

Clonal growth diversity and bud banks of plants in the Czech flora: an evaluation using the CLO-PLA3 database

Diverzita klonálního růstu a banka pupenů u rostlin české flóry: zhodnocení pomocí databáze CLO-PLA3

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The CLO-PLA3 database includes data on vegetative growth relevant to clonality and vegetative regeneration for all (not only clonal) Central-European species. It consists of sheets, with each sheet based on a particular literature reference or our own morphological study documented by drawings. The data are interpreted according to a standardized protocol. The total number of sheets in the database is 7086. A total of 5818 sheets cover the flora of the Czech Republic representing 2775 taxa. Original drawings are available for 938 sheets. There are altogether 17 types of clonal growth organs (CGOs) used to describe morphology of iterative growth. Other clonal traits are the role of CGOs in the life cycle of the plant, shoot cyclicity, persistence of connections between ramets, number of offspring shoots per parent shoot per year, lateral spread per year, type of branching, tillering in graminoids, roots along the CGO, leaf distribution, size of offspring shoot, timing of CGO formation in ontogeny and overlap of shoot generations. Bud bank traits include vertical distribution of buds, their number per shoot and seasonality. Whole-plant traits include taproot persistence, reproduction type, storage organs, age at first flowering and genet life-span. An analysis of the CLO-PLA3 database for the flora of the Czech Republic revealed that plants with epigeogenous and hypogeogenous rhizomes are the most frequent among those growing clonally, followed by root-sprouters, non-clonal plants and plants with rooting above-ground stems. Other types of clonal growth organs like bulbs, stem and root tubers, bulbils, turions, plant fragments and budding are rare. A connection between clonal offspring shoots persisting for more than two years, a shoot longevity of one year, production of one offspring shoot per parent shoot per year and little lateral spread are prevailing trait values in the Czech flora. Seasonal bud banks prevail above ground, perennial bud banks occur mostly in the upper soil layer and the potential bud bank predominantly deeper than 10 cm below ground. From the analysis it follows that even if clonality is widespread in the Czech flora, the overall vegetative multiplication or spreading rates are low. The most common bud bank types reflect the fact that the majority of species in the Czech flora are perennial herbaceous plants.

Key words: bud bank, Central Europe, clonal growth organ, persistence, plant traits, vegetative regeneration

Introduction

Different plant species are successful in different parts of the landscape because they have different traits (Westoby & Wright 2006). Traits are properties supposedly relevant to any ecological function needed by a plant during its life-span (response traits) and/or properties affecting ecosystems functioning (effect traits sensu Lavorel & Garnier 2002). As there is rarely a simple solution to an ecological problem, one trait usually cannot explain differences in plant species distribution (Díaz et al. 2007). Moreover, one trait may be considered both a response and an effect trait (Lavorel & Garnier 2002). This uncertainty leads to an instant need to learn more about the functionality of plant traits.

So far, nearly all research has been on traits relevant to generative regeneration of plants (seed production, seed size, seed dispersal, seed bank – Thompson et al. 1997, Bonn et al. 2000) competitive ability and stress tolerance (plant height, specific leaf area – Garnier et al. 2001; Westoby et al. 2002). There is, however, lack of data on clonal growth and vegetative regeneration collected in a standard way (Weiher et al. 1999) and this information is thus not used in studies on the role of plant traits in response to disturbance and climate change or in determining functional diversity. The reasons for this is it is laborious to collect and difficult to standardize the data and interpret clonal traits (J. Klimešová & F. de Bello, in prep.).

Clonality, defined as the ability to produce potentially independent ramets, is a morphologically very diverse trait, which cannot be expressed as a simple value but rather as a set of traits including multiplication rate, lateral spread and persistence of connections (van Groenendael et al. 1996, Jónsdóttir & Watson 1997, Tamm et al. 2002). Even if these traits are widely accepted as important and relevant for an evaluation of clonal growth, it is not easy to standardize the method of evaluating them for all species. The problem is complicated by the large morphological diversity of plants, plasticity of vegetative growth in relation to plant age, seasonal development and environmental conditions, and by the fact that a lot of species have several ways of growing clonally (Skálová et al. 1997, Klimeš & Klimešová 1999) and may use none, one or all of them in different conditions.

Ability of plants to regenerate vegetatively after a disturbance is another complicated but important trait (Pausas & Lavorel 2003). There are two methods of assessing vegetative regeneration: (i) evaluation of resprouting after experimental disturbance (Cornelissen et al. 2003) or (ii) using bud counts as an indication of regeneration ability (Dalgleish & Hartnett 2006). The first is context-specific and makes comparison between studies, regions, growth forms and types of disturbance difficult. The latter is laborious and has been used only in a few studies. The above-mentioned problems are the reasons why very few comparative studies on clonal growth and vegetative regeneration usually refer to a species pool or complete flora (but see Klimeš & Klimešová 2000, Dalgleish & Hartnett 2006, Pausas & Bradstock 2007).

The aim of our project was to collect data on clonal growth and the bud bank of plants of the flora of Europe, excluding the Mediterranean region, using standardized protocols (Klimeš & Klimešová 2005, Klimešová & Klimeš 2007), publish them on the internet (Klimešová & Klimeš 2006) and evaluate them for a particular area, the Czech Republic. The latter topic is addressed in this study.

The database CLO-PLA3

Data on clonal growth and bud banks were collected from two sources: field morphological studies documented by drawings and literature surveys. The data from those sources were standardized (Klimeš & Klimešová 2005, Klimešová & Klimeš 2007) and are stored in a freely accessible application on the internet (Klimešová & Klimeš 2006). The standardized protocols were published elsewhere, the database and traits used are described here.

Description of the database

CLO-PLA3 is a fully referenced database, which is based on data from literature (5773 sheets) and our own studies (1313 sheets), which were partly also sources for the preced-

ing versions CLO-PLA1 (Klimeš et al. 1997) and CLO-PLA2 (Klimeš & Klimešová 1999), but unlike these version, data from multiple sources are not interpreted here in the form of one value per species but by a complex of data. For each particular reference or studied set of plants there is a particular entry in the database: a sheet. The database covers both modes of clonal growth (simplified in comparison with earlier versions) and numerous plant traits, selected according to potential relevance to the persistence of a plant species in a community (sensu Weiher et al. 1999, Bond & Midgley 2001), such as clonal growth, competitive ability and vegetative regeneration (Table 1). The database traditionally contains not only clonal plants but aims to cover the entire flora of the region (Europe outside of Mediterranean) in particular Central Europe. This database is partly included in the LEDA traitbase of plants of NW Europe (Knevel et al. 2003, 2005).

The total number of sheets in the database is 7086, 5818 of them cover the flora of the Czech Republic and represent 2775 taxa. There are 1 to 19 sheets per taxon. Original drawings are available for 938 of sheets. The only varieties of taxa included are *Allium ampeloprasum* subsp. *ampeloprasum* var. *babingtonii* (Borrer) Syme and *Caltha palustris* var. *radicans* (T. F. Forst.) Hook. Other taxa are either species or subspecies.

