

THE LEDA



TRAITBASE

Collecting and measuring standards of Life-history traits of the Northwest European flora

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for LEDA-participants only***

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SECTION 1. INTRODUCTION

1. THE LEDA TRAITBASE PROJECT

To date there has been considerable effort to build up databases to synthesise information on plant traits. The knowledge of plant traits is currently growing fast, but remains scattered over many sources, i.e. in different journals, large monographs, and herbarium records. Also the sources are presented in various different languages and the data are distributed across many European countries, collected and stored in different ways and mutually not integrated. This severely impedes the functional analysis of plant species-environment relations and the prediction of plant biodiversity after changes in land use in Europe or regions within Europe. Thus the key ecological data for the European flora are too few and too scattered to be effective and without a standardised database of traits for the European flora, planning, nature conservation and restoration instruments will not operate effectively and European biodiversity will continue to decline. Neither the problem nor the flora respect national borders and therefore a response beyond the national level are required.

The LEDA Traitbase

Recently the LEDA Traitbase project started in the fifth framework programme (FP5) of the EC within the energy, environment and sustainable programme (EESD). The project aims to provide an open Europe-wide database of plant traits relevant to the conservation and sustainable use of biodiversity in changing European landscapes. To start with the LEDA Traitbase will deal with the flora of Northwest Europe. The LEDA Traitbase will be a useful tool in planning, in nature conservation and restoration, and in applied research and will focus on plant traits that describe three key features of plant dynamics: *persistence*, *regeneration* and *dispersability*.

The database will be built using several sources of knowledge, including the collation of existing databases, extensive literature compilations, unpublished data from the participants and other colleagues, and additional measurements.

What are the major challenges? The first challenge is to predict plant biodiversity in a changing landscape. For this we need to know if plants can persist and regenerate in their existing habitats and/or can colonise new habitats. Both abilities depend on their biological traits, i.e. vegetative expansion and multiplication, reproduction, seed bank longevity, and dispersability. On theoretical grounds it can be expected that such life-history traits will form distinct functional combinations. The second challenge is to pool transnational expertise on the functional significance of traits, their classification and measurement, while avoiding unnecessary duplication of national initiatives. Knowledge of plant traits is currently growing fast, but remains scattered over many sources, i.e. in dozens of different journals, large monographs, herbarium records. The sources are in several different languages, many even date back to the 19th century. The data are distributed across all different European countries, collected and stored in different ways and mutually not integrated. To date, there has been considerable effort to build up databases to synthesise information on plant traits, but these databases are restricted either to a small species pool or to only one or two traits. The third challenge is to facilitate retrieval. Researchers or land use managers and planners concerned with large species pools are discouraged from attempting to retrieve and use the scattered information. This severely impedes the functional analysis of plant species-environment relations and the prediction of plant biodiversity change in EU landscapes and regions.

To predict plant biodiversity in a changing landscape, information whether plants can persist and regenerate in their existing habitats and/or can colonise new habitats is needed. Both abilities depend on their biological traits, i.e. vegetative expansion and multiplication, reproduction, seed bank longevity, and dispersability. On theoretical grounds it can be expected that such life-history traits will form distinct functional combinations. An important challenge for the use of traits to assess biodiversity is to explicitly link function with response to environmental change. Hence, a detailed understanding of the effects of individual traits

on functions such as persistence, regeneration and dispersability is necessary (Ehrlén & Van Groenendael 1998). Unfortunately, traits that relate to central functions of plant life such as demography (detailed life history tables, e.g. Meyer & Schmid 1999) or photosynthesis (e.g. carbon balance, Diemer & Körner 1996) are hard to quantify for a large number of species. Given the goal to establish a larger species - trait matrix, these "hard" traits with demonstrated links to plant functioning can be replaced by more easily measured "soft" traits (Diaz et al. 1999), where function is inferred from correlations to the "hard" traits. For instance, specific leaf area as an easily measurable trait is positively correlated to relative growth rate (Garnier et al. 1997, Wright & Westoby 1999) and may serve as a surrogate for this "hard" trait. In order to fill the complete species-trait matrix for the Northwest European flora, the LEDA Traitbase will largely compile such "soft" traits and document their predictive use in a re-analysis of existing case studies.

The LEDA Traitbase will be realised through a species-trait matrix with referenced information under control of an editorial board. The species-trait matrix will include *persistence* traits that are correlating with competitive strength, stress/ disturbance tolerance, and vegetative multiplication. These persistence traits include; plant height, leaf size, leaf distribution along the stem, shoot growth form, specific leaf area (SLA), tissue density, clonal extension, clonal growth form, and type of vegetative regeneration. *Regeneration* traits include plant life span, age at first flowering, seed number per inflorescence or shoot, seed weight, size and shape, seed longevity. *Dispersal* traits include morphology of the dispersal unit, terminal velocity (anemochory), attachment capacity of dispersal unit (ectozoochory), survival capacity in digestive tract (endozoochory), buoyancy (hydrochory), seed longevity in the seed bank.

The operating system will be a user-friendly interface to the WWW-based LEDA Traitbase including an intelligent data mining technique to establish trade-off structures in trait combinations on which to base functional types, and advanced data retrieval techniques to aggregate extracted data. E-networking will be established to encourage the user community to continuously update and add to the database during and after the project.

To be accepted by the public, the LEDA Traitbase needs to be as complete as possible, containing a thorough list of species and traits. Also the LEDA Traitbase needs to be accessible, with easy data retrieval, and should be easy to couple to spatial information. The LEDA Traitbase will be tested with a variety of cases on assessment, restoration and conservation of biodiversity. The case studies will comprise different trait distributions on various ecological scales (national, regional, and local) in Germany, The Netherlands, England, Czech Republic and Belgium. For testing of the applicability of the LEDA Traitbase existing vegetation data are re-analysed by collating them to the LEDA Traitbase to detect functional relations between traits and species occurrences or community trends.

LEDA Organisation and Communication

The LEDA Traitbase project is divided into five different workpackages concerned with the collection of data and the assemblage of the species-trait matrix, with building the WWW-based database system together with e-networking, user interfaces, aggregation techniques and with the applicability of the LEDA Traitbase (Fig. 1.1.).

The LEDA Traitbase Workpackages are:

- Workpackage 1: The species - trait matrix (Persistence)
- Workpackage 2: The generative species - trait matrix (Regeneration)
- Workpackage 3: The species - trait matrix (Plant dispersability)
- Workpackage 4: Development of the database server
- Workpackage 5: Application & demonstration of the species-trait database: Case studies

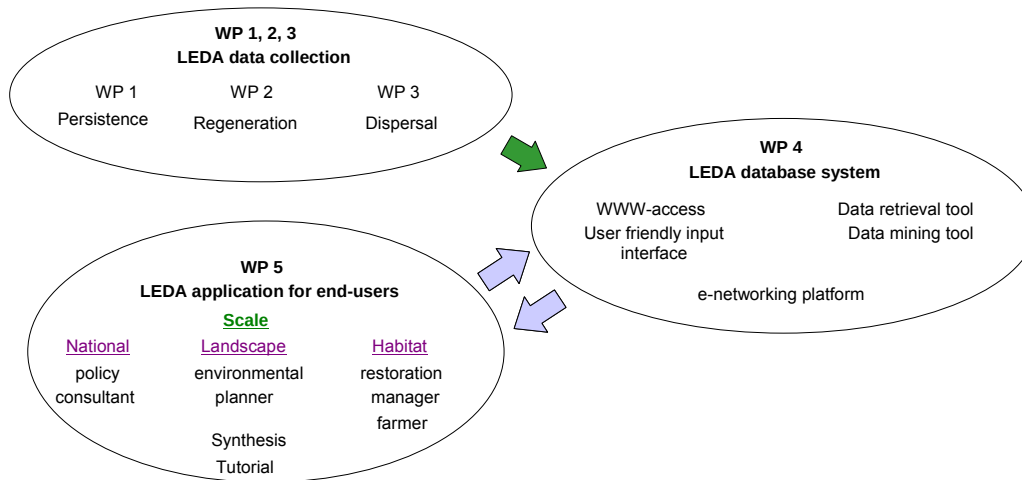


Figure 1.1. LEDA Traitbase workpackage flow diagram.

The LEDA Traitbase consortium

The LEDA Traitbase consortium consists of 10 universities or institutes from five different European countries, within total 30 participants, from which 10 form the project co-ordinating committee (PPC): Prof. Dr. Michael Kleyer - Carl von Ossietzky University of Oldenburg, (Germany) (Project co-ordinator), Prof. Dr. Jan Bakker - University of Groningen (The Netherlands), Prof. Dr. Jan van Groenendael - University of Nijmegen (The Netherlands), Prof. Dr. Peter Poschlod - University of Regensburg (Germany), Prof. Dr. Michael Sonnenschein - Carl von Ossietzky University of Oldenburg (Germany), Dr. Ken Thompson - University of Sheffield (England), Dr. Leos Klimeš - Institute of Botany Trebon (Czech Republic), Dr. Graciela Rusch - Norwegian Institute for Nature Research Trondheim (Norway), Dr. Stefan Klotz - Centre for Environmental Research Leipzig-Halle (Germany), Prof. Dr. Martin Hermy - University of Leuven (Belgium).

An independent editorial board will monitor data standards and provide quality assurance. The editorial board will consist of the partners and external scientists that have expertise in certain traits and are known for their interest in trait databases. A member of the European Environment Agency (EEA) will be invited as an observer to help defining the potential needs from the EEA. This Agency will also be involved in the discussion on the continuation of the LEDA Traitbase after the termination of the current EC-project in October 2005.

An e-networking platform for the consortium and for the scientific community will avoid unnecessary duplication of national initiatives, pool transnational expertise on the functional significance of traits, their classification and measurement, and facilitate the extension of LEDA Traitbase in the future.

SECTION 2. GENERAL STANDARDS

1. REFERENCES CITED AND ORGANISATION

To any single data entry a reference or data source has to be added. In the Traitbase output the references will appear in a short abbreviated format as a result of the queries of the user. A full reference list can always be produced when output of the database is being exported to a user readable file. When new references are entered, it will be possible to check whether this source has already been entered.

1.1. REFERENCE FORMAT

When a reference is a published source, the format followed will be that of the Journal of Ecology, which cites papers, books and chapters in books as follows:

- Boutin, C. & Harper, J.L. (1991) A comparative study of the population dynamics of five species of *Veronica* in natural habitats. *Journal of Ecology*, 79, 199-221.
- Clarke, N.A. (1983) *The ecology of Dunlin (Calidris alpina L.) wintering on the Severn estuary*. PhD thesis, University of Edinburgh.
- Pimm, S.L. (1982) *Food Webs*. Chapman and Hall, London.
- Sibly, R.M. (1981) Strategies of digestion and defecation. In: *Physiological Ecology* (eds C. R. Townsend & P. Calow), pp. 109-139. Blackwell Scientific Publications, Oxford.

Multiple authors (as well as book editors) are entered as separate entries in separate cells, to be able to query the database on author name. When data is originating from grey literature (i.e. MSc thesis, reports) is entered, the field 'location' has to be filled to inform the users of the database where this literature can be found. For published sources this field is optional. The field 'ISXN-number' is for books, and is optional for the other literature sources. A language field is available to store the language of a literature source, as only the original title of the source needs to be stored in the database. When the data source is one of the current partner's databases, the data will be labelled with the subsequent database ID. When data in one of these databases carry information about the original (or old) reference behind a review-type reference, the original reference needs to be stored as well but this will be done separately for each trait.

When the data originate from a non-published source, the data should be entered under the person's name instead of the reference name. A person record will always hold the email address to identify the contributor.

Note: For the time being, this can only be one of the partners of the LEDA Traitbase-consortium, as other contributors need to pass the editorial board to check the validity of the data.

Data structure

<u>Data characteristic</u>	<u>Description</u>	<u>Format</u>	<u>Level</u>
Refname	Short abbreviated name of the data source	text	optional
Reftype	Person, publication or database	text	obligate
Author	List of names of authors - all separately stored	text	obligate
Year	Year of publication	number	obligate
Title	Full title of publication	text	obligate
Publisher	Name of publisher, e.g. Chapman and Hall, London	text	obligate
Journal	Name of journal (chosen from journal list or to add manually)	text	optional
Number	Edition/volume identifier	number	optional
Pages	Range of pages, when part of a large volume, e.g. 199-220	number	optional
Book title	Full title of the book when the source is part of a larger reference	text	optional
Editor	List of names of editors	text	optional
ISXN	ISSN or ISBN number of the source	number	optional
Type	Type of publication e.g. report, PhD-thesis, diplomarbeit	text	optional

Location	Location of the library	text	obligate ¹
Language	Language of the data source	text	optional
Person name	Person name (in reference format) e.g. Thompson, K.	text	optional
Person info	The persons email address	text	optional
Database ID	Unique code for the different partner databases	text	optional
Database admin	Contact address the database (email address)	text	optional
Database address	Name, address or web address (URL) of hosting organisation	text	optional

¹ Only obligate for non-published sources

1.2. GEOGRAPHICAL REFERENCE

Introduction

Each data entry needs to have a geographical reference to be able to map the distribution of trait values within Northwest Europe. For the purpose of detailed research it is crucial to be able to determine the variation of trait values over different regions or countries, and if the variation is large, the user might want to work with values originating from a certain region only. Geographical information will be used in query options as well as for processes such as data aggregation.

For each data entry the county where the measurement was taken has to be recorded. LEDA will use the 2-letter country code of the International Organization for Standardisation (ISO 3166; see Appendix 1).

For the site co-ordinates the Universal Transpose Mercator (UTM) co-ordinates are used. UTM provides a constant distance relationship anywhere on a map. In angular co-ordinate systems like latitude and longitude, the distance covered by a degree of longitude differs as you move towards the poles and only equals the distance covered by a degree of latitude at the equator. The UTM system allows the co-ordinate numbering system to be tied directly to a distance measuring system (see also <http://www.maptools.com/UsingUTM>).

Data structure

<u>Data characteristic</u>	<u>Description</u>	<u>Format</u>	<u>Level</u>
Study area	Whether measurement took place in (1) or outside (0) NW-Europe	0/1	obligate
Country code	ISO-3166 two-letter country code where measurement took place	text	obligate
Altitude	In metres (with unknown projection)	number	optional
Range	Range in radius error when no GPS reading is available of the site, but only of a city nearby (e.g. city 3 km from the field site)	number	obligate ¹
UTMzone	Co-ordinates according to UTM-grid	text	optional
UTMeasting	Co-ordinates according to UTM-grid	text	optional
UTMnorthing	Co-ordinates according to UTM-grid	text	optional
Comment ref	For e.g. comments on nearest town or nature reserve	text	optional
Map date	Date of the map used (month/year or year)	text	optional

¹ Only obligate for non-published sources

Note: When no UTM data is available it can be obtained by converting latitude/longitude co-ordinates at <http://www.dmap.co.uk/ll2tm.htm> (Morton 2003) This site provides a facility to convert the full latitude/longitude co-ordinates to co-ordinates in metres on a Transverse Mercator projection (UTM). When no GPS readings are available from a study or sample site the longitude/latitude and allotted values of cities or towns situated near the study site can be found on <http://www.calle.com/world/index.html>. Please note that the range of error, i.e. how many km the town from which the co-ordinates are used is situated from the study site, is obligatory information when using this method.

