

4. CLONAL TRAITS

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Introduction

About 70% of the species of the NW European flora grow clonally. Diversity of clonal growth is high in this region and most types of clonal growth are remarkably plastic, being affected by local environments. Besides, genetically fixed variation of clonal growth is also considerable. Therefore, it is not surprising that individual authors dealing with clonality differ in their functional evaluation of individual traits and classifications of clonal plants. Other difficulties are caused by terms routinely used in description of clonal plants, such as rhizome, stolon or ramet. These have sometimes different meaning, depending on local tradition and authorities.

About 80% of clonal plants occurring in temperate Europe utilize a single type of clonal growth (Klimeš & Klimešová 1999a). Still, there are several hundreds of species combining several types of clonal growth. For example, long-lived rhizomes are combined with short-lived stolons in *Fragaria vesca*, rhizomes and bulbils may occur together on a single plant of *Dentaria bulbifera*. To reflect this feature, we keep the possibility to characterize individual species by several types of clonal growth.

Snap-shot quantitative data on clonal growth can be misleading because plasticity in traits concerning clonal growth is sometimes as large as differences between species. Measurements from a single environment may be misleading as well, because they cover a small part of plasticity of clonal growth of a given species. On the other hand, measurements from different habitats are available for very few plants. Therefore, we have to rely on less exact data, often based on observations, rather than measurements. Accordingly, we have to use nominal and coarse ordinal scales instead of metric scales suitable for quantitative measurements.

Trait definition

Clonal growth: The way by which plants multiply vegetatively.

How to collect traits of clonal growth?

Dig up several well developed plants, selecting mature and older individuals, on which below-ground stem structures are well developed (large inter-connected systems of ramets, etc.) and which flower and set fruits regularly. The best time for collecting for most clonal traits is at flowering or fruiting time and at the end of a season. In the case of very large inter-connected systems, partial excavation is sufficient.

In plants combining several modes of clonal growth, inspection of a few plants in a single locality is often not sufficient because some clonal growth modes are displayed in special situations only. Therefore, it is worth covering as broad as possible range of habitats in which particular species naturally occur. Literature data are indispensable for obtaining records from various environments. However, be aware that some terms have often different meanings in individual authors (rhizome, stolon, etc.).

Individual traits

This selection focuses on traits potentially important for plants coping with human-induced disturbances. In total 8 clonal traits were selected that will be dealt with separately. The selected clonal traits are:

1. Bud bank - vertical distribution
2. Bud bank - seasonality
3. Clonal growth organs (CGO)
4. Role of CGO in plant growth
5. Life-span of a shoot (shoot cyclicity)
6. Persistence of connection between parent and offspring shoots
7. Number of offspring shoots / parent shoot / year
8. Lateral spread / year

4.1. BUD BANK - VERTICAL DISTRIBUTION

Introduction

Bud banks are partially described by Raunkiaer's life forms (Raunkiaer 1934) because regeneration ability of a plant is partly determined by the number of buds and their location on a plant. However, Raunkiaer's life forms are defined by the position of renewal buds only. These are usually located at the upper part of a plant parts which survive adverse conditions (dry or cold periods), but most plants, bear buds which are higher above the soil surface than those utilised for re-growth after adverse periods. These higher buds are important for regeneration in the same season in which they developed because most plants regenerate from buds situated closely to the removed organs (Klimešová & Klimeš 2003, Huhta *et al.* 2003). For example, if an herbaceous plant with buds located along its stems is cut at 20 cm, then buds situated close to this height ensure regeneration. If a plant is cut close to the soil surface, buds at the soil surface are utilized. And finally, if a root-sprouting plant is damaged by fire up to 10 cm below the soil surface, then buds on roots situated close to this depth ensure its regeneration.

After a severe disturbance affecting upper layers of the soil the depth at which organs bearing the bud bank are situated is important. For example, even if the plant is a hemicryptophyte, it may develop dormant buds on its rhizomes or roots located at a depth of several tens of cm. If a disturbance damages upper layer of the soil (by fire, ploughing, shallow land-slide or erosion of river sediments) containing the buds from which the plant regrows in spring in undisturbed conditions, it may regenerate from dormant buds on rhizomes or on roots which are located deeper in the soil (Korsmo 1930, Wehsarg 1954). Therefore, the bud bank consists not only of renewal buds but also of other buds developed on that plant. Even root buds initiated by a disturbance should be considered, no matter that on undisturbed plants they are not present (Rauh 1937).

In our classification of bud banks we consider vertical distribution of the buds. This distribution indicates the probability of regeneration after a disturbance. For example, mowing results in a loss of biomass at about 10 cm above the soil surface. Large plants with above-ground biomass located high above the soil surface are damaged by mowing more

than smaller or creeping plants. Therefore, with increasing disturbance (grazing and mowing intensity) rosette plants should be favoured (Klimeš & Klimešová 2002, Pavlů *et al.* 2003).

In intensively grazed pastures and in grasslands mown by hand, above-ground plant biomass is lost by regular management. In these conditions plants with buds and biomass accumulated at the soil surface are favoured. Bud bank is usually permanent and does not much fluctuate during a year. On the other hand, the buds are not at the same stage of development during the whole year.