The geographical distribution of records in the database reflects the fact that the data were extracted from particular floras and that our field survey was restricted to several regions in Europe (Electronic Appendix 1). The main literature sources were: Biological flora of Central Europe (Kirchner et al. 1908–1942), Atlas of roots of the Central European flora (Kutschera 1960, Kutschera & Lichtenegger 1982, 1992), Ecological flora of the British Isles (published since 1945 in the Journal of Ecology), Biological flora of Canadian weeds (published in the Canadian Journal of Plant Sciences), Biological flora of the Moscow region (Rabotnov 1974–2000), Rothmaler's flora of Germany (Jäger et al. 1987, Jäger & Werner 2002), Hegi's illustrated flora of Central Europe, morphological works by Irmisch (1850), Wittrock (1884), Warming (1909), Rauh (1937), Troll (1937–1942), Arber (1920, 1934), Serebryakov (1952, 1964), Lukasiewicz (1962), Sculthorpe (1967), Serebryakova (1971), Leaky (1981) and Krumbiegel (2002). Certain habitats like heathlands, dunes and salty habitats, which are very rare in Central Europe, are underrepresented in the database (Electronic Appendix 2).

Description of traits

Whole-plant traits

This is a set of traits that are relevant to a whole plant (genet) and describes some attributes of its vegetative growth (see Table 1 for details).

Clonal growth organs

Clonal growth is defined as the ability of a plant to produce offspring ramets. It can be described by several traits. Types of clonal growth organs (CGOs) are delimited according to their morphological features: origin (stem, root, leaf), placement (above-ground, below-ground), storage function. This categorization is based on our preceding classification of CGOs (see Klimeš et al. 1997), but is simpler, as divisions based on longevity and length of increment are not included. Thus, only 17 categories remain (Appendix 1, Fig. 1). Their relationship to the preceding classification used in CLO-PLA1 is shown in Table 5 and the relationship to other classifications of clonal growth is given in Electronic Appendix 3.

Table 1. – Plant traits listed in the CLO-PLA3 database, their attributes and ecological functions. CGO – clonal growth organ.

| Plant traits | Attributes | Ecological functions |
|---|--|--|
| Whole-plant traits: | | |
| Taproot persistence | yes / no | persistence |
| Reproduction types | vegetative / generative / vegetative & generative | clonality |
| Other storage organs | yes / no | persistence |
| Age at first flowering | in years | persistence |
| Genet life-span | in years | persistence |
| Bud bank traits: | | |
| Number of buds per shoot in layers (more than 10 cm above soil surface; from 10 to 0 cm above soil surface; at the soil surface; from 0 to 10 below soil surface; deeper than 10 cm below soil surface) | 0 / 1–10 / >10 | vegetative regeneration, in relation to disturbance severity |
| Seasonality of bud bank in layers | perennial / seasonal / potential / perennial & potential / seasonal & potential | vegetative regeneration, in relation to disturbance timing |
| Clonal growth traits: | | |
| Clonal growth organ | 17 types (see Appendix 1) | clonality |
| Role of CGO | necessary / additive / regenerative / none | clonality |
| Cyclicality [years] | 1 / 2 / >2 | persistence |
| Persistence of connections between ramets [years] | 1 / 2 / >2 | persistence & clonality |
| Number of shoots/ parent shoot/year | <1 / 1 / 2–10 / >10 | clonality |
| Lateral spread [m/year] | <0.01 / 0.01–0.25 / > 0.25 / dispersible | clonality (foraging) |
| Branching | monopodial / sympodial / dichotomic | clonality |
| Tillering in graminoids | intravaginal / extravaginal / intra- & extravaginal | clonality |
| Roots along CGO | along horizontal stem / on oldest part / on youngest part / on shoot base / not applicable | clonality (foraging) |
| Leaf distribution | no rosette / semi-rosette / rosette | competitive ability |
| Offspring in comparison with parent | about the same / much smaller | competitive ability |
| Reproduction vs. clonality | pre-reproductive / reproductive / post-reproductive | clonality |
| Overlap of shoot generations | yes / no | competitive ability |

The fact that a plant has a CGO does not mean that the plant grows clonally, but indicates the morphological type of iterative growth. When this iterative growth results in the production of potentially independent offspring, the nature of this ability is described by other clonal traits like the role of CGO in plant life, shoot cyclicality, persistence of the connection between parent and offspring shoot etc. (Table 1).

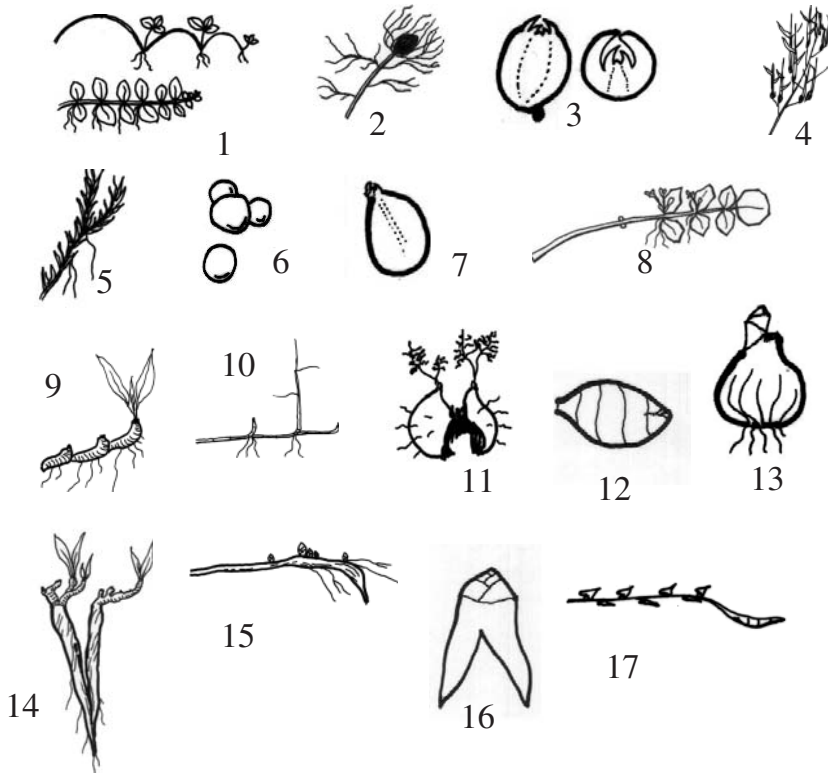


Fig. 1. Morphology of 17 types of CGO. 1 – horizontal rooting stems on or above the soil surface, *Fragaria moschata*, *Lysimachia nummularia*; 2 – turions, *Utricularia vulgaris*; 3 – bulbils and tubers of stem origin on or above the soil surface, *Dentaria bulbifera*, *Saxifraga cernua*; 4 – plantlets (pseudovivipary), *Poa alpina*; 5 – plant fragments of stem origin, *Elodea canadensis*; 6 – budding plants, *Lemna minor*; 7 – root tubers on or above the soil surface, *Ficaria verna*; 8 – buds on leaves (gemmipary), *Cardamine pratensis*; 9 – epigeogenous rhizomes, *Rumex alpinus*; 10 – hypogeogenous rhizomes, *Phalaris arundinacea*; 11 – tuber-splitters, *Corydalis cava*; 12 – stem tubers, *Bolboschoenus maritimus*; 13 – bulbs, *Galanthus nivalis*; 14 – root-splitters, *Verbascum nigrum*; 15 – adventitious buds on roots, *Convolvulus arvensis*; 16 – root tubers below-ground, *Leucorchis albida*; 17 – offspring tubers at distal end of above-ground stems, *Rubus saxatilis*.