2. DESCRIPTION OF ORIGINAL HABITAT AND METHODS

Each data entry needs to have a reference to the habitat characteristics of the habitat in which the measurement took place or where plant material was collected, as well as information on other site characteristics. Obviously, not all data will be assembled in a natural

field situation; therefore the field 'Method of measurement' will explicitly state the origin of the data.

2.1. HABITAT TYPE

Introduction

For the habitat type the EUNIS Habitat Classification (EEA 2002) will be adopted. The EUNIS Habitat classification has been developed to facilitate harmonised description and collection of data across Europe through the use of criteria for habitat identification. It is a comprehensive pan-European system, covering all types of habitats from natural to artificial, from terrestrial to freshwater and marine habitats types. The habitat classification system is hierarchic with each habitat type letter-number coded, with the first levels the letters A to J and for the following habitat levels a number code is added (see also <http://mrw.wallonie.be/dgrne/sibw/EUNIS/home.html>).

LEDA Traitbase habitat type categories

For each data entry a category that indicates the highest hierarchical level (corresponding with the EUNIS codes A to J) has to be filled in. To the EUNIS habitat categories an extra category was added for sites with no vegetation and for greenhouse studies or garden experiments.

The 11 LEDA Traitbase habitat type categories are:

- | | |
|---|----------------|
| 1. Marine habitats | [EUNIS code A] |
| 2. Coastal habitats | [EUNIS code B] |
| 3. Inland surface water habitats | [EUNIS code C] |
| 4. Mire, bog and fen habitats | [EUNIS code D] |
| 5. Grassland and tall forb habitats | [EUNIS code E] |
| 6. Heathland, scrub and tundra habitats | [EUNIS code F] |
| 7. Woodland and forest habitats and other wooded land | [EUNIS code G] |
| 8. Inland unvegetated or sparsely vegetated habitats | [EUNIS code H] |
| 9. Regularly or recently cultivated agricultural, horticultural and domestic habitats | [EUNIS code I] |
| 10. Constructed, industrial and other artificial habitats | [EUNIS code J] |
| 11. No vegetation (also including laboratory, greenhouse or garden experiments) | [LEDA code] |

Note: When entering the data in the Traitbase, a pop-up menu will give the choice of sub-categories consisting of the habitat types of the second and third hierarchical level. See Appendix 2 for overview first three EUNIS habitat levels.

Data structure

<u>Data characteristic</u>	<u>Description</u>	<u>Format</u>	<u>Level</u>
Habitat type	Categories of EUNIS habitat types	category (number) sub-category (number)	obligate optional

2.2. HABITAT CHARACTERISTICS

Habitat characteristics are not available for all species of the NW European flora. We will not measure habitat characteristics for the database. Hence, we will rely on indicator values such as presented by Ellenberg et al. (1992) for 2726 Central European vascular plant species. The most often applied indicator values are those for light, temperature, continentality, moisture, soil reaction (acidity/lime content), and nitrogen. Indicator values for temperature and continentality indicate large-scale biogeographical issues, which are beyond the scope of the LEDA trait-database. We will focus on site characteristics. Indicator values for light may be negatively related to plant productivity; hence, we propose to restrict the habitat characteristics to the soil parameters moisture, acidity and nitrogen status. The Ellenberg indicator values were developed mainly on the basis of field experience, and quantification generally follows a nine-point scale. The indicator values reflect the ecological behaviour of

species, not their physiological preferences (Ellenberg et al. 1992). They summarise complex environmental factors (e.g. groundwater level, soil moisture content, precipitation, humidity etc.) in a single figure. Values do not refer to conditions at one moment, but present integration over time (Schaffers & Sykora 2000).

Although Ellenberg indicator values were designed for Central Europe, they have also been used outside that region, e.g. The Netherlands (Van der Maarel et al. 1985, Bakker 1987), Norway (Vevle & Aase 1980), Sweden (Diekmann 1995), Estonia (Pärtel et al. 1996, 1999), Poland (Roo-Zielinska & Solon 1998), Great Britain (Hawkes et al. 1997) and Northeast France (Thimonier et al. 1994). The values can be used to indicate changes in environmental conditions during restoration management (Bakker et al. 2002).

Ellenberg values are most commonly used in calculations based on the complete species composition of plant communities. The consistency of the Ellenberg indicator values (not the relation to field measurements) has been studied. Van der Maarel (1993) reported that the socio-ecological species-groups defined for the Netherlands contain species with very similar indicator values. Ter Braak & Gremmen (1987) showed that the moisture values have a reasonable internal consistency in the Netherlands.

Bakker (1987) reported that the Ellenberg indicator values assigned to three groups, namely, indicating nutrient-poor, intermediate- and nitrogen-rich soil conditions were similar to the indicator values of other authors (Germany - Klapp 1965; The Netherlands - Kruijne et al. 1967).

Thompson et al. (1993) found a close correlation between Ellenberg indicator values and the affiliation of species with dry or moist habitats or wetlands in Great Britain. Böcker et al. (1983) assert that groundwater level is the parameter that can be expected to show closest relation to moisture values in Germany. However, these authors did not measure soil moisture or groundwater levels.

Schaffers & Sykora (2000) tested the reliability of the Ellenberg indicator values for moisture, soil reaction and nitrogen for the Netherlands, by using measured parameters. They conclude that the Ellenberg indicator system provides a very valuable tool for habitat calibration, provided the appropriate parameters are considered.

Ellenbergs moisture values probably integrate both groundwater level and soil moisture content. At low moisture content, a high groundwater level may still supply deeper plant roots with sufficient water. At a low groundwater level the high moisture content may still be retained if physical soil characteristics are favourable.

Ellenberg nitrogen values provide an effective integration of several ecological parameters and do not reflect the availability of nitrogen only. Various other factors determine productivity, such as moisture availability, soil aeration, soil acidity and phosphate availability. Productivity can be regarded as a measure of fertility as 'perceived' by the vegetation. The results of Schaffers & Sykora (2000) are in line with those of Hill & Carey (1997), and suggest that Ellenberg nitrogen values should rather be referred to as 'productivity values'.

The mean reaction values accurately indicate soil total calcium over a wide range of conditions, whereas the indication of soil pH is problematic. Hence, Schaffers & Sykora (2000) suggest that the Ellenberg reaction values are better referred to as 'calcium values'.

The habitat characteristics 'soil moisture', 'productivity' and 'calcium' for the species of the LEDA trait database can be derived from the most recent version of Ellenberg. Species that are not mentioned by Ellenberg, or are indifferent, might be derived from other sources, such as Landolt (1977). But before using these, they need to be calibrated with Ellenberg values using a number (at least 25, preferably more) of species the sources have in common.

Categories adopted by LEDA

Moisture (F-value; Fig. 2.1)

- | | |
|--|--|
| 1. Indicator of extreme dryness, restricted to soils that often dry out for some time | (<i>Corynephorus canescens</i> , <i>Helianthemum apenninum</i> , <i>Koeleria vallesiana</i>). |
| 2. Between 1 and 3 | (<i>Clinopodium acinos</i> , <i>Saxifraga tridactylites</i> , <i>Sedum acre</i>). |
| 3. Dry-site indicator, more often found on dry ground than in moist places | (<i>Asplenium trichomanes</i> , <i>Centaurea scabiosa</i> , <i>Spergularia rubra</i>). |
| 4. Between 3 and 5 | (<i>Arctium minus</i> , <i>Helictotrichon pratense</i> , <i>Iris foetidissima</i> , <i>Thymus polytrichus</i>). |
| 5. Moist-site indicator, mainly on fresh soils of average dampness | (<i>Anthriscus sylvestris</i> , <i>Euphorbia amygdaloides</i> , <i>Hyacinthoides non-scripta</i> , <i>Solanum nigrum</i>). |
| 6. Between 5 and 6 | (<i>Agrostis stolonifera</i> , <i>Empetrum nigrum</i> , <i>Rumex crispus</i>). |
| 7. Dampness indicator, mainly on constantly moist or damp, but not on wet soils | (<i>Carex ovalis</i> , <i>Dactylorhiza maculata</i> , <i>Pulicaria dysenterica</i> , <i>Ranunculus repens</i>). |
| 8. Between 7 and 9 | (<i>Cardamine pratensis</i> , <i>Equisetum telmateia</i> , <i>Phalaris arundinacea</i> , <i>Schoenus nigricans</i>). |
| 9. Wet-site indicator, often on watersaturated, badly aerated soils | (<i>Drosera rotundifolia</i> , <i>Myosotis scorpioides</i> , <i>Vaccinium oxycoccus</i> , <i>Viola palustris</i>). |
| 10. Indicator of shallow-water sites that may lack standing water for extensive periods | (<i>Alisma plantago-aquatica</i> , <i>Carex limosa</i> , <i>Ranunculus lingua</i> , <i>Typha latifolia</i>). |
| 11. Plant rooting under water, but at least for a time exposed above, or plant floating on the surface | (<i>Lemna minor</i> , <i>Nuphar lutea</i> , <i>Sagittaria sagittifolia</i> , <i>Schoenoplectus lacustris</i>). |
| 12. Submerged plant, permanently or almost constantly under water | (<i>Isoetes lacustris</i> , <i>Potamogeton crispus</i> , <i>Ranunculus circinatus</i> , <i>Zostera marina</i>). |

Acidity (R-value = soil pH, or water pH; Fig. 2.1)

- | | |
|--|---|
| 1. Indicator of extreme acidity, never found on weakly acid or basic soils | (<i>Andromeda polifolia</i> , <i>Lycopodium clavatum</i> , <i>Rubus chamaemorus</i> , <i>Ulex minor</i>). |
| 2. Between 1 and 3 | (<i>Agrostis curtisii</i> , <i>Calluna vulgaris</i> , <i>Drosera rotundifolia</i> , <i>Polygala serpyllifolia</i>). |
| 3. Acidity indicator, mainly on acid soils, but exceptionally also on nearly neutral ones | (<i>Agrostis vinealis</i> , <i>Dactylorhiza maculata</i> , <i>Galium saxatile</i> , <i>Pteridium aquilinum</i>). |
| 4. Between 3 and 5 | (<i>Agrostis capillaris</i> , <i>Carex panicea</i> , <i>Juncus effusus</i> , <i>Teucrium scorodonia</i>). |
| 5. Indicator of moderately acid soils, only occasionally found on very acid or on neutral to basic soils | (<i>Cardamine pratensis</i> , <i>Cirsium palustre</i> , <i>Rubus idaeus</i> , <i>Ulex europaeus</i>). |
| 6. Between 5 and 7 | (<i>Ammophila arenaria</i> , <i>Carex sylvatica</i> , <i>Lolium perenne</i> , <i>Ranunculus ficaria</i>). |
| 7. Indicator of weakly acid to weakly basic conditions; never found on very acid soils | (<i>Agrimonia eupatoria</i> , <i>Atriplex prostrata</i> , <i>Nuphar lutea</i> , <i>Phleum pratense</i>). |
| 8. Between 7 and 9 | (<i>Artemisia vulgaris</i> , <i>Carduus nutans</i> , <i>Iris foetidissima</i> , <i>Viola hirsuta</i>). |
| 9. Indicator of basic reaction, always found on calcareous or other high-pH soils | (<i>Bunium bulbocastanum</i> , <i>Clinopodium calamintha</i> , <i>Dryopteris submontana</i> , <i>Primula farinosa</i>). |



Figure 2.1. The dry-site indicator *Centaurea scabiosa* (a), weakly acid *Ranunculus ficaria* (b) and a species from infertile sites *Pimpinella saxifraga* (c) (Photo: see source list).

Nitrogen status (N-value - in effect a general indicator of soil fertility; Fig. 2.1)

- | | |
|--|--|
| 1. Indicator of extremely infertile sites | (<i>Agrostis curtisii</i> , <i>Clinopodium acinos</i> , <i>Drosera rotundifolia</i> , <i>Rubus chamaemorus</i>). |
| 2. Between 1 and 3 | (<i>Aira praecox</i> , <i>Carex panicea</i> , <i>Linum catharticum</i> , <i>Scabiosa columbaria</i>). |
| 3. Indicator of more or less infertile sites | (<i>Centaurea scabiosa</i> , <i>Galium saxatile</i> , <i>Pimpinella saxifraga</i> , <i>Teucrium scorodonia</i>). |
| 4. Between 3 and 5 | (<i>Agrostis capillaris</i> , <i>Cirsium palustre</i> , <i>Plantago lanceolata</i> , <i>Primula vulgaris</i>). |
| 5. Indicator of sites of intermediate fertility | (<i>Angelica sylvestris</i> , <i>Digitalis purpurea</i> , <i>Iris foetidissima</i> , <i>Trifolium pratense</i>). |
| 6. Between 5 and 7 | (<i>Cirsium arvense</i> , <i>Glyceria fluitans</i> , <i>Poa trivialis</i> , <i>Rumex crispus</i>). |
| 7. Plant often found in richly fertile places | (<i>Atriplex prostrata</i> , <i>Epilobium hirsutum</i> , <i>Stellaria media</i> , <i>Typha latifolia</i>). |
| 8. Between 7 and 9 | (<i>Beta vulgaris</i> , <i>Galium aparine</i> , <i>Lamium album</i> , <i>Urtica dioica</i>). |
| 9. Indicator of extremely rich situations, such as cattle resting places or near polluted rivers | (<i>Arctium lappa</i> , <i>Artemisia absinthium</i> , <i>Hyoscyamus niger</i> , <i>Rumex obtusifolius</i>). |

Data structure

Data characteristic	Description	Format	Level
Habitat characteristics	Moisture status	category (number)	obligate
	Acidity (pH)	category (number)	obligate
	Nitrogen status	category (number)	obligate

2.3. SIZE OF SAMPLE AREA

Introduction

The size of the area sampled is important information that is needed to determine the quality of the sampled data. Therefore, independent of the habitat, the size of the collecting area should be recorded to be able to determine the data quality.

For all data sets, where the size of the collecting area is unknown or where the samples for one record are collected in bigger area's (> 1 ha), the coarse scale should be used.

Size sample area categories

For the size of sample area the choice is between four categories:

1. < 0.5 ha (or <50 m length for line transects/habitats)
2. 0.5-1 ha (or 50-100 m length for line transects/habitats)
3. >1 ha (or > 100 m length for line transects/habitats)
4. Unknown

Data structure

Data characteristic	Description	Format	Level
Size sample area	The size of the sampled area in ha	category (number)	obligate

2.4. SOIL SUBSTRATE

Introduction

Soil texture refers to the relative proportions of sand, silt and clay particles in soil material that has a particle size less than 2 mm in diameter. As only the first three soil substrate categories are based on soil texture classes, the trait was called soil substrate.

The soil texture triangle is used to classify the texture class of a soil (Fig. 2.2). The sides of the soil texture triangle are scaled for the percentages of sand, silt, and clay. Clay percentages are read from left to right across the triangle, whereas silt is read from the upper right to lower left and sand from lower right towards the upper left portion of the triangle. The boundaries of the soil texture classes are marked bold with the intersection of the three sizes on the triangle giving the texture classes. For instance, a soil with 20% clay, 60% silt, and 20% sand it falls in the 'silt loam' class. Soil texture is an indicator of infiltration capacity,

permeability, degree of aeration, and drainage as well as other physical characteristics of a soil material (USDA 1993).

