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CLO-PLA: the database of clonal and bud bank traits of Central European flora§

Klimešová, Jitka[1*] & de Bello, Francesco[2]

[1]*Section of Plant Ecology, Institute of Botany, Czech Academy of Sciences, Dukelská 135, CZ-379 82, Třeboň, Czech Republic;* [2]*Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université Joseph Fourier, BP 53, Domaine Universitarire, 2233 Rue de la Piscine, 38041 Grenoble Cedex 9, France; E-mail fradebello@ctfc.es;* **Corresponding author; Fax 042 384721136; E-mail klimesova@butbn.cas.cz*

Abstract: Clonal growth of plants is mainly a result of the vegetative growth of organs hidden beneath the soil surface and producing potentially independent vegetative offspring. Clonal traits are difficult to measure due to inaccessibility of the space they inhabit and their morphological diversity. This causes great difficulties with descriptions, standardization of measurements across plant growth forms and, probably, a lack of appropriate questions that should be answered using them. The freely available CLO-PLA database (http://clopla.butbn.cas.cz/) can help to assess the roles of vegetative means of regeneration and spread in plant communities under the effect of various biotic and abiotic filters. It can serve as a source of reference on persistence traits of European temperate flora and, eventually, as a guide for trait sampling in other regions of the world.

Keywords: Bud bank; Clonal growth organ; Comparative ecology; Functional trait; Plant clonality.

Nomenclature: Kubát et al. 2002

Plants differ in their ecological functions and therefore are able to inhabit different environments and coexist together (Grime 2006; Wilson 2007). There is a long tradition in ecology of defining and measuring ecological functions by which plants differ in term of their traits. Several attempts have been made to delimit a set of important traits that cover all main plant functions (Westoby 1998; Weiher et al. 1999; Cornelissen et al. 2003). It is remarkable that these approaches, unfortunately, commonly overlook traits such as clonal growth (how a plant can produce potentially independent offspring ramets through vegetative growth) and bud bank characteristics (the reserve meristems necessary for plant regrowth), together with the plant functions related to these traits.

§This paper is dedicated to the memory of Leoš Klimeš, co-author of CLO-PLA, who was lost in Ladakh (West Himalaya) in August 2007.

The almost complete focus on aboveground and ecophysiological traits in the last few decades (e.g. compare descriptions of plant species in the first Biological flora of Central Europe by Kirchner et al. 1908–1942 with more recent approaches) can partly be explained by the diversity of belowground traits and the lack of easy-to-measure characteristics that are relevant to clonality and vegetative regeneration (Weiher et al. 1999). Clonal traits are often connected with belowground organs and, rightly or wrongly, considered by researchers as difficult or time-consuming to measure. However, in cases where clonal growth is taken into account, it has been found to be important for the dynamics of the studied ecosystem (Ozinga et al. 2007; Laanisto et al. 2008) and regarded as a key step to link above- and belowground ecosystem processes (Bardgett et al. 2005).

Here, we introduce CLO-PLA, an on-line database of clonal growth of plants, which contains traits on clonal growth and vegetative regeneration for the European temperate flora; it may also serve as a guide for trait sampling in other regions of the world. The database is freely available at http://clopla.butbn.cas.cz/, together with specific detailed information on how to use it and the nature of clonal and bud bank traits. We also provide an overview on general database features and its philosophy in order to facilitate broad use by plant researchers.