The buds located at the soil surface may substantially differ from other buds in their development. They usually contain several initiated leaves and in some plants even a whole seasonal shoot, including an inflorescence. The renewal buds are prepared for growth at a specific time. If a disturbance takes place earlier, they may break their dormancy, but the number of emerging leaves can be reduced and flowers aborted. In plants with a small number of buds, such as *Aconitum* species with root tubers the shoot developing from a bud prepared for spring re-growth may substitute the shoot lost in autumn. The new tuber bearing a bud may fail to develop due to a time shortage. Instead, an axillary bud on the old tuber may develop next spring. This bud is small and not well prepared for its spring re-growth. Thus, the plant is 're-juvenated' and repeats a part of its ontogenetic development. It may take several years before the plant is able to form a large tuber with well developed over-wintering buds again. In alpine and arctic plants, organs may develop (pre-form) within buds up to two years in advance. Therefore, these plants cannot respond to a disturbance by appropriate morphological changes immediately, but with a delay of one or two years (Diggle 1997).

The depth of 10 cm below the soil surface is crucial for survival of many plants after a disturbance. In most herbaceous plants perennial organs of stem origin bearing a bud bank are concentrated above this level. For most herbaceous plants, including many geophytes, 10 cm corresponds to the maximum depth from which they re-grow and regenerate. There are relatively few plants developing their rhizomes deeper in the soil (*Equisetum*) or capable of root-sprouting (Korsmo 1930, Wehsarg 1954).

Trait definition

Bud bank: Are all viable axillary and adventitious buds which are present on a plant and are at disposal for spring re-growth (renewal buds), branching and replacement of shoots through a season or for vegetative regeneration after an injury (regenerative buds); some adventitious buds may be initiated by an injury. Indicates the probability of regeneration after a disturbance.

Vertical distribution: This trait considers the vertical distribution of the buds in the bud bank.

How to collect?

Excavated plants should be carefully cleaned of soil and dead plant remains should be removed before buds are counted. The best time for the evaluation is the end of a season but in most cases after flowering or fruiting the bud bank can already be evaluated. For

examination of some plants a (hand) lens or binocular microscope is needed. Some buds may be only ephemerally present on a plant (plantlets in inflorescence, turions). Thus, repeated censuses during a season may be required.

Categories

Categories bud bank vertical:	For the layers:
1. no. buds per clonal fragment	1. <-10 cm 2. -10 to 0 cm 3. soil surface 4. 0 to 10 cm 5. >10 cm
2. 1-10 buds per	1. <-10 cm 2. -10 to 0 cm 3. soil surface 4. 0 to 10 cm 5. >10 cm
3. >10 buds per clonal fragment	1. <-10 cm 2. -10 to 0 cm 3. soil surface 4. 0 to 10 cm 5. >10 cm

For example, species X can have buds in one or more layer:

Species	Bud bank vertical	Layer
X	0 buds	<-10 cm
X	1-10 buds	-10 - 0 cm
X	1-10 buds	soil surface
X	>10 buds	0 - 10 cm
X	0 buds	>10 cm

Special cases

Note that in some plants the location of leaf insertions and of buds is different. For example, some grasses belong to rosette or semi-rosette plants by their leaf insertion; however, their leaf sheaths are so tall that leaf blades seem to be inserted high above the soil surface. This false culm enables a lift of canopy high above the soil surface and ensures competitive superiority. Mowing these plants removes a high proportion of their above-ground biomass, however, their bud bank, located at the soil surface, is preserved (e.g. *Molinia caerulea* and *Calamagrostis epigeios*). Similarly, numerous dicotyledonous plants develop tall petioles and form high canopies while their buds are protected at the soil surface (*Petasites officinalis*). Therefore, distinction between vertical distributions of biomass and buds is useful because there are functional differences between these two.

Data structure

To collect: 1-3 observations per species

- Obligate:
- Type of variable: ordinal
 - Number of samples: 1 observation
 - Number of replicates: -
 - Unit: categories
 - Bud bank vertical distribution categories:
 1. No buds per clonal fragment
 2. 1-10 buds per clonal fragment
 3. >10 buds per clonal fragment
 - Vertical distribution bud bank layer categories:
 1. Below soil surface (if depth is unclear)
 2. <-10 cm
 3. 0 > x >-10 cm
 4. Soil surface
 5. Above soil surface (if depth is unclear)
 6. 0 < x <10 cm
 7. >10 cm

Optional: o Comment field: Any information of importance to the trait

4.2. BUD BANK – SEASONALITY

Introduction: Classification of bud banks

We suggest a broad categorisation that reflects responses of plants to disturbance timing and frequency (Iwasa & Kubo 1997, Bellingham & Sparrow 2000). The ability to regenerate is determined by the presence of a bud bank. Therefore, seasonal fluctuations in the number of buds of the bud bank are a key feature of a plant's response to disturbance. As regeneration from soil seed banks (Thompson & Grime 1979) is in many respects similar to regeneration from bud banks, it is convenient use similar categories. We propose to distinguish two basic types, perennial and seasonal bud banks (Fig. 3.10).

The perennial bud bank is represented by perennial plant organs (in trees the whole body, in herbs below-ground parts only) with a large number of buds, which are kept in dormancy by correlative inhibition and usually cannot disperse. The perennial bud bank resembles the persistent seed bank, but longevity of buds usually does not exceed longevity of parent individual. The seasonal bud bank is represented by plant organs which are short-lived (above-ground stems of herbs, below-ground organs of pseudo-annuals), and buds developed on them are usually not as abundant as on perennial organs. Buds are kept dormant either by innate dormancy or by correlative inhibition, and some of them may naturally disperse. The seasonal bud bank resembles the transient seed bank, as the buds are not present permanently on the plant (Verburg 1998; Table 3.1). What to do with adventitious buds which are created only after injury and are not countable on intact plants? Functioning of adventitious buds is in many respects similar to functioning of axillary buds in the bud bank. After correlative inhibition is broken by severe injury, adventi-