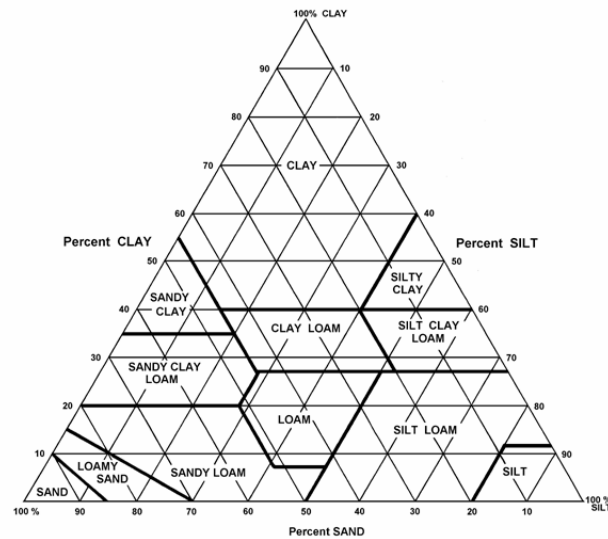


Figure 2.2. Soil texture triangle (USDA 1993)

Soil substrate categories

The main indication will be the choice of six soil substrate categories:

1. Sand (Majority of particle size ranging from 0.05 mm to 2.0 mm in diameter ($\varnothing$))
2. Loam (Particle size ranging from 0.002 mm to 0.05 mm in $\varnothing$)
3. Clay (Particle size less than 0.002 mm in $\varnothing$)
4. Peat (Heterogeneous organically substance (incomplete decomposition of plants))
5. Rocky (Unattached rock pieces of ≥ 2 mm in $\varnothing$)
6. Others (In general an artificial by anthropologically influenced soil substrate (i.e. parks, gardens))

When entering the data into the Traitbase, a pop-up menu will give the choice to choose from more detailed sub-categories for the soil substrate categories sand, loam, clay, and rock (Table 2.1).

Table 2.1. Descriptions of the five soil substrate categories with their sub-categories (for definitions, see the glossary).

Category	Sub-category
Sand	1. Sand 2. Loamy sand 3. Sandy loam
Loam	1. Loam 2. Silt loam 3. Silt 4. Sandy loam 5. Sandy clay loam 6. Silty clay loam
Clay	1. Clay 2. Sandy clay 3. Silty clay
Peat	No sub-categories
Rocky	1. Pebbles 2-75 mm $\varnothing$ 2. Cobbles 75-250 mm $\varnothing$ 3. Stones 250-600 mm $\varnothing$ 4. Boulders >600 mm $\varnothing$

Data structure

<u>Data characteristic</u>	<u>Description</u>	<u>Format</u>	<u>Level</u>
Soil substrate	One of the soil substrate categories	category (number) sub-category (number)	obligate optional

2.5. SOIL TYPE

Introduction

For soil type, the classification system used is based on the World Reference Base for Soil Resources (WRB) (FAO, 1998).

In this classification there are 30 reference soil groups. Soils are assigned to a group based on the presence or absence of a limited number of diagnostic horizons, diagnostic properties, or diagnostic constituents. The 30 major soil groups can be assembled in 10 classes: Organic soils, and mineral soils from which the formation is conditioned by human influences, parent material (i.e. volcanic material, residual and shifting sands, expanding clays), topography/ physiography (i.e. soils in lowlands (wetlands) with level topography), their limited age (not confined to any particular region), (sub-)humid tropics, climate of arid and semi-arid regions, climate of steppes and steppic regions, (sub-)humid temperate climate, and permafrost (see Fig. 2.3; Grissino-Mayer 1999, Zobler 1986).

LEDA Traitbase Soil type categories

The LEDA Traitbase soil types are corresponding with the WRB soil types. One category was added to account for the greenhouse or garden experiments. The 11 soil type categories are:

1. Organic soils
2. Mineral soils - human influences
3. Mineral soils - parent material
4. Mineral soils - topography/physiography
5. Mineral soils - their limited age
6. Mineral soils - (sub-)humid tropics
7. Mineral soils - climate of arid/semi-arid regions
8. Mineral soils - climate of steppes/steppic regions
9. Mineral soils - (sub-)humid temperate climate
10. Mineral soils - permafrost
11. Other (incl. unknown)



Figure 2.3. Some soil profile examples of soil types from the different categories; gleysol (category 4; a), humic cambisol (category 5; b), ferralsol (category 6; c), ferric acrisol (category 6; d) (Kranz 2000).

When entering data in the Traitbase a pop-up menu will give the optional choice of different sub-categories (Table 2.2).

Table 2.2. The soil type categories of LEDA with their sub-categories. Note that the full description of the WRB soil types is given in the glossary (see Appendix 3).

Soil type category	Sub-category
1. Organic soils	1. Histosols
2. Mineral soils (human influences)	1. Anthrosols
3. Mineral soils (parent material)	1. Andosols 2. Arenosols 3. Vertisols
4. Mineral soils (topography/physiography)	1. Fluvisols 2. Gleysols 3. Leptosols 4. Regosols
5. Mineral soils (limited age)	1. Cambisols
6. Mineral soils ((sub-)humid tropics)	1. Plinthosols 2. Ferralsols 3. Nitisols 4. Acrisols 5. Alisols 6. Lixisols
7. Mineral soils (climate of arid and semi-arid regions)	1. Solonchaks 2. Solonetz 3. Gypsisols 4. Durisols 5. Calcisols
8. Mineral soils (climate of steppes and steppic regions)	1. Kastanozems 2. Chernozems 3. Phaeozems
9. Mineral soils ((sub-)humid temperate climate)	1. Podzols 2. Planosols 3. Albeluvisols 4. Luvisols 5. Umbrisols
10. Mineral soils (permafrost)	1. Cryosols

Data structure

<u>Data</u>	<u>Description</u>	<u>Format</u>	<u>Level</u>
<u>characteristic</u>			
Soil type	One of the soil type categories	category (number) sub-category (number)	optional optional

2.6. SOIL MOISTURE CONDITION

Introduction

Soil moisture is often depending on the height of the ground water that in turn is part of precipitation that seeps down through the soil until it reaches rock material. Ground water slowly moves underground, generally at a downward angle (because of gravity), and may eventually seep into streams, lakes, and oceans.

In the LEDA Traitbase the soil with groundwater level of below 60cm depth are called dry, soils with a depth of 20-60 cm is called moist, and soils with a level of ≤ 20 cm is called wet soil. Some species examples of dry soil are listed in table 2.3 together with ecological indicator values for moisture from Ellenberg (1991).

Table 2.3. The definitions of the soil moisture categories with the range of the Ellenberg's moisture indication (mF; after Schaffers & Sýkora 2000).

Ellenberg mF value	Description	Species examples
<5	Indicator of extreme dryness, restricted to soils that often dry out for some time to dry-site indicator, more often found on dry ground than in moist places	<i>Corynephorus canescens</i> , <i>Helianthemum apenninum</i> , <i>Koeleria vallesiana</i> , <i>Clinopodium acinos</i> , <i>Saxifraga tridactylites</i> , <i>Sedum acre</i> , <i>Asplenium trichomanes</i> , <i>Centaurea scabiosa</i> , <i>Spergularia rubra</i> , <i>Arctium minus</i> , <i>Helictotrichon pratense</i> , <i>Iris foetidissima</i> , <i>Thymus polytrichus</i>
5-7	Moist-site indicator, mainly on fresh soils of average dampness to Dampness indicator, mainly on constantly moist or damp, but not on wet soils	<i>Anthriscus sylvestris</i> , <i>Euphorbia amygdaloides</i> , <i>Hyacinthoides nonscripta</i> , <i>Solanum nigrum</i> , <i>Agrostis stolonifera</i> , <i>Empetrum nigrum</i> , <i>Rumex crispus</i> , <i>Carex ovalis</i> , <i>Dactylorhiza maculata</i> , <i>Pulicaria dysenterica</i> , <i>Ranunculus repens</i>
>7	Wet-site indicator, often on water-saturated, badly aerated soils to Indicator of shallow-water sites that may lack standing water for extensive periods to Plant rooting under water, but often time exposed, or plant floating on the surface to Submerged plant, permanently or almost constantly under water	<i>Cardamine pratensis</i> , <i>Equisetum telmateia</i> , <i>Phalaris arundinacea</i> , <i>Schoenus nigricans</i> , <i>Drosera rotundifolia</i> , <i>Myosotis scorpioides</i> , <i>Vaccinium oxycoccus</i> , <i>Viola palustris</i> , <i>Alisma plantago-aquatica</i> , <i>Carex limosa</i> , <i>Ranunculus lingua</i> , <i>Typha latifolia</i> , <i>Lemna minor</i> , <i>Nuphar lutea</i> , <i>Sagittaria sagittifolia</i> , <i>Schoenoplectus lacustris</i> , <i>Isoetes lacustris</i> , <i>Potamogeton crispus</i> , <i>Ranunculus circinatus</i> , <i>Zostera marina</i>

LEDA Traitbase moisture condition classification

This is the condition of the soil measured or estimated in the wettest period of the year. The three moisture condition categories are:

1. Dry >60cm below soil surface [Ellenberg mF<5]
2. Moist 20-60cm below soil surface [Ellenberg mF 5-7]
3. Wet <20cm below soil surface [Ellenberg mF>7]

Data structure

<u>Data characteristic</u>	<u>Description</u>	<u>Format</u>	<u>Level</u>
Soil moisture	Moisture status of the soil of the sample site	category (number)	optional

2.7. SOIL ACIDITY

Introduction

Soil acidity (pH) affects the availability of soil constituents (i.e. nutrients) to plants and soil micro-organisms. For most plants, the ideal soil pH test result is pH 6 - 7.5, although many will tolerate pH 5.5 - 8.5. However, the tolerance to extremes in pH varies between plant species and within species. Some plant species have quite different preferred pH ranges (see table 2.4).

The soil pH is a measure of how acidic or basic the soil is and is measured using a pH scale ranging from 0 to 14. Soil with a pH less than 6.5 is called acid soil and is regarded as 'very acid' when the reaction is less than pH 5.0, whereas soils with a reaction between 6.5 and 7.2 are regarded as neutral (EUNIS 2002). Soils with a pH greater than 7.2 are called alkaline (or basic) soils. The full range of the pH scale (0-14) is not used in soils, as the reaction of most soils is between pH 3.5 and pH 10.0 (EUNIS 2002). Some species examples of acid to alkaline soil are listed in table 2.4 together with ecological indicator values for acidity from Ellenberg (1991).

Note: The Nordic Vegetation Classification defines soils with a reaction of <pH 4.5 as highly acid; pH 4.5-5.5, acid; and pH 5.6-6.5, moderately acid, pH 7.2-8.5 as slightly alkaline; 8.5-9.5 as alkaline; and more than 9.5 as highly alkaline.

Table 2.4. The pH values in rough classes with the corresponding Ellenberg values of acidity (mR; Ellenberg et al. 1991) with some species examples.

Description	pH	mR value	Species example
Extremely acid to acid	<5.0	<4	<i>Andromeda polifolia</i> , <i>Lycopodium clavatum</i> , <i>Rubus chamaemorus</i> , <i>Ulex minor</i> , <i>Agrostis curtisii</i> , <i>Calluna vulgaris</i> , <i>Drosera rotundifolia</i> , <i>Polygala serpyllifolia</i> , <i>Agrostis vinealis</i> , <i>Dactylorhiza maculata</i> , <i>Galium saxatile</i> , <i>Pteridium aquilinum</i>
Acid to weakly acid	5.0-6.4	4-6	<i>Agrostis capillaris</i> , <i>Carex panicea</i> , <i>Juncus effusus</i> , <i>Teucrium scorodonia</i> , <i>Cardamine pratensis</i> , <i>Cirsium palustre</i> , <i>Rubus idaeus</i> , <i>Ulex europaeus</i> , <i>Ammophila arenaria</i> , <i>Carex sylvatica</i> , <i>Lolium perenne</i> , <i>Ranunculus ficaria</i>
Weakly acid to weakly basic	6.5-7.2	7-8	<i>Agrimonia eupatoria</i> , <i>Atriplex prostrata</i> , <i>Nuphar lutea</i> , <i>Phleum pretense</i> , <i>Artemisia vulgaris</i> , <i>Carduus nutans</i> , <i>Iris foetidissima</i> , <i>Viola hirsuta</i>
Basic (or alkaline)	>7.2	9	<i>Bunium bulbocastanum</i> , <i>Clinopodium calamintha</i> , <i>Dryopteris submontana</i> , <i>Primula farinosa</i>

LEDA Traitbase soil acidity classification

The soil pH is usually given in a range and therefore no pH classes will be administered. For data obtained from literature the pH range should be recorded as a mean value with the minimum and a maximum pH value, with the number of replicates (N).

When data is obtained by 'new' measurements (traditionally measured by inserting a pH electrode into a suspension of 1 part soil and 5 parts water), the pH method used (pH H₂O, pH KCl, pH CaCl₂), the number of replicates (minimal 3), the mean, standard deviation/standard error, and the minimum and maximum pH values are all obligatory information.

Data structure

- Type of variable: Numerical
- Sample size: 3 replicated samples per growing area of the species (or per site)
- Unit: -
- Values: N, mean, standard deviation, standard error, minimum, maximum
- Method used: pH H₂O (=1), pH KCl (=2), pH CaCl₂ (=3), unknown (=4)
- Validity range: 0-10
- Collecting date: day/month/year (dd.mm.yy)

2.8. SOIL NUTRIENT STATUS

Introduction

All plants require adequate amounts of water, light, carbon dioxide and nutrients in order to allow them to grow to their maximum potential and a shortage of nutrients can cause serious restrictions to growth. There is a wide range of essential plant nutrients (e.g. N, P, and K). Nitrogen, for example, is essential for plant growth and thus cause problems when it is deficient (Russell 1973), whereas phosphorus plays an essential role in agriculture and for all forms of life: respiration, photosynthesis in green leaves, microbial turnover and decomposing litter all require adequate levels of P in specialised forms (Cole *et al.* 1977).

In extensively managed land, where biodiversity and species richness is a priority, the abundance of soil nutrients (i.e. due to intensive crop production) can reduce the floristic qualities of meadows (Vickery *et al.* 2001). High soil N and P is a key factor limiting increase in botanical diversity of many extensively managed types of grassland after the conversion from intensive agricultural management (Tallowin & Smith 2001) or where atmospheric deposition occurs on upland. Specifically, for example, Goodwin (1998) has shown that high soil P levels are negatively correlated with species diversity.

Soils that are poor in nutrients are called oligotrophic and have in general a low primary productivity. Mesotrophic soils have a moderate or intermediate nutrient status; whereas eutrophic soils have a high nutrient content supporting a high productivity, originally applied to nutrient-rich waters with high primary productivity but now also applied to soils (see Table 2.5).

Table 2.5. The general indicators values of soil fertility of Ellenberg (Nitrogen status (mN); Ellenberg et al. 1991) with some of the indicator species.

