meadows. Similar trends can be expected in virtually all types of grasslands as they are dominated by turf or rhizomatous graminoids with extensive clonal growth (Walter and Breckle 1986-1991).

### Comparative analysis

Any search for patterns between traits or in trait-environment relationships based on comparisons between species such as the ones proposed must exclude the possibility that the patterns are biased as a result of underlying phylogenetic relationships. The closer taxa are related the more likely they will share certain traits independent from the environmental conditions (Felsenstein 1985; van Groenendael *et al.* 1996). This was tested by comparing trait-trait or trait-environment relationships based on individual species with the same relationship at the level of the family. If the relationship is maintained at the family level there is reason to expect a phylogenetic rather than an ecological basis for the pattern found. Mean family values for traits

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Fig. 1. The diversity of clonal growth modes in central Europe and its classification based on the origin, placement and persistence of clonal growth organs. Typical representatives are given. For a detailed description of the types see Appendix.



Table 1. Frequency of types of clonal growth in the central European flora and vegetation. Species combining several modes of clonal growth were counted separately for each type. Therefore, the totals for species (2932) are slightly higher than the number of the species in the database (2760). The participation of clonal growth types in vegetation was estimated as follows:

$$SF_k = \sum_{i=1}^{2760} \sum_{j=1}^{112} f_{ijk}$$
 where  $SF_k$  is participation of the  $k$ th clonal growth type in vegetation and  $f_{ijk}$  is frequency of species  $i$  belonging to the  $k$ th clonal growth type in community  $j$  (based on Oberdorfer et al. 1977-1992).

No.	Clonal growth type	No. of species	%	Ranking (species)	SF	%	Ranking (SF)
1	<i>Trifolium pratense</i>	155	5.29	3	9072	4.47	6
2	<i>Alliaria petiolata</i>	44	1.50	13	3813	1.88	13
3	<i>Rumex acetosella</i>	51	1.74	12	5840	2.88	10
4	<i>Ranunculus ficaria</i>	37	1.26	14	1015	0.50	15
5	<i>Lycopodium annotinum</i>	75	2.56	10	6274	3.09	9
6	<i>Festuca ovina</i>	134	4.57	5	14795	7.29	3
7	<i>Rumex obtusifolius</i>	510	17.39	1	40341	19.87	1
8	<i>Rumex alpinus</i>	86	2.93	7	7753	3.82	7
9	<i>Dactylis glomerata</i>	98	3.34	6	10238	5.04	5
10	<i>Aegopodium podagraria</i>	289	9.86	2	26938	13.27	2
11	<i>Fragaria vesca</i>	148	5.05	4	14037	6.91	4
12	<i>Caltha palustris</i>	57	1.94	11	7552	3.72	8
13	<i>Galium odoratum</i>	83	2.83	8	5109	2.52	11
14	<i>Calystegia sepium</i>	4	0.14	21	416	0.20	18
15	<i>Lycopus europaeus</i>	20	0.68	17	991	0.49	16
16	<i>Corydalis solida</i>	25	0.85	15	1049	0.52	14
17	<i>Corydalis cava</i>	7	0.24	19	43	0.02	21
18	<i>Galanthus nivalis</i>	18	0.61	18	192	0.09	20
19	<i>Ornithogalum gussonei</i>	24	0.82	16	637	0.31	17
20	<i>Tulipa sylvestris</i>	7	0.24	20	251	0.12	19
21	<i>Dentaria bulbifera</i>	79	2.69	9	4669	2.30	12
Non-clonal species		981	33.46		42040	20.70	
Clonal species		1951	66.54		161025	79.30	
SUM		2932	100		203065	100	

or habitat preferences were calculated from the database. To reduce the bias caused by a low number of species in some families, only those families containing 5 and more species were considered.

The position of each species within a phylogenetic tree of plant families was determined using one randomly selected tree from Chase *et al.* (1993), see van Groenendael *et al.* (1996) for details. A phylogenetic tree based on cladistic or molecular approaches is not available for *Rumex*. Therefore we used the current taxonomic classification of the genus (Borodina 1979; Löve 1944; Löve and Kapoor 1967; den Nijs 1984; Rechinger 1937, 1949a,b, 1954, 1984, 1990) to correct for possible phylogenetic bias while exploring the

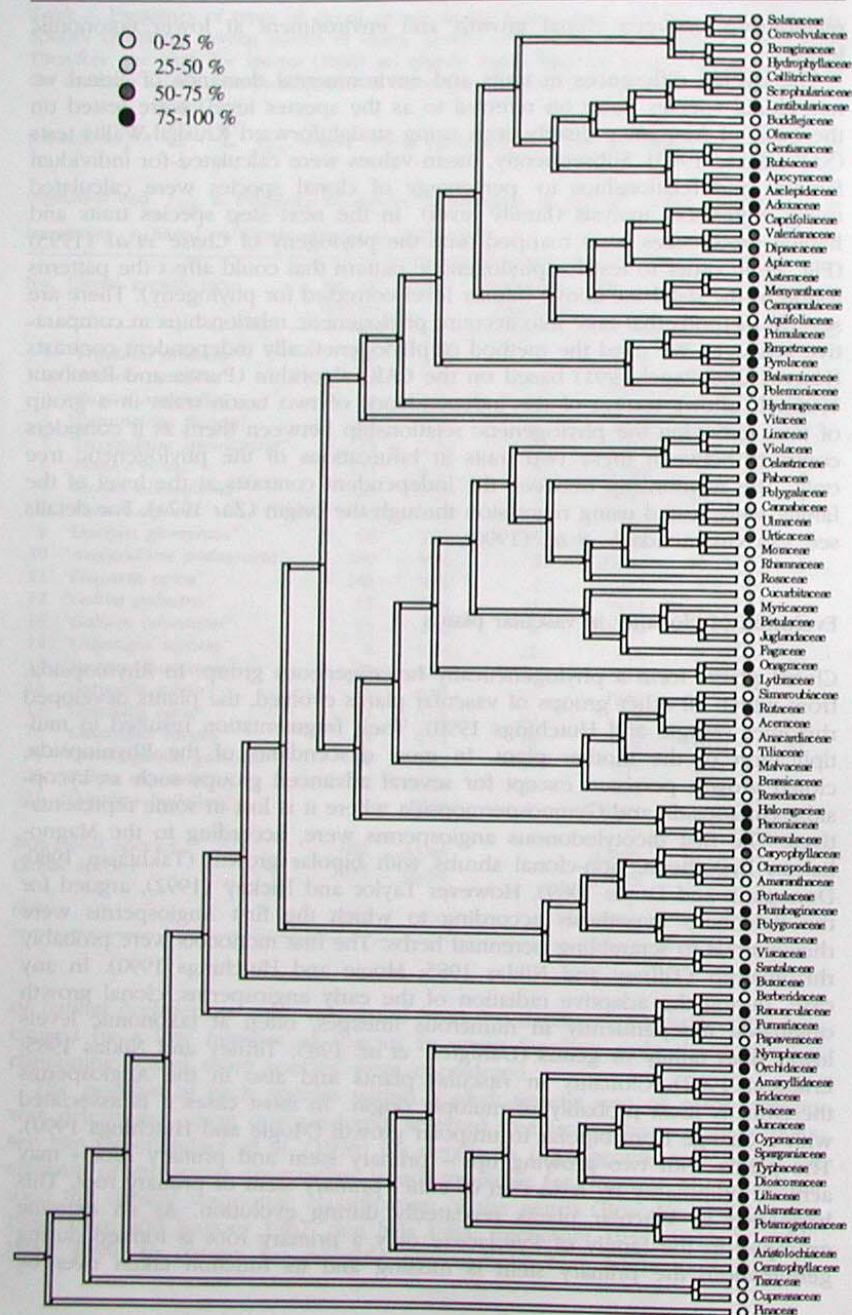
relationship between clonal growth and environment at lower taxonomic levels.

