

CLO-PLA2 – a database of clonal plants in central Europe

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Abstract

'CLO-PLA2' (CLOnal PLAnts, version 2) is a database on architectural aspects of clonal growth in vascular plants of central Europe. The database includes 2749 species, characterised by 25 variables, either directly or indirectly related to clonal growth. The total number of items in the database is over 12750. The structure of the database is described and the variables used to characterise clonal growth of individual species are listed. Two examples of database utilisation are given. The first concerns the relationship between habitat niche width and the mode of clonal growth. Turf graminoids, species with long-lived rhizomes either short to long and formed below-ground, or short and formed above-ground, and short-lived rhizomes formed above-ground, are over-represented among the species with very broad niches and under-represented among the species with narrow niches. In contrast, species multiplying by plant fragments are missing among the species with the broadest niches. The second example explores how individual clonal growth modes are combined in individual species. About 21% of species of clonal plants have more than one mode of clonal growth. Some combinations are over-represented in certain families and environments. The application of phylogenetic independent contrasts (PIC) showed that both phylogenetic constraints and adaptations to particular environmental conditions play important roles in determining the observed pattern.

Introduction

The comparative approach represents one of the most promising directions for future research in ecology (Harvey et al. 1995; Ricklefs 1996; Silvertown et al. 1997). As well as new analytical techniques (Harvey & Pagel 1991; Purvis & Rambaut 1995), extensive databases summarising information scattered over thousands of papers and books have been developed for this purpose. Some of the databases are available as Web sites (http://iopi.csu.edu.au/iopi/iopidpd1.html), others have been published (e.g., Lindacher 1995). Most databases contain floristic and taxonomic data (http://iopi.csu.edu.au/iopi/iopidpd1.html), whereas ecological information has rarely been included (Frank & Klotz 1990; Ellenberg et al. 1992; Fitter & Peat 1994).

Detailed information on the biology of individual species has been summarised in ecological floras. The first was published in Germany (Kirchner et al. 1908–1936). This ambitious series is incomplete but includes more than 300 species, which is more than most other series started at a later date. The autecological oriented approach has further been developed in Great Britain. The Biological Flora of the British Isles was started in 1941 and by the end of 1997 included more than 250 species. The most extensive biological floras following the British concept are published for the Moscow Region (Rabotnov 1974; 13 volumes available in 1997) and for the weeds of Canada – Biological flora of Canadian weeds (Cavers & Mulligan 1972, at present containing about 100 species). A biological flora of Central Europe was recently started in Switzerland (Poschlod et al. 1996).

In some regions, the extensive knowledge of plant naturalists on the distribution of species made it possible to estimate indicator values of individual species for basic environmental factors, such as soil moisture, ambient temperature, light availability, soil pH and nutrients (Ramenskij 1956; Ellenberg 1948, 1950, 1952, 1974; Ellenberg et al. 1992). Later, similar indicator values were tabulated in several European countries, e.g., in Switzerland (Landolt 1977), the Netherlands (de Vries et al. 1957), Russia (Ramenskij et al. 1956; Cyganov 1983), Hungary (Zólyomi et al. 1966; Borhidi 1995); Czechoslovakia (Mráz & Samek 1966; Zlatník 1970), Romania (Donita et al. 1977; Sanda et al. 1983), Slovakia (Jurko 1990), and several successors continued Ellenberg's work in Germany (Petersen 1953; Wagner 1955; Klapp 1965; Hundt 1966). Ellenberg's indicator values of the German flora were later combined with extensive data on life forms, pollination, dispersal (Knuth 1898-1899; Rothmaler 1987), distribution among habitats, and preference for soil conditions in Germany (Oberdorfer 1994) and the Netherlands (Weeda et al. 1985–1993). Further, data on geographic distribution (Meusel & Jäger 1965-1992), hemeroby (plant response to human-induced disturbance), leaf anatomy and leaf persistence were added to the database of biological and ecological data for the flora of the eastern part of Germany (Frank & Klotz 1988, 1990). This database, containing 2208 species, was computerised under the name FLORA D. The latest attempt to combine the available databases of indicator values for central Europe has been made in Switzerland (Lindacher 1995).