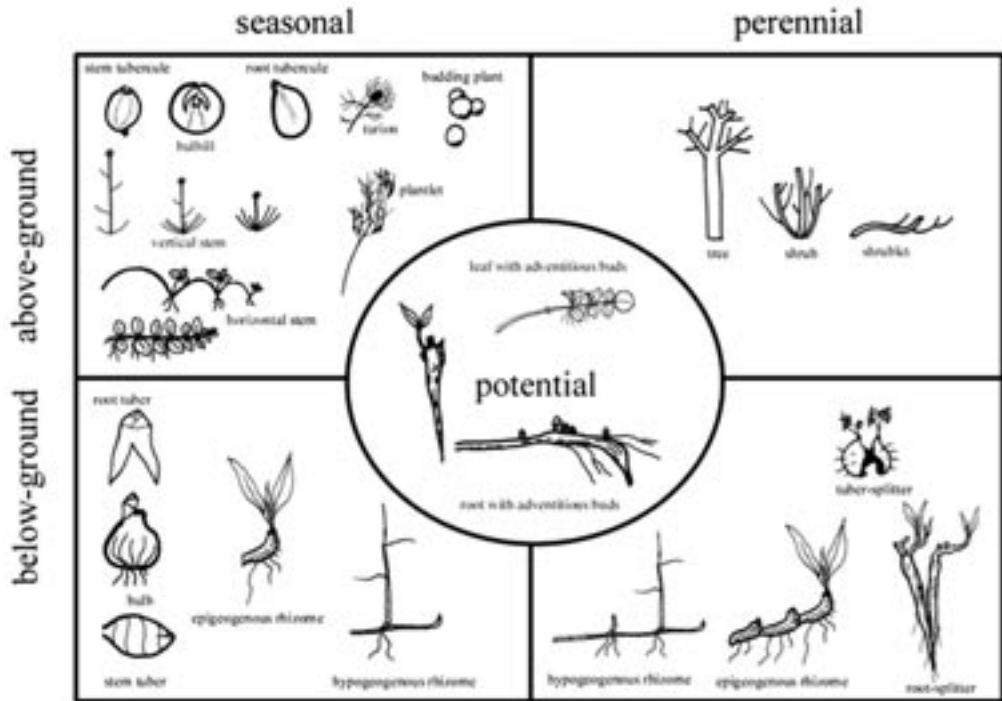


Figure 3.10. Seasonality of bud banks (by J. Klimešová).

tious buds on roots have to awake from their dormancy, similarly to axillary buds on rhizomes (Horvath & Anderson 2002, Horvath *et al.* 2002). Alternatively, they may be formed *de novo*. Accordingly, we may expect a delay in the response of these newly formed buds. There are other differences: roots are usually located deeper in the soil than rhizomes and are better protected against severe disturbance; formation of adventitious buds ensures regeneration from plant fragments and survival after a severe disturbance, such as ploughing (Hamdoun 1972), fire, pulling out, and cutting (Fernández-Santos *et al.* 1999); adventitious buds on roots may undertake the role of buds located on stem organs - these two are rarely combined on a single plant (Klimešová & Martínková in prep.); species which may regenerate by root-sprouting are more common in disturbed communities than in other types of vegetation (Klimešová & Klimeš in prep.).

These are the reasons why we should consider adventitious buds on roots when classifying bud banks. We suggest the bud bank developed on roots after a disturbance is called the potential bud bank (Table 3.1). Seasonal fluctuations in regeneration capacity from perennial and potential bud banks are not caused by a limited number of buds, but by the extent of carbon reserves.

Table 3.1. Characteristics associated with types of seasonality of bud banks.

Bud bank	No. of buds	Seasonal fluctuation	Dispersal	Dormancy	Type of organ bearing buds with examples
Perennial	many	no	no	correlative inhibition	perennial shoot bases (<i>Trifolium pratense</i>), rhizomes (<i>Agropyron repens</i> , <i>Petasites hybridus</i>)
Seasonal	few	yes	no, yes	correlative inhibition innate dormancy	stem tubers (<i>Stachys palustris</i>), root tubers (<i>Ficaria verna</i>), bulbs (<i>Allium vineale</i>), bulbils (<i>Dentaria bulbifera</i>)
Potential	-	-	no	correlative inhibition	roots with regenerative adventitious sprouts (<i>Potentilla anserina</i>), roots with regular adventitious sprouts (<i>Convolvulus arvensis</i>)

Trait definition

Bud bank: Are all viable axillary and adventitious buds which are present on a plant and are at disposal for spring re-growth (renewal buds), branching and replacement of shoots through a season or for vegetative regeneration after an injury (regenerative buds); some adventitious buds may be initiated by an injury (indicates the probability of regeneration after a disturbance).

Seasonality: Number of buds present, or their fluctuations between seasons. Seasonal fluctuations in the number of buds of the bud bank are a key feature of a plant's response to disturbance.

How to assess bud bank types

Injured plants sprout from uppermost buds. Thus, disturbance severity determines which buds are used for resprouting. To assess the bud bank of a particular species, it is necessary to study buds on the whole plant. Data on buds available in floras and species trait databases are also useful (incl. Raunkiaer's life forms, placement of leaves along aerial shoots or clonal growth organs; for Central European flora see Klimeš *et al.* 1997, Jäger & Werner 2002, Klotz *et al.* 2002). None of these surrogates provides complete information about regenerative capacity of a plant, if taken separately. A more complete picture is obtained if these sources are combined. Raunkier's life-forms provide information about longevity of above-ground plant parts. Placement of leaves along the aerial vertical shoot indicates placement of above-ground axillary buds, types of clonal growth organs provide information about morphology of organs bearing buds, and about their longevity. A key to bud bank types is given in figure 3.9, based on categories of clonal growth organs from CLOPLA (Klimeš *et al.* 1997, Klimeš & Klimešová 1999a). Organs responsible for clonal growth are regenerative organs, as well. Exceptions are represented by vertical stems which are not included in CLO-PLA, as they do not provide clonal growth, but they take part in vegetative regeneration. We propose seasonality of the bud bank is considered

separately for above- and below-ground structures. For example, the above-ground bud bank of *Potentilla anserina* is seasonal, whereas its below ground bud bank is perennial and potential.