Other clonal traits

Role of CGO. A first approximation to clonal growth is the role that a CGO plays in a plant's life: (i) a CGO may be necessary for plant growth, i.e. all adult individuals of all populations have it; (ii) an additive role of the CGO means that it is not necessarily found in all populations or individuals of a population; (iii) a regenerative CGO is triggered only by injury; (iv) none role means that clonal multiplication is excluded. Plants having a CGO only with no, an additional or a regenerative role can be regarded as non-clonal. However, even in these species one can find examples of them spreading clonally in particular situations, for example *Armoracia rusticana*. Plants may have two or more types of CGO with different roles.

Lifespan of a shoot (cyclicality). This trait relates to the traditional distinction between monocyclic, dicyclic and polycyclic shoots. Cycles denote years from sprouting of a bud, through growth, flowering and fruiting of the shoot, until its death. This trait is relatively easily identifiable in sympodially growing and root-sprouting plants. In monopodial plants the apical shoot is vegetative and potentially immortal. Lateral shoots may flower, however in some cases they are formed by a single flower, nevertheless in monopodially growing species cyclicality is always relevant only to flowering shoots. The life-span of a shoot may differ between individual CGOs. Some types of clonal growth result in offspring shoots, which are considerably smaller than the parent shoot. Therefore, their development to first flowering is slower and longer. For example, branching of *Dentaria bulbifera* rhizomes results in offspring shoots capable of flowering in the first year of their life if environmental conditions are favourable. In contrast, offspring shoots that originate from bulbils on stems of parent plants are similar in size to seedlings and need several years to develop to flowering size.

Persistence of the connection between parent and offspring shoot (years). Individual CGOs may differ in the persistence of the connections between parent and offspring ramets. For example, offspring plants developed on stolons of *Fragaria vesca* separate from the parent plant after the first season, however offspring plants initiated by branching of the rhizome of the same plant remain connected for many years. The three categories are: (i) ephemeral connections (e.g., between bulbils and parent plant), (ii) offspring plants that develop on stolons that remain connected with the parent plant for one to two seasons (e.g., plantlets on an above-ground stolon), and (iii) pairs of offspring and parent ramets connected for a longer period, often up to several decades (e.g., daughter ramets connected by an underground rhizome). The shorter the persistence of the connection, the lower the support for initiation of its growth and the slower the initial growth of the offspring ramet. This trait characterizes individual CGOs. In clonal plants utilizing a single mode of clonal growth, it is also applicable to species.

Number of offspring shoots per parent shoot per year. This is a measure of the intensity of clonal multiplication. Values lower than 1 occur in shoots living for several years where branching takes place only after flowering or in monopodially growing plants. The value of 1 corresponds to the situation when a single offspring shoot replaces a parent shoot, such as in non-clonal perennials with root tubers (*Orchidaceae*). Higher values refer to successful multiplication, resulting in an increasing number of descendants. This characteristic may markedly differ between individual CGOs on a single plant. For example, the epigeogenous rhizomes of *Fragaria vesca* have a low multiplication rate. However, stolons may produce up to about 10 daughter plants within one season. It is important to realize that even a production of less than one offspring shoot per year may lead to multiplication in the perspective of a plant's lifespan. In the ontogeny of many species, after an initial high clonal multiplication rate, the number of shoots does not increase any more due to competition. This trait characterizes individual CGOs. In clonal plants utilizing a single mode of clonal growth it is also applicable to species.

Lateral spread per year [m/yr]. Lateral spread by means of vegetative organs ensures that daughter plants are placed in an environment that is similar to that in which the mother plant was capable of multiplying. However, clonal plants vary considerably in spreading rate. It ranges from values close to zero to several metres per year. In some plants, such as many orchids, the daughter plant replaces the mother plant and occupies the same position so that there

is virtually no lateral spreading. The other extreme is represented by water plants forming turions or tubers which can be transported. Plants in which the parent and offspring ramets remain connected for a long time can spread laterally by means of their rhizomes or stolons up to several meters per year. As a measure of lateral spread we use the horizontal increment in the clonal growth organ. This trait characterizes individual clonal growth organs. In clonal plants utilizing a single mode of clonal growth it is applicable at the species level.

Branching. If the apical meristem of a stem splits into two similar branches, branching is called dichotomous (relevant to branching ferns). If the apical meristem continues infinitely in vegetative growth and only side-branches flower, branching is called monopodial and if growth of the apical meristem ceases with flowering, branches replace it and development of each branch is again terminated by flowering, branching is called sympodial. This division is applicable only to stem branching and does not include resprouting of adventitious shoots from leaves and roots.

Tillering in grasses. The offspring shoot (tiller) of a grass may grow up enclosed by a leaf sheath (intravaginal growth) or it may grow horizontally, breaking through the sheath of the subtending leaf (extravaginal growth). Both types may occur in a species.

Roots along clonal growth organs. Adventitious roots are developed on a specific part of a CGO of stem origin. In some species a shoot and roots occupy different places in horizontal projection. For example, a shoot of *Asperula cynanchica* may be 15 cm apart from the root system.

Leaf distribution. Leaf position on the above-ground part of a flowering shoot of herbaceous plants reflects its architecture. Plants with leaves high above the soil surface are good competitors but are vulnerable to disturbance or management (cutting or grazing). This trait is associated with the lifespan of the shoot; as herbaceous plants need to be near the ground during winter, the leaves on dicyclic and polycyclic shoots are usually concentrated in a basal rosette. If leaves are spread only along the stem then the shoot has no rosette; if they are concentrated at the base, it is called a semirosette shoot. If leaves are inserted only at the base of the shoot near the ground, the shoot is called a rosette shoot. In monopodial plants this trait denotes only flowering shoots. In the case of a shoot that has a rosette of leaves in the first year and a long leafy shoot in the second year it is a semirosette shoot, even if the rosette leaves are no longer present at the time of flowering.

Offspring size compared with parent. Some types of clonal growth lead to the production of offsprings similar in size to seedlings, for example the bulbils of *Dentaria bulbifera*.