The overall differences in traits and environmental demands of clonal vs. non-clonal species (later on referred to as the species level) were tested on the basis of frequency distributions using straightforward Kruskal-Wallis tests (SAS release 1990). Subsequently, mean values were calculated for individual families and relationships to percentage of clonal species were calculated using regression analysis (family level). In the next step species traits and habitat preferences were mapped onto the phylogeny of Chase *et al.* (1993) (Fig. 2), in order to test for phylogenetic pattern that could affect the patterns found in the database above (family level corrected for phylogeny). There are several methods that take into account phylogenetic relationships in comparative analyses. We used the method of phylogenetically independent contrasts (Harvey and Pagel 1991) based on the CAIC algorithm (Purvis and Rambaut 1995). It allows testing of the independence of two taxon traits in a group of taxa removing the phylogenetic relationship between them as it considers contrasts between these two traits at bifurcations of the phylogenetic tree only. The relationship between the independent contrasts at the level of the family were tested using regression through the origin (Zar 1974). For details see van Groenendael *et al.* (1996).

#### Evolution of clonality in vascular plants

Clonal plants form a phylogenetically heterogeneous group. In Rhyniopsida, from which all other groups of vascular plants evolved, the plants developed rhizomes (Mogie and Hutchings 1990). Their fragmentation resulted in multiplication of the mother plant. In most descendants of the Rhyniopsida, clonal growth persisted except for several advanced groups such as Lycopsidea, Gnetopsida and Gymnospermopsida where it is lost in some representatives. The first dicotyledonous angiosperms were, according to the Magnoliaean hypothesis, non-clonal shrubs with bipolar growth (Takhtajan 1980; Donoghue and Doyle 1989). However Taylor and Hickey (1992), argued for the Paleoherb hypothesis according to which the first Angiosperms were rhizomatous to scrambling perennial herbs. The first monocots were probably rhizomatous (Tiffney and Niklas 1985; Mogie and Hutchings 1990). In any case, during the adaptive radiation of the early angiosperms, clonal growth originated independently in numerous lineages, often at taxonomic levels lower than family or genus (Dahlgren *et al.* 1985; Tiffney and Niklas 1985; Eriksson 1992). Clonality in vascular plants and also in the Angiosperms therefore is most probably of multiple origin. In most cases it is associated with a change from bipolar to unipolar growth (Mogie and Hutchings 1990). The plants with two growing tips – primary stem and primary root – may achieve unipolarity by reduction of either primary stem or primary root. This happened in vascular plants repeatedly during evolution. As an extreme example, in the family of Pyrolaceae only a primary root is formed during germination; the primary stem is missing and its function taken over by





secondary stems developing on the root system (Rauh 1937). Primary stems in Orobanchaceae and Monotropaceae develop as a crippled hypocotyl and do not grow above the soil surface (Rauh 1937). Note that Pyrolaceae, Monotropaceae and Orobanchaceae (related to Scrophulariaceae) belong to different clades in the phylogenetic tree (Fig. 2). Therefore, the extreme reduction to unipolar growth appeared repeatedly and independently during the evolution of angiosperms.

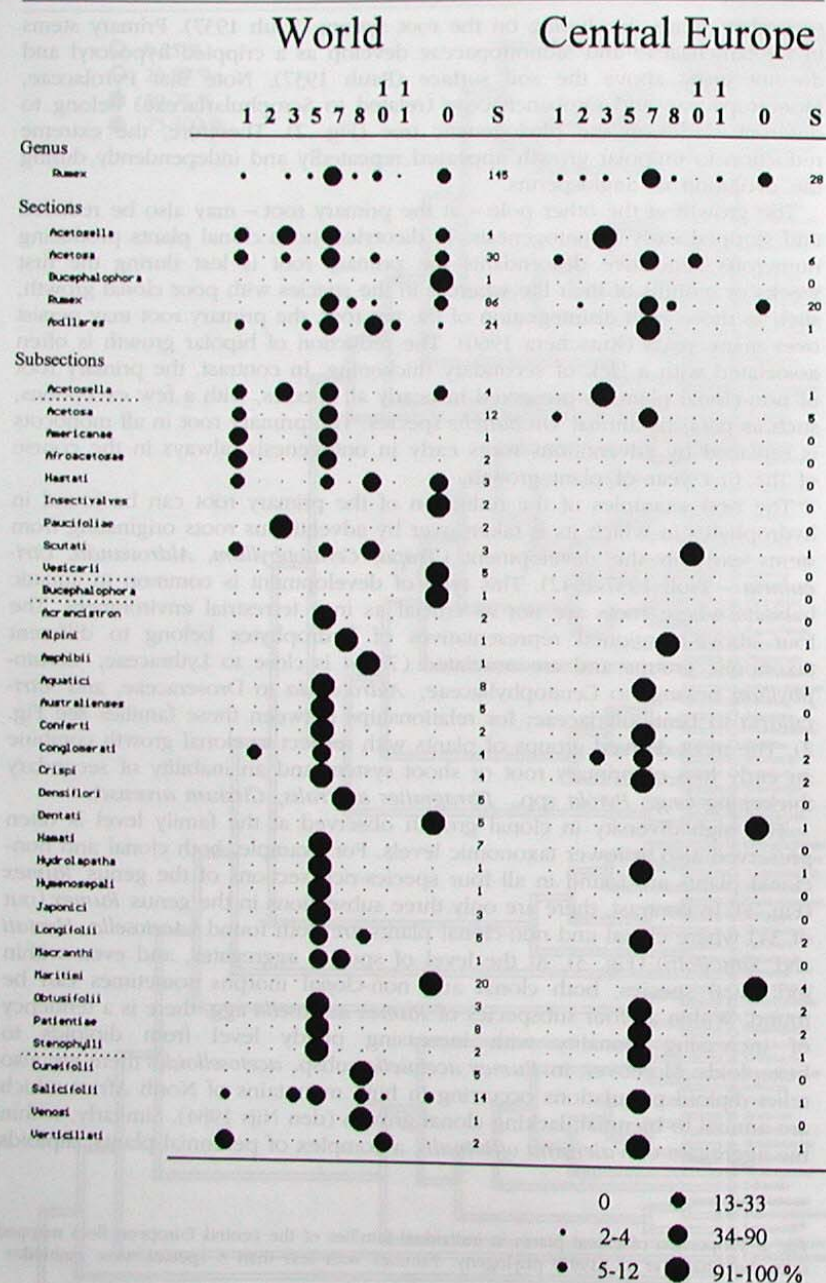
The growth at the other pole – at the primary root – may also be reduced and stopped early in ontogenesis. In dicotyledonous clonal plants producing numerous vegetative descendants the primary root is lost during the first weeks or months of their life whereas in the species with poor clonal growth, such as those with disintegration of the tap root, the primary root may persist over many years (Kutschera 1960). The reduction of bipolar growth is often associated with a lack of secondary thickening. In contrast, the primary root of non-clonal plants is preserved in nearly all species, with a few exceptions, such as parasitic annual *Orobanchae* species. The primary root in all monocots is replaced by adventitious roots early in ontogenesis, always in the course of the first year of plant growth.

The best examples of the reduction of the primary root can be found in hydrophytes in which it is taken over by adventitious roots originating from stems early in the development (*Trapa*, *Ceratophyllum*, *Aldrovanda*, *Utricularia* - Troll 1937-1942). This type of development is common in aquatic habitats where roots are not as crucial as in a terrestrial environment. The four above-mentioned representatives of hydrophytes belong to different taxonomic groups and are unrelated (*Trapa* is close to Lythraceae, *Ceratophyllum* belongs to Ceratophyllaceae, *Aldrovanda* to Droseraceae, and *Utricularia* to Lentibulariaceae; for relationships between these families see Fig. 2). The most derived groups of plants with respect to clonal growth combine an early loss of primary root or shoot system and an inability of secondary thickening (e.g., *Pyrola* spp., *Phragmites australis*, *Cirsium arvense*).

