Available online at www.sciencedirect.com
ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics 8 (2007) 115–129

Perspectives in Plant Ecology, Evolution and Systematics

www.elsevier.de/ppees

Bud banks and their role in vegetative regeneration – A literature review and proposal for simple classification and assessment

Jitka Klimešová*, Leoš Klimeš

Institute of Botany, Section of Plant Ecology, Dukelská 135, 379 82 Třeboň, Czech Republic

Received 12 April 2006; accepted 18 October 2006

Abstract

While sexual regeneration of plants after disturbance is relatively well understood, vegetative regeneration has attracted some attention only recently. Its role along environmental gradients and across biomes is poorly known and standard methods for assessment are not yet established. We review current knowledge about the role of bud banks in vegetative regeneration and the diversity of their modes of functioning. The similarities and differences between bud banks and seed banks are illustrated, focusing on dormancy, dispersability, seasonal dynamics, longevity and storage of carbohydrates. We try to formulate some principles that unify bud bank functioning across habitats and growth forms: (1) the bud banks consist of all buds which may be used for vegetative regeneration, including those formed adventitiously only after injury; (2) vertical distribution of buds reflects avoidance of disturbance; (3) seasonal changes in the bud bank make vegetative regeneration sensitive to timing of disturbance; and (4) ability to form adventitious buds provides a potential for vegetative regeneration from roots, stumps and leaves. Based on these principles, a simple classification of bud banks is presented similar to the classification of seed banks. Bud bank traits are considered in relation to severity, timing and frequency of disturbance. These include vertical distribution and seasonal fluctuations in the number of buds. Methods for quantitative assessment of bud numbers and resprouting capacity are reviewed, and a new approach based on indirect bud counts is proposed. The suggested concept of bud banks may be widely used in studies focusing on plant functional traits in relation to disturbance regimes at the levels of plant individuals, populations and communities. Its further development may incorporate adjustments for areas with non-seasonal climate and refinements for some growth forms, such as epiphytes.

Keywords: Disturbance severity; Disturbance timing; Disturbance tolerance; Plant strategy; Resprouting; Vegetative regeneration

Introduction

While seed banks have been intensively studied since the time of Darwin (Salter, 1857; Leck et al., 1989; Thompson et al., 1997), the role of the bud bank has received relatively little attention until recent times. Compared to the almost 2900 papers concerning seed banks that have been published during the last two decades, only 86 papers have dealt with bud banks in that period (ISI Web of Sciences, August 2006). Apparently, the concept of the bud bank is not yet well established.

Harper (1977), who introduced the term bud bank, defined the seed and bud banks as hidden populations of dormant seeds and meristems, respectively, which differ

---

*Corresponding author.
E-mail address: klimesova@butbn.cas.cz (J. Klimešová).

1433-8319/$ - see front matter © 2007 Rübel Foundation, ETH Zürich. Published by Elsevier GmbH. All rights reserved.
doi:10.1016/j.ppees.2006.10.002

from established vegetation in species composition and by the number of individuals. While dissimilarity in species composition between the seed bank and surrounding vegetation is often considerable (Leck et al., 1989), this contrast is usually less obvious in bud banks (Lee, 2004; but see Combroux et al., 2001). On the other hand, enormous differences in the number of dormant buds between individual species is a typical feature of the bud bank (Richards and Caldwell, 1985).

The crucial role of the bud bank in regeneration after a disturbance event has been documented in numerous environments. For example, in fire-prone areas of Australia, South Africa, the Mediterranean Bassin and California, many woody plants cope with recurrent fire disturbance by resprouting from lignotubers (James, 1984; Bell and Ojeda, 1999; Lloret et al., 1999). These plants are often shrubby and their regeneration from seeds is usually poor. In contrast, seeders, such as fast-growing monotrunk trees, rely on a large production of seeds and do not form below-ground reserves. A similar pattern can be found in shrublands and among herbs colonising fire-prone areas (Meney et al., 1997; Raffaele and Veblen, 1998).

Vegetative regeneration has also been reported from forests disturbed by hurricanes, heavy snowfall, logging and other types of damage (Peterson and Pickett, 1991; Bellingham et al., 1994; Kammesheidt, 1999; Guerrero-Campo et al., 2006).

On arable land, perennials along with annuals, can become troublesome weeds (Leakey, 1981). Perennial herbs rely on dormant meristems hidden deep in the soil, being protected from ploughing, and/or sprouting from fragmented stems or roots (McAllister and Haderlie, 1985; Hakansson, 1995). Seed production in these species may be limited and sexual regeneration less effective.

In pastures, plants have to cope with biomass removal by large mammals. While some species reduce herbivory intensity using special structures, such as spines, or by chemical compounds, there are species which do not possess similar attributes (van der Meijden et al., 1988; Maschinski and Whitham, 1989). They respond to disturbance by rapid regrowth and seed production which may eventually exceed that of undisturbed plants (Lennartsson et al., 1997). The response depends on the vertical distribution of regenerative buds, their dormancy and the proportion of biomass lost due to disturbance (Huhta et al., 2003). Vegetative regeneration is crucial also in mown grasslands (Klimeš and Klimešová, 2002).

Adventitious rooting occurs readily in aquatic environments. Vegetative diaspores, together with plant fragments, are effectively spread by water (Barrat-Segretain et al., 1998; Boedeltje et al., 2003). Vegetative regeneration and clonal growth strongly prevail in some plant species so that reproduction from seeds contributes negligibly to the number of their offspring (Grace, 1993; Eckert, 2002). The number of regenerative modes in aquatic and wetland plants is high due to their architectural diversity (Willby et al., 2000). Switching between the various modes is common, enabling a plastic response to changing environmental conditions.

Extreme climatic factors like drought and frost may be considered as disturbances, after which non-adapted vegetation may resprout from the bud bank (de Bie et al., 1998; Vesk and Westoby, 2003; Brando and Durigan, 2004; Bannister et al., 2005). Correlations among traits responsible for disturbance tolerance have already been noted, for example, between herbivory and frost (Agrawal et al., 2004), drought and fire (Vesk and Westoby, 2003) and frost, fire and drought (MacGillivray et al., 1995). Last, seasonal climate itself might be a selective force for bud bank formation (Raunkiaer, 1934; Dalgleish and Hartnett, 2006).

Despite the large number of studies that illustrate the importance of dormant meristems in regeneration after a disturbance, especially in fire-prone areas with numerous representatives of woody plants, no unifying concept of the bud bank reflecting the enormous diversity of regeneration modes used by herbaceous plants has been developed. Also, there is little agreement about suitable methods for the evaluation of bud banks.

To fill these gaps, we will (1) delimit the term 'bud bank', (2) describe the characteristics of bud banks and compare them with those of seed banks, (3) suggest a new classification of bud banks, (4) review the methods of bud bank assessment, and (5) identify the research fields where the new bud bank concept may be utilized. Although we are aware of the important role of the bud bank in seasonal regrowth (i.e. programmed iterative growth of a plant) the focus here will be mainly on vegetative regeneration of plants after injury. The reason for this restriction is that this role of reserve buds in vegetative regeneration is much more appreciated, because disturbance acts as a natural manipulation of the bud bank. Recently emerging theory of meristem allocation to functions such as dormancy, vegetative growth and flowering would provide a broader context of life-history evolution and the role of bud banks in it, but it is still in a premature state, focusing only on above-ground axillary meristems (see Bonser and Aarssen, 1996, 2001, 2003, 2006).

Definitions of morphological terms are given in the Appendix A.

Delimitation of the bud bank

Harper (1977) was the first to characterise bud banks in detail. According to him, the bud bank is formed by an accumulation of dormant meristems (buds) formed on rhizomes, corms, bulbs, bulbils and tubers in the soil (Fig. 1). We suggest that a bud bank consists of all buds that can be potentially used for vegetative regeneration. Thus, Harper's definition of the bud bank should be extended by including several other types of buds:

(1) Harper (1977) excluded renewal buds from the bud bank, because they cannot serve as organs for long-term storage of meristems. These buds are prepared for regrowth after a seasonal resting (either dry or cold) period. We suggest that the exclusion of renewal buds from the bud bank is not justified, as some organs, which Harper explicitly included in the bud bank, are themselves renewal buds, e.g. bulbs (Irmisch, 1850). Moreover, even renewal buds may take part in the vegetative regeneration of plants. Delimitation of renewal and regenerative buds is difficult, if they do not differ in size, placement or preformation.

(2) Buds forming the bud bank need not be situated in the soil, as supposed by Harper (1977). When severity of a disturbance is relatively low and some above-ground parts of the plants are undamaged, regeneration may take place preferentially from meristems situated above-ground (Tolvanen et al., 2002; Huhta et al., 2003). In many plants, especially some trees and annuals, resting below-ground buds are missing, and plants resprout from above-ground buds which survived the disturbance event (Gill, 1995; Klimešová and Klimeš, 2003).