Bud bank traits

Bud bank traits (Table 1) reflect seasonal variability in numbers and vertical distribution of reserve meristems on a plant. The fact that the part of a plant that survives a disturbance possesses buds means that this feature is a prerequisite for vegetative regeneration. Thus all the buds of a plant that can regenerate vegetatively constitute a pool of reserve meristems called a bud bank (Klimešová & Klimeš 2007). This includes not only axillary buds, which form on stems, but also adventitious buds on roots or leaves, which are formed regularly or are triggered by injury. As disturbances differ in severity and timing, we identify seasonal variation in bud number and vertical distribution of buds as crucial properties of bud banks. The numbers of buds per shoot were assessed according to the occurrence of nodes/leaves, because each node usually bears a viable bud during its entire lifespan (this is a simplification as some nodes may not have buds and some more buds than leaves).

Vertical distribution. The vertical distribution of reserve buds in layers reflects the distribution of buds in relation to certain types of disturbance (e.g., mowing results in removal of above-ground biomass, ploughing in fragmentation of plant organs up to a depth of about 10 cm, etc.). This contrasts with the classification of life-forms by Raunkiaer (1934), who considers only the position of buds surviving one type of disturbance: unfavourable season (cold or dry conditions).

Seasonal variation. Three types of bud bank were distinguished, similar to the seed bank: seasonal bud banks (developing on plant organs with a life-span shorter than two years), perennial bud banks (on plant organs with a life-span of two or more years) and potential bud banks (reflecting the ability of a plant to sprout adventitiously from roots or leaves). Because adventitious buds are not countable on an intact plant we did not assess the number of adventitious buds. Moreover, data on bud numbers are categorized. This simplification enabled us to complete the data in the bud bank for almost all the species in the database.

Relevance of the traits for different growth forms

The database focuses on adult individuals of perennial herbs from the temperate zone and thus uses a categorization and scaling that fits these plants best. A shoot – product of the apical meristem – is considered as the basic unit of plant organization. A shoot is the basic unit in our database on CGOs and bud banks. In the case of monopodially growing plants cyclicality is relevant only to flowering shoots. Even in tussock and cushion plants a shoot is the basic unit even if the whole genet is easily distinguishable.

Another problem is the vertical distribution of bud banks in aquatic plants and epiphytes. In the former, the “0–10 cm” and “> 10 cm” layers denote a water column, in the latter, soil surface is coded as the surface of the host plant.

For trees and shrubs some traits were excluded (e.g., shoot cyclicality, branching, roots along CGO, rosette, offspring in comparison with parent, reproduction versus clonality, generation overlap and bud number) and others modified. For example, instead of the shoot, the trunk with crown was considered the basic unit for traits like persistence of connection, production of offspring shoots and lateral spread.

Annual and biennial plants only have CGOs when they produce more shoots. Such plants may or may not multiply clonally. For plants that during their lifespan only produce a primary shoot, only the bud bank traits, shoot cyclicality and leaf distribution are included in the database.

Tools for searching the database

Data for one species from different sources may differ. There are several reasons for that, not only inherited variability in vegetative growth but also other factors may play a role: (i) the aims of authors differ, e.g. some aim to compile available information into a biological flora, others describe species in an ecological paper (see Electronic Appendix 4); (ii) the opinion of authors differ, as they are not equally experienced; (iii) data in the literature vary from a description of an individual plant to a compendium of all the available information for the species. Due to these problems we avoid automatic aggregation of the data – each user should decide how to handle multiple data for one species. A search can be made

according to plant name or any cell in a sheet. Filtering according to cell content may be accomplished in several steps.

In the current study we analyzed only the species in the flora of the Czech Republic included in the check list of the Czech flora (Chrtěk 2007) and included also plant descriptions that came from abroad. We used all the available data (records, see below), i.e. in the case where there are several sheets for one species we used the information from all of them and in the case of several types of clonal growth organs on one sheet again all the information was used. In the following text we call a piece of information a “record”. For example all data for the lateral spread of a species, independent of how many sources (sheets) or types of clonal growth organs are involved, are individual records.

Trait spectra for plants in the Czech Republic

Whole-plant traits

Loss of the perennial main root during a plant’s lifespan, which is a prerequisite for the vegetative multiplication of a plant, is reported in about two thirds of the records (Table 2). Records of the relative importance of vegetative and generative regeneration (Table 2), age at first flowering (Table 3) and life-span (Table 4) occur less frequently in the database, as they were filed only when explicitly cited in the literature. The distribution of these data does not reflect the situation in the flora but rather the fact that for short-lived species these characteristics are more often available than for perennial species.

Specialized storage organs other than clonal growth organs are reported in only 7% of the records (Table 2). This is probably due to the advantage in the case of plant fragmentation of storing assimilates and having buds in one organ.

Table 2. – Distribution of records in the CLO-PLA3 database of attributes of whole-plant traits of species in the Czech flora. Sp – number of species for which data are available.

| Trait | Number of records |
|-------------------------|-------------------|
| Tap root persistence: | |
| no | 3284 |
| yes | 1905 |
| Sp | 2228 |
| Reproduction types: | |
| generative | 165 |
| vegetative | 83 |
| vegetative & generative | 86 |
| Sp | 299 |
| Other storage organs: | |
| no | 4638 |
| yes | 330 |
| Sp | 2134 |

Table 3. – Categorized records for the “Age at first flowering” trait for species in the Czech flora. The prevalence of short-lived species reflects the fact that more data is available for short- than long-lived plants.

| Age at first flowering | Number of records |
|------------------------|-------------------|
| 1–5 years | 860 |
| 2–9 years | 571 |
| 10–19 years | 22 |
| > 20 | 6 |

Table 4. – Categorized records for the “Plant life span” trait of species in the Czech flora. The prevalence of short lived species reflects the fact that more data is available for short- than long-lived plants.

| Genet life span | Number of records |
|-----------------|-------------------|
| 1–3 years | 803 |
| 2–6 years | 326 |
| 3–10 years | 54 |
| 10–30 years | 10 |
| 20–50 years | 14 |
| >50 years | 8 |

Clonal growth organs

The most common CGOs in the flora are two types of rhizomes: epigeogenous (originated above-ground) and hypogeogenous (originated below-ground) rhizomes are each reported more than 1400 times (e.g., 50% of the records, Fig. 2, Table 5) for the plants in the Czech flora in the CLO-PLA3 database. Another type of CGO is a splitting main root (14% of records), adventitious buds on roots (12% of records) and a horizontal above-ground rooting stem (9% of records). Other types of CGO are rare. The least represented types of clonal growth organs are tuber splitters and above-ground root tubers, for each of which are there 10 records (Fig. 2).