When evaluating the bud bank, we may rely on morphological characteristics because they are easily obtainable for numerous species. Case studies of vegetative regeneration are still scarce so that quantitative data on seasonality of bud banks are lacking for most species. Therefore, we suggest broad categories and do not take into account possible difference in the outcome of plant regeneration which is further affected by morphological and ontogenetical constraints (Richards & Caldwell 1985, Huhta *et al.* 2003, Martínková *et al.* 2004 a, b). If more precise data are needed, buds should be directly counted, similarly to the assessment of the seed banks. Solid data on regeneration capacity of plants can be obtained from experimental studies.

Categories

Bud bank seasonality categories:

1. seasonal
2. perennial
3. seasonal & potential
4. perennial & potential

Layers categories:

1. above-ground
2. below-ground
1. above-ground
2. below-ground
1. above-ground
2. below-ground
1. above-ground
2. below-ground

For example species XY can have a seasonal bud bank in more than one category or layer:

Species	Bud bank seasonality	Layer
XY	seasonal	above-ground
XY	perennial & potential	below-ground

Special cases

- For successful regeneration plant fragments, buds and adventitious roots should be present or developed. A bud may be present on fragments of stem origin or may be formed *de novo* on roots, on shoots out of nodes, or on leaves. Roots are formed *de novo* more easily than buds, so root and leaf fragments of some plants may form new roots but fail to form new buds so that their regeneration is impossible (e.g. leaves of *Lythrum salicaria* and *Scrophularia nodosa*, root fragments of *Rumex obtusifolius*).

Data structure

- To collect: 1-3 observations per species
- Obligate:
- Type of variable: ordinal
 - Number of samples: 1 observation
 - Number of replicates: -
 - Unit: categories
 - Seasonal bud bank categories:
 1. Seasonal
 2. Perennial
 3. Seasonal & potential
 4. Perennial & potential
 - Seasonal bud bank layer:
 1. Above-ground
 2. Below-ground
- Optional: o Comment field: Any information of importance to the trait

4.3. CLONAL GROWTH ORGANS (CGO) AND THEIR ROLE IN PLANT GROWTH

Introduction

This classification does not include categories differing quantitatively only (note that some quantitative characteristics are used as other traits of clonal growth). Categories accepted in the presented classification are hierarchical. At the highest level placement of clonal organs is considered. Origin of the organ of clonal growth is considered next. Remaining levels reflect differences in storage and size of the organ.

Root and stem origins are sometimes considered functionally equivalent. However, there are several functional differences between them.

(1) Plants sprouting from roots have a high plasticity in branching frequency and their growth rate is remarkably high (Drew *et al.* 1973, Burns 1991) when compared with stem-originated organs of clonal growth (Caldwell *et al.* 1991a,b, Jackson & Caldwell 1993).

(2) While roots 'sense' nutrient concentrations, response of rhizomes and stolons to nutrients is indirect, mediated by roots developed on them (Passioura 1988).

(3) In plants with stolons and rhizomes, the number of shoots which may appear on a stem is determined by the number of nodes. This value, multiplied by two in plants with opposite leaves, cannot be exceeded by the number of branches originated on a plant module. In contrast, buds on roots may appear simultaneously in high numbers (Peterson 1975).

(4) The distance between individual buds on a stolon of rhizome is fixed soon after the buds have originated, whereas in plants with buds on roots new buds may establish between buds already present. Therefore, root sprouters may produce potentially an unlimited number of buds on their roots without producing any new root (Klimeš & Klimešová 1999b).

In total 17 types of CGO are recognised in the LEDA Traitbase, divided into categories according their placement to the soil surface and their origin (see Table 3.2).

Trait definition

Clonal growth organs and their role: Is a morphological unit of a plant, which bears a bud-bank and provides vascular connections between shoots. They are characterised by their placement in relation to soil surface, by their origin in relation to the soil surface, by the location of adventitious roots, by the location and preformation of renewal and regenerative buds, and by annual increment and by its lifespan. Knowledge of the role of CGO in plant growth is useful when predicting behaviour of plants in stressful and disturbed environments. Some plants require some CGOs for their survival, such CGOs are called necessary CGO. Environmental conditions such as high nutrient availability or low competition strength can initiate additive CGO's. A CGO which is formed after an injury only and does not occur on intact plants is regenerative.

Detailed comments on identification of CGO categories***Clonal growth present/absent***

We avoid the terms clonal and non-clonal plants as their intuitive meaning is not well established and misunderstanding associated with them is frequent. Instead, we consider whether clonal growth is present or not. Clonal growth is the way by which plants multiply vegetatively. Not all plants showing clonal growth always and in any situation produce viable independent units. However, plants growing clonally may produce them (in some circumstances, at least). This implies that virtually all plants, except for some trees and short-lived herbs, may sometimes show clonal growth.