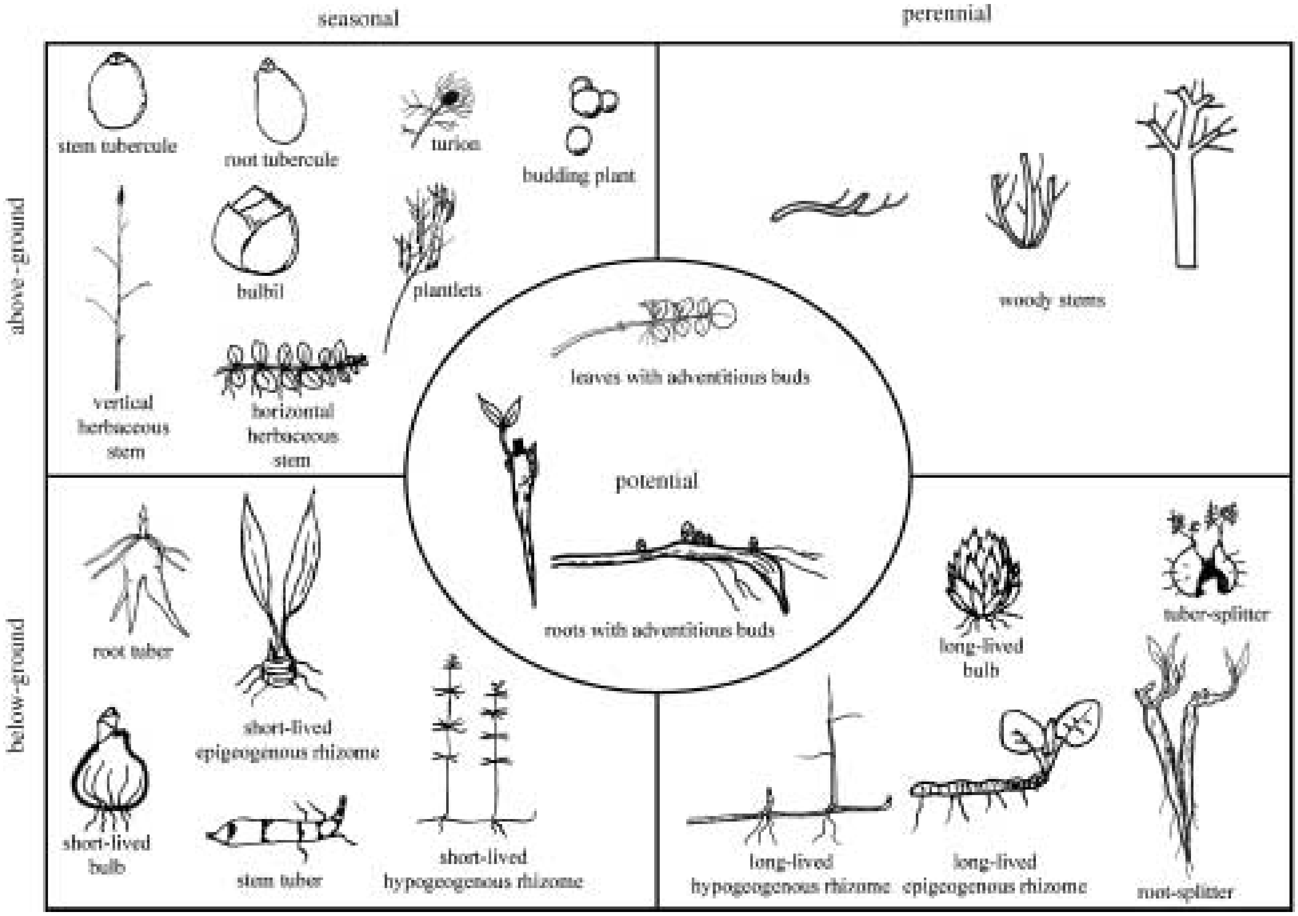

Fig. 1. Bud bank types and organs on which the buds develop. Examples were taken from the central European flora. (1) above-ground seasonal bud bank – stem tubercule (Bistorta vivipara), root tubercule (Ranunculus ficaria), turion (Utricularia vulgaris), budding plant (Lemna minor), vertical herbaceous stem (Phalaris arundinacea), bulbil (Dentaria bulbifera), plantlets (Poa alpina), and horizontal herbaceous stem (Lysimachia nummularia); (2) above-ground perennial bud bank – prostrate woody stem (Pinus mugo), shrubby woody stem (Corylus avellana), and upright woody stem (Tilia platyphyllos); (3) below-ground seasonal bud bank – root-tuber (Nigritella rhellicani), short-lived bulb (Galanthus nivalis), short-lived stem tuber (Stachys palustris), short-lived epigeogenous rhizome (Alisma plantago-aquatica), and short-lived hypogeogenous rhizome (Galium odoratum); (4) below-ground perennial bud bank – long-lived hypogeogenous rhizome (Phalaris arundinacea), long-lived epigeogenous rhizome (Rumex alpinus), long-lived bulb (Lilium martagon), root-splitter (Astragalus glycyphyllos), and tuber-splitter (Corydalis cava); (5) above-ground potential bud bank (Cardamine pratensis); and (6) below-ground potential bud bank (Cichorium intybus, Sonchus arvensis); for definitions of clonal growth organs see Klimeš et al. (1997) and Appendix A.

(3) Buds on transportable plant fragments should also be included in the bud bank. In some habitats, such as wetlands and aquatic habitats, plant fragments play a significant role in regeneration, as they are effectively transported by water to habitats providing conditions suitable for establishment (Barrat-Segretain et al., 1998; Campbell, 2003). However, plant fragments may regenerate in other ecosystems as well. For example, successful establishment from stem fragments has been reported in neotropical shrubs (Sagers, 1993), succulents of arid regions (Bobich and Nobel, 2001; Mandujano et al., 2001) and temperate trees (Jeník, 1994; Karrenberg et al., 2003).

(4) Adventitious buds belong to the bud bank as well. They may develop either spontaneously or after an injury. Unfortunately, the proportion of root-sprouting species is well known in a few relatively small regions only, so that a broader evaluation of the role of root sprouting in natural communities is still impossible. The most complete surveys have been possibly done in central Europe where about 450 species, i.e. 10% of vascular plants, may form buds on their roots (Klimešová and Klimeš, 2006). Besides, several other species (Cardamine pratensis, Drosera sp.) have been reported to regenerate from buds on leaves (Klimešová and Klimeš, 2006). Root-sprouting species are unevenly distributed among life forms; they are rare among perennial herbs and annuals (10% and 2%, respectively), while their proportion is higher among trees and biennials (20% and 12%, respectively; Klimešová and Klimeš, 2003). This pattern probably reflects the fact that, except for woody plants with lignotubers (rare out of fire-prone areas), most trees and biennials do not form below-ground organs of stem origin with axillary buds (Del Tredici, 2001; Huhta et al., 2003) and, therefore, root-sprouting may be crucial for their survival in severely disturbed habitats. While plants forming adventitious buds on leaves are rare in temperate zones, representatives of this group are more common in other parts of the world; they include understorey shrubs of neotropical forests (Sagers, 1993), ferns (Velenovský, 1905–1913) and herbaceous plants in the tropics (Kalanchoe, Sedum, Begonia, Saintpaulia; Troll, 1939–1942; and Utricularia; Rutishauser and Isler, 2001).

A comparison of bud and seed banks

The roles of seed and bud banks in vegetation dynamic are shown on the flow chart in Fig. 2. The processes (ellipses) and compartments (boxes) in seed and bud banks are similar, however, their qualitative and quantitative characters differ. We will compare the main steps in seed- and bud-bank formation (inputs and outputs), persistence (longevity and dormancy), germination and sprouting (seedling and sampling banks, quality of sprouts), quantity, quality and spatial distribution of seeds and buds. Our aim is to show the differences and similarities in the prerequisites for generative and vegetative regeneration.

Inputs and outputs

While seeds forming a seed bank are relatively mobile and may persist in the soil even after the parent plant disappears from the site (Leck et al., 1989), the presence of buds in a bud bank is nearly always associated with the presence of parent plants (see the persistence niche by Bond and Midgley, 2001). A bud bank is formed during stem growth (i.e. in the axils of leaves) whereas, bud formation on roots, leaves and stems outside of the nodes may be triggered in some species by injury or changes in nutrient availability (Rauh, 1937).

Buds cannot disperse without the organ bearing them and plant fragmentation usually results in sprouting of previously dormant buds. Specialised buds, such as bulbils and turions represent exceptional cases because these may be dormant (at least for some time) and can be dispersed to sites where parent plants are missing (Combroux et al., 2001). In disturbed terrestrial habitats, lateral growth of undisturbed plants by stolons and rhizomes (Fahrig et al., 1994; Rogers and Hartnett, 2001), and accidental transport of plant fragments, specialised buds and plantlets by water erosion or human activities contribute to the bud banks (Fig. 2). Establishment from vegetative diaspores imported from other areas is often a crucial step at the onset of plant invasions (Kelly and Skipworth, 1984; Bímová et al., 2003).

Depletion of seed and bud banks is caused by the export of diaspores, their mortality, germination and sprouting (Fig. 2; Simpson et al., 1989). The most important factors responsible for mortality of buds and seeds include predation, pathogens, failed germination and sprouting, and deep burial (Simpson et al., 1989; Stafstrom, 1995).

Longevity and dormancy

Seeds of many species are more persistent than buds formed by these plants. The life-span of seeds is often much longer than that of parent plants and in temperate species was found to be negatively correlated with plant longevity (Rees, 1994). In contrast, bud life-span is closely correlated with the life-span of bud-bearing organs and not necessarily with that of the whole plant.