In addition, several large screening programs have been initiated (DNA content - Bennett & Leitch 1997; RGR – Lambers & Porter 1992; life strategy – Grime et al. 1988, mycorrhiza - Harley & Harley 1987). Finally, an integrated database has been developed (Fitter & Peat 1994) summarising much of the available information on the flora of Great Britain. In 1993 it contained 1777 species of gymnosperms and angiosperms. Over 130 morphological and ecological characteristics are included and the number of items of information extracted from over 1100 literature sources is more than 120000 (Fitter & Peat 1994). This database is available on the Web as BIDS - Ecological Flora of the British Isles (Fitter & Peat 1994; see http://www.bids.ac.uk/ecoflora/ecofl1.html for details). The Botanical Database of the Netherlands is another digital publication containing data on 1781 species of vascular plants occurring in the Netherlands. It includes more than 40 variables on morphology, life history, reproduction and distribution in particular habitats (http://neon.vb.cbs.nl/sec lmi e/ flofau/floveg/ff4bb r00.htm).

The utilisation potential of ecological databases is large, both in basic and applied research. For example, species selection for ecological experiments can be improved, species assemblages can be defined, and correlations between plant features for large numbers of species can be studied (e.g., Peat & Fitter 1994). Tables of indicator values are frequently used for bioindication of environmental conditions and in gradient analysis (Ter Braak & Barendregt 1986; Jongman et al. 1987).

Databases on clonal growth of plants

The available biological/ecological flora databases do not cover all aspects of plant biology in detail. More specialised databases that focus on selected topics are also needed. Clonality, defined as plant growth resulting in potentially independent units, is one of the aspects treated rather marginally in the computerised plant databases mentioned above. However, three databases have been developed specifically for clonal plants. 'CLO-PLA1' (van Groenendael et al. 1996; Klimeš et al. 1997) is a database of clonal growth forms and includes 2686 species occurring in central Europe. This database is now being prepared as a Website. The second database is based on Estonian wooded meadows (Kull 1997) and contains quantitative data on the clonal growth of 130 grassland species. The third database - 'CLO-PLA2' - is introduced here. The aim of this database is to extend the previous database by including several more characteristics of plant growth, extensive literature and figures. We combined data from the literature (Irmisch 1850; Velenovský 1905-1913; Kirchner et al. 1908-1936; Rauh 1937; Troll 1937-1942; Lukasiewicz 1962; Rabotnov 1974; Rothmaler 1987; Kutchera and Lichtenegger 1982-1992; Lichtenegger et al. 1997; Sculthorpe 1985; Smirnova 1987, Rysin and Rysina 1987, Kästner & Karrer 1995, and others) with our field experience. At present 2749 species of the central European flora are included in the database. The total number of items is over 12750. For the 446 species which were studied in the field, detailed information on their clonality is available, including frequency of clonal growth in different habitats, life-span of ramets and spacers, number of ramets produced per season, etc. (see Appendix 1). In addition, drawings of the plants are included, showing peculiarities and morphological details relevant to the clonal growth of individual species. Altogether 25 plant characteristics relating to

clonal growth are tabulated for these species. Based on these data, clonal plants were classified into 31 categories of clonal growth mode (Appendix 2). These categories mostly correspond to those in 'CLO-PLA1' where only 21 growth modes were described, but some categories were split.

To evaluate the frequency and importance of individual modes of clonal growth in the field we developed a database of vegetation types ('VEGET'). This database contains the frequency (percentage of record plots where a species was recorded) of 1726 species in 112 vegetation types of Southern Germany (Oberdorfer et al. 1977–1992), based on 20761 plot records. The mean number of plot records per vegetation type was 120.

Use of the database 'CLO-PLA'

The database 'CLO-PLA1' has been used in a comparative study of clonal plants along environmental gradients in central Europe (van Groenendael et al. 1996), to assess the role of clonality in the central European flora and vegetation (Klimeš et al. 1997), to relate plant traits and invasive behaviour of plants (Pyšek 1997), and to evaluate plant mobility in a species-rich grassland (Klimeš 1998). Moreover, the database can be used to test how individual clonal growth modes are combined in real plant communities see Malanson 1982; Wilson & Roxburgh 1994; Wilson & Watkins 1994; Weither & Keddy 1995).

Here we present two examples based on a comparative approach. Firstly, we asked what is the frequency of plants using different modes of clonal growth in the central European vegetation types? We also assessed the relationship between modes of clonal growth and width of the habitat niche. Secondly, we tested whether individual types of clonal growth in individual plant species are combined randomly or not.