Data synthesis from old literature

Clonal traits, even if overlooked in functional ecology, are well known for the majority of central European species. Traditionally, however, trait descriptions were scattered throughout older literature, which was not written in English (e.g. Irmisch 1850; Lukasiewitz 1962; Rysin & Rysina 1987). This problem is overcome by the CLO-PLA database, which contains information from old and new literature sources, newly interpreted and translated into several defined traits for nearly the entire central European flora. Data on clonal and bud bank traits for temperate plant taxa are excerpted from basic sources such as, e.g. Biological Flora of the Moscow Region (Rabotnov 1974), Life History of Central European Plants (Kirchner et al. 1908–1942), Comparative Morphology (Troll 1935–1942), Root Atlas (Kutschera 1960; Kutschera & Lichtenegger 1982–1992), Ecological Flora of the British Isles (Published in the *Journal of Ecology*), Biology of Canadian Weeds (Published in the *Canadian Journal of Plant Sciences*), and ecological journals, including regional publications (*Botanicheskii Zhurnal*, *Biulletin MOIP*, *Preslia*, *Flora*). The CLO-PLA database may not only serve as a valuable source of information on clonal and bud bank traits, but also as a library of references on plant life histories. In fact, different sources of information are taken into account for each species.

Typification of clonal growth organs and related traits

Morphological descriptions of clonal traits have traditionally been undertaken by particularly experienced researchers who have attempted to typify different strategies, i.e. grouping species into different "types". This approach, and in general all approaches that try to typify species into different groups, is difficult to apply for a vast number of species and can be highly subjective. The number of types of clonal growth organs in the literature for central Europe usually exceeds 20 (Kästner & Karrer 1995 distinguished nearly 100 growth forms, and Klimeš et al. 1997 distinguished 21 types of clonal growth organs), and some of these are represented by only a few plant species. Morphological descriptions for clonal growth traits also need many term definitions, which traditionally differ between European morphological schools (Klimešová & Klimeš 2008). As a result, clonal growth "types" have not been readily understandable for the non-specialist.

In the CLO-PLA database, the approach is to complement classical "types" of clonal growth organs (Fig. 1) with information on other related plant traits. Information concerning morphological type of a clonal growth organ, in fact, contains limited information on clonal function, e.g. the fact that a plant has a rhizome cannot elucidate how fast the species spreads by lateral growth or how many vegetative offspring it produces. Therefore, information on clonal growth type is combined with various, more functional, plant characters: whole plant traits, bud bank traits and specific clonal traits (Table 1).

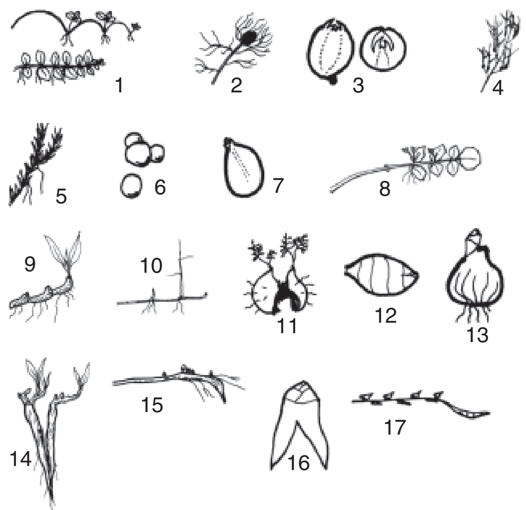

Fig. 1. Seventeen morphologically delimited types of clonal growth organs (CGO) used in the CLO-PLA3 database. (1) Rooting horizontal stems at or above soil surface, *Fragaria moschata, Lysimachia nummularia*; (2) turions, *Utricularia vulgaris*; (3) bulbils and tubers of stem origin at or above soil surface, *Dentaria bulbifera, Saxifraga cernua*; (4) plantlets (pseudovivipary), *Poa alpina*; (5) plant fragments of stem origin, *Elodea canadensis*; (6) budding plants, *Lemna minor*; (7) root tubers at or above soil surface, *Ficaria verna*; (8) buds on leaves (gemmipary), *Cardamine pratensis*; (9) epigeogenous rhizomes, *Rumex alpinus*; (10) hypogeogenous rhizomes, *Phalaris arundinacea*; (11) tuber-splitters, *Corydalis cava*; (12) stem tubers, *Bolboschoenus maritimus*; (13) bulbs, *Galanthus nivalis*; (14) root-splitters, *Verbascum nigrum*; (15) adventitious buds on roots, *Convolvulus arvensis*; (16) root tubers belowground, *Leucorchis albida*; (17) offspring tubers at distal end of aboveground stems, *Rubus saxatilis*. Reprinted from Klimešová & Klimeš (2008) with permission.