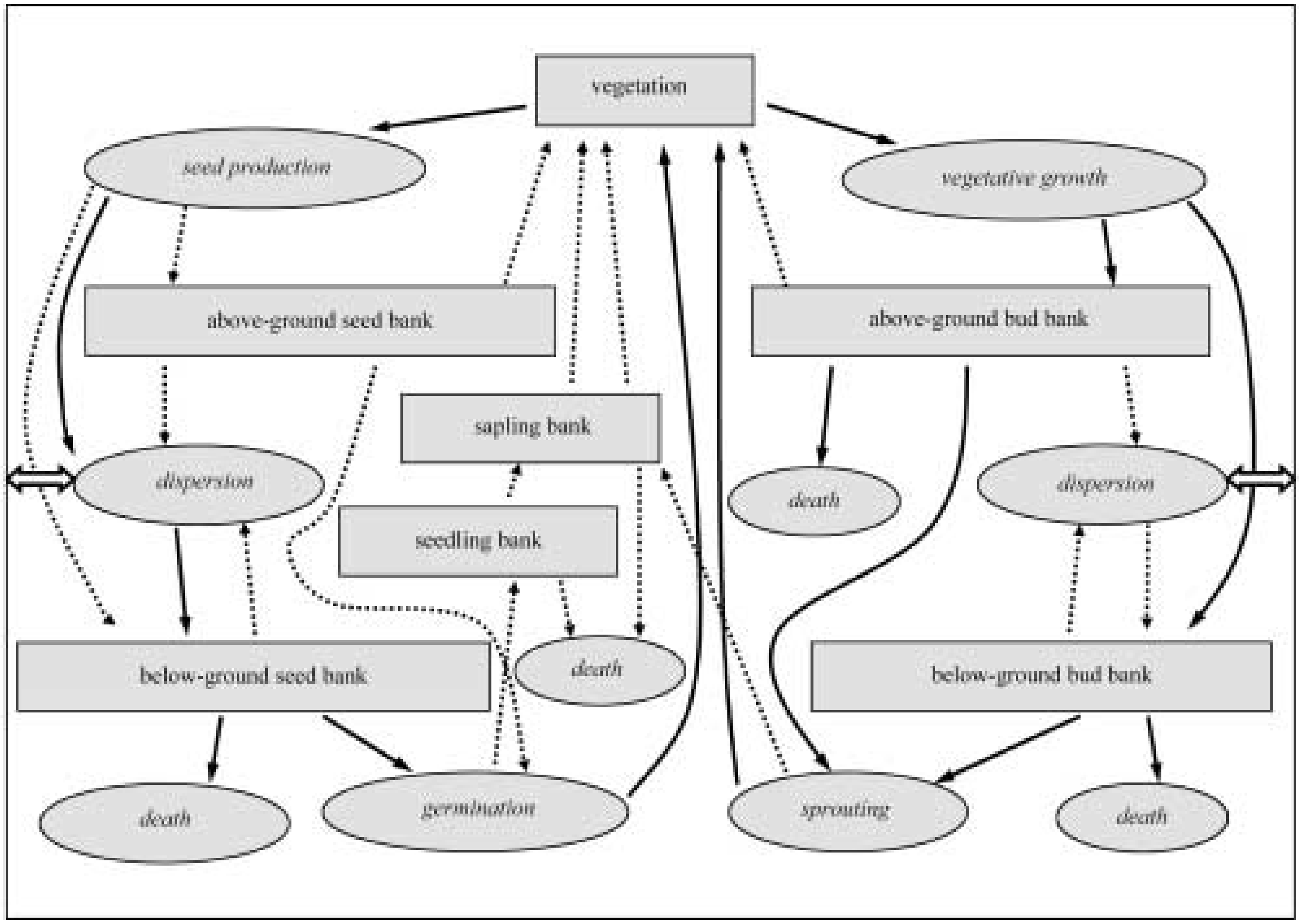

Fig. 2. Functioning of the seed and bud banks. Boxes denote emerged vegetation and stored propagules, ellipses indicate processes. Solid arrows describe the most frequent pathways; dotted arrows less frequent pathways. Box arrows directed into and out of the system are inputs ('import of diaspores') and outputs ('export of diaspores'). Adapted from Simpson et al. (1989).

For example, rhizomes of Rumex alpinus live up to 20 years, bearing dormant buds of the same age (Klimeš, 1992), while all vegetative parts of pseudoannuals die off within 1 year (Krumbiegel, 2001).

The characteristics shared by the seed and bud banks are innate dormancy and induced dormancy, which is often enforced by cold or drought (Anderson et al., 2001). Another type of dormancy which is even more important for bud bank functioning, is correlative inhibition, which is represented mainly by apical dominance. Through this mechanism, actively growing apical buds prevent growth of axillary and adventitious buds situated below the apical meristem. Thus, the buds remain available for vegetative regeneration until an injury breaks the apical dominance (Tuomi et al., 1994; Stafstrom, 1995). This type of quiescence has no counterpart in seeds. On the other hand, buds or whole bud-bearing organs rarely stay dormant (do not produce above-ground shoots) over the whole vegetation season or longer, in contrast to seeds (e.g. Morrow and Olfelt, 2003).

Banks of seedlings and saplings

Sometimes, seedlings or samplings are prepared to replace dying adults, but not seeds or buds (Fig. 2). For example, in the root-sprouting tree Ailanthus altissima, small root-sprouts grow in the understorey and develop into large trees only after the parent tree is damaged (Kowarik, 1995). Consequently, after the death of the parent tree, the sprouts have a competitive advantage over seedlings (Loehle, 2000). Similarly, seedling growth is often retarded beneath parent trees due to shading or intraspecific competition. After the parent tree dies, a gap is formed and seedling growth becomes vigorous (e.g. Catovski and Bazzaz, 2002).

Quality of sprouts

Architecture, life-span and life history of shoots may differ between regenerated and intact plants due to differences in bud anatomy, disturbed hormonal and carbon/nitrogen balance, and healing processes. For example, branching pattern is often modified in regenerating shoots of trees and herbs (Dubard, 1903; Hallé, 1999). Differences in the life-span have been reported between long-lived single trunks in trees and short lived stump sprouts which are often infested by fungi (McVean, 1953) or suppressed due to mutual shading (Kubo et al., 2005). Differences in life history characteristics have been documented in short-lived monocarpic herbaceous plants in which resprouting shoots of severely injured plants leads to a postponement of flowering (Klimešová, 2003). They may also differ from intact plants in seed production (Huhta et al., 2003).

Vertical distribution

Seeds and buds may be stored both above- and below-ground, and reason for it may be protection of diaspores from particular type of disturbance, ontogeny or time. While the depth of seed burial in the soil almost always correlates positively with seed age, for buds this holds only in some habitats and for some growth forms. In screes and sand dunes, for example, older parts of rhizome systems are usually buried deeper than younger parts (Hess, 1909; Maun, 1998). Similarly, older parts of epigeogenous rhizomes are situated deeper in the soil than younger parts, which are gradually pulled into the soil by contracting roots, while their youngest tips are always situated at the soil surface. In contrast, there is no relationship between the depth at which plants with other growth forms grow and their age (Serebriakov and Serebriakova, 1965). Diaspores hidden in the soil are better protected, but have a lower probability of germination and regrowth (Raju et al., 1964; Klimeš et al., 1993).

Carbon reserves

While reserves stored in seeds are utilized mainly for germination and early growth, the resources accumulated in bud-bearing organs are used not only for resprouting (Richards and Caldwell, 1985; Bell and Ojeda, 1999). Maintenance expenses are higher in bud-bearing organs (e.g. rhizomes) than in seeds, and parent plants are sometimes supported from reserves stored in the bud-bearing organs. In areas with a seasonal climate, carbon storage in bud-bearing organs fluctuates over the course of a year, being depleted by respiration, seasonal regrowth, flowering and fruiting (Masuzawa and Hogetsu, 1977; Kubín et al., 1994; Suzuki and Stuefer, 1999). The regeneration capacity of a plant may be affected by these fluctuations (Hogg and Lieffers, 1991; Cruz et al., 2003). If there is no supply of assimilates provided by photosynthesis or via mycorrhiza (Lerat et al., 2002), carbon availability can be a factor limiting regeneration. In contrast to most types of bud-bearing organs situated below-ground, some vegetative fragments, such as plantlets developed in the inflorescences of Bistorta vivipara and Poa alpina, stem fragments of aquatic plants and budding fronds of Lemna, assimilate carbon and do not require support from the parent plant.

Seeds and bud-bearing organs of about the same size are functionally similar if vegetative diaspores bear only one bud (bulbs, some tubers) or if one bud is dominant. Otherwise, resprouting shoots compete for carbohydrates (Hamdoun, 1972; Suzuki and Hutchings, 1997), and this represents a way in which resprouting plants differ from seedlings.

Bud preformation

In seed banks, seeds of individual sexually reproducing species are genetically different from parent plants or genetically uniform in apomictic plants. In contrast, all buds developed on a plant are almost always genetically uniform (with the exception of periclinal chimeras and somatic mutants; see Klekowski, 2003), but they may differ in other characteristics. Buds differ in size and in the number of leaf and flower primordia (Vodolazsky, 1979). Renewal buds are sometimes preformed for 1–3 years and may include not only stems and leaves, but also inflorescences (Warming, 1908; Geber et al., 1997). In plants with preformed buds, a response to disturbance can be delayed by time for which the organs within the buds are preformed at the time of disturbance (Diggle, 1997). The fact that not all buds produced by a plant are the same (Vesk and Westoby, 2004b) corresponds functionally to the heterocarpy of seeds.

Diaspore density

Another important characteristic, yet for buds poorly known, is propagule density in individual species. For seed banks, up to 10^5 seeds have been reported per m^2 (Thompson et al., 1997). Interspecific differences between bud banks are also considerable. For example, tuberous terrestrial orchids usually develop a single below-ground bud per plant per year (Ziegenspeck, 1936). In contrast, in weedy perennials of arable land, the number of below-ground buds ranges from several hundred (Cirsium arvense: 530) to tens of thousands per m^2 (Agropyron repens: 25,980; Korsmo, 1930).