Trees grow clonally if they sprout from roots (many species) or produce rhizomes (few species) (Del Tredici 2001). Root-sprouting trees are usually surrounded by saplings of root origin. Their below-ground root connection to the parent plants indicates that these are not seedlings established from generative propagules. The saplings are distributed around the trunk but sometimes they occur beneath the whole tree crown. Spacers connecting the offspring with the parent tree are sometimes situated deep in the soil but it is usually not necessary to dig out the whole spacer because morphology of the below-ground organs indicates offspring origin. If the below-ground axis is segmented, consisting of nodes bearing scale leaves, roots and buds, and internodes (it is formed by a stem and not by a root) offspring is of vegetative origin (Fig. 3.11).

Other traits discriminating saplings of root and seed origin are visible above ground. While shaded saplings originated from seeds have about constant annual increments, vegetatively originated saplings have markedly longer first annual increments and then their growth rate slows down. They may finally develop into mature trees, but only if their parent tree dies or is heavily injured (Del Tredici 2001).

In small trees and shrubby woody plants descendants of clonal origin may reach about the same size as parent plants and they usually form clones in the form of a thicket (*Prunus spinosa*) or small wood (*Rhus typhina*, *Robinia pseudoacacia*). In this case we have to find whether young shoots situated at thicket margin are linked with other shoots or not. Trees occurring close to the border of their distribution limit grow clonally more often than in the centre of their distributional area (Koop 1987).

duced by clonal growth, ramets) originate as buds. Roots and leaves may also serve as CGOs, if buds are formed on them adventitiously (Holm 1925, Rauh 1937).

Among root-derived CGOs we include not only roots with adventitious buds, but also root tubers and splitting main roots which bear buds of stem origin, even if the majority of their biomass is formed by the storage root. Distinction between root- and stem-originated organs is not always easy. Problems may arise in below-ground horizontal stems and horizontal roots with adventitious buds. Stems are segmented, bearing buds and scale leaves, sometimes also roots initiated at nodes. Roots are not segmented and buds on them are distributed irregularly, sometimes in rows or at the onset of side roots. Adventitious shoots originated from roots are never terminal (with exception of terminal-like position in *Neottia* ssp., *Listera cordata*; Domin 1925), whereas tips of below-ground (hypogeous) stems growing horizontally turn up at some distance and produce aerial shoots (the only exceptions are *Adoxa moschatellina* and *Paris quadrifolia*; Irmisch 1850).

In unclear cases anatomical structure should be assessed to decide the origin of the below-ground organ (Fig. 3.11). On cross-section of a root the vascular bundle is in the centre, whereas in stems, the vascular tissue forms a hollow cylinder. Root tubers differ from stem tubers by the absence of nodes and internodes. Stem tubers may bear remains of leaves or leaf scales and there is usually a terminal bud. Root tubers are usually smooth, often branched, and their bud need not be terminal. In the case of small organs, tuber anatomy should be examined on cross-sections using a microscope. On stem tubers we can find a central cylinder and the tissue of a bud at the tip of the tuber is not separated from the tissue of the tuber. On cross-sections of root tubers we do not see the central cylinder and the tissue of the bud at the tip of the tuber is clearly separated from the tissue of the tuber. If the main storage tissue is formed by scale leaves of the bud, rather than by a root or stem, then we call this vegetative diaspore a bulbil; we put it with CGOs of stem origin (Troll 1937-1941, Wagenitz 1996). Leaves may serve as CGOs if they form adventitious buds (*Drosera rotundifolia*; Domin 1925; *Cardamine pratensis*, Hansen 1881) or if they transform into a stem (*Utricularia* sp. div.; Arber 1920). These cases are often not readily observable in the field because they appear transiently or are induced by injury. Therefore, it is desirable to pay attention to the surrounding of the target plants, and to ground and fallen leaves.

Clonal Growth Organs (CGO)

In total 17 types of CGO are distinguished in the LEDA Traitbase and they are divided into categories according their placement with respect to the soil surface and their origin (Figure 3.12, Appendix D). See also Table 3.2 for categorisation of the CGO types.

How to collect?

Careful examination of the whole inter-connected clonal fragment is usually necessary, either in the field or in a laboratory (see Table 3.2 for categorisation of the CGO types). Dig up several well developed plants and select mature and older individuals on which below-ground stem structures are well developed (large inter-connected systems of ramets) and which flower/set fruits regularly. The best time for collecting is at flowering or fruiting time and at the end of a season. In the case of very large inter-connected systems partial excavation is sufficient. In plants combining several modes of clonal growth inspection of a few

plants is often not sufficient because some clonal growth modes are utilised in special situations only. Therefore, it is worth covering as broad as possible range of habitat conditions in which particular species naturally occur. Literature data are indispensable for obtaining records from various environments.

Note that one species can have multiple levels of clonal growth organs, for example the species *Potentilla anserina* can combine 3 levels of CGO:

Example	CGO 1	CGO 2	CGO 3
A	epigeogenous stems	adventitious buds on roots	above or at soil surface
B	CGO of stem-origin	above or at soil surface	-

The second example is also correct, as not all plants always form buds on roots and higher hierarchical categories can be accepted as well.