Clonal growth and bud bank measurement philosophy

Because different organs (stem, root) can exhibit clonal growth, clonal descendants may soon be separated from a mother plant, resulting in an extreme variety of clonal growth forms in different environments, making standardization of clonal traits relatively difficult (Klimeš et al. 1997). The important prerequisite for approaching and simplifying this complexity, and the key to understanding clonal traits, is to have an appropriate definition of "individual". When we consider one shoot (i.e. product of an apical meristem) as an individual, we can define the multiplication rate as "number of offspring shoots per parent shoot per year," and lateral spread as "distance between parent and offspring shoot reached per year." Also, in this way, morphological descriptions (which are still important for analysing how the parent shoot is replaced by an offspring shoot) can be integrated into a common framework that describes different characteristics of

Table 1. Description of traits listed in the CLO-PLA database and examples of the output for *Geranium sanguineum* and *Fragaria viridis* (for details, and an explanation of sections in bold, see text). *Bud bank includes all buds on a plant that are available for vegetative regeneration. **Clonal growth traits are evaluated separately for a particular clonal growth organ (CGO); one plant may have more CGOs (see Figs 2 and 3).

Traits	Description and categorization	Example 1 *Geranium sanguineum*	Example 2 *Fragaria viridis*
Whole plant (genet) traits			
Tap root persistence	Primary root survives over entire plant life-span (yes/no)	No	No
Reproductive types	Prevailing mode of reproduction (vegetative/generative/ vegetative and generative)	Vegetative and generative	Vegetative and generative
Other storage organs	Existence of storage organ not utilized for clonal growth (yes/no)	No	No
Age at first flowering	Life period when plant may regenerate only vegetatively (years)	10-12	No data
Genet life span	Life span of plant arising from one zygote (years)	No data	No data
Leaf distribution	Distribution of leaves along the flowering shoot (no-rosette/semirosette/rosette)	No rosette	Semirosette
Bud bank traits*			
Bud bank distribution	Vertical distribution of buds (five layers > 10/10 to 0/0/0 to -10/ < -10 cm in relation to soil surface)		
Seasonality of bud bank	Mode of perennation of bud-bearing organs (perennial/seasonal/potential/perennial and potential/seasonal and potential)	Seasonal/seasonal/ seasonal/seasonal and potential/**potential**	0/ seasonal / seasonal / perennial / 0
Number of buds per shoot	Numbers of buds per shoot and layer in well-developed plants (0/1-10/ > 10)	1-10/1-10/1-10/ > 10/0	0/1-10/1-10/ > 10/0
Clonal growth traits**			
Clonal growth organs (CGO)	Morphologically delimited types (17 types—see Fig. 1)	CGO 1: 10; CGO 2: 15	CGO 1: 9; CGO 2: 1
Role of CGO	CGO are necessary (If all adult plants in all populations develop CGOs), additive (If CGO is not needed for flowering and overwintering or is absent in some populations) or regenerative (If CGO develops after an injury)	CGO 1: necessary; CGO 2: regenerative	CGO 1: necessary; CGO 2: ***additive***
Cyclicity	Cyclicity corresponds to the life span of a shoot, starting from sprouting of a bud, followed by vegetative growth, flowering and fruiting, until shoot death. (1/2/ > 2 years)	CGO 1: 1; CGO 2: > 2	CGO 1: 2; CGO 2: > 2
Persistence	Persistence of connection, such as stolons or rhizomes, between parent and offspring ramets (1/2/ > 2 years)	CGO 1: > 2; CGO 2: 1	CGO 1: > 2; CGO 2: 1
No. of shoots/parent shoots	Rate of clonal multiplication (< 1/1/2-10/ > 10 per year)	CGO 1: 1; CGO 2: no data	CGO 1: 1; ***CGO 2: 2-10***
Lateral spread	Horizontal increment of clonal growth organ. Some water plants form turions or tubers that can be dispersed independent of the parent plant (< 0.01/0.01—0.25/ > 0.25 m/year/dispersable)	CGO 1: 0.01-0.25; CGO 2: no data	CGO 1: < 0.01; ***CGO 2: > 0.25***
Branching	Morphological type of stem branching (monopodial/sympodial/dichotomic)	CGO 1: sympodial; CGO 2: not relevant	CGO 1: sympodial; CGO 2: sympodial
Tillering in graminoids	Morphological type of branching in graminoids. (intravaginal/extravaginal/intra- and extravaginal)	Not relevant	Not relevant
Roots along CGO	Placement of roots on clonal growth organs of stem origin (along horizontal stem/on oldest part/on youngest part/on shoot base/not applicable)	CGO 1: along horizontal stem; CGO 2: not relevant	CGO 1: along horizontal stem; CGO 2: on shoot base
Leaf distribution	Leaf distribution along flowering shoot (no rosette/ semirosette/rosette)	CGO 1: no rosette; CGO 2: no rosette	CGO 1: rosette; CGO 2: rosette
Offspring comparison with parents	Relative size of clonal offspring (about the same/much smaller)	CGO 1: about the same; CGO 2: much smaller	CGO 1: about the same; CGO 2: much smaller
Reproduction *vs.* clonality	When, in ontogeny, clonal type of clonal growth organs are formed (prereproductive/reproductive/postreproductive)	CGO 1: prereproductive; CGO 2: prereproductive	CGO 1: prereproductive; CGO 2: prereproductive
Generation overlap	Shoots from following generations present (Yes/No)	CGO 1: no; CGO 2: no	CGO 1: yes; CGO 2: yes