The high diversity in clonal growth observed at the family level is often preserved also at lower taxonomic levels. For example, both clonal and non-clonal plants are found in all four species-rich sections of the genus *Rumex* (Fig. 3). In contrast, there are only three subsections in the genus *Rumex* (out of 34) where clonal and non-clonal plants are both found (*Acetosella*, *Hastati* and *Salicifolii*) (Fig. 3). At the level of species aggregates, and even within individual species, both clonal and non-clonal morphs sometimes can be found. Within all four subspecies of *Rumex acetosella* agg. there is a tendency of increasing clonality with increasing ploidy level from diploids to hexaploids. Moreover, in *Rumex acetosella* subsp. *acetoselloides* there are also relict diploid populations occurring in high mountains of North Africa which are annual to biennial, lacking clonal growth (den Nijs 1984). Similarly, within the aggregate of *Valeriana officinalis*, a complex of perennial plants, diploids

Fig. 2. Proportion of clonal plants in individual families of the central European flora mapped onto the Chase et al. (1993) phylogeny. Families with less than 5 species were omitted.





occur (*V. officinalis* s.s.) which lack clonal growth whereas plants with higher ploidies develop below-ground (in *V. pratensis* and *V. wallrothii* which are tetraploids and in *V. versifolia*, an octoploid) or both below- and above-ground plagiotropic stems (in *V. procurrens* and *V. sambucifolia*, both are octoploids) (Titz 1984). There are a number of other examples documenting how clonality varies in related species and in species aggregates (Mogie and Hutchings 1990; Krahulec 1994). On the other hand there are also many species groups in which all members are either clonal or non-clonal. Even among the 45 families containing 10 and more species in central Europe there are 6 families with exclusively clonal members (Aspidiaceae, Aspleniaceae, Equisetaceae, Iridaceae, Orchidaceae, Potamogetonaceae – Fig. 4) and 2 with exclusively non-clonal plants (Amaranthaceae, Oleaceae). The large families of exclusively clonal plants belong to three groups only: Filicopsida, Sphenopsida and Monocotyledonae. This indicates a strong phylogenetic factor in the evolution of clonality although this does not preclude ecological interpretations (van Groenendael *et al.* 1996).

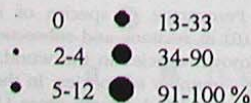
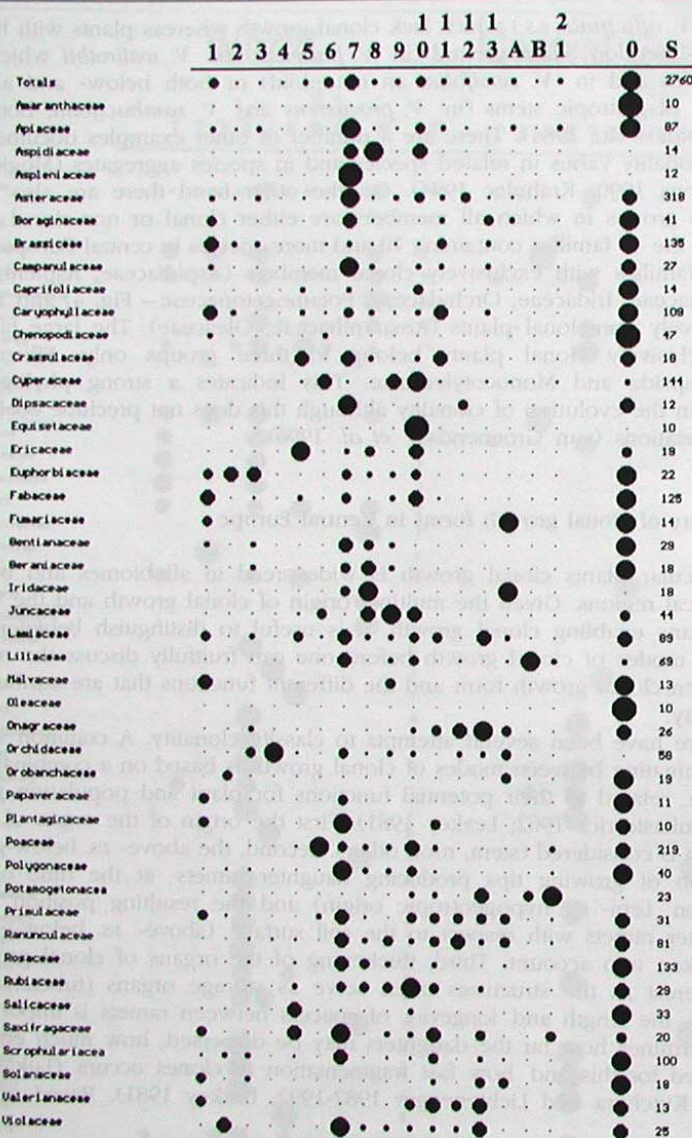
#### Diversity of clonal growth forms in Central Europe

In vascular plants clonal growth is widespread in all biomes and biogeographical regions. Given the multiple origin of clonal growth and the variety of organs enabling clonal growth, it is useful to distinguish between individual modes of clonal growth before one can fruitfully discuss the relation between clonal growth form and the different functions that are attributed to clonality.

There have been several attempts to classify clonality. A common way of discriminating between modes of clonal growth is based on a combination of criteria, related to their potential functions for plant and population growth (e.g. Lukasiewicz 1962; Leakey 1981). First the origin of the organ of clonal growth is considered (stem, root, other). Second, the above- vs. below-ground position of growing tips producing daughter ramets at the time of their initiation (epi- vs. hypogeotropic origin) and the resulting position of the daughter ramets with respect to the soil surface (above- vs. below-ground) are taken into account. Third, thickening of the organs of clonal growth is of interest 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 occurs (Lukasiewicz 1962; Kutcher and Lichtenegger 1982-1992; Leakey 1981). Based on these

Fig. 3. Percentage of species of individual types of clonal growth (1-11) and non-clonal growth (0) in sections and subsections of the genus of *Rumex* based on 145 species, i.e. 74% of the known species in the world, including all 28 central European species. 0 – non-clonal plants; S – number of species. In the list of subsections, sections are delimited by dotted lines. For codes of clonal growth types (1-11) see Table 1 (other types of clonal growth (12 to 21) are not known for *Rumex*).





characteristics a robust qualitative morphological classification of clonal plants has been obtained consisting of 21 hierarchically related categories and spanning the clonal diversity in vascular plants of central Europe (Figs. 1 and 5). All clonal plants in our database belong to one (rarely two or three) of these 21 categories, named after typical representatives (Fig. 1, see Appendix 1 for details). The number of species of vascular plants belonging to these types are given in Table 1. The most abundant are the "*Rumex obtusifolius*" type representing 17.4 % vascular plants and the "*Aegopodium podagraria*" type with 9.9 %. All other types contain less than 6% of vascular plants of the central European flora. The rarest modes of clonal growth are found among several species with specialised types of tubers and bulbs represented each by less than 10 species in central Europe. The types that are most represented among species are also most frequently found in the more than 20,000 field plots in the data base (Table 1). The more rare clonal growth forms are also the ones that are infrequently encountered in the field. There is a very close similarity between the ranking of clonal growth types over species and over field plots (Kendall's rank correlation coefficient 0.762,  $n = 19$ ,  $p < 0.001$ ). When there is a difference in percentage of species belonging to a particular clonal growth type between species and vegetation data (Table 1), this indicates the adaptive value of an individual clonal growth type, e.g. the "*Callitha palustris*" type is relatively overrepresented whereas most types with below-ground tubers and bulbs are underrepresented in the vegetation data, indicating their narrower specialisation and inability to colonize various habitats.