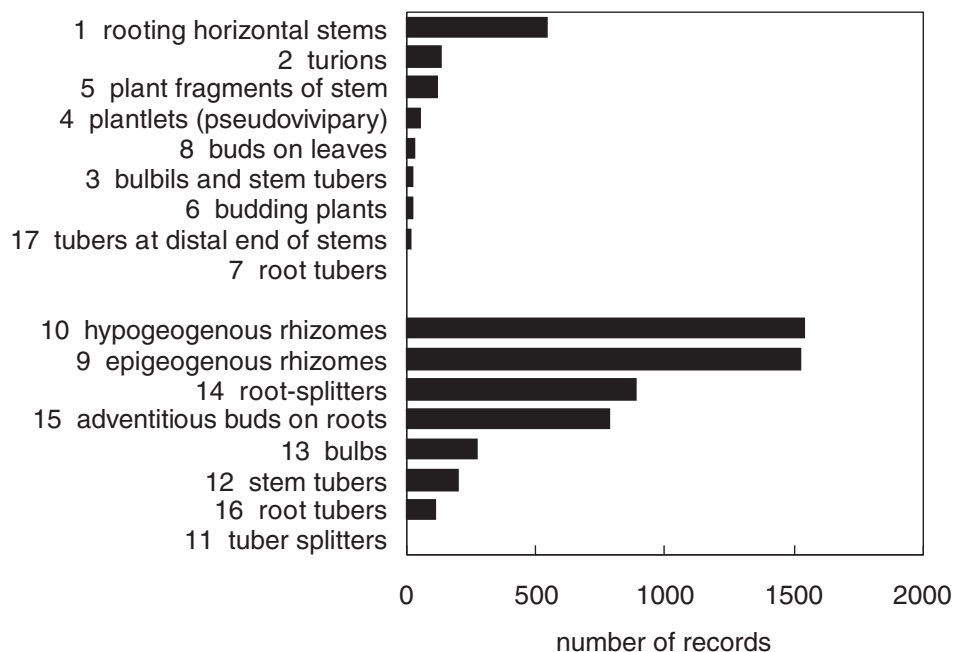


Fig. 2. – Distribution of records for 17 types of clonal growth organs in the CLO-PLA3 database for 2226 plant species in the Czech flora. In the upper part of the graph above-ground and in the lower part, below-ground clonal growth organs are shown.

Table 5. – Comparison of the proportion of clonal growth organs in the Czech flora (according to the CLO-PLA 3 database) and in data for Central Europe (according to the CLO-PLA1 database). Relevant names for clonal growth organs in both databases are shown. CLO-PLA3: behind numerical code of the clonal growth organ (CGO) type is the name of the type according to its morphology; CLO-PLA1: behind numerical code the CGO type is the name of the type according to its typical representative.

| CLO-PLA3 | Records (%) | CLO-PLA1 (Klimeš et al. 1997) | Species(%) |
|---|-------------|--|------------|
| 17 offspring tubers at distal end of aboveground stems | 0.25 | 14 <i>Calystegia sepium</i> | 0.14 |
| 11 tuber splitters | 0.16 | 17 <i>Corydalis cava</i> | 0.24 |
| 16 root tubers belowground | 1.83 | 4 <i>Ranunculus ficaria</i> | 1.26 |
| 12 stem tubers | 3.12 | 15 <i>Lycopus europaeus</i> , 16 <i>Corydalis solida</i> | 1.53 |
| 13 bulbs | 4.35 | 18 <i>Galanthus nivalis</i> , 19 <i>Ornithogalum gussonei</i> , 20 <i>Tulipa sylvestris</i> | 1.67 |
| 7 root tubers aboveground, 6 budding plants, 3 bulbils and stem tubers aboveground, 8 buds on leaves, 4 plantlets (pseudovivipary), 5 plant fragments of stem origin, 2 turions | 6.21 | 21 <i>Dentaria bulbifera</i> | 2.69 |
| 1 rooting horizontal stems aboveground | 8.62 | 5 <i>Lycopodium annotinum</i> , 11 <i>Fragaria vesca</i> | 7.61 |
| 15 adventitious buds on roots | 12.42 | 2 <i>Alliaria petiolata</i> , 3 <i>Rumex acetosella</i> | 3.24 |
| 14 root-splitters | 14.11 | 1 <i>Trifolium pratense</i> | 5.29 |
| 9 epigeogenous rhizomes | 24.32 | 6 <i>Festuca ovina</i> , 7 <i>Rumex obtusifolius</i> , 8 <i>Rumex alpinus</i> , 12 <i>Caltha palustris</i> | 26.83 |
| 10 hypogeogenous rhizomes | 24.61 | 9 <i>Dactylis glomerata</i> , 10 <i>Aegopodium podagraria</i> , 13 <i>Galium odoratum</i> | 16.03 |

Table 5 presents a comparison of the proportions of types of clonal growth organs recorded for plants in the Czech flora in the CLO-PLA 3 database and plants in Central Europe according to CLO-PLA1 (Klimeš et al. 1997). Ranking of types of clonal growth organs is similar, except for a few details: (i) the higher proportion of root splitters (CGO 14) in the new version of the database is because all the plants with a perennial main root but unable to form adventitious roots are classified as root-splitters whereas in CLO-PLA1 these plants were partly classified as non-clonal; (ii) the higher proportion of plants with adventitious buds on that roots reflects the great effort invested in literature surveys, and field and experimental studies of species able to develop adventitious buds on their roots (CGO 15) (e.g., Klimešová 2001, 2003, 2007, Klimešová et al. 2004, 2007, 2008, Martínková et al. 2004a, b, 2006, 2008, Klimešová & Martínková 2004); (iii) an increasing proportion of other categories is probably caused by both, including morphological types of growth that do not involve clonal multiplication and the higher quality of the data.

Other clonal traits

A plant spreads and multiplies clonally if its CGO is reported to be necessary or have an additive role in the life history of the plant. A necessary CGO is reported in 3890 records, an additive CGO in 917 records. This means that 80% of the recorded CGOs might be considered to be important for clonal growth of plants. A regenerative CGO is reported 407 times, i.e. in these cases clonal growth is triggered by injury. When the role of the CGO is reported as none (796 times), it means that the plant does not grow clonally (Table 6). In

Table 6. – Distribution of records in the CLO-PLA3 database for attributes of quantitative clonal traits of species in the Czech flora. Sp – number of species for which data are available.

| Trait | Number of records |
|-------------------|-------------------|
| CGO role: | |
| additive | 917 |
| necessary | 3890 |
| regenerative | 407 |
| none | 796 |
| Sp | 1637 |
| Cyclicality: | |
| > 2 | 381 |
| 1 | 3120 |
| 2 | 1751 |
| Sp | 1945 |
| Persistence: | |
| > 2 | 3233 |
| 1 | 1103 |
| 2 | 636 |
| Sp | 1573 |
| Number of shoots: | |
| < 1 | 472 |
| > 10 | 86 |
| 1 | 2285 |
| 2–10 | 1683 |
| Sp | 1499 |
| Lateral spread: | |
| < 0.01 | 2580 |
| > 0.25 | 376 |
| 0.01–0.25 | 1861 |
| dispersible | 363 |
| Sp | 1552 |