Niche width of plants using different modes of clonal growth

The term niche is used in ecology with various meanings (Giller 1984; Leibold 1995). An important distinction between fundamental and realised niches (Hutchinson 1957) reflects the difference between resource utilisation by organisms in isolation and when competing with other species (see also Ellenberg

1953; Giller 1984; MacNally 1995). Grubb (1977) defined habitat niche as the environment in which a species occurs. Niche width may differ between plants of early and late successional stages (Odum 1969; Bazzaz 1987); large niches are expected in good colonisers and plants occurring in wide ranges of habitats (Schmid 1984). In general, plants with broad environmental tolerances and/or high competitive capacity occur in more vegetation types and are more frequent there than specialised species with a poor capacity to compete with their neighbours (Grime 1979; Crawley 1997). Here we use the term niche width within the concept of the habitat niche, i.e., the range of environmental conditions under which a species occurs when competing with other species. The hypothesis to be tested was that niche width is independent of clonal growth mode. Alternatively, plants using some modes of clonal growth may be over-represented among species with broad, medium or narrow niches. An important possible bias is involved in the analysis. The range of environmental conditions under which individual vegetation types occur may differ. Therefore, two species found in the same number but different vegetation types need not have exactly the same niche width. However, among phytosociologists there is a tendency to define plant communities by species combinations in order to divide the vegetation continuum into equal parts (Whittaker 1973). Moreover, the wide range of the conditions included in the analysis and the high number of species make the results of the analysis relatively robust.

For testing we used 1722 species present in both the 'CLO-PLA2' and 'VEGET' databases. Niche width was estimated as (a) the number of vegetation types (NVT_i) in which species *i* occurs, and (b) sum of frequencies (SF_i) of species *i* in all vegetation types. As SF strongly depended on NVT (SF = 23.74 * NVT - 23.412, r = 0.904, df = 1720, P < 0.0001; regression analysis) and the results for SF and NVT were very similar we present here only the results for SF.

We ranked the 1722 species, including non-clonal plants, according to SF_i . First, we tested the differences between the mean niche width of species divided over the individual clonal growth modes with the Kruskal–Wallis test. The results were strongly significant ($\chi^2 = 110.8$, df = 33, P < 0.00001). Then we asked at which part of the niche width gradient the differences appeared. We divided the ranked 1722 species into 6 frequency classes, with an equal number of members (class 1 includes species with ranks 1 to 287, class 2: 288 to 574, ... class 6: 1436 to

1722). Using randomisation tests (Manly 1991, 1997) we tested the frequency of plants belonging to individual clonal growth modes in these groups against their overall frequency. The results for other sizes of niche width groups (2, 14) were very similar and are therefore omitted.

Out of the 31 types of clonal growth, species belonging to 11 types showed non-random distribution (Table 1). Clonal growth modes which are overrepresented among species with the broadest niches ensure a high year-to-year survival due to extensive long-lived rhizomes or root systems with a bud bank. Their dispersal to distances of a few decimetres to metres is efficient due to long spacers. Plants with wide ecological niches and with short-lived rhizomes formed above-ground combine this type of clonal growth with above-ground plagiotropic stems enhancing their dispersal potential. In other species dispersal is guaranteed by a high investment in generative reproduction.

Plants utilising individual modes of clonal growth are often more related than species using different modes of clonal growth. This phylogenetic constraint may result in an accumulation of related species among plants with a similar mode of clonal growth or with a particular niche width. Consequently, the number of degrees of freedom in any analysis in which species are considered as independent units is reduced to an unknown extent (Harvey & Pagel 1991; Silvertown et al. 1997). There are a number of examples of phylogenetic constraints in our data. For example, multiplication by plant fragments, which is underrepresented among species with the broadest niches, is limited to the Potamogetonaceae, Callitrichaceae, Lentibulariaceae and a few members of other families. Within these families most species use this means of multiplication. In other families there are only a few species multiplying by plant fragments (e.g., Hottonia palustris of the Primulaceae). Similarly, species of the Orchidaceae and Gentianaceae, two families well represented in the central European flora, are completely missing among the first 20% of species with broad ecological niches. Bulbs are characteristic of many members of the Liliaceae. However, there are Liliaceae species without bulbs and some other families include a few members with bulbs also (Juncaginaceae - Triglochin palustre, Lentibulariaceae - Pinguicula vulgaris, Oxalidaceae - Oxalis debilis). Lastly, the large group of turf graminoids is formed mainly by Poaceae and Cyperaceae species.