Some of the important characteristics of each of the 21 morphological types of clonal growth are summarised in Table 2. Species belonging to different morphological types differ in the number of daughter ramets produced per season, in fragmentation process, anchorage, photosynthetic activity of clonal growth organ, degree of protection of buds initiating clonal growth, etc. There are no two types of clonal growth with the same characteristics. The list given in Table 2, however, indicates that some types of clonal growth are quite similar, such as types 7 and 8, and 9 and 10. Others are more distinct and perhaps more specialised for particular habitats (types 2, 11, 21). Using cluster analysis on the form-function matrix of Table 2, it can be shown that the growth types can be ordered in a hierarchical fashion according to their function and that there are four basic groups of clonal types (Fig. 5). The first includes plants with disintegrating tap root and is associated with two types developing buds on roots (types 1, 2, 3). Bulbs and root-originating tubers represent the second group (types 4, 16-20). The third group is identical with the "*Dentaria bulbifera*" type (detached adventitious and axillary buds, dor-

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Fig. 4. Distribution of individual types of clonal growth over the plant families of the central European flora. Families with 10 and more species are given. Type A: clonal growth modes 14-17. Type B: clonal growth modes 18-20. 0 – non-clonal plants; S – total number of species belonging to individual families in central Europe. For codes of clonal growth modes 1 - 21 see Table 1.



**Table 2.** Characteristics of individual modes of clonal growth (1 to 21, see Fig. 1). 1 denotes presence of a characteristic in most species belonging to a clonal growth type (1 to 21, see Appendix for their detailed description), 0 means the absence of a characteristic in most species belonging to individual types. CGO: clonal growth organ.

No. Characteristic	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1 CGO is of root origin	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 CGO is of stem origin	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
3 CGO is a specialised bud or plantlet formed above-ground	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
4 CGO has a special adaptation for storage	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
5 Origin of organs used for storage and clonal growth is different	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
6 CGO photosynthesises	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1
7 CGO used for anchorage	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0
8 Bud bank large and permanent	0	0	0	0	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0
9 A large bud bank may develop	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10 Bud bank small and permanent	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1
11 Descendants much smaller than mother plant (resembling a seedling)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
12 Multiplication frequent (numerous ramets produced every year)	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1
13 Multiplication infrequent (ramets produced in some years only)	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
14 Insignificant vegetative spreading (< 0.05 m per year)	1	1	0	1	0	1	1	0	1	0	0	1	0	0	0	1	1	1	1	0	0
15 Daughter ramet photosynthesises immediately after its initiation	1	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1
16 Creeping shoots	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
17 Pseudo-annuals	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0
18 Extensive perennial root system	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
19 Perennial primary root	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20 Primary root system without adventitious roots	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21 Secondary thickening	1	1	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0
22 More than 1 organ of clonal growth in some species	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	1
23 Ramets integrated for $\geq 2$ years	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0
24 Connection mother and daughter decays after ramet initiation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
25 Clonal growth starts above-ground: buds above-ground	1	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	1
26 Buds protected by specialised scale leaves	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1



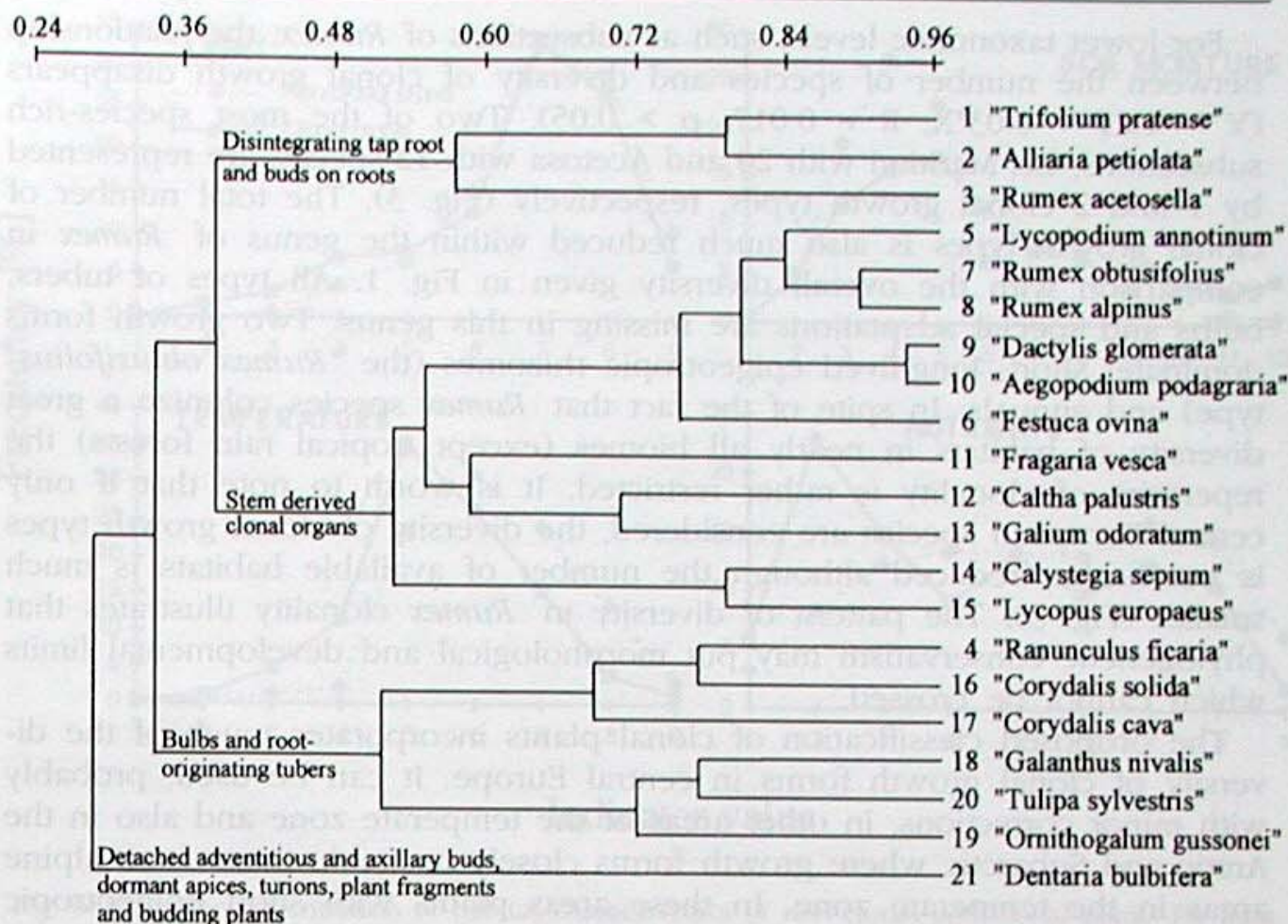


Fig. 5. Cluster analysis of 21 clonal growth types based on origin, morphology, longevity and other characteristics given in Table 2 (UPGMA – unweighted pair group method using arithmetic average, Euclidean distance was used as sample dissimilarity measure – Orłóci 1978). The numbers correspond to codes given in Table 1.

mant apices, turions, plant fragments and budding plants). The rest of the types containing the majority of species, belong to the last group (types 5-15). Plants with different types of stem-derived clonal organs, both below- and above-ground, belong there.

The diversity of clonal growth is unevenly and non-randomly distributed among plant families (Fig. 4). For example, some types are restricted to monocots (all types of bulbs: types 18-20, and most species belonging to the "*Ranunculus ficaria*" type), other families also belong to a single type (Aspleniaceae and Plumbaginaceae – the "*Rumex obtusifolius*" type, Equisetaceae – the "*Aegopodium podagraria*" type, Lycopodiaceae – the "*Lycopodium annotinum*" type) or belong to two types only (e.g., Dipsacaceae – the "*Rumex obtusifolius*" and "*Caltha palustris*" types). The number of clonal growth types (Y) strongly correlates with the number of clonal species in families (X) ( $Y = 1.05 + X^{0.4915}$ ;  $R^2 = 0.735$ ,  $p < 0.0001$ ). The highest positive values of residuals were found in Primulaceae and Ranunculaceae, indicating unexpectedly high diversity of clonal growth types. In contrast, the highest negative values of residuals were found in some monocots, such as Juncaceae and Iridaceae, and also in Equisetaceae and Aspleniaceae, indicating phylogenetic constraints.