clonal features. For example, there may be several possible ways in which offspring shoots are produced in a particular species. These may differ in terms of their role in plant life history (necessary, additive, regenerative), rate of multiplication, lateral spread, etc. (Table 1, Figs 2 and 3).

Another important set of traits relates to bud bank type. Belowground clonal growth organs usually bear a pool of dormant meristems for seasonal regrowth and regeneration after disturbance. Here, the vertical distribution of buds is important, as pointed out by Raunkiaer (1934). However, different buds and their functions need to be considered (Table 1), not only those surviving unfavourable conditions in winter or summer, e.g. when considering disturbance, which is unpredictable in relation to its extent and timing for plant development (Latzel et al. 2008). Standard methods for considering

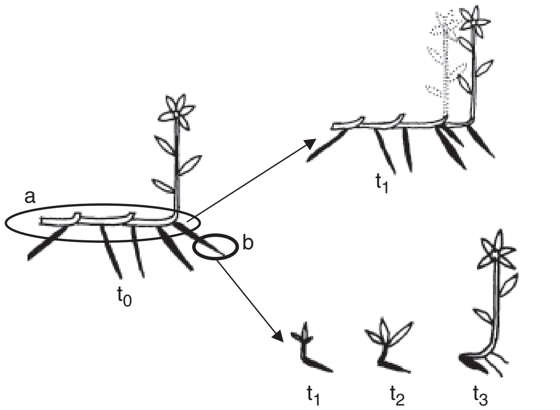

Fig. 2. Example of clonal and bud bank trait description using the growth of *Geranium sanguineum* as a model, a species with necessary and regenerative clonal growth organs (CGO). The hypogeogenous rhizome is a necessary CGO (a), while adventitious sprouting from injured roots functions as a regenerative CGO (b). The hypogeogenous rhizome is formed by perennial bases of sympodially growing shoots (a). The bases are parts of shoots growing horizontally below the soil surface and bearing scale leaves. Aboveground parts of the shoots are non-rosette and annual, flowering every year (t_0 and t_1; the dotted shoot was formed last spring and died last autumn). Sizes of sprouts originating on root fragments are similar to those of seedlings. The shoots are replaced by sympodially growing new shoots every year, producing hypogeogenous rhizomes with short increments. It takes several years (t_1, t_2, t_3) before the new shoots flower for the first time. Reserve meristems, which can be used for vegetative regeneration, are all buds on plants (bud bank). Non-rosette shoots bear an aboveground seasonal bud bank, perennial hypogeogenous rhizomes bear a perennial bud bank placed several centimeters belowground, and roots capable of adventitious sprouting bear a potential bud bank with the same vertical distribution as the roots. Reprinted from Klimešová & Klimeš (2005) with permission.

specific clonal and bud bank traits, based on published description (Klimeš & Klimešová 2005; Klimešová & Klimeš 2006, 2007), are applied throughout CLO-PLA.

Morphological terminology made understandable for non-specialists

Morphological terminology of clonal organs and traits is generally poorly known among ecologists. CLO-PLA provides basic and detailed information referring to the most widely applied terms required for studying vegetative organs. This offers an easy self-education opportunity for researchers willing to improve their expertise in this field. There are also more than 1000 black and white drawings of clonal growth organs available in the