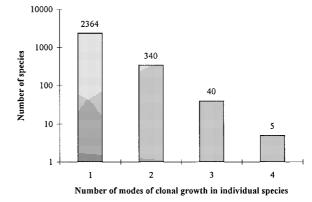


Figure 1. Number of species with a single mode of clonal growth and combining 2, 3 and 4 modes of clonal growth. The total number of species was 2749. Note logarithmic scale on the *y*-axis.

We tested the strength of the phylogenetic constraint at the family level using PIC (phylogenetic independent constraints - Harvey & Pagel 1991; calculated by the CAIC program - Purvis & Rambaut 1995). Mean niche width was used as the dependent variable and the percentage of species using particular modes of clonal growth as the independent variable. The phylogeny by Chase et al. (1993), based on molecular data, was adopted as a source of evolutionary relationships between the families, independent of plant morphology (see van Groenendael et al. 1996 for details). Families containing less than five species for which data were available were excluded from the analysis to reduce estimation errors in calculating family mean values of the relevant parameters. Also, some of the modes of clonal growth are represented in so few families that testing becomes difficult. Therefore, only clonal growth modes that are present in at least five families are included. The significance of the relationship between independent and dependent variables was tested using regression through the origin (see Table 2).

Most significant results obtained at the species level disappeared at the family level (compare Table 1). Moreover, some of the significant or marginally significant relationships at the family level disappeared after phylogenetic correction. The correction weakened the strength of the relationship at the family level in most cases. Nevertheless, the wide niches in plants with long-lived rhizomes formed below-ground was found at the species level (Table 2), as well as the family level, both before and after the phylogenetic correction. In contrast, the narrow niches of the '*Corydalis solida*' type (attached tubers) found at the family

Growth mode/Niche width class and range per class	1 1–287	2 288–574	3 575–861	4 862–1148	5 1149–1435	6 1436–1722
2. Alliaria petiolata	•	•	+	•	•	_
3. Rumex acetosella	+	•	•			
4. Ranunculus ficaria						++
6. Festuca ovina	+					
7. Rumex obtusifolius						
8. Rumex alpinus	+	•	•		_	
9. Dactylis glomerata	++					
10. Aegopodium podagraria	+					_
12. Caltha palustris	++	•	•			_
14. Calystegia sepium	+					
26. Elodea canadensis	_					
Annuals		•	•			++
Shrubs		•	-			

Table 2. Relationship between percentage of species using individual modes of clonal growth and mean habitat niche width, evaluated at the family level (n = 43). The results show correlation coefficients (r), slope of the regression and significance of the slope for the relationship, uncorrected and corrected by PIC. Only results for clonal growth modes represented in 5 or more families were tested. Non-significant results (clonal growth modes 2, 3, 5, 7–9, 11–13 and 21) are not shown.

	Before l	Before PIC		After PI	After PIC		
	r	Slope	Р	r	Slope	Р	
1. Trifolium pratense	-0.29	-0.116	0.062	-0.25	-0.089	0.122	
10. Aegopodium podagraria	0.31	0.061	0.048	0.34	0.063	0.032	
16. Corydalis solida	-0.32	-0.047	0.043	-0.22	-0.035	0.164	
Trees	0.34	0.205	0.028	0.42	0.182	0.006	

level disappeared when PIC was applied (Table 2). This indicates that the fact that plants with attached mother and daughter tubers are relatively specialised, considering their habitat demands and tolerances, is due to the phylogenetic position of the species rather than adaptation processes that originate independently in different lineages.