The number of seeds in transient seed banks may fluctuate considerably over the year. In some species, similar fluctuations can be seen in the number of buds in bud banks. For example, in pseudoannuals, where overwintering organs bearing buds are formed at the end of a season, resprouting is reduced by bud and carbon limitation in spring, following seasonal regrowth by renewal buds (Verburg, 1998; Piqueras, 1999).

Classification of bud banks

Most characteristics of bud banks are largely determined by plant growth architecture. Clonal growth types can therefore be used as a proxy in the classification of bud banks. The diversity of clonal growth types is considerable (Fig. 1; see also Klimeš et al., 1997); therefore, it is suggested that the classification should contain rather broad categories in which some traditional types of clonal growth are merged. These categories reflect plant response to disturbance severity and timing/frequency. Vertical distribution of buds in the bud bank and the ability to sprout from plant fragments determine plant regeneration after disturbances differing in severity (Bellingham and Sparrow, 2000; Vesk et al., 2004b; Vesk and Westoby, 2004c), whereas seasonal fluctuations in the number of buds determine the response to different timing of disturbances (Piqueras, 1999; Barrat-Segretain and Bornette, 2000).

Disturbance has been defined as an external factor causing biomass removal (Grime, 2001). The greater the disturbance severity, the higher the proportion of lost biomass. Most disturbances of low severity directly affect above-ground parts of the plant only (leaf herbivory, mowing, browsing and grazing by ungulates) whereas severe disturbances often remove both above- and below-ground plant biomass (windthrows, ploughing, soil erosion, landslides). Therefore, the effect on plants and their bud banks generally extends from above-ground to below-ground with increasing intensity of disturbance. Exceptions may be found in fire-prone areas where above-ground seed and bud storage may be an important strategy (Hodgkinson, 1998; Ne'eman et al., 2004). However, plants subjected in the below-ground to a disturbance of low severity (e.g. by root herbivory) do not require a bud bank for regeneration, as buds are not utilized for growth of adventitious roots. Consequently, the response of a plant to disturbance severity can be estimated according to the distribution of buds along the vertical axis of the plant. Thus, above- and below-ground bud banks are distinguished in our classification.

Seasonal and perennial bud banks can be distinguished when considering the effect of disturbance frequency and timing on buds. The seasonal bud bank develops on short-lived plant organs (above-ground stems of herbs, below-ground organs of pseudo-annuals). Its buds are usually not as abundant as on perennial organs, and are kept dormant either by innate dormancy or correlative inhibition. Some of them may also be dispersed. Thus, the seasonal bud bank resembles a transient seed bank, because the buds are not available for regenerative sprouting in some parts of the year. The perennial bud bank develops on perennial plant organs. The buds are usually numerous, kept dormant by correlative inhibition and are not dispersable (buds on all woody parts in trees and buds on perennial below-ground organs in herbs). The perennial bud bank resembles a long-term persistent seed bank, but bud longevity usually does not exceed that of the parent plant (Table 1, Fig. 1).

In contrast to buds on stem-originated organs, a definitive number of adventitious buds formed on roots and leaves cannot be estimated a priori because some of them are formed de novo after an injury or due to other triggering factors (Peterson, 1975). Therefore, the bud bank of adventitious buds on roots and leaves forms a special category. Superficially, the functioning of adventitious buds does not differ from the functioning of axillary buds. After correlative inhibition is broken by an injury, adventitious buds on roots start to sprout similarly to axillary buds on rhizomes (Horvath et al., 2002), or are formed de novo (Beijerinck, 1887; Bosela and Ewers, 1997). Thus, the response to a disturbance is delayed in the latter case (Geranium sanguineum; Dubard, 1903; Trifolium montanum; Golubeva and Golubev, 1964).

There are also other differences. Roots on which adventitious buds are usually formed are located deeper in the soil than rhizomes and are better protected against severe disturbance. Formation of adventitious buds thus enables regeneration of even very small plant fragments. In this way, survival of plants after severe disturbance, such as ploughing in arable fields (Hamdoun, 1972), fire, pulling out, and cutting (Fernández-Santos et al., 1999), is ensured. Adventitious buds on roots may substitute functionally for buds of stem-originated organs, as these two types are usually not found together in one species (Klimešová and Martínková, 2004). Root-sprouting herbaceous plants are more frequent in severely disturbed communities, such as arable fields, than in other types of vegetation (Klimeš et al., 1997). As timing of the development of buds on roots often depends on disturbances whose timing is unpredictable, adventitious buds are classified as a potential bud bank (Fig. 1).

This classification of bud banks includes two levels of seasonality (seasonal and perennial) and two levels of vertical distribution (above- and below-ground), resulting in four categories. Moreover, each of them can be combined with the potential bud bank ('adventitious sprouting') and the potential bud bank need not be associated with other types of bud banks. A plant population may develop one or several types of bud bank, depending on its growth form, plasticity and disturbance severity and timing.

Table 1. Some characteristics of three types of bud banks

Bud bank	Number of buds	Seasonal fluctuations	Dispersability of buds	Type of dormancy
Perennial	Many	No	No	Correlative inhibition, induced dormancy
Seasonal	Few	Yes	No or yes	Correlative inhibition, induced dormancy, innate dormancy
Potential	Estimation uncertain[a]	Estimation uncertain[a]	No	Correlative inhibition, induced dormancy

[a] Buds in the potential bud bank are partly formed de novo, often after an injury, and thus their number may change within a short time.

Main principles of classification may be summarised as follows:

1. The bud bank consists of all buds which may be used for vegetative regeneration, including those formed adventitiously only after injury.
2. Vertical distribution of buds reflects disturbance avoidance.
3. Seasonal changes in the bud bank make vegetative regeneration sensitive to disturbance timing.
4. The ability to form adventitious buds provides potential for vegetative regeneration from roots, stumps and leaves.

Quantitative assessment of resprouting capacity and bud numbers

The ability of plants to resprout can be assessed experimentally in the field or ex situ. Cornelissen et al. (2003) suggested a standardised procedure to assess vegetative regeneration in the field after episodic major disturbances. They defined 'resprouting capacity' as the proportion of damaged plants multiplied by the proportion of resprouting damaged plants (i.e. plants developing new shoots on basal or below-ground organs). Evaluation of vegetative regeneration should be made up to 5 years after the disturbance for trees and in the year of the disturbance for herbs (Cornelissen et al., 2003). This approach produces accurate data for a given species and its environment. However, it is very time-consuming because it requires an exact evaluation of plant mortality which cannot be usually estimated from snap-shot data. Another disadvantage of this method is its dependence on natural disturbances or relatively large-scale experimental disturbances, which cannot be always applied, due to restrictions by nature protection authorities, for example.

In semiarid shrublands, Vesk et al. (2004b) and Vesk and Westoby (2004c) clipped and/or burned only targeted plant individuals, recorded their resprouting and monitored several other plant traits. This method gave important results on the impact of disturbances differing in intensity on plants with various growth forms and different vertical distribution of buds. Application of this approach is more difficult in dense vegetation, where plants with extensive clonal growth are intermingled but it has been successfully applied to non-clonal plants in pastures (e.g. Huhta et al., 2003).

Ex situ assessment of resprouting capacity was used by Lee (2004) in an aspen-dominated boreal forest: several soil cores were sampled, sprouting was recorded in a greenhouse, sprouts were identified to species and counted. Unfortunately, this technique, similar to that used for seed bank estimation, considerably underestimated the number of sprouting species. About one-third of species sprouting in the field were recorded by this method, because plants with less extensive below-ground clonal organs were underrepresented in the cores. A similar approach was used for screening of regenerative capacity of different species for stem fragments by Hodgson et al. (1993) and for root fragments by Kociánová (2005). Ex situ experiments estimate the potential for regeneration after very severe disturbances. These often result in plant fragmentation (for example in arable land) where not only the bud bank but also the ability to produce adventitious roots plays an important role (Guerrero-Campo et al., 2006). A less severe disturbance can be easily applied in pot or garden experiments with a single or a limited number of species (e.g. Martínková et al., 2004a, b).

Results of resprouting experiments can be relatively easily obtained for a large number of species. On the other hand, generalizations beyond the studied type, intensity and timing of disturbance and environmental conditions used in the experiment can be made only cautiously.

An alternative is an indirect assessment of plant regeneration, based on bud counts and the knowledge of their role in regeneration after various types of disturbances. As bud counting in the field is very time-consuming and in woody plants usually impossible, it has been done only for selected species in a community (Busso et al., 1989; Hendrickson and Briske, 1997; Noble, 2001; Flemmer et al., 2002; Hartnett et al., 2006) or the estimates were obtained for the whole community without identification of individual species (Benson et al., 2004; Dalgleish and Hartnett, 2006). The estimates of resprouting capacity can be much improved if living and dead meristems are distinguished. Still, the number of living meristems is usually much higher than the number of shoots resprouting after a disturbance. Also, we may expect great differences in the proportion of resprouting shoots between individual bud bank types. On the other hand, this approach is more advantageous than experimental assessment of sprouting ability in some cases, because its results are less dependent on particular disturbance types and environmental conditions.