For lower taxonomic levels, such as subsections of *Rumex*, the relationship between the number of species and diversity of clonal growth disappears ( $Y = 1.21 + 0.03 \cdot X$ ,  $R = 0.017$ ,  $p > 0.05$ ). Two of the most species-rich subsections, i.e. Maritimi with 20 and Acetosa with 12 species are represented by 1 and 2 clonal growth types, respectively (Fig. 3). The total number of clonal growth types is also much reduced within the genus of *Rumex* in comparison with the overall diversity given in Fig. 1. All types of tubers, bulbs and special adaptations are missing in this genus. Two growth forms dominate: short, long-lived epigeotropic rhizomes (the "*Rumex obtusifolius*" type) and annuals. In spite of the fact that *Rumex* species colonize a great diversity of habitats in nearly all biomes (except tropical rain forests) the repertoire of clonality is rather restricted. It is worth to note that if only central European species are considered, the diversity of clonal growth types is not further reduced although the number of available habitats is much smaller (Fig. 3). The pattern of diversity in *Rumex* clonality illustrates that phylogenetic conservatism may put morphological and developmental limits which cannot be crossed.

The proposed classification of clonal plants incorporates much of the diversity of clonal growth forms in central Europe. It can be used, probably with minor corrections, in other areas of the temperate zone and also in the Arctic and Subarctic where growth forms closely resemble those from alpine areas in the temperate zone. In these areas plants with short epigeotropic rhizomes are more common and perhaps also more differentiated than in central Europe. Clonal growth forms in Mediterranean areas are characterised by geophytes with bulbs and other structures hiding growing apices during dry and hot summers. More forms based on bulbs, tubers, etc. can be expected there. Clonal growth in wet subtropical and tropical forests is very different from the clonal growth forms presented here. Clonality of woody species is common and diversified there (Hallé *et al.* 1978; Jeník 1994) and epiphytes in the tropics represent a species- and form-rich group which is poorly known and definitely requires further attention from the point of view of clonal growth.

#### The ecological preferences of clonal plants

It follows from our trait-to-environment analysis based on indicator values of Ellenberg (1979) that there is a marked difference in the distribution of clonal and non-clonal species among different habitats (Fig. 6). Clonal plants are more common at low soil nitrogen and the reverse is true for non-clonals. A similar pattern can be observed for soil moisture. On drier soils non-clonal plants prevail, on wetter soils, in wetlands and water bodies clonal plants are more frequently found. However, for the driest soils (i.e. dry sandy dunes) there is no difference between representation of clonal and non-clonal species. Non-clonals are more frequent at the warmer end of the temperature gradient which corresponds to a preference for lower altitudes and latitudes. At the cold end of the gradient, i.e. at higher elevations clonal species do-

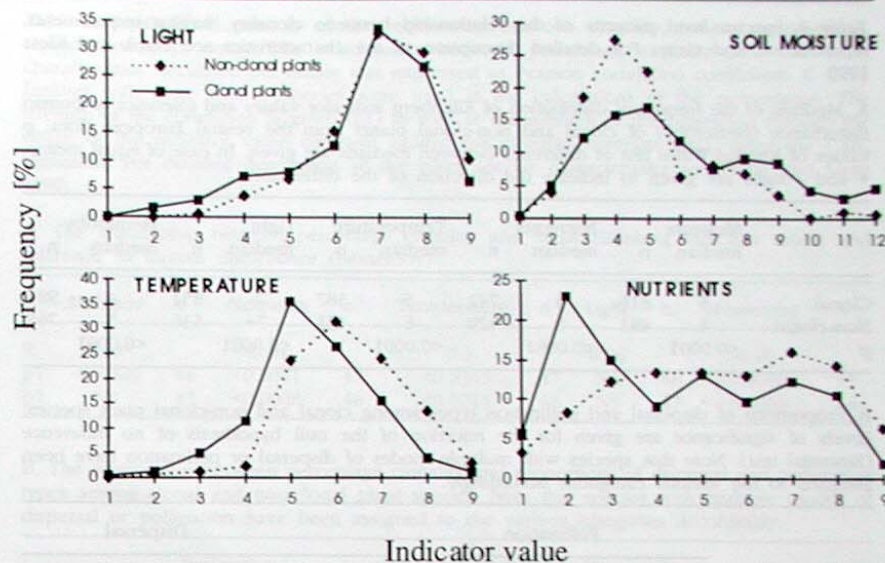


Fig. 6. Frequency distribution of habitat characteristics of non-clonal and clonal plants for light intensity, soil moisture, mean annual ambient temperature and soil nutrients (nitrogen) based on Ellenberg indicator values.

minate. With respect to light intensity the trend is similar but not as distinct as for the other environmental factors: clonal plants are slightly more present in shaded habitats whereas non-clonals are more frequent in the open. Non-clonal plants are also more frequent in disturbed habitats compared to clonals. The differences between modal values of these distributions for clonal *vs.* non-clonal plants are strongly significant (Table 3a). We carried out a similar analysis for soil pH and continentality. However, in these cases no differences were found between clonal and non-clonal plant species (data not shown). Other interesting patterns that emerge from the analysis are that clonal plant species are less frequently selfing or using insects for their pollination and also show less assisted dispersal by e.g. animals or wind (Table 3b). Very common as well as very rare species are more frequently non-clonal and clonals tend to be less invasive (Table 3c, see Pyšek, this volume).

To what degree the patterns described above represent a phylogenetic rather than an ecological relationship has been tested at the level of the family. The relationship between clonality and environmental factors is maintained at the level of the family except for the relationship between clonality and light (Table 4a). When a trait-environment relationship is maintained at the family level, this suggests a strong phylogenetic component in these relationships. After calculating independent contrasts, however, the relationships remain irrespective of any underlying phylogenetic pattern, pointing to



**Table 3.** Species level patterns of the relationship between clonality, habitat requirements, reproduction and rarity. For detailed description of the characteristics see Frank and Klotz 1990.

A. Medians of the frequency distribution of Ellenberg indicator values and tolerance to human disturbance (hemeroby) of clonal and non-clonal plants from the central European flora; p values of Kruskal-Wallis test of difference between medians are given. In case of equal means, + and - signs are given to indicate the direction of the difference.

	Moisture		Nutrients		Temperature		Light		Hemeroby	
	median	n	median	n	median	n	median	n	median	n
Clonal	5	816	4	742	5	587	7-	851	4	985
Non-clonal	4	481	5	429	6	431	7+	536	5	765
p	<0.0001		<0.0001		<0.0001		<0.0001		<0.0001	

B. Proportions of dispersal and pollination types among clonal and non-clonal plant species. Levels of significance are given for the rejection of the null hypothesis of no difference (Binomial test). Note that species with multiple modes of dispersal or pollination have been assigned to the various categories accordingly.

	Pollination								Dispersal							
	Insect				Selfing				Wind				Animals			
	Total	%	n	%	n	%	n	%	n	%	n	%	%	n	%	n
Clonal	1437	52	744	29	423	21	306	49	709	18	265	54	780	10	143	
Non-clonal	822	76	622	47	388	20	162	55	452	16	131	61	500	10	82	
p	<0.001		<0.001		NS		<0.05		NS		<0.025		NS			

C. Proportions of three classes of rarity and two trends of recent changes in the number of localities among clonal and non-clonal plant species. Levels of significance are given for the Kruskal-Wallis test of difference.

	Rarity								Trend			
	Common				Scattered				Spreading		Declining	
	Total	%	n	%	n	%	n	%	%	n	%	n
Clonal	1437	23	328	25	357	24	349	4	57	44	632	
Non-clonal	822	26	217	25	205	40	332	8	65	41	337	
p	<0.05		NS		<0.001		<0.001		NS			

an evolutionary significant trait-environment relationship. Only the relation between clonality and moisture disappears due to the frequent occurrence of clonal plants among aquatic species. These species also frequently belong to the monocots. This raises the classical chicken and egg question whether aquatics are clonal because they are monocots or whether aquatics are monocots because clonality is more common among monocots and constitutes an advantage for life under water (Duarte *et al.* 1994; van Groenendael *et al.* 1996).