Combination of two or more modes of clonal growth

The number of species in the central European flora, with two or more modes of clonal growth, is 385, i.e., 21% of all potentially clonal plants (1825 species). We recorded two modes of clonal growth in 340 species, three modes in 40 species, and four modes in 5 species (Figure 1) in which short-lived below-ground rhizomes, annual below-ground tubers on the distal part of plagiotropic stems, turions and plant fragments are combined (e.g. in some *Potamogeton* species). Individual types of clonal growth are non-randomly combined. Many significantly over-represented combinations of clonal growth modes are found within groups of similar clonal growth modes, such as plants with stem-derived organs of clonal growth or plants with special adaptations. On the other hand, the definition of the clonal growth modes makes some of the missing combinations impossible (sprouting from buds on lateral roots cannot be combined with a disintegrating tap root, etc.). The over- and under-represented combinations are presented in Figure 2 where individual

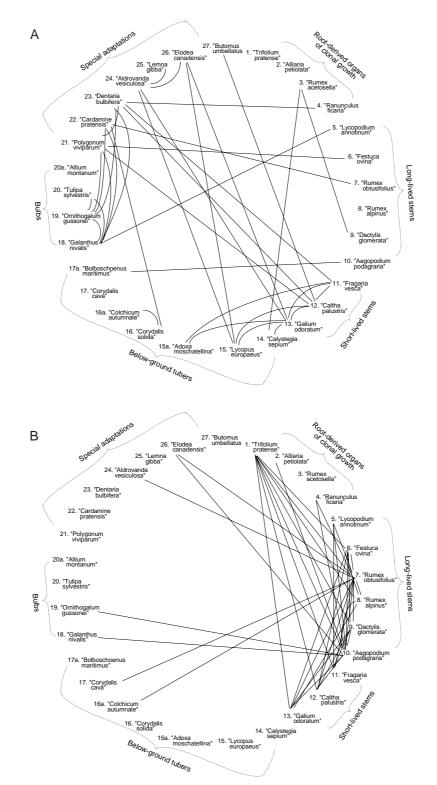


Figure 2. Combination of individual modes of clonal growth (codes 1 to 27, see Appendix for explanation) in 2749 species of the central European flora. Over-represented (A) and under-represented (B) combinations of clonal growth modes are indicated. Departures from the expected number of species combining individual pairs of clonal growth modes were tested using χ^2 .

growth modes are grouped according to the hierarchy of clonal growth modes given in Appendix 2.

Plants with buds on roots rarely utilise any other type of clonal growth with the exception of long-lived rhizomes formed below-ground. In contrast to other plants, the rhizomes of root-sprouters are vertical and their main role is in connecting the roots with the shoots. This confirms the views of Wittrock (1884) and Rauh (1937), who claimed that root-sprouters rarely use any other mode of clonal growth for lateral spread.

Long-lived creeping stems (No. 5) are often combined with long-lived rhizomes formed above-ground (No. 8) because the plagiotropic stems growing at the soil surface are often buried and become belowground. Long-lived rhizomes formed above- and below-ground are rarely combined. In contrast, shortlived rhizomes formed above- (No. 12) and belowground (No. 13) are combined more frequently than expected. Both pairs are found in members of various unrelated families. This indicates that a high investment into long-lived organs limits these combinations more strongly than the phylogenetic constraint. Growth of short-lived rhizomes is not very expensive in terms of biomass investment, so that short-lived rhizomes formed above- and below-ground can more easily be combined. Short-lived rhizomes (Nos. 12 and 13) are also unexpectedly combined with tubers (No. 15), pseudovivipary (No. 21), gemnipary (No. 22), production of axillary buds (No. 23), turions (No. 24) and plant fragments (No. 26). Individual types of stem tubers are never combined with each other because the same meristem can only be used for one type of clonal growth. Their combination with short-lived rhizomes is often made possible by the existence of several generations of rhizomes per year, of which the last one in autumn produces tubers which overwinter. The various types of bulbs are often combined with each other as well as with potentially detached buds formed on stems or inflorescences. In the latter case, most species belong to the family Liliaceae, with some in the Saxifragaceae and a few other families. Plants producing turions have a tendency to multiply by plant fragments. This is often combined with short-lived rhizomes formed below-ground and with tubers formed on distal parts of the rhizomes. Budding plants (Lemnaceae) often form turions. Specialised types of clonal growth with different types of detachable buds (Nos. 16a, 19, 21, 22 and 23) are often combined with other types of clonal growth with little horizontal spreading.