Our approach (see also Klimeš and Klimešová, 2005), developed for herbaceous plants, simplifies and also refines the methods of direct counting of buds. For the estimation of bud number, we suggest counting nodes on individual shoots. The number of buds at a node depends on the number of leaves attached to it (usually one or two, but in some plants with bulbs even much more; see Klimešová and Klimeš, 2006). There are only scale leaves at the nodes of below-ground organs, but their number per node is the same as above-ground. It is necessary to dig up entire clonal fragments of the plant with one or several shoots for such assessment. The number of buds is estimated for the plant parts expected to survive the disturbance in question and above- and below-ground parts of the shoot separately, and expressed per shoot. This estimate is accurate under the assumption that the bud life-span is about the same as that of the organ on which it develops (rhizome, above-ground part of the shoot) and that buds develop at each axil. The real number of buds per shoot is usually somewhat lower, because some nodes do not develop buds (Bell, 1991), while other buds are not alive.

Buds on secondarily thickened below-ground organs of herbs have to be counted directly as the secondary thickening obscures the primary structure of the organs, including the nodes. The number of buds cannot be estimated directly in species adventitiously sprouting from roots, shoots and leaves, as some of the buds are formed after an injury only. For such species, experimental evaluation of resprouting capacity is necessary (see above). Unfortunately, lists of root-sprouting plants are available for some areas only, usually being more complete for woody plants (Del Tredici, 2001; Rodrigues et al., 2004) than for herbs (but see Klimešová and Klimeš, 2006).

In contrast to the experimental assessment of resprouting capacity, the estimation of bud numbers from plant morphology can be easily done for many species. In addition, the differences between various types of disturbances and environments may be considered using this method. Therefore, bud bank dynamics may be elucidated for different growth forms, bud bank types or types of disturbance. Bud bank types (vertical distribution and seasonality) with categorised bud numbers per shoot are currently available for central and northwest European species in the LEDA database (Knevel et al., 2003; Klimeš and Klimešová, 2005) and for central European species in the CLO-PLA database (Klimešová and Klimeš, 2005, 2006).

Implications of the bud bank concept

In the traditional concepts of plant strategies (Mac Arthur and Wilson, 1967; Grime, 2001), short generation time and large seed production were considered as adaptative traits in disturbed environments. However, it has been shown that regrowth from reserve meristems is also a successful strategy in severely and repeatedly disturbed habitats (Noble and Slatyer, 1980; van der Meijden et al., 1988; Bond and Midgley, 2001; Klimešová and Klimeš, 2003). Thus, the bud bank should not be neglected in studies focusing on the response of plants to disturbance at individual, population and also community levels.

The two most elaborated concepts of vegetative regeneration were built (i) around the seeder–sprouter dichotomy developed for tree strategies in fire-prone areas (Bond and Midgley, 2001, and references therein) and (ii) for regrowth strategy in plants subjected to herbivory (van der Meijden et al., 1988; Stowe et al., 2000). While the seeder–sprouter concept has been mostly applied to woody plants subjected to severe disturbance, regrowth strategy after biomass removal by herbivores has been studied usually in short-lived herbs subjected to a disturbance of low severity. Although several reviews on plant responses to various types of disturbances have been recently published (Bellingham and Sparrow, 2000; Pausas and Lavorel, 2003; Vesk and Westoby, 2004a; Bond and Keeley, 2005), the tools available for the evaluation of plant resprouting potential are still inadequate.

The advantage of the bud bank concept, as originally developed by Harper (1977) and then extended in this paper, is in its independence of plant growth forms and habitat types, as buds are utilised for resprouting by all vascular plants. Therefore, it can be used across biomes and life forms. Some minor modifications of the bud bank assessment will probably be useful for areas where special life forms, such as epiphytes or lianas, are abundant. Further, development of the concept may require adjustments for areas with non-seasonal climate where dynamics of plant development may follow plant's internal rhythms, not always synchronised across species, or is continuous throughout the year (Hallé et al., 1978). On the other hand, the bud bank concept might profit from incorporation into meristem allocation strategies which are currently being developed (see Bonser and Aarssen, 2006).

Four broad topics were identified in which utilization of the new bud bank concept may be stimulative.

(1) As buds are basic elements of plant architecture (together with nodes, internodes and leaves), there should be evolutionary constraints in the developmental programmes of modular plant growth (Hallé et al., 1978; Watson, 1984) and environmentally induced variation in these programmes (Watson et al., 1995). The concept of the bud bank can be used, for example, when testing the effect of various types of disturbance on the number of dormant meristems, their vertical distribution and seasonal variation among related taxa.

(2) Because the bud bank is closely linked with plant architecture, it has to be affected not only by disturbance but also by habitat productivity and competition. Therefore, correlations and/or trade-offs can be expected between the bud banks and other architectural traits, such as plant height, branching and woodiness (Givnish, 1995).

(3) The bud bank concept enables a comparison of vegetative regeneration with regeneration by seeds, because both seed banks and seed dispersal respond to the timing and severity of a disturbance. We may ask what the role of individual regeneration modes in plant communities is and test for correlations and trade-offs among them. For example, does competition between seed production and bud storage for assimilates result in a trade-off between these two processes?

(4) The bud bank, as a relatively easily obtainable trait, can be used in the delimitation of plant functional types in plant communities subjected to various types of disturbance. In the current literature dealing with different management regimes, much attention is paid to plant traits enabling avoidance of disturbance, such as plant height, phenology and Raunkiaer's life forms (e.g. Lavorel et al., 1997; Diaz et al., 2001), rather than to traits responsible for disturbance tolerance. However, plants usually fail to avoid the disturbance completely and have to cope with it. Therefore, it is not surprising that attempts to find plant traits shared by plants dominating in plots with various management regimes sometimes do not give satisfactory results (Vesk et al., 2004a). We suggest that regeneration potential, as indicated by the bud banks, their vertical distribution, seasonality and bud number, provide a promising tool which could be more efficient in such studies, in comparison with the plant traits used so far.

Acknowledgments

Invaluable comments to previous versions of the manuscript were provided by J.M. van Groenendael, G. Austrheim, R.M. Bekker, A. Krumbiegel, E.J. Jäger and L.W. Aarssen. Language help by J.W. Jongepier and K. Edwards is acknowledged. The work was funded by the Grant Agency of the Czech Republic (206/01/1039 and 206/01/1037), by project AV0Z6005908 of the Czech Academy of Sciences and the LEDA project founded by the European Commission (EVR1-CT-2002-40022).

Appendix A. Glossary on terms related to bud banks

Adventitious bud: a bud formed de novo mainly endogenously; usually develops on roots, less often on stems or leaves; its formation may be stimulated by plant injury.

Axillary bud: a bud situated on a stem in the axil of a leaf; it develops exogenously at the shoot apex.

Bud bank: all viable axillary and adventitious buds which are present on a plant and are available for regrowth, branching and replacement of shoots through a season or for vegetative regeneration after an injury (regenerative buds); some buds may be initiated by an injury.

Budding plant: a plant formed by a small frond (e.g. in Lemna); an extremely reduced plant body of aquatic plants; its growth results in the production of similar structures which are soon detached from parent plant.

Bulb: a storage organ consisting of storage leaves and a shortened stem base; the bulb is formed by organs produced within a single season or in the course of several seasons; by itself it represents one renewal bud; in addition, some plants produce smaller bulbs and/or bulbils; plants growing from them morphologically and in size resemble seedlings.

Bulbils and tubercules: small vegetative diaspores produced in axils of leaves on stems above-ground or below-ground; depending on the location of storage within the buds they are called bulbils (storage located in scale leaves), stem tubercules (storage located in the stem part) or root tubers (storage located in an adventitious root); they soon fall down from the parent plant and immediately start to grow, having no dormancy, whereas below-ground bulbils and tubercules may postpone their development until spring; young plants regenerating from bulbils and tubercules resemble seedlings in their morphology and size.

Clonal fragment: physically inter-connected ramets of a partially disintegrated clonally growing plant.

Epigeogenous rhizome: a perennating stem-originated organ formed above-ground (Serebriakov and Serebriakova, 1965); its distal part is covered by soil and litter or pulled into the soil by the contraction of roots; nodes bear green leaves, the internodes are usually short; the rhizomes bear roots and serve as a bud bank and storage organs; vegetative spreading is usually slow (up to a few cm year^{-1}), persistence of epigeogenous rhizomes differ considerably among species.

Horizontal above-ground stem: a clonal growth organ rooting in the soil and providing connection between offspring plants or formed by a creeping axis of a plant; nodes on the stem bear leaves, internodes are usually long, the stem serves as a storage organ and a bud bank; vegetative spreading may be fast and persistence of the horizontal above-ground stems differs considerably among species.

Hypogeogenous rhizome: a clonal growth organ formed below-ground (Serebriakov and Serebriakova, 1965); the rhizome usually grows horizontally at a species-specific depth and after some time it becomes orthotropic and forms above-ground shoots; the horizontal part of the rhizome bears bracts, a few roots developed at the nodes, and has long internodes; vegetative spreading is often fast, up to several m year^{-1}; persistence of the hypogeogenous rhizome differs considerably among species.

Leaves with adventitious buds (gemmipary): adventitious buds on leaves formed after shedding or detaching of leaves from the parent plant; on bare wet soil they develop into plantlets resembling seedlings in their aboveground morphology and size.

Lignotuber: swollen below-ground stem base of a woody plant, usually partly of root origin; it bears axillary buds and contains large carbohydrate reserves used for regeneration after a disturbance, usually fire.