**Table 4.** Family level patterns of the relationship between clonality, habitat requirements, reproduction and rarity. The relationship between percentage clonality and the other characteristics calculated per family was expressed as Pearson correlation coefficients R. Only families with more than 5 species were used in the calculations of the percentages. The strength of the correlation is given (p1) as well as the strength of the regression through the origin of the indicator value contrasts against the clonality contrasts (p2), using the CAIC algorithm. For detailed description of the plant species characteristics see Frank and Klotz 1990.

A. The relationship between percentage clonality and mean Ellenberg indicator values and tolerance to human disturbance (hemeroby).

	Moisture	n	Nutrients	n	Temperature	n	Light	n	Hemeroby	n
R	0.31		-0.54		-0.3		0.08		-0.49	
p1	<0.0320	48	<0.0001	47	<0.0365	47	NS	48	<0.0006	45
p2	NS	47	<0.0008	46	<0.0211	46	NS	47	<0.0003	44

B. The relationship between percentage clonality and proportions of dispersal and pollination types among clonal and non-clonal plant species. Note that species with multiple modes of dispersal or pollination have been assigned to the various categories accordingly.

	Pollination								Dispersal							
	Insect				Selfing				Wind				Animals			
	Total	%	n	%	n	%	n	%	%	n	%	%	%	n	%	n
R	0.1		0.12		-0.34		-0.06		0.03		-0.09		0.11			
p1	NS	47	NS	47	<0.020	47	NS	47	NS	47	NS	47	NS	47	NS	47
p2	NS	46	<0.035	46	<0.003	46	NS	46	NS	46	NS	46	NS	46	NS	46

C. The relationship between percentage clonality and percentage rarity in three classes and percentage of trend in change in spatial distribution in two classes.

	Rarity								Trend			
	Common				Scattered				Spreading		Declining	
	Total	%	n	%	n	%	n	%	%	n	%	n
R	-0.38		-0.03		0.14		-0.32		0.59			
p1	<0.007	47	NS	47	NS	47	<0.03	47	<0.0001	47		
p2	NS	46	NS	46	NS	46	<0.015	46	<0.0001	46		

These ecological preferences of clonal vs non-clonal plants correspond to the ideas by Tiffney and Niklas (1985) and Grace (1993) who suggested that clonal growth is adaptive under stressed conditions as in nutrient-poor, cold habitats or under shaded or wet conditions, whereas under more optimal conditions non-clonal plants are favoured.

At the family level the relations between clonality and pollination and between clonality and dispersal mode that were present at the species level disappear. After taking out the phylogenetic pattern, it proved that clonal plant families are less wind pollinated and (weakly) more selfing, this in

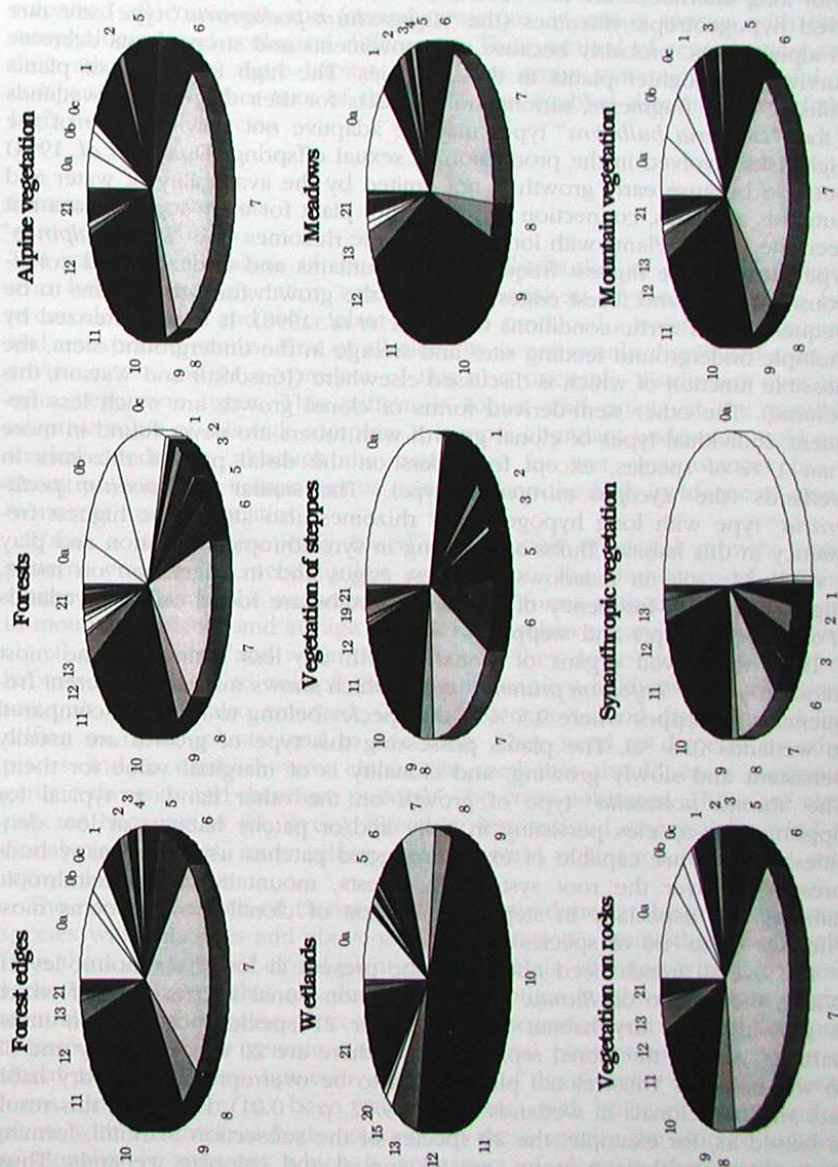


contrast to the species level where selfing was prominent among the non-clonal (annual) species (Table 4b). The relations between clonality and rarity and between clonality and changes in distribution are largely maintained at the family level. Common species tend to be non-clonal but there is a strong phylogenetic component to this relationship as many of the common species are weedy annuals from related families, causing the relationship to disappear after taking phylogenetically independent contrasts (Table 4c). The relationship between rarity and clonality is also lost at the family level (Table 4c). Plant families containing a high number of invasive species tend to be non-clonal, a trend also shown at the species level. Surprisingly, however, the weak tendency for clonal species to decline in recent time (Table 3c) proves to be a strong relationship at higher taxonomic levels. Families with a high number of clonal species also contain a high number of endangered species irrespective of the position of the family in the phylogenetic framework (Table 4c).

#### The distribution of clonal plants

The occurrence of non-clonal and clonal plants is markedly different among plant communities. Their distribution over 9 basic vegetation types is shown in Fig. 7. There is a clear gradient in clonality. Clonal growth forms are most abundant under cold and wet conditions and under dense shade as in forest edges and less frequent under disturbed conditions and in steppes. Clearly clonal growth seems less advantageous when disturbance is frequent. Stem-derived organs of clonal growth are most abundant, especially the rhizomatous and stoloniferous types (5-13). Of these the "*Rumex obtusifolius*" type (long-lived, short epigeotropic stems) plays a prominent role in most vegetation types, except for wetlands where clonal plants with long-lived and long hypogeotropic stems (the "*Aegopodium podagraria*" type), short-lived above-ground stems (the "*Fragaria vesca*" type) and plants with special ad-

Fig. 7. Distribution of non-clonal plants (white) and individual types of clonal plants (different patterns) over main vegetation types. For each main vegetation type, mean percentages of species belonging to particular growth forms were calculated from (6 to 25) plant communities belonging to each main vegetation type. The calculation was based on the species presence/absence data for each plant community according to Oberdorfer *et al.* (1977-1992). Growth forms more frequent than 1% are labeled by following numbers: 0: non-clonal plants (0a - annuals, 0b - shrubs, 0c - trees); woody vines (0d) did not reach 1% in any vegetation type; 1 to 21: clonal plants, see Table 1 for codes. "Forest edges" - woodland-related herbaceous perennial and shrub communities at lower altitudes, "Forests" - woodlands in lowlands and in mountains, "Alpine vegetation" - alpine grasslands and stony sites above tree-line, "Wetlands" - freshwater and mire vegetation, "Vegetation of steppes" - more or less arid swards, "Meadows" - cultivated meadows and pastures, "Vegetation on rocks" - stony sites below tree-line, "Synanthropic vegetation" - herbaceous vegetation of frequently disturbed sites, "Mountain vegetation" - mountain vegetation at the tree-line. For detailed description of these vegetation types see Ellenberg (1986).