Table 7. – Distribution of records in the CLO-PLA3 database for attributes of qualitative clonal traits of species in the Czech flora. Sp – number of species for which data are available.

| Trait | Number of records |
|---|-------------------|
| Branching: | |
| dichotomous | 66 |
| monopodial | 437 |
| sympodial | 3956 |
| Sp | 1471 |
| Tillering: | |
| extravaginal | 313 |
| intra- and extravaginal | 9 |
| intravaginal | 350 |
| Sp | 267 |
| Roots along CGO: | |
| Along horizontal stem | 2049 |
| on oldest part | 102 |
| on shoot base | 894 |
| on youngest part | 21 |
| Sp | 1205 |
| Shoot architecture: | |
| no rosette | 2875 |
| rosette | 695 |
| semi-rosette | 2035 |
| Sp | 2024 |
| Offspring size in comparison with parent: | |
| about the same | 4600 |
| much smaller | 411 |
| Sp | 1537 |
| Reproduction versus clonality: | |
| postreproductive | 14 |
| prereproductive | 235 |
| reproductive | 435 |
| Sp | 322 |
| Generation overlap: | |
| no | 1903 |
| yes | 2525 |
| Sp | 1415 |

the database there are records for 2226 species in the Czech flora with at least one CGO, but the role of the CGO is reported only for 1637 of them, so that we have no information on the role of the CGOs in the 589 remaining species.

CGOs of particular species may be characterized by quantitative (Table 6) and qualitative traits (Table 7). In the Czech flora, the following quantitative trait attributes prevail: life span of shoot lasting one year (monocyclic shoot, i.e. shoot that sprouts from a bud in spring and flowers and dies in the same season); persistence of connections between shoots that last for more than two years; only one offspring shoot per mother shoot per year; and very poor lateral spread (Table 6).

Table 8. – Distribution of records in the CLO-PLA3 database for attributes of bud-bank traits (bud number) of species in the Czech flora. Sp – number of species for which data are available.

| Categories of bud numbers | Vertical distribution in relation to soil surface | | | | |
|---------------------------|---|--------------|------|-------------|----------|
| | > 10 cm | > 0 to 10 cm | 0 cm | 0 to –10 cm | < –10 cm |
| > 10 | 445 | 251 | 251 | 2881 | 122 |
| 0 | 1502 | 891 | 891 | 1259 | 5120 |
| 1–10 | 3336 | 4130 | 4130 | 1225 | 44 |
| Sp | 2563 | 2339 | 2339 | 2665 | 2155 |

Among quantitative traits, the following attributes prevail in plants in the Czech flora (Table 7): sympodial branching of clonal growth organs of stem origin prevail over monopodial and dichotomous branching; extravaginal tillering of graminoids is as common as intravaginal tillering; roots most usually develop along the entire clonal growth organ of stem origin; leaves are usually distributed along the entire shoot or form leafy stems with a rosette at its base, whereas shoots with all the leaves in a basal rosette are less common; offspring shoots are usually of the same size as parent shoots, and clonal growth is usually characteristic of reproductive plants and shoot generations usually overlap in time (Table 7).

Bud bank traits

Reserve meristems are concentrated in the top soil layer (from 0 to –10 cm) (Table 8). The predominant type of bud bank located above-ground is a seasonal bud bank, perennial bud bank is the dominant type close to the soil and the potential bud bank prevails deeper in the soil (Table 9). These bud bank characteristics reflect the fact that most species in the Czech flora are perennial herbaceous plants.

Table 9. – Distribution of records in the CLO-PLA3 database for attributes of bud-bank traits (seasonality) of species in the Czech flora. Sp – number of species for which data are available.

| Categories of seasonality | Vertical distribution in relation to soil surface | | | | |
|---------------------------|---|--------------|------|-------------|----------|
| | > 10 cm | > 0 to 10 cm | 0 cm | 0 to –10 cm | < –10 cm |
| perennial | 138 | 281 | 1640 | 2633 | 116 |
| potential | 5 | 17 | 16 | 253 | 615 |
| seasonal | 3638 | 4088 | 3062 | 1003 | 25 |
| perennial & seasonal | – | – | – | 359 | 17 |
| potential & seasonal | 4 | 6 | 21 | 56 | 13 |
| not applicable | 1487 | 863 | 489 | 1221 | 4709 |
| Sp | 2409 | 2306 | 2577 | 2775 | 2338 |

Ecological relevance of traits

Clonal traits

The CGO is a complex trait, which is correlated with many functional traits. However, functional differences among CGOs are indirectly confirmed by studies that reveal different CGO spectra in different communities (Klimeš et al. 1997, Halassy 2005, Sosnová 2007), in invasive versus non-invasive species (Pyšek 1997) and rare versus common plants (Klimeš & Klimešová 2000). The CGOs of plants determine the growth strategy of plant roots (Šmilauerová & Šmilauer 2007).

For example, defining the categories splitting/non-splitting plants, by the persistence of the connection between offspring shoots, and spreading/non-spreading plants, by the lateral spread per year, revealed different affinities for nutrients, moisture and light gradients (van Groenendael et al. 1996). Shoot life-span was found to be negatively correlated with nutrient addition and species diversity in species rich grasslands (Sammul et al. 2003), and was higher in abandoned, shrubby than in regularly mown, open grassland. Similarly, average species mobility of plants, measured as the year to year increment in the growth of a rhizome, was higher in abandoned than managed grassland (Tamm et al. 2001). Differences in clonal trait spectra were found in wetland communities in the Netherlands. Splitting clones with dispersable offspring ramets and low cyclicality of shoots were typical of open water communities, persistent clones with high cyclicality and poor spreading prevailed in fens and bogs, and in floodplains and salt marsh intermediate clonal growth characteristics were found (M. Sosnová et al., in prep).

Probably the most often analyzed clonal trait is persistence of connection among ramets. Long persistence of connection i.e. “conservative strategy” sensu de Kroon & Schieving (1990) or “integrators” sensu Jónsdóttir & Watson (1997), the clonal growth strategy in resource-poor environments, is a common feature of plants in the flora of Central Europe (van Groenendael et al. 1996), Trans Himalayas (Klimeš 2008) and wetland communities in the Netherlands (M. Sosnová et al., in prep).

An appreciation of the role of CGOs in plant life allows an assessment of intermediate growth forms, which may be useful for determining the functioning of clonality. For example, potential root sprouters forming adventitious shoots only after injury (regenerative role of CGOs) may regularly spread and multiply clonally in recurrently disturbed habitats (Klimešová & Martínková 2004, Palacio et al. 2007).