Plantlet (pseudovivipary): a meristem which would normally develop into a flower, forms a vegetative bud (plantlet, bulbil, root or stem tubercule) and may be soon detached from the parent plant; alternatively the whole inflorescence lays down and plantlets root at the soil surface; offspring morphology and size is similar to seedlings.

Regenerative bud: dormant (resting) axillary, adventitious buds which break their dormancy and adventitious buds formed de novo and substituting for lost shoots after an injury; the regenerative buds may be located on any living plant part, including above-ground shoots; they form a bud bank together with renewal buds.

Regrowth: see vegetative regeneration.

Renewal buds: dormant (resting) apical, axillary and adventitious buds which are used for spring regrowth or replacement of shoots during a season; renewal buds usually form a small proportion of the buds on a plant, their location is species-specific and similar in plants with the same morphology; their location is used in the definition of Raunkiaer's life-forms and their development is seasonal; in comparison with regenerative buds, structures in the renewal buds are usually more preformed, and may include leaves, stems and in some cases even flowers; their dormancy may be broken by a disturbance, however, this often results in flower abortion or malformation; in many plants no sharp distinction between renewal and regenerative buds exists; the renewal buds together with regenerative buds form a bud bank.

Root-splitter: a plant possessing a primary root system without adventitious roots and buds; senescing tap root of old plants decays from the root center, in some species causing plant fragmentation; an old individual genet disintegrates into ramets bearing parts of the main root and one or a few shoots; vegetative spreading is poor; the tap root serves as a storage organ and vascular link between shoots; the bud bank is situated on the perennial bases of shoots ('caudex').

Roots with adventitious buds: plant roots (main root including the hypocotyle, and adventitious roots) form adventitious buds spontaneously or after an injury; when buds are formed on horizontal roots they may enable an extensive clonal growth; persistence of the roots with adventitious buds considerably differs among species.

Root tuber: a below-ground storage organ; in some plants it serves as a regenerative organ of root origin bearing a bud or buds of stem origin; in that case the plant dies back in autumn, except for the root tuber(s) with the buds, later utilised for spring regrowth; in summer old tubers decay and new ones are formed.

Shoot: product of an apical meristem, usually consisting of a stem with leaves and generative structures (flowers and fruits).

Stem tuber: below-ground, usually short-lived storage and regenerative organ of shoot origin; offspring tubers are attached to a parent tuber or produced at the end of a hypogeogenous rhizome; the parent plant dies back in autumn, except for the stem tuber(s) which bear one dominant bud, each utilised for spring regrowth; in summer old tubers decay and new ones are formed; in addition some plants produce smaller tubers and/or tubercules; plants growing from them resemble in aboveground morphology and size seedlings.

Tuber-splitter: a plant develops only one perennial tuber (usually formed by the hypocotyle), no offspring tubers are produced; in senescing plants tubers may start to decay from their center resulting eventually in plant fragmentation.

Turion: a detachable over-wintering bud of water plants composed of tightly arranged leaves filled by storage compounds; the turion develops axially or apically, is usually dormant and needs vernalization to regrow.

Vegetative regeneration: growth of plant which follows after loss of biomass due to disturbance and results in at least partial restoration of plant functions ('vegetative growth').

References

Agrawal, A.A., Conner, J.K., Stinchcombe, J.R., 2004. Evolution of plant resistance and tolerance to frost damage. Ecol. Lett. 7, 1199–1208.

Anderson, J.V., Chao, W.S., Horvath, D.P., 2001. A current review on the regulation of dormancy in vegetative buds. Weed Sci. 49, 581–589.

Bannister, P., Maegli, T., Dickinson, K.J.M., Halloy, S.R.P., Knight, A., Lord, J.M., Mark, A.F., Spencer, K.L., 2005. Will loss of snow cover during climatic warming expose New Zealand alpine plants to increased frost damage? Oecologia 144, 245–256.

Barrat-Segretain, M.H., Bornette, G., 2000. Regeneration and colonization abilities of aquatic plant fragments: effect of disturbance seasonality. Hydrobiologia 421, 31–39.

Barrat-Segretain, M.H., Bornette, G., Vilas-Boas, H.A., 1998. Comparative abilities of vegetative resprouting among aquatic plants growing in disturbed habitats. Aquat. Bot. 60, 201–211.

Beijerinck, M., 1887. Wurzelknospen und Nebenwurzeln. Verh. Koninkl. Nederl. Akad. Wet. 25/3, 1–150.

Bell, A.D., 1991. Plant Form. An Illustrated Guide to Flowering Plant Morphology. Oxford University Press, Oxford.

Bell, T.L., Ojeda, F., 1999. Underground starch storage in Erica species of the Cape Floristic Region – differences between seeders and resprouters. New Phytol. 144, 143–152.

Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89, 409–416.

Bellingham, P.J., Tanner, E.V.J., Healey, J.R., 1994. Sprouting of trees in Jamaican montane forests, after a hurricane. J. Ecol. 82, 747–758.

Benson, E.J., Hartnett, D.C., Mann, K.H., 2004. Belowground bud banks and meristem limitation in tallgrass prairie plant population. Am. J. Bot. 91, 416–421.

Bímová, K., Mandák, B., Pyšek, P., 2003. Experimental study of vegetative regeneration in four invasive Reynoutria taxa (Polygonaceae). Plant Ecol. 166, 1–11.

Bobich, E.G., Nobel, P.S., 2001. Vegetative reproduction as related to biomechanics, morphology and anatomy of four cholla cactus species in the Sonoran Desert. Ann. Bot. 87, 485–493.

Boedeltje, G., Bakker, J.P., Bekker, R.M., van Groenendael, J.M., Soesbergen, M., 2003. Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. J. Ecol. 91, 855–866.

Bond, J.W., Keeley, J.E., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20, 387–394.

Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. Trends Ecol. Evol. 16, 45–51.

Bonser, S.P., Aarssen, L.W., 1996. Meristem allocation: a new classification theory for adaptive strategies in herbaceous plants. Oikos 77, 347–352.

Bonser, S.P., Aarssen, L.W., 2001. Allometry and plasticity of meristem allocation throughout development in Arabidopsis thaliana. J. Ecol. 89, 72–79.

Bonser, S.P., Aarssen, L.W., 2003. Allometry and development in herbaceous plants: functional responses of meristem allocation to light and nutrient availability. Am. J. Bot. 90, 404–412.

Bonser, S.P., Aarssen, L.W., 2006. Meristem allocation and life-history evolution in herbaceous plants. Can. J. Bot. 84, 143–150.

Bosela, M.J., Ewers, F.W., 1997. The mode of origin of root buds and root sprouts in the clonal tree Sassafras albidum (Lauraceae). Am. J. Bot. 84, 1466–1481.

Busso, C.A., Mueller, R.J., Richards, J.H., 1989. Effects of drought and defoliation on bud viability in 2 caespitose grasses. Ann. Bot. 63, 477–485.

Brando, P.M., Durigan, G., 2004. Changes in cerrado vegetation after disturbance by frost (Sao Paulo State, Brazil). Plant Ecol. 175, 205–215.

Campbell, M.L., 2003. Recruitment and colonisation of vegetative fragments of Posidonia australis and Posidonia coriacea. Aquat. Bot. 76, 175–184.

Catovski, S., Bazzaz, F.A., 2002. Nitrogen availability influences regeneration of temperate tree species in the understory seedling bank. Ecol. Appl. 12, 1056–1070.

Combroux, I., Bornette, G., Willby, N.J., Amoros, C., 2001. Regenerative strategies of aquatic plants in disturbed habitats: the role of the propagule bank. Arch. Hydrobiol. 152, 215–235.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51, 335–380.

Cruz, A., Perez, B., Moreno, J.M., 2003. Resprouting of the Mediterranean-type shrub Erica australis with modified lignotuber carbohydrate content. J. Ecol. 91, 348–356.

Dalgleish, H.J., Hartnett, D.C., 2006. Below-ground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis. New Phytol. 171, 81–89.

De Bie, S., Ketner, P., Paasse, M., Geerling, C., 1998. Woody plant phenology in the West Africa savanna. J. Biogeogr. 25, 883–900.

Del Tredici, P., 2001. Sprouting in temperate trees: a morphological and ecological review. Bot. Rev. 67, 121–140.

Diaz, S., Noy-Meir, I., Cabido, M., 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? J. Appl. Ecol. 38, 497–508.

Diggle, P.K., 1997. Extreme preformation in alpine Polygonum viviparum: an architectural and developmental analysis. Am. J. Bot. 84, 154–169.

Dubard, M., 1903. Recherches sur les plantes a bourgeons radicaux. Ann. Sci. Natur.-Bot. 17, 109–225.

Eckert, C.G., 2002. The loss of sex in clonal plants. Evol. Ecol. 15, 501–520.

Fahrig, L., Coffin, D.P., Lauenroth, W.K., Shugart, H.H., 1994. The advantage of long-distance clonal spreading in highly disturbed habitats. Evol. Ecol. 8, 172–187.

Fernández-Santos, B., Gómez-Gutiérez, J.M., Moreno-Marcos, G., 1999. Effects of disturbance caused by traditional Spanish rural land use on the regeneration of Cytisus multiflorus. Appl. Veg. Sci. 2, 239–250.

Flemmer, A.C., Busso, C.A., Fernandez, O.A., 2002. Bud viability in perennial grasses: water stress and defoliation effects. J. Range Manage. 55, 150–163.

Geber, M.A., de Kroon, H., Watson, M.A., 1997. Organ preformation in mayapple as a mechanism for historical effects on demography. J. Ecol. 85, 211–223.