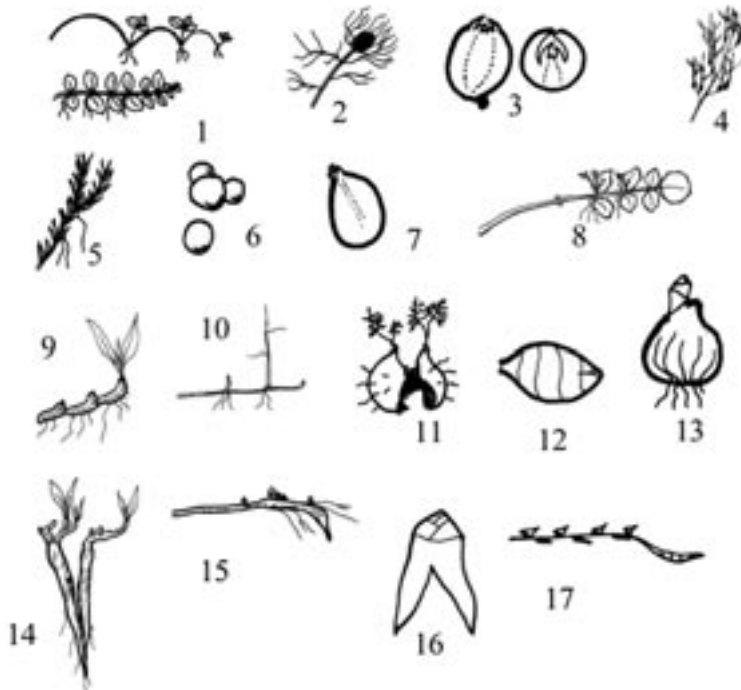


Figure 3.12. Morphology of 17 types of clonal growth organs (CGO): 1 - rooting horizontal stems at or above soil surface; 2 - turions; 3 - bulbils and tubers of stem origin at or above soil surface; 4 - plantlets (pseudovivipary); 5 - plant fragments of stem origin; 6 - budding plants; 7 - root tubers at or above soil surface; 8 - buds on leaves (gemmae); 9 - epigeogenous stems; 10 - hypogeogenous stems; 11 - tuber-splitters; 12 - stem tubers; 13 - bulbs; 14 - root-splitters; 15 - adventitious buds on roots; 16 - root tubers below-ground; 17 - offspring tubers at distal end of above-ground stems (by J. Klimešová).

Special cases

- Development of some detachable vegetative units is usually strongly seasonal. Therefore, a single examination need not be sufficient for some plants. For example, aquatic plants form turions only in autumn, pseudovivipary can be observed only on flowering stems, and short-lived below-ground structures are best developed at the end of a season as they decay in winter. Root tubers usually complete their development in summer, requiring long days, while stem tubers complete their development in autumn, when days are short.

Role of CGO in plant growth

Knowledge of the role of CGO in plant growth is useful when predicting behaviour of plants in stressful and disturbed environments. For example, plants of *Achillea millefolium* producing long hypogeous rhizomes in abandoned meadows do not develop them in regularly mown meadows and produce epigeous rhizomes only. These are less effective in horizontal spreading. Other species sprout from roots in special conditions only or after being injured (Rauh 1937).

Some plants require some CGOs for their survival; such CGOs are necessary. An additive CGO is initiated by some environmental conditions, such as high nutrient availability or low competition strength. A CGO which is formed after an injury only and does not occur on intact plants is regenerative. This classification was developed by Wittrock (1884), who used it to classify root-sprouting plants. This trait characterises individual CGO. In clonal plants utilising a single mode of clonal growth it is applicable to the species as well.

How to collect?

A regularly occurring mode of clonal growth is usually necessary for plant survival, while the mode of clonal growth observed in some mature individuals only is usually additive. To obtain information on all additive modes of clonal growth, inspection of populations from various environments is usually needed. Detailed descriptions and/or pictures given in literature can also be considered as a reliable source of information.

Categories

Classification of the role of CGO is as follows:

1. No CGO
2. Regenerative CGO
3. Additive CGO
4. Necessary CGO
5. Unknown

Table 3.2. The 17 CGO type categories are ordered according to their placement (above soil surface, at soil surface, below soil surface) and their origin (stem origin, root origin, leaf origin). The numbers in brackets behind the CGO types correspond with the CGO types in figure 3.12 and Appendix D.

Clonal growth		Present/Absent:	
1. Present	1.1 CGO above or at soil surface	1.1.1 CGO of stem-origin	1.1.1.1 rooting horizontal stems at or above soil surface (1)
			1.1.1.2 turions (2)
			1.1.1.3 bulbils and tubers of stem origin at or above soil surface (3)
			1.1.1.4 plantlets (pseudovivipary) (4)
			1.1.1.5 plant fragments of stem origin (5)
			1.1.1.6 budding plants (6)
		1.1.2 CGO of root-origin: root tubers at or above soil surface (7)	
		1.1.3 CGO of leaf-origin: buds on leaves (gemmipary) (8)	
	1.2 CGO below soil surface	1.2.1 CGO of stem-origin	1.2.1.1 stems
			1.2.1.1.1 epigeogenous stems (9)
			1.2.1.1.2 hypogeogenous stems (10)
			1.2.1.2 tuber-splitters (11)
			1.2.1.3 stem tubers (12)
			1.2.1.4 bulbs (13)
		1.2.2 CGO of root-origin	1.2.2.1 root-splitters (14)
			1.2.2.2 adventitious buds on roots (15)
			1.2.2.3 root tubers below-ground (16)
	1.3 spacers above and renewal buds below soil surface: offspring tubers at distal end of above-ground stems (17)		
2. Absent			

Data structure

To collect: 1-3 observations per species

Obligate: ● Type of variable: Nominal

● Unit: Categories

● Categories role CGO:

1. No CGO

2. Regenerative CGO

3. Additive CGO

4. Necessary CGO

5. Unknown

● Clonal growth organs (CGO) categories (Note maximum of 4 CGO categories per database record):

1. Present

1.1. CGO above or at soil surface

1.1.1. CGO of stem-origin

1.1.1.1. rooting horizontal stems at or above soil surface

1.1.1.2. turions

1.1.1.3. bulbils and tubers of stem origin at or above soil surface

1.1.1.4. plantlets (pseudovivipary)