Ellenberg (mN)	Description	Example species
<4	Extremely infertile sites - More or less infertile sites	<i>Agrostis curtisii</i> , <i>Clinopodium acinos</i> , <i>Drosera rotundifolia</i> , <i>Rubus chamaemorus</i> , <i>Aira praecox</i> , <i>Carex panicea</i> , <i>Linum catharticum</i> , <i>Scabiosa columbaria</i> , <i>Centaurea scabiosa</i> , <i>Galium saxatile</i> , <i>Pimpinella saxifraga</i> , <i>Teucrium scorodonia</i> .
4-6	Intermediate fertile sites	<i>Agrostis capillaris</i> , <i>Cirsium palustre</i> , <i>Plantago lanceolata</i> , <i>Primula vulgaris</i> , <i>Angelica sylvestris</i> , <i>Digitalis purpurea</i> , <i>Iris foetidissima</i> , <i>Trifolium pratense</i> , <i>Cirsium arvense</i> , <i>Glyceria fluitans</i> , <i>Poa trivialis</i> , <i>Rumex crispus</i>
≥7	Fertile places (e.g. cattle resting places)	<i>Atriplex prostrata</i> , <i>Epilobium hirsutum</i> , <i>Stellaria media</i> , <i>Typha latifolia</i> , <i>Beta vulgaris</i> , <i>Galium aparine</i> , <i>Lamium album</i> , <i>Urtica dioica</i> , <i>Arctium lappa</i> , <i>Artemisia absinthium</i> , <i>Hyoscyamus niger</i> , <i>Rumex obtusifolius</i>

LEDA Traitbase soil nutrient categories

Information on the soil nutrient status of the sampled sites in the literature is often not given, hence the soil nutrient status has to be derived/ estimated from the species pool of the present vegetation. Therefore the nutrient status is divided into three coarse categories:

1. Oligotrophic [Ellenberg mN <4]
2. Mesotrophic [Ellenberg mN 4-6]
3. Eutrophic [Ellenberg mN ≥7]

Data structure

Data characteristic	Description	Format	Level
Soil nutrient status	Nutrient status the sample sites estimated from vegetation present	category (number)	optional

2.9. INDICATOR VALUES OF AQUATIC PLANTS

Introduction

Between 1978 and 1983 an extensive survey was carried out to record the flora and vegetation and physico-chemical parameters of the water column and sediment of c. 600 fresh water bodies including ditches, streams, rivers, canals, ponds, lakes and fens throughout The Netherlands (De Lyon & Roelofs 1986). This comprehensive dataset was used to calculate the weighted mean value and an 'indication weight' of each parameter measured for the species involved. From this dataset, the species' responses to three parameters were selected to be incorporated into the LEDA Traitbase including pH and alkalinity of the water layer and redox potential of the sediment. These factors are known to be important in determining the distribution of aquatic plants (Wetzel 2001).

Trait definition

The pH is a measure of the acid balance of a solution and is defined as the negative of the logarithm to the base 10 of the hydrogen concentration. As it influences many biological and chemical processes, it is considered an important parameter in water quality assessments (Chapman 1996). In unpolluted waters, pH is principally controlled by the balance between the carbon dioxide, bicarbonate and carbonate ions (Fig. 2.4). On account of the

photosynthesis and respiration cycles of aquatic plants, seasonal and diel variations in pH are common.

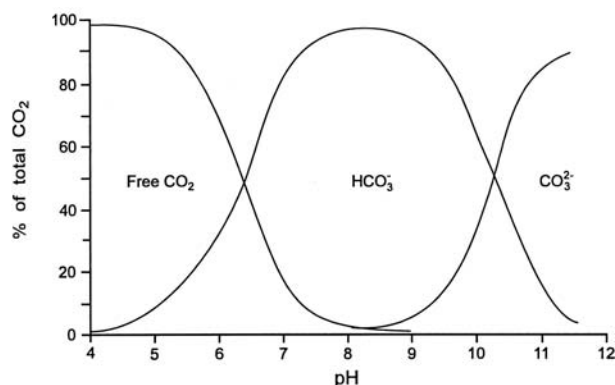


Figure 2.4. The relative proportions of different forms of inorganic carbon in relation to the pH of water (Golterman 1969).

The term alkalinity is used to express the total quantity of base (usually in equilibrium with carbonate or bicarbonate) that can be determined by titration with a strong acid. The milliequivalents of acid required neutralising the hydroxyl, carbonate, and bicarbonate ions in 1 L water are known as the total alkalinity (Wetzel 2001).

The redox potential characterizes the oxidation-reduction state of sediments of natural waters. Ions of the same element but different oxidation states form the redox system which is characterised by a certain value. The co-existence of a number of such systems leads to an equilibrium which determines the redox state of the sediment (Chapman 1996). The redox potential controls to a large extent the microbial pathways that contribute to the oxidation of organic matter.

Measurements

For additional measurements the following guidelines should be taken into account. The pH of the water column should be determined *in situ* with a standard KCl pH-electrode at a depth of 20 cm below water surface after calibration against buffer solutions pH 4.00, pH 7.00 or pH 10.00 (depending on the water body to be sampled).

Samples of the water column should be taken at a depth of 20 cm below water surface after which 50 mL of the sample is titrated down to pH 4.2 using 0.01 M L⁻¹ HCl. The amount of HCl required (expressed as meq L⁻¹) is the total alkalinity.

Redox potential should be measured in the upper 0-5 cm of the sediment with a Pt Ag/AgCl electrode. A constant stabilization time of three minutes should be used for each measurement. Redox-values should next be converted to the potential relative to a normal hydrogen reference electrode (E_h).

All parameters should be measured during the growing season within the aquatic vegetation to be sampled. Because pH features diel variations, measurements are taken preferably between 8.00 and 12.00 a.m.

Classification

For each parameter, species are divided into two groups of aquatic plants: i) floating and submerged aquatic plants and ii) emergent aquatic plants.

pH of the watercolumn (see Appendix 1)

Within both aquatic plants groups, species are classified into six categories according to the weighted mean (wm) value of the pH:

- I Species of acid waters ($\text{wm} < 5.0$)
- II Species of weakly acid waters ($5.0 \leq \text{wm} < 6.0$)
- III Species of weakly acid waters – circumneutral waters ($6.0 \leq \text{wm} < 7.3$)
- IV Species of circumneutral waters – alkaline waters ($7.3 \leq \text{wm} < 8.5$)
- V Species of alkaline waters ($\text{wm} \geq 8.5$)
- VI Indifferent species

Alkalinity of the water column

Within both aquatic plants groups, species are classified into seven categories according to the weighted mean (wm) value of the alkalinity:

- I Species of un-buffered waters ($\text{wm} \leq 0.1 \text{ meq L}^{-1}$)
- II Species of very soft waters ($0.1 < \text{wm} < 0.5 \text{ meq L}^{-1}$)
- III Species of soft waters ($0.5 \leq \text{wm} < 1.0 \text{ meq L}^{-1}$)
- IV Species of soft waters – moderately hard waters ($1.0 \leq \text{wm} < 2.0 \text{ meq L}^{-1}$)
- V Species of hard waters ($2.0 \leq \text{wm} < 4.0 \text{ meq L}^{-1}$)
- VI Species of very hard waters ($\text{wm} \geq 4.0 \text{ meq L}^{-1}$)
- VII Indifferent species

Sediment redox potential

Within both aquatic plants groups, species are classified into six categories according to the weighted mean (wm) value of E_h ¹:

- I Species of very reductive sediments ($\text{wm} < -175 \text{ mV}$)
- II Species of reductive sediments ($-175 \leq \text{wm} < -100 \text{ mV}$)
- III Species of moderately reductive sediments ($-100 \leq \text{wm} < 0 \text{ mV}$)
- IV Species of moderately oxidizing sediments ($0 \leq \text{wm} < 100 \text{ mV}$)
- V Species of oxidizing sediments ($\text{wm} \geq 100 \text{ mV}$)
- VI Indifferent species

Minimal requirements

At least 6 populations of each species with a minimum surface area of 10 m^2 occurring in different water bodies should be sampled. Furthermore columns conform to general data standards (e.g. country, UTM, altitude).

Data structure

To collect: 1 measurement of pH, alkalinity and sediment redox potential within each population

- Obligate:
- Type of variable: Numerical
 - Number of replicates: 6
 - Units: none; mequiv. L^{-1} ; mV
 - Values: N, mean, median, standard deviation, standard error
 - Method used: 1 - Obtained by measurements (standardised protocol), 2 – Obtained from published data
 - Collecting date: day/month/year (dd.mm.yy)

2.10. MANAGEMENT & FERTILISER APPLICATION

Different management practices as well as fertiliser application are of influence on plant communities and should therefore be indicated when this information is available. The different management categories for LEDA are:

Management: 1. Grazing

¹ At this moment it is not clear whether this value refers to E_h or to the uncorrected value

2. Hay-making
3. Burning
4. Unmanaged
5. Other (the rest)
6. Unknown

When information is available on the use of fertiliser on the site this should also be indicated, in the comment field details on the fertiliser used can be given when appropriate.

Fertiliser application: 1: Yes
0: No

Data structure

<u>Data characteristic</u>	<u>Description</u>	<u>Format</u>	<u>Level</u>
Management	Management practices	category (number)	optional
Fertiliser application	Fertiliser application yes or no	category (number)	optional

2.11. METHOD OF MEASUREMENT

Introduction

Data entries may have many different origins and in various ways of being obtained. To be able to query the database on different methods of measurement each entry must be allocated one of the below listed choices. The ranking of each method responsible for high or low data quality (e.g. to indicate different levels of data aggregation per plant species) will be indicated at each individual trait standard.

- Method of measurement:
1. Estimation
 2. Derivation from morphologies or other plant traits
 3. Derivation from photos or drawings
 4. Observation (like obvious taxonomical traits)
 5. Measurement (actual measurements)
 6. Field experiment
 7. Laboratory/greenhouse/garden experiments
 8. Modelling
 9. Other
 10. Unknown

To each of the methods choices comments field will be attached as an optional field that may contain information on the original method, if second hand data are used, or that may contain more details about a used method.

Data structure

<u>Data characteristic</u>	<u>Description</u>	<u>Format</u>	<u>Level</u>
Method of measurement	Method used to obtain data	category (number)	obligate

3. SUMMARY

Summary of the data structure of the characteristics of the general standards with their description, data format and indication if the information is obligatory (indicated by X):

Data characteristic	Description	Format	Obligate
References cited			
Refname	Short abbreviated name of the data source	text	
Reftype	Person, publication or database	text	X
Author	List of names of authors, all separately stored (in J. Ecol. format)	text	X
Year	Year of publication	number	X
Title	Full title of publication	text	X

Publisher	Name of publisher, e.g. Chapman and Hall, London	text	X
Journal	Name of journal	text	
Number	Edition/volume identifier	number	
Pages	Range of pages, when part of a large volume, e.g. 199-220	number	
Book title	Full title of the book when the source is part of a larger reference	text	
Editor	List of names of editors	text	
ISXN	ISSN or ISBN number of the source	number	
Type	Type of publication e.g. report, PhD-thesis, diplomarbeit	text	
Location	Location of the library	text	
Language	Language of the data source	text	
Number of Trials	Total number of trials per source number	text	
Person name	Person name in the reference format e.g. Thompson, K.	text	
Person info	The persons email address	text	
Database ID	Unique code of one of the five different databases	text	
Database admin	Contact email address	text	
Database address	Name, address or web address (URL) of hosting organisation	text	
Geographical reference			
Study area	Where measurement took place in (1) or outside(0) of NW-Europe	number	X
Country code	ISO-3166 two-letter country code where measurement took place	text	X
Altitude	In metres with unknown projection	number	
Range	Radius range GPS reading	number	
UTM zone	Co-ordinates according to UTM-grid	text	
UTM easting	Co-ordinates according to UTM-grid	text	
UTM northing	Co-ordinates according to UTM-grid	text	
Comment ref	For e.g. comments on nearest town or nature reserve	text	
Map date	Date of the map used (month/year or year)	text	
Description habitat			
Habitat type	Categories that corresponds with EUNIS habitat types	number	X
Sample area	The size of the sampled area in m ² (or m length for line transects)	number	X
Soil substrate	One of the categories	number	X
Soil type	One of the main soil type categories	number	
Soil acidity	pH of the soil of the sample site	range	
Soil moisture	Moisture status of the soil of the sample site	number	
Soil nutrients	Nutrient status the sample sites	number	
Management	Management practices of sample site	number	
Fertiliser application	Fertilised used (yes/no)	number	
Method of measurement	Method used to obtain data	number	X

SECTION 3. TRAIT STANDARDS

For any data entered into the Traitbase it is required to record the obligate fields of the general standards and trait standards concerned. For the general standards information on the data reference (literature, database), geographical references (study area, area code), and description of the sample site (habitat type, sample area size, soil substrate, method of measurement) is required. For each of the trait standards the required information is stated for each trait. When trait data is obtained from literature the original data source (original reference) should be filled in separately for each trait when the data is originating from a review paper (i.e. data used in one paper that is originating from another source).

Note: Criteria for refusing data to be entered into the LEDA Traitbase will be the lacking of any obligate information required for the general and/or trait standard, as well as missing information on the number of replicates and the standard deviation or standard error of the mean values of the concerning trait value(s).

1. CANOPY HEIGHT

Introduction

Canopy height is associated with competitive vigour, whole plant fecundity and generation time after disturbance. Between canopy height and tolerance or avoidance of, for instance, environmental stress there are important trade-offs. On broad interspecific comparisons height tends to correlate allometrically with other size traits such as aboveground biomass, rooting depth, lateral spread and leaf size (Cornelissen *et al.* 2003). Note that in the LEDA Traitbase canopy height is not the same as plant height. Plant height is defined as the highest point of the plant (i.e. inflorescence) and therefore plant height can be greater than canopy height.

Trait definition

Canopy height: Is defined as the distance between the highest photosynthetic tissue and the base of the plant (Weiher *et al.* 1999; see Glossary).

How to measure

The canopy height is measured in metres as the difference between the highest photosynthetic tissue (the foliage) of the individual and the base of the plant. Within a plant species the canopy height can be highly variable. Therefore a minimum of 25 representative healthy, adult individuals should be randomly selected for measurement per species per site. The randomly selected individuals should be situated with their foliage exposed to the light (i.e. sunny spot; Cornelissen *et al.* 2003). For the determination of the height of trees, a (telescopic) stick with metre marks will be the most straightforward way to measure tree height. Height sticks provide a direct method for measuring tree height and are the most reliable instrument for measuring tree height (Brack & Wood 1997). Each stick is usually 1.5 m long and constructed of tubular duralumin or fibreglass, and graduated in decimetres. Use of height sticks is generally confined to trees less than 25 m tall. For taller trees situated on flat areas or on slopes, an estimate of tree height can be obtained by indirect measurements using trigonometric principles in combination with hypsometers or other (optical) instruments for measuring height (i.e. Vertex, Releskop, Suunto clinometer, Blume Leiss, Haga, Criterion laser dendrometer, and Abney level; see Fig. 3.1; Brack & Wood 1997).