Gill, A.M., 1995. Stem and fires. In: Gartner, B.L. (Ed.), Plant Stems. Physiology and Functional Morphology. Academic Press, San Diego, pp. 323–342.

Givnish, T.J., 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. In: Gartner, B.L. (Ed.), Plant Stems. Physiology and Functional Morphology. Academic Press, San Diego, pp. 3–49.

Golubeva, I.V., Golubev, V.N., 1964. O fakul'tativnoi korneotpryskovosti klevera gornogo v usloviiakh lugovoi stepi. Bot. Zh. 49, 1624–1628.

Grace, J.B., 1993. The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. Aquat. Bot. 44, 159–180.

Grime, J.P., 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. Wiley, Chichester.

Guerrero-Campo, J., Palacio, S., Pérez-Rontomé, Monserrat-Martí, G., 2006. Effect of root system morphology on root-sprouting and shoot-rooting abilities in 123 plant species from eroded lands in North-east Spain. Ann. Bot. 98, 439–447.

Hakansson, S., 1995. Weeds in agricultural crops 2. Life-forms and occurrence in a European perspective. Swedish J. Agric. Res. 25, 155–161.

Hallé, F., 1999. Ecology of reiteration in tropical trees. In: Kurmann, M.H., Hemsley, A.R. (Eds.), The Evolution of Plant Architecture. Royal Botanical Garden, Kew, pp. 93–107.

Hallé, F., Oldeman, R.A.A., Tomlinson, P.B., 1978. Tropical Trees and Forests. An Architectural Analysis. Springer, Berlin.

Hamdoun, A.M., 1972. Regenerative capacity of root fragments of Cirsium arvense (L.) SCOP. Weed Res. 12, 128–136.

Hartnett, D.C., Setshogo, M.P., Dalgleish, H.J., 2006. Bud bank of perennial savanna grasses in Botswana. Afr. J. Ecol. 44, 256–263.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, New York.

Hendrickson, J.R., Briske, D.D., 1997. Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence. Oecologia 110, 584–591.

Hess, E., 1909. Über die Wuchsformen der alpinen Geröllpflanzen. Arbeit aus dem Botanischen Museum des Eidg. Polytechnikum Zürich, Heinrich, Dresden.

Hodgkinson, K.C., 1998. Sprouting success of shrubs after fire: height-dependent relationship for different strategies. Oecologia 115, 64–72.

Hodgson, J.G., Pearce, A.M.K., Booth, R.E., 1993. Adventitious rooting of cuttings. In: Hendry, G.A.F., Grime, J.P. (Eds.), Methods in Comparative Plant Ecology. Chapman & Hall, London, pp. 74–77.

Hogg, E.H., Lieffers, V.J., 1991. Seasonal changes in shoot regrowth potential in Calamagrostis canadensis. Oecologia 85, 596–602.

Horvath, D.P., Chao, W.S., Anderson, J.V., 2002. Molecular analysis of signals controlling dormancy and growth in underground adventitious buds of leafy spurge. Plant Physiol. 128, 1439–1446.

Huhta, A.-P., Hellström, K., Rautio, P., Tuomi, J., 2003. Grazing tolerance of Gentianella amarella and other monocarpic herbs: why is tolerance highest at low damage levels? Plant Ecol. 166, 49–61.

Irmisch, T., 1850. Zur Morphologie der monokotylischen Knollen- und Zwiebelgewächse. G. Reimer Verlag, Berlin.

James, S., 1984. Lignotubers and burls – their structure, function and ecological significance in Mediterranean ecosystems. Bot. Rev. 50, 225–266.

Jeník, J., 1994. Clonal growth in woody plants: a review. Folia Geobot. Phytotax. 29, 291–306.

Kammesheidt, L., 1999. Forest recovery by root suckers and above-ground sprouts after slash-and-burn agriculture, fire and logging in Paraguay and Venezuela. J. Trop. Ecol. 15, 143–157.

Karrenberg, S., Blaser, S., Kollmann, J., Speck, T., Edwards, P.J., 2003. Root anchorage of saplings and cuttings of woody pioneer species in a riparian environment. Funct. Ecol. 17, 170–177.

Kelly, D., Skipworth, J.P., 1984. Tradescantia fluminensis in a Manawatu (New Zealand) forest: I. Growth and effects on regeneration. NZ J. Bot. 22, 393–397.

Klimeš, L., 1992. The clone architecture of Rumex alpinus (Polygonaceae). Oikos 63, 402–409.

Klimeš, L., Klimešová, J., 1999. CLO-PLA2 – a database of clonal plants in central Europe. Plant Ecol. 141, 9–19.

Klimeš, L., Klimešová, J., 2002. The effects of mowing and fertilization on carbohydrate reserves and regrowth of grasses: do they promote plant coexistence in species-rich meadows? Evol. Ecol. 15, 363–382.

Klimeš, L., Klimešová, J., 2005. Clonal traits. In: Knevel, I.C., Bekker, R.M., Kunzmann, D., Stadler, M., Thompson, K. (Eds.), Collecting and Measuring Standards of Life-history Traits of the Northwest European Flora, LEDA Traitbase Project. University of Groningen, Community and Conservation Ecology Group, UK, pp. 66–88.

Klimeš, L., Klimešová, J., Osbornová, J., 1993. Regeneration capacity and carbohydrate reserves in a clonal plant Rumex alpinus: effect of burial. Vegetatio 109, 153–160.

Klimeš, L., Klimešová, J., Hendriks, R., van Groenendael, J., 1997. Clonal plant architecture: comparative analysis of form and function. In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Backhuys Publishers, Leiden, pp. 1–29.

Klimešová, J., 2003. Monokarpické rostliny schopné přežít silnou disturbanci. Zprávy Čes. Bot. Společ., Praha, 38, Mater 19, 37–48.

Klimešová, J., Klimeš, L., 2003. Resprouting of herbs in disturbed habitats: is it adequately described by Bellingham–Sparrow's model? Oikos 103, 225–229.

Klimešová, J., Klimeš, L., 2005. CLO-PLA: databáze architektury klonálního růstu rostlin střední Evropy. Zprávy Čes. Bot. Společ., Praha, 40 Mater. 20, 53–64.

Klimešová, J., Klimeš, L., 2006. CLO-PLA3. 〈http://clopla.butbn.cas.cz/〉.

Klimešová, J., Martínková, J., 2004. Intermediate growth forms as a model for the study of plant clonality functioning: an example with root sprouters. Evol. Ecol. 18, 669–681.

Klekowski, E.J., 2003. Plant clonality, mutation, diplontic selection and mutational meltdown. Biol. J. Linn. Soc. 79, 61–67.

Knevel, I.C., Bekker, R.M., Bakker, J.P., Kleyer, M., 2003. Life-history traits of the Northwest European flora: the LEDA database. J. Veg. Sci. 14, 611–614 The database is accessible at 〈www.leda-traitbase.org.〉.

Kociánová, A., 2005. Banka pupenů na kořenových fragmentech. Zprávy Čes. Bot. Společ., Praha, 40 Mater. 20, 113–120.

Korsmo, E., 1930. Unkräuter im Ackerbau der Neuzeit. Springer, Berlin.

Kowarik, I., 1995. Clonal growth in Ailanthus altissima on a natural site in West Virginia. J. Veg. Sci. 6, 853–856.

Krumbiegel, A., 2001. Vegetative reproduction strategies of pseudoannual plants in central Europe. Beitr. Biol. Pfl. 72, 287–313.

Kubín, P., Melzner, A., Čížková, H., 1994. The relationship between starch content in rhizomes of Phragmites australis (Cav) Trin. ex Steud. and trophic conditions of habitat. Proc. R. Bot. Soc. Edinburgh 102B, 433–438.

Kubo, M., Sakio, H., Shimano, K., Ohno, K., 2005. Age structure and dynamics of Cercidiphyllum japonicum sprouts based on growth ring analysis. Forest Ecol. Manage. 213, 253–260.

Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T.D.A., 1997. Plant functional calssifications: from general groups to specific groups based on response to disturbance. Trends Ecol. Evol. 12, 474–478.

Leakey, R.R.B., 1981. Adaptive biology of vegetatively regenerating weeds. Adv. Appl. Biol. 6, 57–90.

Leck, M.A., Parker, V.T., Simpson, R.L., 1989. Ecology of Soil Seed Banks. Academic Press, San Diego.

Lee, P., 2004. The impact of burn intensity from wildfires on seed and vegetative banks, and emergent understory in aspen-dominated boreal forests. Can. J. Bot. 82, 1468–1480.

Lennartsson, T., Tuomi, J., Nilsson, P., 1997. Evidence for an evolutionary history of overcompensation in the grassland biennial Gentianella campestris (Gentianaceae). Am. Nat. 149, 1147–1156.

Lerat, S., Gauci, R., Carfore, J.G., Vierheilig, H., Piche, Y., Lapointe, L., 2002. ^{14}C transfer between the spring ephemeral Erythronium americanum and sugar maple saplings via arbuscular mycorrhizal fungi in natural stands. Oecologia 132, 181–187.

Lloret, F., Verdú, M., Flores-Hernández, N., Valiente-Banuet, A., 1999. Fire and resprouting in Mediterranean ecosystems: insights from an external biogeographical region, the Mexical shrubland. Am. J. Bot. 86, 1655–1661.

Loehle, C., 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. Am. Nat. 156, 14–33.