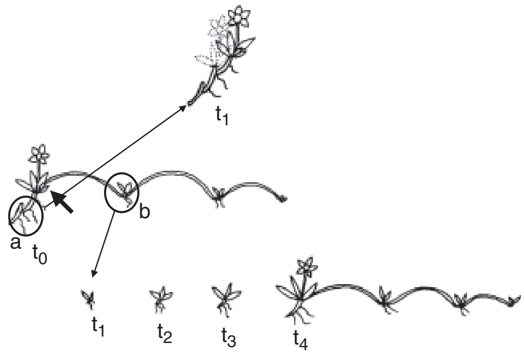

Fig. 3. Example of clonal and bud bank trait description using the growth of *Fragaria viridis*, a species with necessary and additive clonal growth organs (CGO). The epigeogenous rhizome is a necessary CGO and an aboveground horizontal rooting stem (stolon) is an additive CGO. The epigeogenous rhizome is formed by perennial stem bases of sympodial shoots. The rhizome growing at the soil surface has shortened internodes and is gradually pulled into the soil by roots. Its youngest parts bear green leaves at the nodes. During the first year of life, the shoot corresponds to a rosette of leaves (arrow) (t_0), the apical meristem modifies into an inflorescence in the second year. An offspring rosette arises from the axil of the uppermost leaf of the rosette in the same year. Generations of shoots overlap and the plant flowers every year (t_0 and t_1; the dotted shoot was formed last spring and died last autumn). The aboveground rooting stem consists of several generations of offspring shoots that arose during one season. Their first internodium is always long and is followed by several short internodes. The spacer between offspring rosettes splits in winter. Offspring plants grow for several years (t_1, t_2, t_3) as rosette shoots and produce their first stolons between the second and fourth year. Offspring usually flower in the fifth year of life. Reserve meristems, which can be used for vegetative regeneration, are all buds on the plant (bud bank). Semirosette shoots bear an aboveground seasonal bud bank, and perennial epigeogenous rhizomes bear a perennial bud bank, which extends from the soil surface to a depth of several centimeters belowground. Reprinted from Klimešová & Klimeš (2005) with permission.

database, which facilitate understanding of these terms using practical examples.

Practical data selection and export

The built-in Internet application in CLO-PLA3 provides the possibility to easily search and extract trait data from the CLO-PLA 3 database. Data can be searched according to either plant Latin name and/or according to any trait or combination of traits. The result of a query is one or more sheets containing the requested information (together with all other information for the species from one data source). Consequently, for one species there may be several sheets with different trait characteristics, i.e. because the data from different sources may differ. Displayed sheets can be selected (by ticking the "shopping basket") and then exported in the form of a table (sent by email), which can be easily used in Excel, R, etc. The researcher, according to the specific ecological questions, should decide how to handle cases when (1) trait information from multiple sources differs, or (2) various possibilities for a given trait are shown in the same sheet (e.g. several ways in which to grow clonally, see examples in Table 1).