Figure 3.1. Instruments used for indirect tree height measurement (A) with left to right the Abney level, Suunto, Blume Leiss, and Haga (source: Brack and Wood 1997).

For estimations of tree height in flat areas you assume that the tree is truly vertical (i.e. point A is directly above point B; Fig. 3.2a), the operator's eye (point O) is above the level of the base of the tree (point C), and the distance to the tree is the horizontal distance from the operator to the geometric centre of the tree at the appropriate position on the trunk (OC; see Fig. 3.2a). To estimate the height of the tree the observer stands at any distance (OC) from the tree that is convenient for observation of both the tip and base of the tree. The distance OC is measured and the angles between the horizontal plain and the tree top ($\text{AOC} = \alpha$) and between the horizontal plain and the tree base ($\text{COB} = \beta$) are determined using a hypsometer. The total tree height (H) is subsequently calculated as $H = \text{OC} \times [\text{TAN}(\alpha) + \text{TAN}(\beta)]$.

In the case described above it is assumed that the operator is above the level of the tree base. On sloping grounds this may not be the case and it may also be difficult to determine the horizontal distance to the tree (OC; see Fig. 3.2b). In this situation you calculate the horizontal distance OC (from slope distance OB and angle BOC) and subtract the length BC from AC. $H = \text{AC} - \text{BC} = \text{OC} \times [\text{TAN}(\alpha) - \text{TAN}(\beta)]$ where $\text{OC} = \text{OB} \times \text{COS}(\beta)$. Alternatively an object of known height is placed against the tree trunk, and the height (H) is calculated using the formula $H = h \times [\tan(\alpha) - \tan(\gamma)] / [\tan(\beta) - \tan(\gamma)]$ where α is the angle between the horizontal plane and the tree top, β is the angle between the horizontal plane and the top of an object of known height (h) that is positioned vertically next to the trunk of the tree, and γ is the angle between the horizontal plane and the tree base (which is the similar as the base of an object or person).

If the slope is not severe, the horizontal distance OC can be measured by holding a measuring tape at point B and stretching it out horizontally until it is exactly above point O (Fig. 3.2b).

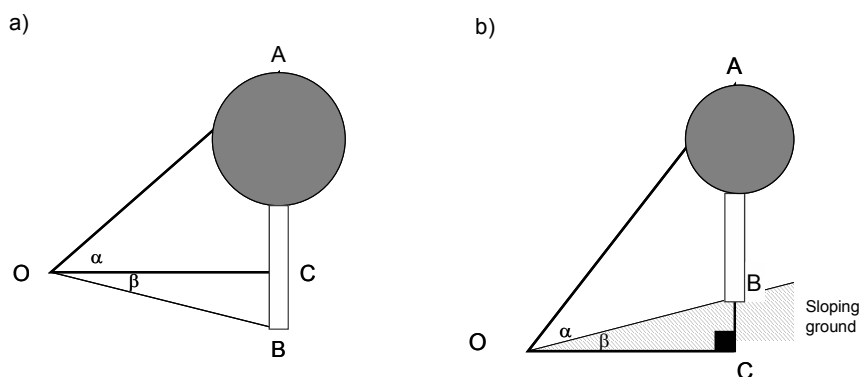


Figure 3.2. Trigonometric principles to estimate tree height in flat (a) and sloped (b) areas (Brack and Wood 1997).

Special cases

- Major leaf rosettes plants canopy height is based on height of the rosette leaves, as these species often have little photosynthetic tissue higher up (*Capsella bursa-pastoris*, *Onopordum acanthium*; Cornelissen *et al.* 2003).
- In the case of epiphytes canopy height is defined as the shortest distance between the upper foliage boundary and centre of their basal point of attachment.
- In the case species that use a support structure to grow (i.e. twines, climbers, lianas, scramblers, hemi-epiphytes and certain hemi-parasites), the canopy height is defined as the shortest distance between the upper foliage boundary and the soil surface. Please, make a note if the species use support structures as trees, shrubs or other plants.
- The canopy height for water plants is measured as the distance between the highest point of photosynthetic tissue and the water surface.

- For herbaceous species an additional method called 'stretched length' can be used to assess the potential occupied space. Select a stem of which the youngest leaf is healthy and fully active (or a tiller in the case of graminoids) and stretch the axis of the leaf to its maximum height. The distance between the plant base and the top of the leaf is the 'stretched length' (Cornelissen *et al.* 2003).

Minimal requirements

To estimate the canopy height the database BIOPOP1 used drawings from the German flora (Rothmaler 2000; see Poschlod *et al.* 2003). This data will be incorporated into the LEDA Traitbase, however note that the statistical quality of this method is low, due to the fact that the ranges of minimum and maximum height are only field observations with an unknown number of replicates.

To obtain the canopy height of the species missing from the BIOPOP list, the standardised measuring protocol of canopy height (as described above) should be used.

When in any published source the canopy height is a real measurement (i.e. not derived from drawings), information on the number of sampled individuals, mean or median with the standard deviation or standard error is obligatory. Missing information on one of the above mentioned criteria will result in rejection of the data. In the cases of estimation by drawings and of published data sets LEDA accepted the unknown number of replicates as a single observation.

For any data entered into the Traitbase it is required to record the obligate fields of the general standards on the description of the sample site (i.e. geo-reference, habitat, method), including the size of collecting area to estimate data quality. For canopy height field data with 25 replicates per species per site are preferred, but data from garden experiments are accepted with additional information about the sample site (see general standards). For small populations or rare species a lower number of replicates are accepted with a minimum of 3 replicates per species per site.

In the LEDA Traitbase the canopy height will be expressed in metres. Data expressed in other units needs to be converted to metres before entering the data into the database to be able to compare the data.

Data structure

- To collect: 1 height measurement of 25 different individuals = 25 heights in total per species (per site)
- Obligate:
- Type of variable: Numerical
 - Number of individuals per sample (sample size, n): 25
 - Number of replicates per individual (N): 1
 - Unit: m
 - Values: N, mean, median, minimum, maximum, standard deviation, standard error
 - Method used: 1 - Obtained by measurements (standardised protocol), 2 - Obtained from measurements of published data, 3 - Estimated from drawings
 - Validity range: 0-70 (for European plants)
 - External support structure²: yes = 1 or no = 2, unknown = 3

2. LEAF TRAITS

Introduction

Interspecific variation in leaf size has been connected with climatic variation, geology, altitude or latitude, where heat stress, cold stress, drought stress and high-radiation stress all tend to select for relatively small leaves. Hence, leaf size has important consequences for the leaf energy and water balance. Leaf size variation can also be linked to allometric factors (plant size, twig size, anatomy and architecture) and ecological strategy with respect to

² = "yes" is only to use for lianas, climbers and epiphytes, which were measured with their support structure! In all other cases is to use "no".

environmental nutrient stress and disturbances within climatic zone, while phylogenetic factors can also play an important role (Cornelissen *et al.* 2003).

In many cases the specific leaf area (SLA) of a species is positively correlated with its potential relative growth rate mass-based maximum photosynthetic rate (Cornelissen *et al.* 2003). Lower values of SLA tend to correspond with a long leaf lifespan and species with a relatively high investment in leaf 'defences' (particularly structural ones). Some shade-tolerant woodland under storey species are known to have remarkably high SLA, as well as species in resource-rich environments compared to those in environments with resource stress (Cornelissen *et al.* 2003).

SLA is the one-sided area of a fresh leaf divided by its oven-dry mass, hence leaf mass is one component of the SLA measurements, expressed as leaf dry mass (see Wright *et al.* 2002). Note that this expression does not mean the same as leaf mass per area or specific leaf mass (SLM; Pynakow *et al.* 1999).

As a measure for the tissues density the trait leaf dry matter content (LDMC) will be measured. Tissue density plays a central role in the nutrient utilisation of a species by determining the rate of biomass turnover (i.e. low tissue density is associated with high growth rate). Although variation in tissue density is often correlated with differences in life history traits among species, for the bulk of the organ tissue density is relatively constant for each species (Niklas 1994, Enquist *et al.* 1999). Leaves with a high LDMC tend to be relatively tough, and are as such assumed to be more resistant to physical hazards (e.g. herbivory, wind, hail) compared to leaves with a low LDMC. Species with a low LDMC tend to be associated with productive often high-disturbance environments (Cornelissen *et al.* 2003). The LDMC is the ratio dry leaf mass to fresh leaf mass after the definition of Ryser (1996) with the assumption that leaf tissue density $\approx$ leaf dry matter content. Thus a tight relationship between volume and fresh mass of the leaf is assumed (see Garnier & Laurent 1994). In general the LDMC is negatively correlated to potential relative growth rate and positively with leaf life span, however these correlation are weaker than compared to for instance the correlation between leaf life span and SLA (Cornelissen *et al.* 2003).

The LDMC can be used in cases where the leaf area is difficult to measure (Cornelissen *et al.* 2003), even though LDMC and SLA are not the same, the average density of the leaf tissues is related to the LDMC and tends to scale with $1/\text{SLA}$.

Trait definition

- SLA: Specific leaf area (SLA) is the ratio of leaf area to leaf dry mass: $\text{SLA} = \text{leaf area} / \text{leaf dry mass}$, expressed in $\text{mm}^2 \text{mg}^{-1}$
- Leaf size: Leaf size is the one-sided projected surface area of an individual leaf or lamina expressed in mm^2 .
- Leaf mass: Is the dry weight of a leaf, expressed in mg.
- LDMC: Leaf dry matter content, a measure of tissue density, is the ratio dry leaf mass to fresh leaf mass and is expressed in mg/g.

2.1. SLA, LEAF SIZE, LEAF MASS & LDMC

What and how to collect

For the collection of leaves, the individuals of herbaceous and small woody species should be randomly selected and should have their foliage exposed to the light (i.e. sunny spot). Whole leaves (including the petiole) should be collected and for tall woody species the leaves most exposed to direct sunlight ('outer canopy' leaves) should be sampled (Cornelissen *et al.* 2003).

As most leaf traits are rather variable within plants, it is recommended that for each species 2 randomly selected leaves exposed to the light should be collected from each of 10 different individuals for each sample site. If it is impossible to collect leaves from 10 different individuals, i.e. due to small populations or rarity of the species, more than 2 leaves could be collected from the minimum of 3 individuals per species per sample site. For small species it

is recommended to collect complete plants or branches. As LDMC can vary during the day, it is recommended to sample the leaves before (or close to) sunset or after sunrise (Cornelissen *et al.* 2003 see also Garnier *et al.* 2001).

Note that to economise on collecting time, the same leaves could be used to determine leaf size, SLA, leaf mass and LDMC.

Storing and processing

When collected, the leaf samples should be wrapped in moist (filter)paper, sealed in plastic bags, and transported to the laboratory in cooler boxes to prevent weight (or turgor) loss. In the laboratory the leaves should be stored in the plastic bags in the fridge at 5°C until further measurements. Note to store the leaves as flat as possible when SLA needs to be obtained from the leaves. If no cool box is available and temperatures are high, it is better to store the samples in plastic bags without any additional moisture. If storage during rehydration is to last for more than 24h, low temperatures (2-6°C) are essential to avoid rotting (Cornelissen *et al.* 2003). The leaves of some xerophytic species (e.g. bromeliads, cacti) decompose very quickly when stored too wet and should therefore be stored dry in paper bags. A 1-3 hour rehydration period is suggested for these leaves before measurements.

When uncertain about the best storage method, store plant material under both dry and wet circumstances. For 'soft' leaves, such as those of many herbaceous and deciduous woody species, the leaves should be rehydrated with de-ionised water when kept under dry conditions prior to measurements in order not to underestimate the measurements. Note that the measurements should preferably be carried out as soon as possible (within 24 hours) after collecting (Cornelissen *et al.* 2003). If this is not possible, the leaves should be stored between moist filter paper in sealed plastic bags in the freezer until further measurements. When ready to measure the leaves, the frozen leaves should be defrosted in water and remain in the water until the fresh weight and area measurement are finalised. Note that the freezer treatment is not suitable for all leaves.

How to measure

SLA: Each leaf (including petiole) is gently rubbed dry before measurement. Projected area (as in a photo) can be measured with specialised leaf area meters (i.e. Li-Cor), or, if a leaf area meter is not available, an alternative is to scan leaves with a flatbed scanner (Cornelissen *et al.* 2003). From the leaf a computer image is generated and the area can be measured using appropriate analysis software (i.e. Lafore Fig. 3.3; Lehsten 2002). Documentation of sampled leaves by reference pictures of scanned leaves, scanned at 300 DPI, is preferred and that the readings of the area meter should be checked by using coins or pieces of paper of known area before measuring leaves. The latter also applies to leaf areas measured using a flatbed scanner.

LEDA prefers to use a flat bed scanner, because in practice the measurements with this scanner are more exact, and can be used in the field with electricity from a laptop. Where none of these facilities are available, the area can be estimated by weighing paper or plastic cut-outs of similar shape and size and then multiplying by the known area/weight ratio of the paper, as long as the paper or plastic is of a constant quality.

When measuring the leaves, the leaves should be positioned as flat as possible (e.g. by using a glass cover), in the position that gives the largest area, but without squashing and damaging the leaves.

The use of the methods mentioned above may give a large error for small or narrow leaves or needles, partly due to the pixel size of the projected images (Cornelissen *et al.* 2003). For such leaves it is recommended to calibrate the image analysis equipment with objects of similar shape, size and colour (e.g. green paper cuttings of the desired dimensions) and treat several leaves as if they were one (Cornelissen *et al.* 2003). For very small leaves and needles the projected area can best be obtained by placing the leaves on millimetre grid paper and estimated the area by using a binocular microscope (10x magnification), after which large drawings of both the

leaves and millimetre squares could be compared using the leaf area meter (Cornelissen *et al.* 2003).

On the other hand, very large leaves might not fit in the area meter or on the flatbed scanner. In this case the leaf needs to be cut up in smaller leaf parts and the total area is determined by taking the cumulative area of all parts (Cornelissen *et al.* 2003).

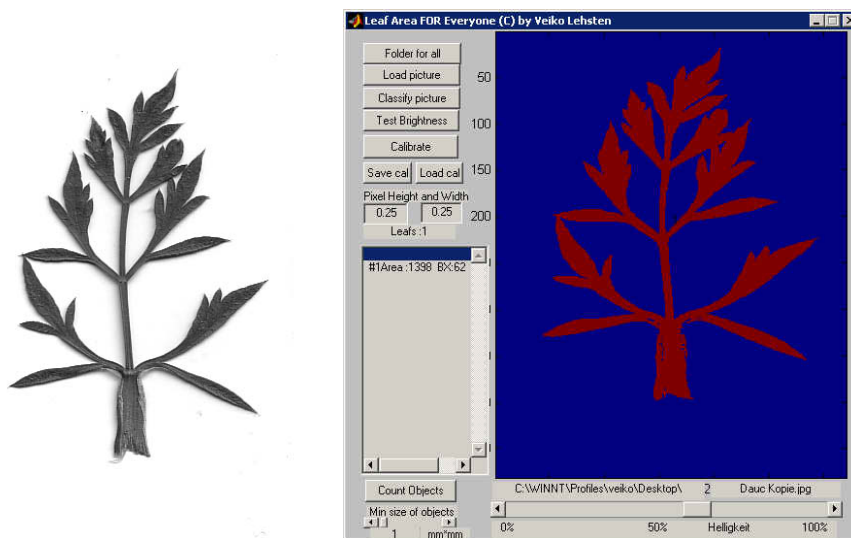


Figure 3.3. Lafore scan software for image classification for plant leaf investigations and seed counting, with an example of *Daucus carota* (Lehsten 2002).