1.1.1.5. plant fragments of stem origin

1.1.1.6. budding plants

1.1.2. CGO of root-origin: root tubers at or above soil surface

1.1.3. CGO of leaf-origin: buds on leaves (gemmipary)

1.2. CGO below soil surface

1.2.1. CGO of stem-origin

1.2.1.1. stems

1.2.1.1.1. epigeogenous stems

1.2.1.1.2. hypogeogenous stems

1.2.1.2. tuber-splitters

1.2.1.3. stem tubers

1.2.1.4. bulbils

1.2.2. CGO of root-origin

1.2.2.1. root-splitters

1.2.2.2. adventitious buds on roots

1.2.2.3. root tubers below-ground

1.3. Spacers above and renewal buds below soil surface:

2. Absent

Optional: ○ Comment field: Any information of importance to the trait

4.4. LIFESPAN OF A SHOOT

Introduction

This corresponds to the traditional distinction between monocyclic, dicyclic and polycyclic shoots. We define the life-span of a shoot as the duration of a small life-cycle sensu Rabotnov (1974), i.e. from sprouting of a bud, through the growth, flowering and fruiting of the shoot, until its death. This trait is relatively easily applicable 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 so that it makes little sense to consider their life-span.

Life-span of a shoot may differ between individual CGOs. Some types of clonal growth result in offspring shoots which are considerably smaller in comparison with the parent shoot. Therefore, their development is longer until first flowering. 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 originated from bulbils on stems of parent plants are similar to seedlings in size and require several years before they flower.

This trait has attracted little attention in ecological literature so far (but see Tamm *et al.* 2002, Sammul *et al.* 2003). However, shoot cyclicity is undoubtedly one of the traits determining persistence and regeneration of plants. This trait characterises individual CGOs. In clonal plants utilising a single mode of clonal growth it is applicable to the species as well.

Trait definition

Lifespan of a shoot: Is defined as the duration of a small life-cycle, i.e. from sprouting of a bud, through the growth, flowering and fruiting of the shoot, until its death (sensu Rabotnov 1974). Also known as shoot cyclicity.

How to collect?

Observation of marked shoots over their life-span is the best and most reliable source of information about shoot cyclicity. In some cases indirect evidence can be utilised: If a clonal fragment bears both sterile and fertile shoots then its shoots are usually di- or polycyclic. If all shoots are of the same size and developmental stage, and there is a larger renewed bud on the perennating organ, the shoots are usually monocyclic. Note that there are plants with all shoots at the same developmental stage not only within a plant individual, but even in the whole population or across distributional area. Still, they do not have monocyclic shoots; their shoots are polycyclic, synchronised in their development.

Categories

Lifespan of a shoot categories are:

1. 1 year (monocyclic)
2. > 1 year (dicyclic or polycyclic)

Data structure

- To collect: 1-3 observations per species
- Obligate:
- Type of variable: ordinal
 - Unit: Categories
 - Life cyclicity categories
 1. Monocyclic (1 year)
 2. Dicyclic or polycyclic (> 1year)

4.5. PERSISTENCE OF CONNECTION BETWEEN PARENT AND OFFSPRING SHOOTS

Introduction

Individual clonal growth organs may differ in persistence of spacers connecting parent and offspring ramets (Jónsdóttir & Watson 1997, Oborny *et al.* 2000). They either split into physically and physiologically independent units after a short time (splitters) or remain inter-connected for a long time (integrators). For example, offspring plants developed on stolons of *Fragaria vesca* separate from the parent plant after the first season already; however, offspring plants initiated by branching of rhizome of the same plant remain inter-connected for many years.

This trait indicates for offspring ramets that are potentially supported by resources from their parent ramet through the possible inter-connected clonal system (Jónsdóttir & Watson 1997). The shorter persistence of the interconnection is, the lower is the amount of storage for initiation of its growth and the slower is the initial growth of the offspring ramet (Klimeš & Klimešová 1999b).

Trait definition

Persistence of connection parent-offspring: Duration (or persistence) of the connection between parent and offspring shoots.

How to collect?

Connection persistence can often be inferred from its morphology: thickened spacers with remains of shoots, sheaths, bracts and woody structures are usually long-lived, non-woody, soft and thin spacers without remains of shoots, sheaths and bracts are usually short-lived. However, using observation data from a single date a conclusive decision is usually possible only in species with distinct morphology. In other cases repeated observations of marked individuals are necessary because evaluation of this trait from snap-shot data could be somewhat tricky.

To estimate persistence of the connection between shoots, a careful examination of inter-connected clonal fragments is necessary, either in the field or in a laboratory. The procedure is similar to that of the 'Clonal growth organ' trait. Dig up several well developed plants and select mature and older individuals on which below-ground stem structures are well developed and which flower/set fruits regularly. The best time for collecting is in spring when connections persisting for one year or less already split or are decaying.



Figure 3.13. *Fragaria vesca* can remain inter-connected for many years to the parent plant (Photo: see Source list).

The three categories which we suggest separate are 1) ephemeral connection between e.g. bulbils and parent plant, 2) offspring plants developed on stolons which remain inter-connected with the parent plant for one to two seasons, and 3) pairs of parent and offspring ramets inter-connected for a longer period, often up to several decades. This trait characterises individual CGOs. In clonal plants utilising a single mode of clonal growth it is applicable to the species as well.

Categories

For the persistence of connection between parent and offspring shoots there are three categories:

1. <1 year
2. 1-2years
3. >2 years

Special cases

- Pseudo-annuals fit into the first category by definition (Piqueras & Klimeš 1998, Krumbiegel 2001). See also comments on seedling-like clonal offspring.