In the first case, multiplicity of information for a given trait can be used to provide a measure of species plasticity for a specific trait (which could be treated, e.g. as a fuzzy variable in dummy coding in statistical analyses). Alternatively, another way to deal with cases of multiple data sheets is to prioritize first-hand information (obtained by authors of the database from living material in the field) or guess the quality of information from (a) the number of filled cells in the sheet, or (b) according to the source type (biological flora are normally based on more extensive surveys than a description of the species in an ecological paper).

In the second case, two simple examples can show which kinds of trait data can be selected depending on the research question of interest. Consider, for example, that we are interested in knowing whether a given species is able to regenerate vegetatively from a bud bank after management by sod cutting, i.e. removing the upper 10-cm soil layer. The result for the selected species in Table 1 is that *Geranium sanguineum* could regenerate, because this species has a potential bud bank on roots at greater depths in the soil, while *Fragaria viridis* could not. If we are interested in whether a species is able to show remarkable clonal spread (e.g. more than 25 cm per year) and vegetative multiplication (more than two offspring per year), the result of the query given in Table 1 shows that only *Fragaria viridis* is able to do so, but not in all populations nor in all individuals in a population (see relevant values in italics for the species in Table 1).

Conclusions

Why use clonal and bud bank traits and which questions can they help to answer? Clonal organs reflect plant persistence strategies in communities and therefore are a major axis of specialization (McIntyre et al. 1999; Klimešová et al. 2008). They also reflect adaptations to different habitat conditions (van Groenendael et al. 1996; de Bello et al. 2005; Klimeš 2008; Sosnová et al. unpubl. data), and are relevant for species coexistence (Tamm et al. 2002; de Bello et al. 2006) and plant regeneration (Latzel et al. 2008). There are probably different demands on the functions of clonal growth and the bud bank in different habitats, resulting in differing relevance of the various clonal traits in different species pools (Klimeš & Klimešová 2000; de Bello et al. 2005) and the relative extent of phylogenetic conservatism in different habitats (Klimeš 2008). Nevertheless, the ecological role of clonal traits in species coexistence and adaptation, i.e. abiotic and biotic environmental filtering, remains mostly unknown and represents an open field for research that can be assessed using CLO-PLA data.

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References

Bardgett, R.D., Bowman, W.D., Kaufmann, R. & Schmidt, S.K. 2005. A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology & Evolution* 20: 634–641.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Stege, 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. *Australian Journal of Botany* 51: 335–380.

de Bello, F., Lepš, J. & Sebastià, M-.T. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology* 42: 824–833.

de Bello, F., Lepš, J. & Sebastià, M.T. 2006. Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* 29: 801–810.

Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science* 17: 255–260.

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

Kästner, A. & Karrer, G. 1995. Übersicht der Wuchsformtypen als Grundlage für deren Erfassung in der "Flora von Österreich". *Florae Austriacae Novitates* 3: 1–50.

Kirchner, O., Loew, E. & Schröter, C. (eds.) 1908–1942. *Lebensgeschichte der Blütenpflanzen Mitteleuropas*. Bd 1 – 4, Eugen Ulmer Verlag, Stuttgart, DE.

Klimeš, L. 2008. Clonal splitters and integrators in harsh environments of the Trans-Himalaya. *Evolutionary Ecology* 22: 351–367.

Klimeš, L. & Klimešová, J. 2000. Plant rarity and the type of clonal growth. *Zeitung für Ökologie und Naturschutz* 9: 43–52.

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*. pp. 66–88. LEDA Traitbase project, University of Groningen, Groningen, NL.

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*. pp. 1–29. Backhuys Publishers, Leiden, NL.