Mac Arthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

MacGillivray, C.W., Grime, J.P., Band, S.R., Booth, R.E., Campbell, B., Hendry, G.A.F., Hillier, S.H., Hodgson, J.G., Hunt, R., Jalili, A., Mackey, J.L.M., Mowforth, M.A., Neal, A.M., Reader, R., Rorison, I.H., Spencer, R.E., Thompson, K., Thorpe, P.C., 1995. Testing predictions of the resistance and resilience of the vegetation subjected to extreme events. Funct. Ecol. 9, 640–649.

Mandujano, M.C., Montana, C., Franco, M., Golubov, J., Flores-Martinez, A., 2001. Integration of demographic annual variability in a clonal desert cactus. Ecology 82, 344–359.

Martínková, J., Klimešová, J., Mihulka, S., 2004a. Resprouting after disturbance: an experimental study with short-lived monocarpic herbs. Folia Geobot. 39, 1–12.

Martínková, J., Kočvarová, M., Klimešová, J., 2004b. Resprouting after disturbance in the short-lived herb Rorippa palustris (Brassicaceae): an experiment with juveniles. Acta Oecol. 25, 143–150.

Maschinski, J., Whitham, T.G., 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. Am. Nat. 134, 1–19.

Masuzawa, T., Hogetsu, K., 1977. Seasonal changes in the amount of carbohydrate and crude protein in the rhizome of Miscanthus sacchariflorus. Bot. Mag., Tokyo 90, 181–191.

Maun, M.A., 1998. Adaptations of plants to burial in coastal sand dunes. Can. J. Bot. 76, 713–738.

McAllister, R.S., Haderlie, L.C., 1985. Seasonal variation in canada thistle (Cirsium arvense). Root bud growth and root carbohydrate reserves. Weed Sci. 33, 44–49.

McVean, D.N., 1953. Alnus glutinosa (L.) Gaertn. J. Ecol. 41, 447–466.

Meney, K.A., Dixon, K.W., Pate, J.S., 1997. Reproductive potential of obligate seeder and resprouter herbaceous perennial monocots (Restionaceae, Anarthriaceae, Ecdeiocoleaceae) from South-western Western Australia. Aust. J. Bot. 45, 771–782.

Morrow, P.A., Olfelt, J.P., 2003. Phoenix clones: recovery after long-term defoliation-induced dormancy. Ecol. Lett. 6, 119–125.

Ne'eman, G., Goubitz, S., Nathan, R., 2004. Reproductive traits of Pinus halepensis in the light of fire – a critical review. Plant Ecol. 171, 69–79.

Noble, J.C., 2001. Lignotubers and meristem dependence in mallee (Eucalyptus spp.) coppicing after fire. Aust. J. Bot. 49, 31–41.

Noble, I.R., Slatyer, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43, 5–21.

Pausas, J.G., Lavorel, S., 2003. A hierarchical deductive approach for functional types in disturbed ecosystems. J. Veg. Sci. 14, 409–416.

Peterson, R.L., 1975. The initiation and development of root buds. In: Torrey, J.G., Clarkson, D.T. (Eds.), The Development and Function of Roots. Academic Press, London, pp. 125–161.

Peterson, C.J., Pickett, S.T.A., 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. Forest Ecol. Manage. 42, 205–217.

Piqueras, J., 1999. Herbivory and ramet performance in the clonal herb Trientalis europaea L. J. Ecol. 87, 1–12.

Raffaele, E., Veblen, T.T., 1998. Facilitation by nurse shrubs of resprouting behaviour in a post-fire shrubland in northern Patagonia, Argentina. J. Veg. Sci. 9, 693–698.

Raju, M.V.S., Steeves, T.A., Coupland, R.T., 1964. On the regeneration of the root fragments of leafy spurge (Euphorbia esula L.). Weed Res. 4, 36–41.

Rauh, W., 1937. Die Bildung von Hypokotyl- und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. Nova Acta Leop. 4, 395–553.

Raunkiaer, C., 1934. The Life-forms of Plants and Statistical Plant Geography. Clarendon Press, Oxford.

Rees, M., 1994. Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. Am. Nat. 144, 43–64.

Richards, J.H., Caldwell, M.M., 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with Agropyron species. J. Appl. Ecol. 22, 907–920.

Rodrigues, R.R., Torres, R.B., Metthes, L.A.F., Pentha, A.S., 2004. Tree species sprouting from root buds in a semideciduous forest affected by fires. Braz. Arch. Biol. Technol. 47, 127–133.

Rogers, W.E., Hartnett, D.C., 2001. Temporal variation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. Am. J. Bot. 88, 1634–1642.

Rutishauser, R., Isler, B., 2001. Developmental genetics and morphological evolution of flowering plants, especially Bladderworts (Utricularia): fuzzy Arberian morphology complements classical morphology. Ann. Bot. 88, 1173–1202.

Sagers, C.L., 1993. Reproduction in neotropical shrubs: the occurrence and some mechanisms of asexuality. Ecology 74, 615–618.

Salter, J., 1857. On the viability of seeds after prolonged submersion in the sea. J. Linn. Soc., London 1, 140–142.

Serebriakov, I.G., Serebriakova, T.I., 1965. O dvukh tipakh formirovaniia kornevishch u travianistykh mnogoletnikov. Biull. Moskov. Obshch. Ispyt. Prir., Biologia 70/2, 67–81.

Simpson, R.L., Leck, M.A., Parker, V.T., 1989. Seed banks: General concepts and methodological issues. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Banks. Academic Press, San Diego, pp. 3–8.

Stafstrom, J.P., 1995. Developmental potential of shoot buds. In: Gartner, B.L. (Ed.), Plant Stems. Physiology and Functional Morphology. Academic Press, San Diego, pp. 257–279.

Stowe, K.A., Marquis, R.J., Hochwender, C.G., Simms, E.L., 2000. The evolutionary ecology of tolerance to consumer damage. Annu. Rev. Ecol. Syst. 31, 565–595.

Suzuki, J.-I., Hutchings, M.J., 1997. Interactions between shoots in clonal plants and the effects of stored resources on the structure of shoot populations. In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Backhuys Publishers, Leiden, pp. 311–329.

Suzuki, J.-I., Stuefer, J., 1999. On the ecological and evolutionary significance of storage in clonal plants. Plant Spec. Biol. 14, 11–17.

Thompson, K., Bakker, J.P., Bekker, R.M., 1997. Soil Seed Banks of North-West Europe: Methodology, Density and Longevity. Cambridge University Press, Cambridge.

Tolvanen, A., Schroderus, J., Henry, G.H.R., 2002. Age- and stage-based bud demography of Salix arctica under contrasting muskox grazing pressure in the High Arctic. Evol. Ecol. 15, 443–462.

Troll, W., 1939–1942. Vergleichende Morphologie der höheren Pflanzen. Band 1 – Vegetationsorgane. Borntraeger, Berlin.

Tuomi, J., Nilsson, P., Aström, M., 1994. Plant compensatory responses: bud dormancy as an adaptation to herbivory. Ecology 75, 1429–1436.

Van der Meijden, E., Wijn, M., Verkaar, H.J., 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. Oikos 51, 355–363.

Velenovský, J., 1905–1913. Vergleichende Morphologie der Pflanzen. Fr. Řivnáč Ver., Praha.

Verburg, R.G., 1998. The witch at the forest floor. Reproductive allocation and clonal diversity in the pseudo-annual Circaea lutetiana L. Ph.D. Thesis, Utrecht University, Utrecht.

Vesk, P.A., Westoby, M., 2003. Drought damage and recovery – a conceptual model. New Phytol. 160, 7–14.

Vesk, P.A., Westoby, M., 2004a. Sprouting ability across diverse disturbances and vegetation types worldwide. J. Ecol. 92, 310–320.

Vesk, P.A., Westoby, M., 2004b. Funding the bud bank: a review of the costs of buds. Oikos 106, 200–208.

Vesk, P.A., Westoby, M., 2004c. Sprouting by plants: the effect of modular organization. Funct. Ecol. 18, 939–946.

Vesk, P.A., Leishman, M.R., Westoby, M., 2004a. Simple traits do not predict grazing response in Australian dry shrublands and woodlands. J. Appl. Ecol. 41, 22–31.

Vesk, P.A., Warton, D.J., Westoby, M., 2004b. Sprouting by semi-arid plants: testing a dichotomy and tredictive traits. Oikos 107, 72–89.

Vodolazsky, L.E., 1979. O raznoobrazii pridatochnykh pochek i pobegov u korneotpriskovogo travianistogo mnogoletnika Chamaenerion angustifolium (L.) Scop. (Onagraceae). Bot. Zh. 64, 734–738.

Warming, E., 1908. The structure and biology of Arctic flowering plants I. Ericineae (Ericaceae, Pirolaceae). Medd. Grönl. 36, 2–71.

Watson, M.A., 1984. Developmental constrains: effect on population growth and patterns of resource allocation in a clonal plant. Am. Nat. 123, 411–426.

Watson, M.A., Geber, M.A., Jones, C.S., 1995. Ontogenetic contingency and the expression of plant plasticity. Trends Evol. Ecol. 10, 474–475.

Willby, N.J., Abernethy, V.J., Demars, B.O.L., 2000. Attribute-based classification of European hydrophytes and its relationship to habitat utilization. Freshwater Biol. 43, 43–74.

Ziegenspeck, H., 1936. Orchidaceae. In: Wangerin, W., Schröter, C. (Eds.), Lebensgeschichte der Blütenpflanzen Mitteleuropas, Vol. 4. Ulmer, Stuttgart, Band I, Abt., pp. 1–840.