aptations (the "*Dentaria bulbifera*" type) are more frequent. This is possibly caused by the fact that in the water environment the mechanistic problems with long internodes are less severe. In contrast, plants with long and long-lived hypogeotropic rhizomes (the "*Aegopodium podagraria*" type) are rare in alpine areas, probably because soil movements and strong frosts decrease survival of daughter plants in these species. The high frequency of plants utilising plant fragments, turions and plantlets for their dispersal in wetlands (the "*Dentaria bulbifera*" type) may be adaptive not only because of the high risks involved in the production of sexual offspring (Duarte *et al.* 1994) but also because early growth is not limited by the availability of water and nutrients and thus, connection to the mother plant for early support does not seem necessary. Plants with long epigeotropic rhizomes (the "*Rumex alpinus*" type) achieve the highest frequency in mountains and under shaded conditions in forests and forest edges. It is also the growth form that seems to be frequent under arctic conditions (Carlsson *et al.* 1990). It is characterized by multiple underground feeding sites and storage in the underground stem, the possible function of which is discussed elsewhere (Jónsdóttir and Watson, this volume). The other stem-derived forms of clonal growth are much less frequent. Individual types of clonal growth with tubers are never found in more than 1 % of species, except for tubers on the distal part of rhizomes in wetlands (the "*Lycopus europaeus*" type). The similar "*Aegopodium podagraria*" type with long hypogeotropic rhizomes also attains the highest frequency in this habitat. Bulbs are missing in synanthropic vegetation and play a negligible role in meadows, at forest edges and in vegetation on rocks. Higher values of frequency of plants with bulbs are found only in wetlands (*Potamogeton* spp.) and steppes.

The root-derived organs of clonal growth are less abundant. The most frequent is the "*Trifolium pratense*" type, which shows markedly different frequencies in steppes where 9.5 % of the species belong to this type compared to wetlands (0.4 %). The plants possessing this type of growth are usually persistent and slowly growing, and clonality is of marginal value for them. The "*Rumex acetosella*" type of growth on the other hand, is typical for opportunistic species persisting in risky and/or patchy habitats at low densities, as they are capable of exploiting good patches using the many buds present all over the root system. In forests, mountains and synanthropic habitats and especially in steppes, this type of clonal growth seems most effective (2 to 4% of species).

The overall trends need not always be present at lower taxonomic levels. Within the section of *Rumex* there are 22 non-clonal species, one of which is growing in a dry habitat and the other 21 species occurring in moist habitats. Among the clonal representatives there are 20 species in dry and 31 in wet habitats. Thus, clonal plants seem to be overrepresented in dry habitats and non-clonals in wetlands ( $\chi^2 = 9.02$ ,  $p < 0.01$ ). However, this result is biased as, for example, the 20 species of the subsection Maritimi, forming a clearly monophyletic group, are all annual and colonize wetlands. Thus, there are no phylogenetically independent contrasts within this group and therefore, the number of taxa that can be used in a comparative analysis is

in fact much lower. As a result, the significance of the relationship disappears. On the other hand, there is an important message from this observation: the subsection Maritimi is the only group within the whole genus which colonized all continents and formed numerous vicarious species with little morphological and ecological differences. Their method of reproduction and their adaptation to shore habitats made the group extremely successful in comparison with other taxa of the genus and enabled diversification of the high number of species.

### Summary and prospects

The comparative analysis of the pattern of distribution of clonal plant traits over habitats and vegetation types and the analysis of the relationship between clonal traits and other plant traits has produced a number of expected and unexpected results. First of all clonality is not evenly distributed over all environments and as a correlate of this also unevenly distributed over the main vegetation types. This pattern is robust and points at the possible adaptive value of this trait complex. It is more abundant under wet, cold and shaded conditions, although the preference for wet circumstances has a strong phylogenetic component as it is based on the high incidence of clonal monocots among aquatics.

Using a morphogenetically based classification of clonal growth forms, patterns emerge that need further investigation: the abundance of splitting clones in wetlands, the occurrence of growth forms with tap root on rocks, in mountain habitats and at high altitudes, the relative scarcity of root-derived clonal growth forms and when they do occur they do so mainly in disturbed habitats. In addition to unexplored trait-environment relationships, interesting trait-trait relations also emerged. One would expect good dispersal and less selfing as clonal plants tend to live long. They need to disperse to other places and to establish new clones via seed that should carry maximum genetic diversity and therefore preferably be cross-pollinated. There are clear patterns here but in the wrong direction: less assisted dispersal by wind in clonal plant species; more selfing and less wind pollination in families with many clonal species.

The current research on clonal plants is mostly done on the group of clonal species with rhizomes and above-ground plagiotropic stems that traditionally form the focal point of clonal plant research. Main attention is paid to those aspects of clonality, that are dealing with 'mother-daughter' relations: architectural patterns, foraging processes, clonal integration and internal transport of resources and the genetic structure of clonal populations. This group of clonal plants represent, however, only a part of the diversity of clonal growth forms. Less attention has been paid to species with bulbs or tubers and to plants with adventitious buds on roots. In these species the storage function of clonality is apparent which is an aspect of clonality that needs more fundamental research. Also, clonality in plants with detached adventitious and axillary buds, dormant apices, turions and other plant fragments that together



represent the dispersal function of clonality have not received enough attention so far. We therefore would argue that because of the attention in the past for clonal organisation, other aspects of clonality such as storage and dispersal are less well investigated. The generalisations applied to clonal plants therefore should be compared on the whole range of clonal growth modes to test the mechanistic explanations for the observed patterns in clonal plants.

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## Appendix

Description of 21 types of clonal growth in vascular plants growing in central Europe. We avoided vague terms, such as stolon, corm, layer and rootstock, which have very different meaning with individual authors. The rhizome is defined as any below-ground stem. Plant names follow Ehrendorfer (1973). Long-lived organs senesce after more than 2 years, short-lived ones earlier.

1. "*Trifolium pratense*" type. Main (tap) root of the primary root system without adventitious roots and buds. Senescing tap root decays from root centre causing plant fragmentation. Old genets disintegrate into ramets bearing parts of the main root and one or a few shoots. Vegetative spreading is poor. The tap root serves as storage organ and vascular link between shoots. Bud bank is on perennial bases of shoots (caudex) [other examples: *Artemisia campestris*, *Cichorium intybus*, *Dorycnium herbaceum*].
2. "*Alliaria petiolata*" type. Main root of the primary root system with adventitious buds. This type differs from the preceding one by the bud bank. The species forms adventitious buds on hypocotyl and/or tap root. Sprouting may start in young plants, but fragmentation proceeds in old plants only, much in the same way as in the "*Trifolium pratense*" type [other examples: *Aristolochia clematitis*, *Linaria alpina*, *Viola pumila*].
3. "*Rumex acetosella*" type. Lateral roots of the primary root system or adventitious roots with adventitious buds. The roots with adventitious buds serve as storage organ and a connection between ramets. The lateral and adventitious roots decay within a few years causing fragmentation of the mother plant. Sprouting from adventitious buds on horizontal roots results in extensive vegetative spreading [other examples: *Ajuga genevensis*, *Convolvulus arvensis*, *Epilobium angustifolium*].
4. "*Ranunculus ficaria*" type. Root tubers. The tubers are short-lived and serve as storage and regenerative organ. The plant dies back in autumn, except for the root tuber(s) which bear just one bud each for spring regrowth. During summer old tubers decay and new ones are formed. Vegetative spreading in non-disturbed habitats is poor. The number of ramets produced during the life-span of a genet is usually low [other examples: *Dactylorhiza fuchsii*, *Orchis morio*, *Trautsteinera globosa*].
5. "*Lycopodium annotinum*" type. Long-lived above-ground creeping stems. Flowers of some plants develop on orthotropic branches which bend down later and become horizontal. Fragmentation starts after several years, due to decaying of the oldest parts of the plagiotropic stem. Nodes on plagiotropic stems bear leaves, internodes are usually long, branching is monopodial or sympodial. The stems serve as vascular connections between old and young parts of a plant. Vegetative spreading may be fast and persistence is variable [other examples: *Linnaea borealis*, *Oxycoccus microcarpus*, *Salix reticulata*, *Veronica fruticulosa*].
- 6-8. Long-lived below-ground stems formed above-ground (= epigeotropic rhizomes sensu Serebrjakov and Serebrjakova 1965). Distal part of stem is covered by soil and litter or pulled into the soil by contraction of roots. Nodes bear green leaves, the internodes are short. The



rhizomes serve as storage organs and as a bud bank and bear roots. Vegetative spreading is usually slow (up to a few cm/year). Decay from the basal part of the rhizome starts usually after more than ten years. Branching is monopodial or sympodial. Disintegration starts with the decay of the primary root and continues with the oldest parts of the rhizome.