Two combinations of clonal growth modes are relatively frequent. In water plants rhizomes are combined with turions, plant fragments and vivipary. In plants growing in a strongly seasonal environment with soils drying out in summer, big and small bulbs are often combined with axillary buds and pseudovivipary. Water bodies and habitats affected by a strongly seasonal climate represent environments which are risky for generative reproduction. The combination of two or more modes of clonal growth ensures both persistence and spreading to neighbouring areas. These environments stimulate the production of vegetative multiplication by detachable vegetative fragments which have properties between seeds and vegetative offspring directly connected to the mother plant, and serve as an alternative to seeds (Elmquist & Cox 1996). Such fragments are larger than seeds therefore they contain more resources, and are transported some way from the mother plant (van der Pijl 1969). Plants with bulbs are much more frequent in regions with more seasonal precipitation, such as the Mediterranean. In water plants the ready regeneration of stem fragments may increase the probability of successful vegetative multiplication. The combination of several types of clonal growth may solve the problems with generative reproduction in some environments.

The final question is whether plants utilising several modes of clonal growth are more widespread over habitat types than plants with a single mode of clonal multiplication. We found that plants using a single mode of clonal growth are under-represented, and those with two modes of clonal growth overrepresented among plants with the broadest niches (Table 3). Niche width (NW) increased with the number of clonal growth modes (CGM) used by individual plants (NW = 65.201 + 40.069 * CGM, n = 1190, r = 0.121, P = 0.00003; regression analysis). This indicates that the combination of two modes of clonal growth may increase the range of conditions under which individual plants may occur. However, at the family level the relationship disappeared (y =-37.813 * x + 138.13, r = 0.197, P = 0.153; regression analysis) and the application of the PIC did not change the result (y = -33.699 * x, r = 0.184, P = 0.183; regression line through origin).

Clonal growth forms occur across plant families as does ecological tolerance. Thus at higher taxonomic levels the relationship which is apparent at the species level becomes diffuse. Therefore, the relationship should be studied and phylogenetically corrected at the species level to obtain clearer results.

Table 3. Frequency of species using 1 to 4 clonal growth modes in 14 classes of niche width. Only classes with results significantly different from the expected one are given. Over-representation is labelled by '+', under-representation by '-'. The niche width classes contain an equal number of species. The first class contains the most frequent species. + or -: P < 0.05, ++ or --: P < 0.01, \cdot non-significant. Randomisation tests were used for testing.

Number of clonal growth modes per plant/			
Niche width class	1	13	14
1		_	++
2	++	•	
3			
4			

Summary

(1) The structure of a new database on architectural aspects of clonal growth in vascular plants of central Europe ('CLO-PLA2') is presented.

(2) Using the data from the database the relationship between habitat niche width and the mode of clonal growth was tested. Turf graminoids and several types of rhizomatous plants are over-represented among the species with very broad niches and underrepresented among the species with narrow niches. In contrast, species multiplying by plant fragments are missing among the species with the broadest habitat niches.

(3). About 21% of species of central European flora use a combination of several modes of clonal growth. Some combinations of clonal growth modes are over-represented in certain families and environments, indicating that both phylogenetic constraints and adaptations to particular environmental conditions play important roles in determining the observed pattern.

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Appendix 1

Plant characteristics used in the CLO-PLA2 database. Alternatives are in brackets. Not all characteristics are relevant for all species. CGO – clonal growth organ.

General characteristics:

1. type of clonal growth organ - see Appendix 2

Characteristics of individual CGO:

- 1. response to injury (y/n)
- 2. seasonality of formation of CGO (y/n)
- 3. CGO is formed rarely/commonly
- 4. number of shoots in a clonal fragment (1, 2–5, more)
- 5. number of shoots per shoot produced per year (1, 2–5, more)
- 6. branching (monopodial, sympodial, dichotomic)
- 7. lateral spread per year (less than 0.05 m, 0.05–0.25 m, more, transportable fragments)
- 8. length of internodes (less than 2 mm, more)
- 9. location of leaves on generative shoots (without rosette, semi-rosette, rosette)
- 10. life-span of shoots (years to flowering: 1, 2, more)
- 11. spacer longevity (1 season, 1 year, 2 to 10 years, more)
- 12. number of generations of shoots per year (1, more)
- 13. tillering of grasses (intravaginal, extravaginal)

- 14. ontogenetic development of mother plant during formation of CGO (pre-reproductive, reproductive, postreproductive)
- 15. ontogenetic development of mother and daughter plants is the same (y/n)
- 16. generations of shoots are overlapping (y/n)
- 17. location of adventitious roots on spacer of stem origin (along whole spacer, on youngest part, on oldest part, on bases of shoots, without adventitious roots)