Leaf size: Individual leaf laminas (or leaflets in compound leaves) should be measured with and without the petiole and rachis (see also Special cases). The average leaf size of the leaves collected from one individual will represent one statistical observation (Cornelissen *et al.* 2003).

Leaf mass: After the leaf area is measured, each leaf sample is dried in the oven at 70 °C for 48- 72 hours and subsequently the dried leaves weighed to determine their dry mass (=leaf mass). If the leaf samples cannot be weighed immediately after cooling down, put them in the desiccator until weighing, or else back in the oven to dry off again. As is the case for leaf area, the weighing several tiny leaves as if they were one will improve the accuracy, depending on the type of balance used (Cornelissen *et al.* 2003).

LDMC: For measurements of LDMC a combination of the standardised protocol of the “fresh leaf method” from Wilson *et al.* (1999) and Cornelissen *et al.* (2003) will be used. The rehydration (or saturated) method for LDMC of Garnier *et al.* (2001) is not used in the LEDA Traitbase, but is one of the methods that can be chosen for data obtained from published sources. When measuring the LDMC, the leaves with and without the petiole should be measured to be able to compare with other published data sets as in general both leaf 'states' are measured.

After collection the leaves are weighed (fresh weight) after which the sample was dried in a paper bag/envelope at 70°C for 48-72 hours and subsequently re-weighed to obtain the over-dry weight of the leaf (dry weight). Note that before weighing the leaves; the leaf lamina should be blotted dry with tissue paper to remove any surface water (Wilson *et al.* 1999). LDMC is expressed in mg g^{-1} and calculated by dividing the oven-dry weight (mg) by the fresh weight (g). Values for the dry matter content were calculated as dry weight, expressed as a percentage of saturated weight.

Special cases

- For leafless plants the functional analogue of a leaf is sampled and treated as a leaf. For instance for spiny species such as *Ulex*, the top 2 cm of a young twig should be sampled, whereas for cacti and other succulents it is recommend to cut off a slice ('the scalp') of

the epidermis plus some parenchyma of a relatively young part. Also the younger stems of some rushes and sedges (*Juncus*, *Eleocharis*) and green leafless shoots and/or the 'branches' of horsetails (*Equisetum*) can be treated as leaves (Cornelissen *et al.* 2003). Data collectors have to decide what they consider to be the leaf analogue, but note that it is important to record the exact method used in when this is the case.

- For heterophyllous species which have, for instance, both rosette and stem leaves, both leaf types should be collected in proportion to the total leaf number in order to obtain a representative SLA.
- It might be relevant to determine SLA on the basis of actual (rather than projected) one-sided leaf area, as an additional measurement. In needles (e.g. *Pinus*) or rolled-up grass leaves (e.g. some *Festuca*) this makes a large difference. By taking the ratio of the upper half of the circumference and leaf width of a leaf cross section, using a microscope, a true one-sided leaf area may be estimated.
- It should be noted that interspecific rankings of SLA are rather robust to methodological factors (e.g. with or without petioles). For comparisons on a coarse scale SLA data from several sources may be combined, only as long as (at least) possible methodological artefacts are acknowledged (Cornelissen *et al.* 2003).
- Whole-leaf sizes may be added as they can be relevant for some allometric analyses. For whole leaf measurements of compound leaves, all leaflets should be included as well as any petiole and rachis. Note that these whole-leaf measurements are part of SLA measurements (Cornelissen *et al.* 2003).
- Record leaf size for leafless plant species as zero and not as a missing value as it is an important functional trait. Note that from certain data analyses these zero values may need to be excluded (Cornelissen *et al.* 2003).
- For heterophyllous plants (e.g. plants with both rosette and stem leaves) leaves of both types should be collected in proportion to the total leaf number in order to obtain a representative species leaf size (Cornelissen *et al.* 2003).
- For leaves with massive midrib support structures (e.g. *Petasites hybridus* Fig. 3.4) excise a lamina sample from the leaves (Wilson *et al.* 1999).
- For resinous and succulent xerophyte species, rehydration in the laboratory may prove difficult. For these species an alternative method could be to collect the leaves the morning after a rainfall event (Cornelissen *et al.* 2003).



Figure 3.4. Special case example *Petasites hybridus* with leaves with massive midrib support structures (Source: Strøm 2000).

Minimal requirements

For any data entered into the Traitbase it is requested to record the obligate fields of the general standards on the description of the sample site (i.e. georeference, habitat, method), including the size of collecting area to estimate data quality.

Measurement obtained from literature (or other published sources) data of SLA, Leaf size and Leaf mass can not be accepted by the LEDA Traitbase when the mean or median is given without the number of replicates (N) and the standard deviation or standard error. For information obtained from literature sources, details of the method used (i.e. leaf area meter or scanner) and the state of the leaf (measured with or without petiole/rachis) are obligatory. When data obtained by measurements is entered in the Traitbase, the mean or the median with the standard deviation or standard error with a minimum number of 3 replicates of individuals is obligatory. A minimum of 2 leaves should be collected within each individual, with the exception of species that only produce one leaf. Leaf trait data obtained from greenhouse or garden experiments are only accepted when all obligate fields can be completed.

The leaf traits SLA, Leaf size and Leaf mass will be expressed in $\text{mm}^2 \text{mg}^{-1}$, mm^2 , mg , respectively. Data collected from literature or other sources expressed in other units will need to be converted to the above mentioned units before entering the data to the Traitbase. Leaf size data obtained from greenhouse or garden experiments are only accepted when all obligate fields can be completed, including additional information on the use of e.g. fertilisers during the experiments. The lack of information on one of the obligate points mentioned above will result in rejection of the data.

Data structure

To Collect: 2 leaves of 10 different individuals = 20 leaves in total per species (per site)

Obligate:

- Type of variable: Numerical
- Number of individuals per sample (n): 10
- Number of replicates per individual (N): 2
- Unit: SLA $\text{mm}^2 \text{mg}^{-1}$, Leaf mass mg , Leaf size mm^2 , LDMC mg / g
- Values: N-number, mean, median, minimum, maximum, standard deviation, standard error

Note: The average leaf trait data for each individual plant (which is in general 2 leaves) is taken as one statistical observation when calculating mean, standard deviation or standard error (Cornelissen *et al.* 2003).

- Validity range: SLA 0-100, Leaf mass 0-1.000.000, Leaf size 0-3.000.000, LDMC 0-1000
- Leaf state: without petiole and rachis (= 0) or with (= 1) or unknown (= 2)
- Rehydration (saturated) method: yes (= 1), no (= 0)
- Plant stage: seedling (= 1), juvenile (= 2), adult (= 3), unknown (= 4)

Optional: o Error of balance: mg

3. STEM TRAITS

Stem traits included in the LEDA Traitbase are Woodiness (or stem specific density), shoot growth form (including branching), leaf distribution along the stem

3.1. WOODINESS & STEM SPECIFIC DENSITY

Introduction

Tissue density plays a central role in the nutrient utilisation of a species by determining the rate of biomass turnover (i.e. low tissue density is associated with high growth rate). Although variation in tissue density is often correlated with differences in life history traits among species, for the most of the organ tissue density is relatively constant for each species (Niklas 1994, Enquist *et al.* 1999).

In general the definition for 'density' is the mass of an object divided by its volume, the density of a plant organ is therefore the mass of the plant organ divided by its volume. Hence, the density of the dry matter of an organ is its dry mass divided by its volume. The dry matter concentration of an organ is the mass of its dry matter divided by volume of the organ itself. An indirect measure of dry matter concentration is the dry matter content (or mass fraction of dry matter in the international system of units), with the dry matter content defined as the ratio of organ dry mass to fresh mass (Shipley & Thi-Tam Vu 2002). The dry matter content of an organ is referred to as tissue density (see Ryser 1996, Westoby 1998), which is defined as the dry weight per unit volume (Wilson *et al.* 1999).

As a measure for the tissues density the traits leaf dry matter content (see Leaf traits) will be measured and the woodiness of the stem will be observed. As an extra (optional) choice the stem specific density (SSD) can be included.

A stem provides the structural strength that a plant needs to stand upright and the durability it needs to live sufficiently long. Stem density appears to be central in a trade-off between plant (relative) growth rate (high rate at low stem densities) and stem defences against pathogens, herbivores or physical damage by abiotic factors (high defence at high stem densities). In combination with plant size related traits, stem density also plays an important role in the aboveground storage of carbon (Cornelissen *et al.* 2003, see also Niklas 1993, 1995). The persistence, the stiffness and longevity of stems is depending on their tissue density (Wilson 1995). Therefore, stem tissue density plays an indirect role to the placement of flowers and fruits in space and time (Niklas 1994, Waller & Steingraeber 1995), e.g. for wind-pollinators and wind-dispersers.

The stem density (or wood density) is determined by dividing the dry mass of a stem segment by its fresh volume (Weiher *et al.* 1999). This value is referred to as stem specific density (SSD), which quantifies woodiness and stem water content (Castro- Díez *et al.* 1998, Hacke *et al.* 2001, Cornelissen *et al.* 2003)³. Woodiness is an easy trait, to determine tissue density of each species in two very coarse categories; woody and non-woody. Note that the term woodiness means also the occurrence and distribution of wood along the stem (e.g. semi-woody $\approx$ woody at base; see Woodiness categories). In the LEDA Traitbase woodiness is an obligate trait obtained by observation, while the SSD measurements are an optional choice.

Trait definition

Woodiness: The occurrence and distribution of wood along the stem.

SSD: Stem specific density quantifies woodiness and stem water content and is determined by dividing the dry mass of a stem segment by its fresh volume, expressed in g/cm³.

What and how to collect for Woodiness

The trait woodiness will be obtained from published sources (see General standards for reference system). In many published sources (e.g. flora's) woodiness is a nominal trait with three main categories:

1. Woody = including 'real' hard wood (defined as ≥ 0.50 g/ cm³ wood density e.g. *Quercus* species) and soft wood (defined as < 0.50 g/ cm³ wood density e.g. conifers and *Salix* species)⁴.
2. Semi-woody = including species that are often 'woody at base' such as *Solanum dulcamara* or *Rubus* species; the wood density of semi-woody species is not clear due to too few available measurements. It will be expected, that you can also find species with hard woody shoots than with soft woody shoots at their base.
3. Non-woody = including all other species (most herbaceous and graminoid species)

³ = See also Twig dry matter content (TDMC) and twig drying time referred by Cornelissen *et al.* (2003)

⁴ Note, that wood density, referred in forestry literature, often estimated as "air-dry weight (ADW)" per volume vs. "oven-dry weight (ODW)" per volume (to measure SSD).

In the absence of quantitative data sets the above mentioned nominal categories (hard and soft wood, semi wood, non woody) should be used to make a rough estimate.

What and how to collect for stem specific density (SSD)

A minimum of 5 replicates (i.e. individuals) of representative healthy adults should be sampled, as described for canopy height (foliage exposed to sunlight). For herbaceous and woody species with a main stem diameter of ≤ 6 cm, a branchless section of at least 10 cm long section is cut out (knife) at approximately one third of the total stem height measured from the base of the stem (Note: Remove branches when necessary). For shorter stems the whole stem is used with the apical part and loose bark removed. Any firmly attached bark or equivalent phloem tissue is considered to be an integral part of the functioning stem and therefore it needs to be included in stem density measurement. Note that if this method causes unacceptable damage to shrubs or small trees, the 'slice method' may therefore be a compromise alternative (Cornelissen *et al.* 2003).

For woody (or thick succulent) plants with stem diameters of > 6 cm, a pie-shaped slice from the trunk is removed at approximately at one third of trunk height when measured from the base, or at approximately 1.3 m for trees when tree over 4m in height. The pie-shaped slice (2 to 10 cm in height) needs to represent a cross-section area of approximately $1/8^{\text{th}}$ of the total cross-section.

Hard-wooded samples should be stored cool in a sealed plastic bag, whereas the herbaceous samples (more sensitive dehydration) are stored cool between moist filter paper in plastic bags until future use.

How to measure stem specific density (SSD)

The optional trait stem specific density is determined by the oven-dry mass of a section of a plant's main stem divided by the volume of the same section when still fresh, expressed in mg mm^{-3} (corresponding with kg dm^{-3}) with values ≤ 1 (only tropical hardwood have values of >1). The idea is that large spaces in relation to the stem diameter are considered air or water spaces, and as such do not belong to the stem tissue, whereas smaller spaces do. Accordingly, the central hollow of a hollow stem is not included in the volume, but smaller xylem vessels will be included. The volume can be determined by the volume replacement method. With this method the volume of a fresh stem sample (rubbed dry) is measured by immersing the stem section in a volumetric flask filled with water and the increase of volume is measured. During the 5 second interval, the larger but not yet the smaller spaces should fill with water.

For very small samples, or species with unusual tissue, this volume replacement method may not work. For those species the mean diameter (D) and the length (L) of the cylindrical sample is measured with a calliper or ruler. If the stem is very thin, the stem diameter should be determined using a cross-section under the microscope (e.g. small annuals). The volume (V) of the cylinder is subsequently calculated using: $V = (0.5 D)^2 * \pi * L$. In the case of hollow stems, estimate the diameter of the hollow and subtract the cross-sectional area of the hollow from the stem cross-section before calculating the volume.

After volume measurement the sample is dried in the oven at 70°C for 48 to 72 hours (depending on the size of the stem samples) and the oven-dry weight determined (Cornelissen *et al.* 2003).

To determine wood density of lower shrubs (often with multiple stems), herbs, grasses or seedlings the use of 5-10 short stem segments (0.3 - 2.5 cm long) per individual will be accepted (e.g. grasses Ryser 1996; shrubs Hacke *et al.* 2000; seedlings Castro- Díez *et al.* 1998).

An additional forestry method to determine stem density is the use of tree cores. Although this method is not always using a representative part of the stem volume, similar data from

tree cores are acceptable for use in broader comparisons where small deviations are not critical. The mass component of wood density is often measured at 12 % moisture content, and density reported as 'air dry weight' (ADW) or 'air-dried timber'. Stem specific density as described in this protocol is called 'oven dry weight' (ODW) in technical timber journals. Data obtained by ODW, directly measurement or derivation from ADW, can be used as stem specific density for trees. After Reyes *et al.* (1992), ADW can be transformed to ODW or SSD as follows: $SSD = 0.800 \text{ ADW} + 0.0134$ ($R^2 = 0.99$). For further details see Cornelissen *et al.* (2003).

Special cases

- Some plant species without a well-defined stems (i.e. rosette plants, grasses, sedges), the central aboveground area from which the leaves grow is isolated and treated as the stem. The stem density is reported as zero if the plant species has no recognisable aboveground support structure (Cornelissen *et al.* 2003, Ryser 1996).
- When plants are branching at ground level, the apparent main branch or a random branch should be selected to measure (Hacke 2000, Cornelissen *et al.* 2003).
- To compare SSD with other traits as the relative growth rate, it is interesting to measure adult plants as well as seedlings (see Castro- Díez *et al.* 1998).