(6) Turf graminoids: **"Festuca ovina" type** [other examples: *Agrostis alpina*, *Carex montana*, *Deschampsia cespitosa*].

(7) Stems < 10 cm in length: **"Rumex obtusifolius" type** [other examples: *Armeria alpina*, *Calamagrostis arundinacea*, *Lamium* (*Lamium*) *galeobdolon*, *Sanicula europaea*].

(8) Stems > 10 cm in length: **"Rumex alpinus" type** [other examples: *Asarum europaeum*, *Geum rivale*, *Filipendula ulmaria*].

9.–10. Long-lived below-ground plagiotropic stems formed below-ground (= hypogeotropic rhizomes *sensu* Serebrjakov and Serebrjakova 1965). The stem usually grows horizontally at a species-specific depth. After some time the stem becomes orthotropic and forms above-ground shoots. The plagiotropic part of the stem bears bracts, a few roots at nodes and has long internodes. Branching is usually sympodial. Life-span of the rhizomes is about 2 to 9 years. Vegetative spreading can be fast and cover several metres per year. Disintegration starts from oldest part of the below-ground stem.

(9) Stems < 10 cm in length: **"Dactylis glomerata" type** [other examples: *Antioxanthum odoratum*, *Carex atrata*, *Juncus trifidus*, *Molinia caerulea*].

(10) Stems > 10 cm in length: **"Aegopodium podagraria" type** [other examples: *Achillea pannonica*, *Agropyron repens*, *Anemone nemorosa*, *Brachypodium pinnatum*, *Carex arenaria*, *C. bigelowii*, *Calamagrostis epigejos*, *Galium boreale*, *Mercurialis perennis*, *Phragmites australis*, *Pteridium aquilinum*, *Solidago altissima*, *S. canadensis*].

11. **"Fragaria vesca" type**. Short-lived plagiotropic above-ground stems are specialised for spreading. They provide temporal vascular connections between daughter and mother plants during the first growing season. The stem may bear roots and leaves and it serves as temporal storage organ of food reserves and buds. Growth is monopodial or sympodial. Fragmentation is caused by decaying of plagiotropic stems. The daughter ramets may be long-lived [other examples: *Ajuga reptans*, *Geum reptans*, *Glechoma hederacea*, *Potentilla anserina*, *Trifolium repens*].

12. **"Caltha palustris" type**. Short-lived below-ground plagiotropic stems formed above-ground. Characteristics of this type are the same as for the types 6–8 except for longevity [other examples: *Bellis perennis*, *Ranunculus acris*, *Viola biflora*].

13. **"Galium odoratum" type**. Short-lived below-ground plagiotropic stems formed below-ground. Characteristics of this type are the same as for the types 9–10 except for longevity [other examples: *Dentaria enneaphyllos*, *Mentha longifolia*, *Stachys sylvatica*].

14. **"Calystegia sepium" type**. Annual below-ground tubers on distal part of plagiotropic above-ground stems. The tubers serve as storage organs and have a bud bank. The tuber is formed on a stem in autumn when the plagiotropic above-ground stem penetrates into soil and transforms. One or several apical internodes thicken, food reserves are deposited in the swollen part of the stem. The plagiotropic stem provides a connection to the mother plant. It may bear green leaves and roots and decays completely after the tuber is formed. This type ensures a fast vegetative spreading, high mobility in space and a short persistence at a particular site [other examples: *Calystegia silvatica*, *Rubus caesius*, *Rubus fruticosus* agg.].

15. **"Lycopus europaeus" type**. Annual below-ground tubers on distal part of below-ground plagiotropic stems. The tubers serve as storage organ and bear buds used for spring regrowth. The below-ground plagiotropic stems bear roots and bracts. At an apical part of the below-ground stem, a single tuber is formed or several tubers originate along the rhizome. The below-ground plagiotropic stems serve as vascular connection to the mother plants [other examples: *Adoxa moschatellina*, *Helianthus tuberosus*, *Trientalis europaea*].

16. **"Corydalis solida" type**. Mother and daughter below-ground tubers are annual and attached. Growth is sympodial. The tubers serve as storage organs and a bud bank. Vegetative spreading is very limited, a production of more than one daughter tuber during one season is rare [other examples: *Aconitum napellus*, *Glaucololus imbricatus*, *Ranunculus bulbosus*].

17. **"Corydalis cava" type**. Perennial below-ground stem tuber. Its senescence may result in plant fragmentation. No daughter tubers are produced. The mother tuber grows monopodially and thickens due to secondary growth. Decaying of the tuber starts from its centre.

The perennial stem tuber serves as storage organ and as a bud bank. Vegetative spreading is poor [other examples: *Allium angulosum*, *Cyclamen purpurascens*, *Eranthis hyemalis*].

18.–20. Bulbs – shortened basal parts of stem with one or several thickened storage bracts or basal parts of leaves. The bulb growth is usually sympodially.

(18) Daughter bulb is formed inside the mother bulb; the daughter bulb is of the same size as the mother bulb: **"Galanthus nivalis" type** [other examples: *Leucojum vernum*, *Ornithogalum nutans*, *Scilla bifolia*].

(19) Daughter bulb is formed inside the mother bulb; the daughter bulb is much smaller than the mother bulb: **"Ornithogalum gussonii" type** [other examples: *Allium flavum*, *Gagea bobemica*, *Muscari comosum*].

(20) A bulb is formed on a distal part of a below-ground stem: **"Tulipa sylvestris" type** [other examples: *Butomus umbellatus*, *Lloydia serotina*, *Potamogeton filiformis*].

21. **"Dentaria bulbifera" type**. Detached adventitious and axillary buds, dormant apices, turions, plant fragments, and budding plants, i.e., specialised buds or plantlets formed on the above-ground plant parts which decay afterwards. The daughter plant often loses its connection to the mother plants before regrowth. It has its own storage tissue (bulbils, turions) or assimilation capacity (plantlets) [adventitious buds on leaves: *Cardamine pratensis*, *Drosera rotundifolia*; axillary buds on stems: *Saxifraga bulbifera*, *Lilium bulbiferum*; dormant apices and turions: *Aldrovanda vesiculosa*, *Ceratophyllum demersum*; plant fragments: *Elodea canadensis*, *Myriophyllum spicatum*; and budding plants: *Azolla caroliniana*, *Lemna gibba*].

Some of the well-known clonal plants combine 2 or even three types of clonal growth (ordered according to their importance): *Carex flacca* 10, 6; *Cynodon dactylon* 10, 11; *Festuca rubra* 6, 10; *Hieracium pilosella* 12, 11; *Hydrocotyle vulgaris* 11, 13; *Potentilla reptans* 7, 11; *Prunella vulgaris* 11, 12; *Ranunculus repens* 11, 12; *Rubus saxatilis* 7, 14; *Juncus bulbosus* 6, 21, 11; *Lobelia dortmanna* 12 (rarely 21).