Characteristics of the whole plant

- 1. main root is perennial (y/n)
- 2. depth of root system (less than 10 cm, more, non-rooting in soil)
- 3. generative reproduction (rare, common, abundant)
- 4. storage organ other than CGO (y/n)
- 5. secondary thickening (y/n)
- 6. branching (monopodial, sympodial, dichotomic)
- 7. source of data / references

Appendix 2

The 31 types of clonal growth in vascular plants growing in central Europe (modified from Klimeš et al. 1997: the 21 types of 'CLO-PLA1' were used with 'special adaptations' (no. 21) divided into six types (21–26); newly added types are labelled 'a'). Vague terms, such as stolon, corm, layer and rootstock, which have different meanings with individual authors are not used. Plant names follow Ehrendorfer (1973). Long-lived organs show senescence after more than two years, short-lived ones after less than two years.

- A. Root-derived organs of clonal growth (1-4)
- Trifolium pratense type. Main (tap) root of the primary root system without adventitious roots and buds. Vegetative spreading is poor.
- 2. *Alliaria petiolata* type. Main root of the primary root system with adventitious buds.
- 3. *Rumex acetosella* type. Lateral roots of the primary root system or adventitious roots with adventitious buds.
- 4. *Ranunculus ficaria* type. Root tubers.
 B. Stem-derived organs of clonal growth (5–20a)
 Ba. Long-lived stems (5–10)
 B. Long-lived stems (5–10)
 - Ba1. Stems growing above-ground (5)
- 5. *Lycopodium annotinum* type. Creeping stems. Ba2. Stems growing below-ground (6–10)
- 6. *Festuca ovina* type. Below-ground stems formed aboveground. Turf graminoids.
- 7. *Rumex obtusifolius* type. Below-ground stems formed above-ground. Stems <10 cm in length.
- 8. *Rumex alpinus* type. Below-ground stems formed aboveground. Stems >10 cm in length.

- 9. *Dactylis glomerata* type. Below-ground stems formed below-ground. Stems <10 cm in length.
- 10. Aegopodium podagraria type. Below-ground stems formed below-ground. Stems >10 cm in length. Bb. Short-lived stems (11–13)
- 11. Fragaria vesca type. Plagiotropic above-ground stems specialised in spreading.
- 12. Caltha palustris type. Below-ground stems formed above-ground.
- 13. *Galium odoratum* type. Below-ground stems formed below-ground.

Bc. Below-ground tubers (14-17a)

- 14. *Calystegia sepium* type. Annual below-ground tubers on distal part of plagiotropic above-ground stems.
- 15. *Lycopus europaeus* type. Annual below-ground tubers on distal part of below-ground stems.
- 15a. *Adoxa moschatellina* type. Annual below-ground tubers on distal part of below-ground stems with thickened scale leaves or leaf bases.
- 16. *Corydalis solida* type. Mother and daughter belowground tubers annual and attached.
- 16a. *Colchicum autumnale* type. Daughter tuber attached to the mother tuber; daughter tuber much smaller than the mother tuber.
- 17. Corydalis cava type. A single perennial below-ground stem tuber.

17a. *Bolboschoenus maritimus* type. Perennial tubers on below-ground stem which is formed in the below-ground.

Bd. Bulbs (18–20a)

- 18. *Galanthus nivalis* type. Daughter bulb formed inside the mother bulb; daughter bulb of the same size as the mother bulb.
- 19. *Ornithogalum gussonei* type. Daughter bulb formed inside the mother bulb; daughter bulb much smaller than the mother bulb.
- 20. *Tulipa sylvestris* type. Bulb formed on distal part of a below-ground stem.
- 20a. *Allium montanum* type. Below-ground stem preserved behind the bulb.
 - C. Special adaptations (21–27)
- 21. Polygonum viviparum type. Pseudovivipary.
- 22. *Cardamine pratensis* type. Gemnipary (adventitious buds on leaves).
- 23. Dentaria bulbifera type. Axillary buds.
- 24. Aldrovanda vesiculosa type. Turions.
- 25. Lemna gibba type. Budding plants.
- 26. Elodea canadensis type. Plant fragments.
- 27. *Butomus umbellatus* type. Buds on below-ground stem which may be detached.