Data structure

To collect: 1-3 observations per species

- Obligate:
- Type of variable: ordinal
 - Unit: categories
 - Persistence categories:
 1. <1 year
 2. 1-2years
 3. >2 years

Optional: o Comment field: Any information of importance to the trait

4.6. NUMBER OF OFFSPRING SHOOTS PER PARENT SHOOT PER YEAR

Introduction

This is a measure of intensity of clonal multiplication. Values <1 apply to shoots living for several years in which branching takes place after flowering only. The value of 1 denotes the situation when a single offspring shoot replaces the parent shoot, such as in non-clonal perennials with root tubers (*Orchidaceae*; Ziegenspeck 1936). Higher values refer to a successful multiplication, resulting in an increasing number of descendants (Piqueras & Klimeš 1998). This characteristic may markedly differ between individual CGOs on a single plant, for example the dicyclic and after flowering branching rhizome of *Fragaria vesca* displays a low multiplication rate. However, it may produce up to about 10 offspring plants within one season using its stolons. This trait characterises individual CGOs. In clonal plants utilising a single mode of clonal growth it is applicable to the species as well.

Trait definition

No. offspring shoots/parent shoot/year: Is a measure of intensity of clonal multiplication given as the number of offspring shoots produced per year per parent shoot.

How to collect?

This trait can be estimated if a parent shoot or its remains are preserved and offspring shoots are still connected to it. Otherwise, evaluation is somewhat tricky.

Categories

The four LEDA categories of the number of offspring shoots per parent shoot per year are:

1. <1 shoot/parent shoot/year
2. 1 shoot/parent shoot/year
3. 2-10 shoots/parent shoot/year
4. >10 shoots/parent shoot/year

Special cases

- In sympodially growing plants which branch after flowering, the parent shoot is regularly replaced by an offspring shoot. This process does not result in multiplication. In contrast, in monopodally growing shoots, branching implies multiplication.

tion, as parent shoots may survive and continue their growth. It follows from this difference that, if the number of offspring per parent shoot per year of a monopo-dially growing plant is <1 , numerous descendants may arise in the course of several years.

Data structure

To collect: 1-3 observations per species

Obligate:

- Type of variable: ordinal
- Unit: categories
- Number of offspring shoots/parent/year categories:
 1. <1 shoot/parent shoot/year
 2. 1 shoot/parent shoot/year
 3. 2-10 shoots/parent shoot/year
 4. >10 shoots/parent shoot/year

Optional: o Comment field: Any information of importance to the trait

4.7. LATERAL SPREAD PER YEAR

Introduction

Vegetative multiplication is usually considered as an efficient way of spreading to local neighbourhood of the parent plant (Harper 1981). Lateral spreading by means of vegetative organs ensures that offspring plants are placed in the environment which is similar to that where the parent plant multiplied. Therefore, persistence of the parent genotype at a location is ensured. However, variation in spreading rates of clonal plants is considerable. They range from values close to zero to several metres per year and are variable at the levels of individuals, populations and species. In some plants, such as many clonal orchids, the offspring plant replaces the parent plant and occupies its position so that virtually no lateral spreading takes place (Ziegenspeck 1936). The other extreme is represented by water plants forming turions or tubers that can be transported across continents within a short time (Cook 1987). Plants with parent and offspring ramets inter-connected for a longer time can laterally spread by their rhizomes or stolons up to several metres per year (Haslam 1972).

As a measure of lateral spread we use increment of clonal growth organ in the horizontal direction. This trait characterises individual clonal growth organs. In clonal plants utilising a single mode of clonal growth it is applicable at the species level.

Trait definition

Lateral spread/year: Distance covered by lateral spread in one year, given in metres. Note that this trait should not be confused with the distance between offspring ramets or the distance between parent and offspring ramets.

How to collect?

Annual increments of a plant are often recognizable as repeating structures along a horizontal stem. For example, in plants which flower every year, remains of flowering shoots

may mark annual increments. In monopodially growing epigeogenous stems, thicker parts are produced in summer and thinner ones in spring and autumn (*Rumex alpinus*, (Fig 3.14) *Alchemilla monticola*). In sympodially growing plants with perennial rhizome and one generation of shoots per season, annual increments can be estimated by measuring the length of a horizontal shoot increment (*Polygonatum multiflorum*). If several values are known for a given species and locality, modal value should be used as input data.

Categories

Categories of lateral spread per year are:

1. Lateral spread of <0.01 m
2. Lateral spread of 0.01-0.25m
3. Lateral spread of >0.25m
4. Dispersable vegetative diaspores (see Chapter 6).

There is an optional option to fill in actual measured data of lateral spread (in metres), together with the minimum and maximum in the database.

Special cases

- In some pseudo-annuals and plants with short-lived above-ground horizontal stems this trait can be evaluated during a short time period only because after offspring are established the parent plant dies and the spacer between them eventually decays as well. Difficulties arise when evaluating lateral spread of root-sprouting plants. Adventitious shoots can easily be established on older roots and annual increments cannot be easily evaluated on roots. Moreover, after an initial expansion of the root system perennial root-sprouters start to produce shoots from the base of established shoots and stop their lateral spreading. In this case we recommend finding remnants of this-year and last-year adventitious shoots and to measure distance between them.

Data structure

To collect: 1-3 observations per species

- Obligate:
- Type of variable: nominal
 - Unit: categories
 - Lateral spread categories:
 1. <0.01m/year
 2. 0.01-0.25m/year
 3. 0.25m/year
 4. Dispersable vegetative diaspores

- Optional:
- o Lateral spread original value: m
 - o Values: minimum, maximum
 - o Comment field: Any information of importance to the trait



Figure 3.14. *Rumex alpinus* (A) with part of its rhizome (B) (Photo: see Source list).