Klimešová, J. & Klimeš, L. 2005. CLO-PLA: databáze architektury klonálního růstu rostlin střední Evropy. *Zprávy České Botanické Společnosti, Praha, 40 Materiály* 20: 53–64.

Klimešová, J. & Klimeš, L. 2006. CLO-PLA3: a database of clonal growth architecture of Central European plants. Available at http://clopla.butbn.cas.cz

Klimešová, J. & Klimeš, L. 2007. Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 115–129.

Klimešová, J. & Klimeš, L. 2008. Clonal growth diversity and bud banks in the Czech flora: evaluation using CLO-PLA3 database. *Preslia* 80: 255–275.

Klimešová, J., Latzel, V., de Bello, F. & van Groenendael, J.M. 2008. Plant functional traits in studies of vegetation changes under grazing and mowing: towards a use of more specific traits. *Preslia* 80: 245–253.

Kubát, K., Hrouda, L., Chrtek, J. Jr., Kaplan, Z., Kirschner, J. & Štěpánek, J. 2002. *Klíč ke květeně České republiky*. Academia, Praha, CZ.

Kutschera, L. 1960. *Wurzelatlas miteleuropäischer Ackerunkräuter und Kulturpflanzen*. DLG Verlag, Frankfurt.

Kutschera, L. & Lichtenegger, E. 1982-1992. *Wurzelatlas miteleuropäischerGrünlandpflanzen*. Vols. 1–2, Gustav Fischer, Stuttgart, DE.

Laanisto, L., Urbas, P. & Pärtel, M. 2008. Why does the unimodal species richness–productivity relationship not apply to woody species: a lack of clonality or a legacy of tropical evolutionary history. *Global Ecology and Biogeography* 17: 320–326.

Latzel, V., Mihulka, S. & Klimešová, J. 2008. Plant traits and regeneration of urban plant community after disturbance: Does bud bank play any role? *Applied Vegetation Science* 11: 387–394.

Lukasiewitz, A. 1962. Morphological–developmental types of herbs. *Prace Komisii Biologicznej, PTPN* 27/1: 1–398. (in Polish).

McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T.D.A. 1999. Disturbance response in vegetation towards a global perspective on functional traits. *Journal of Vegetation Science* 10: 621–630.

Ozinga, W.A., Hennekens, S.M., Schaminee, J.H.J., Smits, N.A.C., Bekker, R.M., Roemermann, Ch., Klimeš, L., Bakker, J.P. & van Groenendael, J.M. 2007. Local above-ground persistence of vascular plants: Life-history trade-offs and environmental constraints. *Journal of Vegetation Science* 18: 489–497.

Rabotnov, T.A. (ed.) 1974. *Biological flora of the Moscow region*. Izdatelstvo Moskovskogo Universiteta, Moskva, RU. (in Russian).

Raunkiaer, C. 1934. *The life forms of plants and statistical plant geography*. Clarendon Press, Oxford, UK.

Rysin, L.P. & Rysina, G.P. 1987. *Morphology and structure of below-ground organs of forest herbs*. Nauka, Moskva, RU. (in Russian).

Tamm, A., Kull, K. & Sammul, M. 2002. Classifying clonal growth forms based on vegetative mobility and ramet longevity: a whole community analysis. *Evolutionary Ecology* 15: 384–401.

Troll, W. 1935-1942. *Vergleichende Morphologie der höheren Pflanzen: Vegetationsorgane*. Verlag von Gebrüder Borntraeger, Berlin, DE.

van Groenendael, J.M., Klimeš, L., Klimešová, J. & Hendriks, R.J.J. 1996. Comparative ecology of clonal plants. *Philosophical Transactions of the Royal Society of London B* 351: 1331–1339.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999. Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal Vegetation Science* 10: 609–620.

Westoby, M. 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213–227.

Wilson, J.B. 2007. Trait-divergence assembly rules have been demonstrated: Limiting similarity lives! A reply to Grime. *Journal of Vegetation Science* 18: 451–452.

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