Vegetative regeneration after an injury based on a bud bank

The bud bank, originally elaborated by Harper (1977) and recently reviewed by Klimešová & Klimeš (2007), is a trait independent of plant growth-form and ecosystem that can be used as a tool to assess resprouting ability of plants in communities subjected to disturbance. All buds on a plant may contribute to vegetative regeneration. After a moderate disturbance, i.e. removal of part of the above-ground biomass, the buds situated on above-ground parts of the plant resprout (Bellingham & Sparrow 2000). After a severe disturbance removing the above-ground parts of a plant completely, resprouting is based on buds situated below-ground (Klimešová & Klimeš 2003). Thus, vertical distribution of buds is an important characteristic of the bud bank, indicating the potential to resprout after disturbances differing in severity (Vesk et al. 2004, Vesk & Westoby 2004).

As the number of buds on a plant may fluctuate in the course of a year, timing of disturbance may strongly affect the response of a plant to disturbance (Barrat-Segretain & Bornette 2000). Geographical differences in bud bank properties may cause certain regions to be more vulnerable to environmental change (Dalglish & Hartnett 2006) and specific types of disturbance may be associated with particular traits of the bud bank. For example, in eroded lands in Spain plants with the ability to form adventitious buds on roots are more common in heavily disturbed areas (Guerrero-Campo et al. 2006) and root sprouting is a common strategy in Brazilian semi-deciduous forest affected by fires (Rodrigues et al. 2004). Taking into account bud bank traits in areas other than the traditional ones like fire prone ecosystems and arable land, may result in a better understanding of persistence traits (Klimešová & Klimeš 2003).

Potential use of the CLO-PLA3 database

The database can be used for searching data and literature about persistence traits of species. For example, studies on the regeneration of vegetation after disturbance, population dynamics of plants capable of vegetative multiplication, risk assessment in endangered species etc., will profit from easy access to the data. When clonal growth or vegetative regeneration is considered in similar studies, usually only two categories for the evaluation of a plant's possibility to multiply clonally or regenerate vegetatively are used: yes or no. This has led to an underestimate of the role of vegetative persistence traits in the life history of plants. CLO-PLA 3 provides a tool to determine the role of persistence traits more accurately in future studies.

See <http://www.preslia.cz> for Electronic Appendices 1–4.

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Souhrn

Navzdory skutečnosti, že většina rostlin je klonálních a má zásobní meristémy pro vegetativní regeneraci (banka pupenů), informace o parametrech klonálního růstu jsou roztroušeny v literatuře a nebyly dosud syntetizovány pro žádné území, takže role banky pupenů je přehlížena. Zde prezentujeme první zhodnocení parametrů klonálního růstu a banky pupenů pro českou flóru s využitím databáze CLO-PLA 3, která je zaměřena na funkční vlastnosti spojené s perzistencí rostlin, a představujeme její strukturu.

Databáze CLO-PLA3 obsahuje data o vegetativním růstu, která jsou relevantní pro klonalitu a vegetativní regeneraci pro všechny (nejen klonální) druhy rostlin Evropy bez Mediteránu. Databáze je uspořádána jako sada tabulek, každá tabulka je založena na datech z jednoho literárního zdroje nebo na vlastním studiu rostlin jednoho druhu na jedné lokalitě. Jedná se vlastně o interpretaci literárního popisu, obrázku nebo vlastní studie podle standardního protokolu. Celkový počet tabulek v databázi je 7086, z čehož 5818 tabulek se týká 2775 druhů české flóry. Jednotlivé druhy české flóry jsou dokumentovány 1 až 19 tabulkami, originální kresby orgánů klonálního růstu jsou k dispozici u 938 tabulek. V každé tabulce může být vyplněno maximálně 80 políček, 52 pro vlastnosti spojené s klonalitou, 10 pro vlastnosti banky pupenů, 5 pro vlastnosti celé rostliny a 13 pro doplňující informace jako je citace zdroje nebo geografický původ studovaného rostlinného jedince.

Vlastnosti klonálního růstu jsou uvedeny v databázi zvlášť pro každý orgán klonálního růstu (CGO), je-li jich pro jeden druh zaznamenáno více typů. CGO je definován svou morfologií, ovšem to, že jej rostlina má, neznamená automaticky, že roste klonálně. CGO vlastně vyjadřuje způsob, jak jsou produkovány následné generace prýtů, což v důsledku může nebo nemusí vést ke klonálnímu růstu. Samotná míra klonální multiplikace je vyjádřena atributy dalších vlastností klonálního růstu.

Orgány klonálního růstu jsou klasifikovány do 17 typů, maximálně jsou uvedeny 4 pro jeden druh v jedné tabulce. Ostatní vlastnosti klonálního růstu jsou role orgánu klonálního růstu v životě rostliny, cyklicita prýtu, vytrvávání spojení mezi rametami, počet dceřinných prýtů vytvořených mateřským prýtem za jeden rok, boční šíření za rok, typ větvení, odnožování u travin, umístění kořenů podél orgánu klonálního růstu, rozložení listů podél stonku, velikost dceřinného prýtu ve srovnání s mateřským prýtem, načasování růstu orgánu klonálního růstu v ontogenezi rostliny a překryv generací prýtů. Vlastnosti banky pupenů jsou vertikální distribuce pupenů vzhledem k povrchu půdy, počet pupenů na prýt a sezónnost. Vlastnosti celé rostliny zahrnují persistenci hlavního kořene, typ reprodukce, zásobní orgán, věk prvního kvetení a délku života genety.

Analýza databáze CLO-PLA3 pro druhy české květeny ukázala, že epigeogenní a hypogeogenní oddenky jsou nejčastějšími typy orgánů klonálního růstu, následovány jsou odnožováním z kořenů a neklonálními rostlinami s vytrvalým hlavním kořenem a rostlinami s horizontálním kořenícím stonkem. Ostatní typy klonálního růstu, jako jsou cibule, stonkové a kořenové hlízy, pacibulky, turiony, fragmenty rostlin a pučící rostliny, jsou vzácné. Vytrvávání spojení mezi rametami déle než dva roky, délka života prýtů více než jeden rok, jeden dceřinný prýt vyprodukovaný mateřským prýtem za rok a boční šíření na velmi krátkou vzdálenost jsou převažujícími hodnotami dalších charakteristik klonálního růstu pro celou flóru. Sezónní banka pupenů převažuje v nadzemí, vytrvalá banka pupenů převažuje ve svrchní vrstvě půdy a potenciální banka pupenů převažuje v hloubce půdy víc než 10 cm.

Z analýzy vyplývá, že i když je klonalita široce rozšířena mezi druhy české květeny, celkový stupeň multiplikace a bočního šíření klonů je nízký. Nejběžnější zaznamenané typy banky pupenů odrážejí fakt, že většina druhů flóry jsou vytrvalé byliny.

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Appendix 1. – Key for the identification of clonal growth organs (CGOs).