The table below presented the relationships between woodiness, a nominal trait to categorise the distribution of wood along the shoot, and stem specific density, a numerical trait to measure the density of herbaceous or woody tissue.

obligate		optional	
Woodiness		Stem specific density	
Nominal or ordinal: categories		Numerical as unit: g/cm³	
Woody	Woody	Hard wood	≥ 0.50
		Soft wood	< 0.50
	Semi-woody	Semi-woody: Hard	≥ 0.50
		woody at base	
		Semi-woody: soft woody at base	< 0.50, but known records ≤ 0.04 for seedlings ⁵
Non woody	Non woody	Non woody	< 0.50, but known records ≤ 0.26 ⁶

Minimal requirements

In the case of SSD the mean or the median with the standard deviation or with the standard error has to be given with a minimum of 3 replicates (i.e. 3 different individuals per species). A criterion for data rejection is the missing of the number of replicates and/or the standard deviation or standard error.

For any data entered into the Traitbase it is required to record the obligate fields of the general standards on the description of the sample site (i.e. georeference, habitat, method), including the size of collecting area to estimate data quality. For SSD it is obligate to give information on if the measurement was from seedling or adult stage. Woodiness or SSD data obtained from greenhouse or garden experiments are only accepted when all obligate fields can be completed. In the case the data is obtained from literature, the LEDA Traitbase accepts data in other unit's but these have to be converted to mg/mm³ before entered into the database.

Data structure

Woodiness

To collect: 1 observation per species for Woodiness

⁵ e.g. Castro- Díez *et al.* (1998)

⁶ e.g. Shipley, B. and T.-T. Vu (2002)

- Obligate: • Type of variable: nominal and ordinal
 • Unit: categories

SSD

To collect: 1 stem piece from 5 different individuals per species = 5 stem pieces in total per species

- Optional: o Type of variable: numerical
 o Number of individuals per sample size (n): 5
 o Number of replicates (N): 1 (up to 10 for multiple stem plants or branched herbs)
 o Unit: g cm⁻³
 o Values: n-number, mean, median, minimum, maximum, standard deviation, standard error, quartiles (Q₁, Q₃)
 o Validity range: from 0-1.5
 o Trait specific methods: Volumetric flask method (1), Volume calculation method (2) or unknown (3)
 o Plant stage: Measuring of seedlings (=1), juveniles (=2), adults (=3) or unknown(=4)

3.2. SHOOT GROWTH FORM (including branching)

Introduction

Shoot form can be described as the canopy structure of shoots (including branching). Barkman (1988) synthesised the discussion about several systems of plant growth forms of the last 200 years, which are inconsistent and confounding. For example, growth form and life form are often used as synonyms in literature and therefore the many proposals for growth form systems are the result of the mixing of two or more combined concepts. Barkman (1988) distinguished between the important main concepts “growth form” and “life form” and gave the following definitions:

- Life form: Types of plant having the same kind of morphological and/or physiological adaptation to a certain ecological factor.
- Growth form: Types of plants with the same growth morphology or architecture (the concept is therefore free of any hypotheses about adaptation).

Many growth form classifications regard only a part of plant form or only regard specific species groups such as the system rosette plants prefer hemi-cryptophytes after Raunkiaer's definition. Old systems before the plant form systems of hydrophytes from Hartog & Segal (1964) or Sculthorpe (1967) regarded often only terrestrial plants, sometimes only herbs and grasses.

The German database BIOLFLOR (Klotz *et al.* 2002) regards several arrays of growth form and life form classifications, preferring exact definitions for all classes and uses consistent systems, but often only for one specific species group or a specific adaptation of plant. Another more pragmatically way was chosen by Cornelissen *et al.* (2003), who prefer a mixed system of growth form, life form and nutritional adaptations. Barkman (1988) made a proposal for a new consistent system of plant growth form, but that is too detailed for LEDA. To determine shoot form the LEDA Traitbase will follow a modified version of short classification systems, referred by Kleyer (1995). The categories of shoot form supplemented by the question after branching: yes or no (more details of branching classification systems see Bell (1991).

Trait definition

Shoot growth form: Shoot form describes as the canopy structure of shoots.

How and what to measure

To estimate the shoot form of each species, a nominal classification system will be used (defined by Kleyer 1995, revised and emphasised for aquatic plants by Sculthorpe 1967).

Note that the shoot of many rosette plants is very short (e.g. *Bellis perennis* up to 1 cm; Kutschera & Lichtenberger 1992), but the inflorescence is erect; therefore it would fit in category 2, stem erect.

In this classification the categories 1-4 are for terrestrial plants, 5-8 are for aquatic plants:

- | | |
|---|--|
| 1. Lianas, climbers and scramblers | (e.g. <i>Hedera helix</i>) |
| 2. Stem erect | (e.g. <i>Fagus sylvatica</i>) |
| 3. Stem ascending to prostrate | (e.g. <i>Veronica prostata</i> , <i>Calluna vulgaris</i>) |
| 4. Stem prostrate | (e.g. <i>Lysimachia nummularia</i>) |
| 5. Free-floating plants | (e.g. <i>Lemna</i> , <i>Salvinia</i> , <i>Stratiotes</i>) |
| 6. Emergent, attached to the substrate | (e.g. <i>Butomus</i> , <i>Typha</i> , <i>Glyceria</i>) |
| 7. Floating leaves, attached to the substrate | (e.g. <i>Nuphar</i> , <i>Nymphaea</i> , <i>Nymphoides</i> , <i>Luronium</i>) |
| 8. Submerged, attached to the substrate | (e.g. <i>Elodea</i> , <i>Najas</i> , <i>Isoetes</i> , <i>Vallisneria</i> , <i>Potamogeton pectinatus</i>) |

Special cases

- Species with special substratum as facultative epiphytes (e.g. *Phyllitis scolopendrium*) or nutrition's as holo- and hemi-parasites (e.g. *Orobanchae spec.*) will be categorised in the same way as well as all other species (see Fig. 3.5).



Figure 3.5. Examples of the special cases for shoot growth form *Phyllitis scolopendrium* (a) and *Orobanchae hederae* (b) (Photo: See Source list).

Minimal requirements

For any data entered into the Traitbase it is required to record the obligate fields of the general standards on the description of the sample site (i.e. georeference, habitat, method), including the size of collecting area to estimate data quality. Shoot form data obtained from greenhouse or garden experiments are only accepted when all obligate fields can be completed. In the LEDA Traitbase obligate information about the sub-trait branching is needed. The presence or absence (yes/no) of branching is possible with all shoot growth form categories.

Branching

Branching is a simple binominal trait giving information about the capacity of a plant species to fill lateral space above ground, thus it is an indicator of competitive capacity.

Most of the data on branching in the BIOPOP database incorporated in LEDA were derived from the scientific drawings in Jäger & Werner (2000). A species was classified as a branching species when lateral shoots were produced above the epicotyl and below the inflorescence. When branching was unclear it was primarily decided according to the

capacity of the species to fill lateral space, i.e. if a species is only branching above the most basal flower but the inflorescence contains photosynthetic active leaves, it is classified as branching (e.g. *Verbascum lychnitis*). Tussock grasses were regarded as branching species as well (Hegi 1998), also species able to produce vegetative parts (i.e. daughter rosettes) that grow very near to the main ramet were regarded as a branching species (e.g. *Saxifraga paniculata*).

Data structure

To collect: 1 observation per species

- Obligate:
- Type of variable: nominal in classes
 - Number of samples (n): 1 observation per species
 - Number of replicates (N): -
 - Unit: category (number)
 - Branching: yes (1), no (0)*

* The presence or absence (yes/no) of branching is possible with all shoot growth form categories.

3.3. LEAF DISTRIBUTION ALONG THE STEM

Introduction

This simple trait describes the distribution of leaves along the stem of an adult plant⁷. This trait gives information about the canopy structure of a plant, or more precise the distribution of photosynthetically active organs. Leaf distribution along the shoot also gives information on the partitioning of allocated biomass between leaves and stem (see also Niklas & Enquist 2002).

Definition: Leaf distribution along the stem is the distribution of leaves along the stem of an adult plant.

How to and what to measure

To estimate the distribution of leaves used the following six nominal categories will be used (Note that it is possible to use different categories for the same species; see also Fig. 3.6):

- | | |
|---|--|
| 1. Rosette / tufted plant above ground, above ground, in water or on the water surface (leaves concentrated near soil or water surface) | (e.g. <i>Menyanthes</i> , <i>Primula vulgaris</i> , <i>Festuca ovina</i> , <i>Trapa natans</i> , <i>Stratiotes</i>) |
| 2. Semi-rosette | (e.g. <i>Crepis spec.</i> , <i>Ajuga</i> , <i>Antennaria</i> , <i>Aegopodium</i> , <i>Pedicularis palustris</i>) |
| 3. Leaves distributed regularly along the stem * | (e.g. <i>Helianthus tuberosus</i> , <i>Origanum vulgare</i> , <i>Myriophyllum</i> and <i>Elodea</i>) |
| 4. Shoot scarcely foliated | (e.g. <i>Orobancha spec.</i> , <i>Chondrilla juncea</i>) |
| 5. Tufts and crowns, leaves concentrated as a rosette at the top of taller shoot or vegetative stem | (e.g. <i>Daphne mezereum</i> , but also <i>Trientalis</i> and trees with concentrated crowns) |
| 6. Other | (e.g. plant without obvious stems such as <i>Lemna minor</i> ; <i>Wolffia</i>) |

* Also includes multiple-stemmed shrubs or trees, winding herbs e.g. *Convolvulus*).

⁷ = more details about growth form and leaf distribution referred by Troll (1935)



Figure 3.6. Examples of some of the leaf stem distribution categories; *Lemna minor* (a), *Helianthus tuberosus* (b), *Chondrilla juncea* (c), *Daphne mezereum* (d) (Photo: see source list).

Special cases

- Species with special substratum as e.g. facultative epiphytes (e.g. *Phyllitis scolopendrium*), other supported plants (*Hedera*) or nutrition's as Holo- and Hemi parasites (e.g. *Orobancha spec.*) will be categorised in the same way as well as all other species.
- In the case of aquatic plants the leaf position is recorded.

Minimal requirements

For any data entered into the Traitbase it is required to record the obligate fields of the general standards on the description of the sample site (i.e. georeference, habitat, method), including the size of collecting area to estimate data quality. Leaf distribution data obtained from garden experiments are only accepted when all obligate fields can be completed.

Data structure

- To collect: 1 observation per species
- Obligate:
- Type of variable: nominal classes
 - Number of samples: 1 observation
 - Number of replicates: -
 - Unit: categories

4. CLONAL TRAITS

Introduction

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

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

Snap-shot quantitative data on clonal growth can be misleading because plasticity in traits concerning clonal growth is sometimes as large as differences between species.

Measurements from a single environment may be misleading as well, because they cover a

small part of plasticity of clonal growth of a given species. On the other hand, measurements from different habitats are available for very few plants. Therefore, we have to rely on less exact data, often based on observations, rather than measurements. Accordingly, we have to use nominal and coarse ordinal scales instead of metric scales suitable for quantitative measurements.

How to collect traits of clonal growth?

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

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

Individual traits

In total 8 clonal traits were selected. This selection focuses on traits potentially important for plants coping with human-induced disturbances.

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

4.1. BUD BANK - VERTICAL DISTRIBUTION

Introduction

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

After a strong disturbance affecting upper layers of the soil the depth in which organs bearing the bud bank are situated is important. For example, even if the plant is a hemicryptophyte, it may develop dormant buds on its rhizomes or roots located at a depth of several tens of cm. If a disturbance damages upper layer of the soil (by fire, ploughing, shallow land-slide or erosion of river sediments) with all buds from which the plant re-growths in spring in undisturbed conditions, it may regenerate from dormant buds on rhizomes or on roots which are located deeper in the soil (Korsmo 1930, Wehsarg 1954). Therefore, the bud bank consists not only of renewal buds but also from other buds developed on that plant. Even

root buds initiated by a disturbance should be considered, no matter that on undisturbed plants they are not present (Rauh 1937).

In our classification of bud banks we consider vertical distribution of the buds. This distribution indicates the probability of regeneration after a disturbance. For example, mowing results in a loss of biomass at about 10 cm above the soil surface. Large plants with above-ground biomass located high above the soil surface are damaged by mowing more than smaller or creeping plants. Therefore, with increasing disturbance (grazing and mowing intensity) rosette plants should be favoured (Klimeš & Klimešová 2002, Pavlů *et al.* 2003). In intensively grazed pastures and in grasslands mown by hand, above-ground plant biomass is lost by regular management. In these conditions plants with buds and biomass accumulated at the soil surface are favoured. Bud bank is usually permanent and does not much fluctuate during a year. On the other hand, the buds are not at the same stage of development during the whole year. The buds located at the soil surface may substantially differ from other buds in their development. They usually contain several initiated leaves and in some plants even a whole seasonal shoot, including an inflorescence. The renewal buds are prepared for growth at a specific time. If a disturbance takes place earlier, they may break their dormancy too, however, number of emerging leaves can be reduced and flowers aborted. In plants with a small number of buds, such as *Aconitum* species with root tubers, the shoot developing from a bud prepared for spring re-growth may substitute the shoot lost in autumn. The new tuber bearing a bud may fail to develop due to a time shortage. Instead, an axillary bud on the old tuber may develop next spring. This bud is small and not well prepared for its spring re-growth. Thus, the plant is "rejuvenated" and repeats a part of its ontogenetic development. It may take several years before the plant is able to form a large tuber with well developed over-wintering buds again. In alpine and arctic plants, organs may develop (pre-form) within buds for up to two next years. Therefore, these plants cannot response to a disturbance by appropriate morphological changes immediately, but with a delay of one or two years (Diggle 1997).

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

How to collect?

Dug plants should be carefully cleaned of soil and dead plant remains should be removed before buds are counted. The best time for the evaluation is the end of a season but in most cases after flowering or fruiting bud bank can already be evaluated. For examination of some plants magnifier or binocular microscope is needed. Some buds may be only ephemerally present on a plant (plantlets in inflorescence, turions). Thus, repeated censuses during a season may be required.

Categories bud bank vertical:

- 0 - no buds per clonal fragment
- 1-10 buds per clonal fragment
- >10 buds per clonal fragment

for layers:

- 1: <-10 cm
- 2: 0<x<-10 cm
- 3: soil surface
- 4: 0>x>10 cm
- 5: >10 cm

Example	Layer			
	<-10 cm	-10<x<0 cm	0<x<10 cm	>10 cm
Species X	0	1-10	>10	0

Special cases

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

Data structure

To collect: 1-3 observations per species

- Obligate:
- Type of variable: ordinal
 - Number of samples: 1 observation
 - Number of replicates: -
 - Unit: categories
 - Categories: (0) - no buds per clonal fragment, (1) - 1-10 buds per clonal fragment, (3) >10 buds per clonal fragment
 - Layer: (1) <-10 cm, (2) 0<x<-10 cm, (3) soil surface, (4) 0>x>10 cm, (5) >10 cm

4.2. BUD BANK – SEASONALITY

Introduction: Classification of bud banks

We suggest a broad categorisation, which reflects responses of plants to disturbance timing and frequency (Iwasa & Kubo 1997, Bellingham & Sparrow 2000). The ability to regenerate is determined by the presence of bud bank. Therefore, seasonal fluctuations in the number of buds of the bud bank are a key feature of plant's response to disturbance. As regeneration from seed banks (Thompson & Grime 1979) is in many respects similar to regeneration from bud banks, it is convenient to use similar categories. We propose to distinguish two basic types, perennial and seasonal bud banks (Fig. 4.1).