- 1 stems only above ground2
- 1 stems also below ground8
- 2 horizontal or bowing rooting stem3
- 2 plant fragments4
- 2 neither adventitious roots nor buds are present on roots non-clonal plants (11)
- 3 below-ground tubers produced at distal end of above-ground stem or along it (17)
- Offspring tubers at distal end of above-ground stems:**
- below-ground storage and regenerative organ of shoot origin; offspring tubers produced at the end of a rooting horizontal, above-ground leafy stem (*Rubus saxatilis*, Fig. 1/17)
- 3 plantlets produced along an above-ground stem or at its end (1)
- Rooting horizontal stems on or above soil surface:**
- clonal growth organ rooting in the soil and providing connection between offspring plants or formed by a creeping plant axis; nodes on stem bearing leaves, internodes usually long, stem serving as a storage organ and a bud bank; vegetative spreading sometimes fast and persistence of horizontal above-ground stems differs considerably among species (*Fragaria moschata*, Fig. 1/1)
- 3 creeping plant (*Lysimachia nummularia*) (1)
- 4 plant fragments that are shed and disposed during the growing season5
- 4 plant fragments specialized for overwintering (turions) (2)
- Turions:**
- detachable over-wintering buds (usually of water plants) composed of tightly arranged leaves filled with food reserves; turions develop axially or apically usually dormant and needing vernalization to re-grow (*Utricularia vulgaris*, Fig. 1/2)
- 5 unspecialized plant fragments (5)
- Plant fragments of stem origin:**
- detached parts of shoot with rooting ability (*Elodea canadensis*, Fig. 1/5)

- 5 budding plants(6)
- Budding plants:**
plant formed by a small frond (e.g. *Lemna*); extremely reduced plant body of aquatic plants; its growth results in the production of similar structures, which are quickly detached from parent plant (*Lemna minor*)
- 5 detachable offspring6
- 6 offspring on leaves (gemmaipary) (*Cardamine pratensis*)(8)
- Buds on leaves (gemmaipary):**
adventitious buds on leaves formed sometimes only after shedding or detaching of leaves from parent plant; on bare wet soil develop into plantlets resembling seedlings in size (*Cardamine pratensis*, Fig. 1/8)
- 6 offsprings in inflorescence (pseudovivipary)(4)
- Plantlets (pseudovivipary):**
meristem normally develops into a flower, but forms vegetative buds (plantlets, bulbils, roots or stem tubercules), which sometimes are quickly detached from parent plant; alternatively the entire inflorescence falls to the ground and the plantlets root at the soil surface; offspring size similar to seedlings (*Poa alpina*, Fig. 1/4)
- 6 offspring in axils of leaves7
- 7 storage in leaves or stems (*Saxifraga cernua*)(3)
- Bulbils and tubers of stem origin on or above soil surface:**
small vegetative diaspores produced in axils of leaves on stems above-ground; called bulbils (food stored in scales) or stem tubercules (food stored in the stem) depending on where the food is stored within the buds; quickly shed from the parent plant and begins to grow immediately; young plants regenerating from bulbils and tubercules resemble seedlings in size (*Dentaria bulbifera*, *Saxifraga cernua*, Fig. 1/3)
- 7 food storage in adventitious root (root tubercules) (*Ficaria verna*)(7)
- Root tubers:**
small vegetative diaspores produced in axils of leaves on stems above-ground; called root tubers (food stored in an adventitious root); young plants regenerating from tubercules resemble seedlings in size (*Ficaria verna*, Fig. 1/7)
- 8 below-ground stems lack specialized storage organs9
- 8 below-ground stems have specialized storage organs, stems sometimes reduced12
- 8 roots with adventitious buds(15)
- Adventitious buds on roots:**
plant roots (main root including the hypocotyle, and adventitious roots) forming adventitious buds spontaneously or after injury; after bud formation on horizontal roots extensive clonal growth sometimes occurs; persistence of roots with adventitious buds differ considerably among species (*Convolvulus arvensis*, Fig. 1/15)
- 9 adventitious roots present10
- 9 adventitious roots absent11
- 10 renewal buds localized below-ground (hypogeogenous rhizome)(10)
- Hypogeogenous rhizomes:**
perennial organs of stem origin formed below-ground; rhizome usually growing horizontally at a species-specific depth, which periodically becomes orthotropic and forms above-ground shoots; horizontal part of the rhizome bearing bracts, some roots and having long internodes; vegetative spreading often fast, up to several metres · yr⁻¹; persistence of hypogeogenous rhizome differs considerably among species (*Phalaris arundinacea*, Fig. 1/10)
- 10 renewal buds localized at soil surface, stem pulled below ground by roots or buried in litter (epigeogenous rhizome)(9)
- Epigeogenous rhizomes:**
perennial organs of stem origin formed above-ground; its distal part covered by soil and litter or pulled into the soil by contraction of roots; nodes bearing green leaves, internodes usually short; rhizomes bearing roots and serving as a bud bank and storage organ; vegetative spreading usually slow (up to a few cm · year⁻¹), persistence of epigeogenous rhizomes differs considerably among species (*Rumex alpinus*, Fig. 1/9)
- 11 main (primary) root surviving for the entire life of the plant(14)
- Root-splitters:**
plant possessing primary root system lacking adventitious roots and buds; centre of senescing tap root of old plants decays and in some species results in plant fragmentation; old individual genet disintegrating into ramets bearing parts of main root and one or a few shoots; vegetative spreading poor; tap root serving as storage organ and vascular link between shoots; bud bank situated on perennial bases of shoots (caudex). (*Verbascum nigrum*, Fig. 1/14).

- 11 hypocotyl surviving for the entire life of the plant, forming a tuber(11)
Tuber-splitter:
 plant develops only one perennial tuber (usually formed by hypocotyle), no offspring tubers produced; in senescing plants tubers sometimes decay from centre resulting eventually in plant fragmentation (*Corydalis cava*, Fig. 1/11)
- 12 storage in leaves(13)
Bulbs:
 storage organ consisting of storage leaves and shortened stem base; bulb formed by organs produced in one season or over the course of several seasons; representing one renewal bud; in addition, some plants produce small bulbs and/or bulbils; plants growing from them resemble seedlings (*Galanthus nivalis*, Fig. 1/13)
- 12 storage in stem(12)
Stem tubers:
 below-ground, usually short-lived storage and regenerative organ of shoot origin; offspring tubers attached to a parent tuber or produced at the end of a hypogeogenous rhizome; parent plant dies back in autumn, except for stem tuber(s) bearing one dominant bud, each utilised for spring regrowth; in summer old tubers decay and new ones form; in addition some plants produce small tubers and/or tubercules; plants growing from them resemble seedlings in size (*Bolboschoenus maritimus*, Fig. 1/12)
- 12 storage in adventitious root(16)
Root tubers:
 below-ground storage and overwintering organ of root origin bearing a bud or buds of stem origin; plant dies back in autumn, except for root tuber(s) with buds, which produce the regrowth in spring; in summer old tubers decay and new ones form (*Leucorchis albida*, Fig. 1/16). Root tubers serving only as a perennial storage organ are not included (e.g. *Cirsium tuberosum* and *Sedum telephium*)