The perennial bud bank is represented by perennial plant organs (in trees the whole body, in herbs below-ground parts only) with a large number of buds, which are kept in dormancy by correlative inhibition and usually cannot disperse. The perennial bud bank resembles the permanent seed bank, but longevity of buds usually does not exceed longevity of parent individual (Table 4.1). The seasonal bud bank is represented by plant organs which are short-lived (above-ground stems of herbs, below-ground organs of pseudo-annuals), and buds developed on them are usually not as abundant as on perennial organs. Buds are kept dormant either by innate dormancy or by correlative inhibition, and some of them may naturally disperse. The seasonal bud bank resembles the transient seed bank, as the buds are not present permanently on the plant (Verburg 1998; Table 4.1).

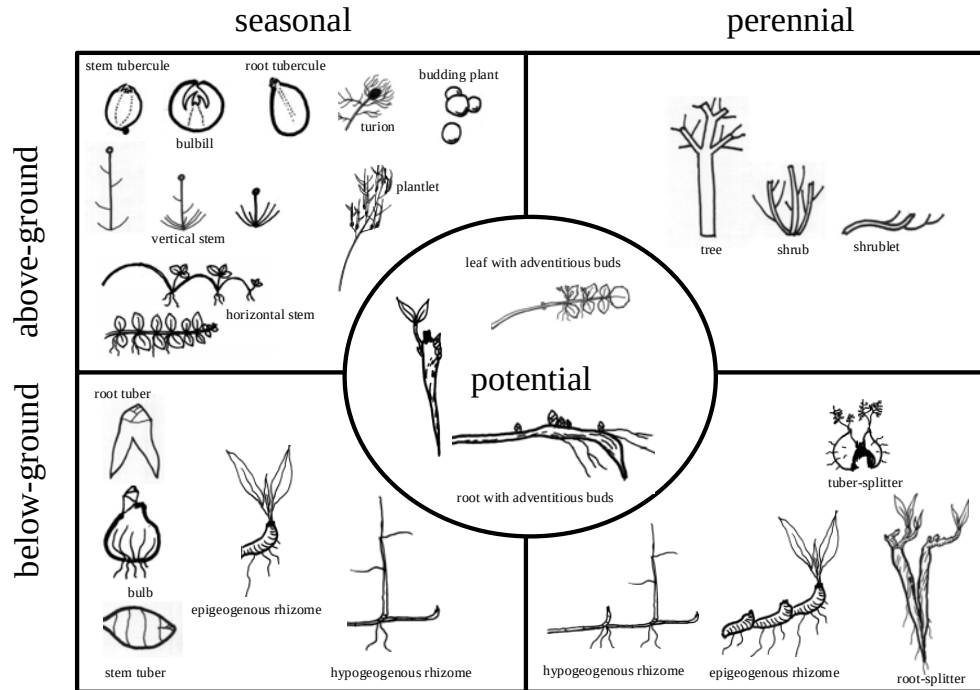


Figure 4.1. Seasonality of bud banks. Most examples represent types of clonal growth organs, as described in Figs. 4.2 and 4.3.

What to do with adventitious buds which are created only after injury and are not countable on intact plants? Functioning of adventitious buds is in many respects similar to functioning of axillary buds in the bud bank. After correlative inhibition is broken by severe injury, adventitious buds on roots have to awake from their dormancy, similarly to axillary buds on rhizomes (Horvath & Anderson 2002, Horvath *et al.* 2002). Alternatively, they may be formed *de novo*. Accordingly, we may expect a delay in the response of these newly formed buds. There are other differences: roots are usually located deeper in the soil than rhizomes and better protected against severe disturbance; formation of adventitious buds ensures regeneration from plant fragments and survival after a severe disturbance, such as ploughing (Hamdoun 1972), fire, pulling out, and cutting (Fernández-Santos *et al.* 1999); adventitious buds on roots may undertake the role of buds located on stem organs - these two are rarely combined on a single plant (Klimešová & Martínková in prep.); species which may regenerate by root-sprouting are more common in disturbed communities than in other types of vegetation (Klimešová & Klimeš in prep.).

Table 4.1. Characteristics associated with types of seasonality of bud banks.

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

These are the reasons why to consider adventitious buds on roots when classifying bud banks. We suggest to call the bud bank developed on roots after a disturbance the potential bud bank (Table 4.1).

Seasonal fluctuations in regeneration capacity from perennial and potential bud banks are not caused by a limited number of buds, but by the extent of carbon reserves.

How to assess bud bank types

Injured plants sprout from uppermost buds. Thus, disturbance severity determines which buds are used for resprouting. To assess the bud bank of a particular species, it is necessary to study buds on the whole plant. Data on buds available in floras and species trait databases are also useful (incl. Raunkiaer's life forms, placement of leaves along aerial shoots or clonal growth organs; for Central European flora see Klimeš *et al.* 1997, Jäger & Werner 2002, Klotz *et al.* 2002). None of these surrogates provides a complete information about regenerative capacity of a plant, if taken separately. A more complete picture is obtained if these sources are combined. Raunkiaer's life-forms provide information about longevity of above-ground plant parts. Placement of leaves along the aerial vertical shoot indicates placement of above-ground axillary buds, types clonal growth organs provide information about morphology of organs bearing buds, and about their longevity. A key to bud bank types is given in figure 4.1, based on categories of clonal growth organs from CLO-PLA (Klimeš *et al.* 1997, Klimeš & Klimešová 1999a). Organs responsible for clonal growth are regenerative organs, as well. Exceptions are represented by vertical stems which are not included into CLO-PLA, as they do not provide clonal growth, but they take part in vegetative regeneration. We propose to consider seasonality of the bud bank separately for above- and below-ground structures. For example, above-ground bud bank of *Potentilla anserina* is seasonal, whereas its below ground bud bank is perennial and potential.

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

Categories bud bank seasonality:

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

for layers: above- and below-ground

An example for species XY:

vertical layers	seasonality
above-ground	seasonal
below-ground	perennial & potential

Special cases

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

Data structure

To collect: 1-3 observations per species

Obligate: • Type of variable: ordinal

- Number of samples: 1 observation
- Number of replicates: -
- Unit: categories
- Categories: (1) seasonal, (2) perennial, (3) seasonal & potential, (4) perennial & potential
- Layer: (1) above-ground, (2) below-ground

4.3. CLONAL GROWTH ORGANS (GCO)

Introduction

This classification does not include categories differing quantitatively only (note that some quantitative characteristics are used as other traits of clonal growth). Categories accepted in the presented classification are hierarchical. At the highest level placement of clonal organs is considered. Origin of the organ of clonal growth is considered next. Remaining levels reflect differences in storage and size of the organ (Fig. 4.2).

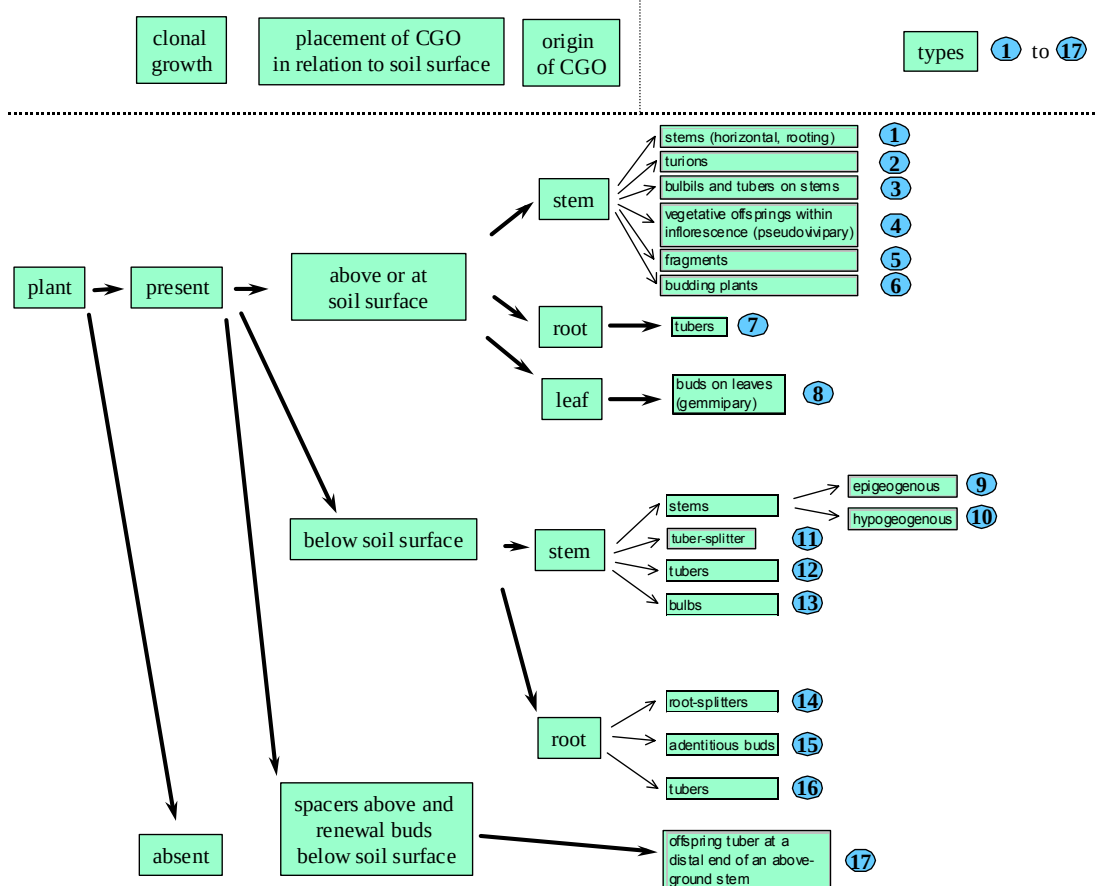


Figure 4.2. Hierarchy of 17 categories of clonal growth organs.

Root and stem origin is sometimes considered functionally equivalent. However, there are several functional differences between them. (1) Plants sprouting from roots have a high plasticity in branching frequency and their growth rate is remarkably high (Drew *et al.* 1973; Burns 1991) when compared with stem-originated organs of clonal growth (Caldwell *et al.* 1991a, b; Jackson & Caldwell 1993). (2) While roots are 'sensing' nutrient concentrations, response of rhizomes and stolons to nutrients is indirect, mediated by roots developed on

them (Passioura 1988). Moreover, (3) in plants with stolons and rhizomes, number of shoots which may appear on a stem is determined by the number of nodes. This value, multiplied by two in plants with opposite leaves, cannot be exceeded by the number of branches originated on a plant module. In contrast, buds on roots may appear simultaneously in high numbers (Peterson 1975). (4) The distance between individual buds on a stolon of rhizome is fixed soon after the buds have originated, whereas in plants with buds on roots new buds may establish between buds already present. Therefore, root sprouters may produce potentially an unlimited number of buds on their roots without producing any new root (Klimeš & Klimešová 1999b). Morphology of representative plants with different CGO's is shown in figure 4.3.

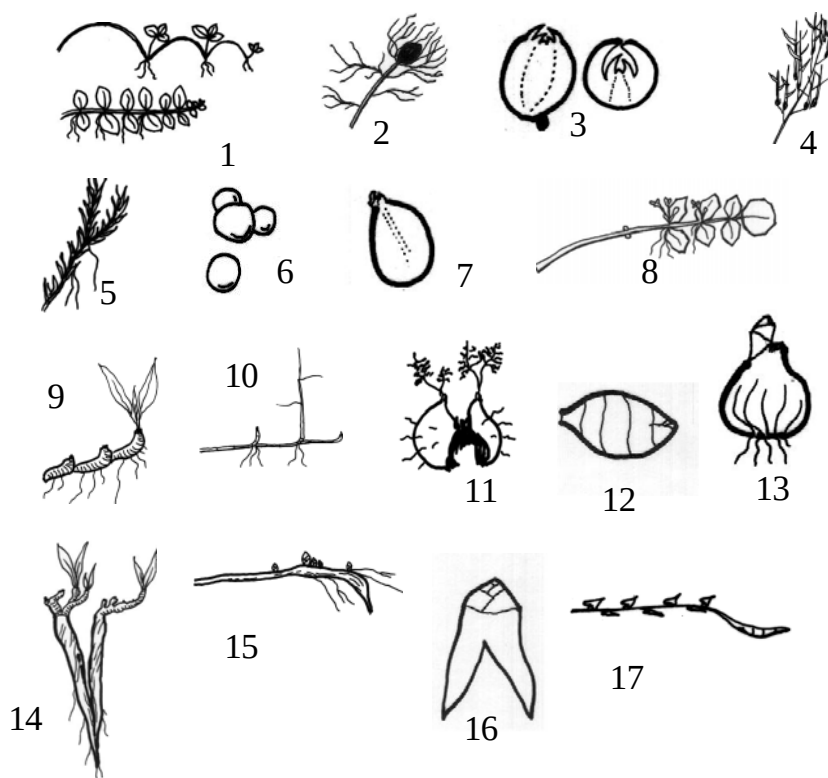


Figure 4.3. Morphology of 17 types of clonal growth organs (CGO): 1 - rooting horizontal stems at or above soil surface; 2 - turions; 3 - bulbils and tubers of stem origin at or above soil surface; 4 - plantlets (pseudovivipary); 5 - plant fragments of stem origin; 6 - budding plants; 7 - root tubers at or above soil surface; 8 - buds on leaves (gemmaipary); 9 - epigeogenous stems; 10 - hypogeogenous stems; 11 - tuber-splitters; 12 - stem tubers; 13 - bulbs; 14 - root-splitters; 15 - adventitious buds on roots; 16 - root tubers below-ground; 17 - offspring tubers at distal end of above-ground stems

How to collect?

Careful examination of the whole inter-connected clonal fragment is usually necessary, either in the field or in a laboratory. Dig up several well developed plants and select mature and older individuals on which below-ground stem structures are well developed (large inter-connected systems of ramets) and which flower/set fruits regularly. The best time for collecting is at flowering or fruiting time and in the end of a season. In the case of very large inter-connected systems partial excavation is sufficient. In plants combining several modes of clonal growth inspection of a few plants is often not sufficient because some clonal growth modes are utilised in special situations only. Therefore, it is worth to cover as broad as possible range of habitat conditions in which particular species naturally occur. Literature data are indispensable for obtaining records from various environments.

Categories CGO

1	CGO above or at soil surface	1.1	CGO of stem-origin	1.1.1	rooting horizontal stems at or above soil surface				
				1.1.2	turions				
				1.1.3	bulbils and tubers of stem origin at or above soil surface				
				1.1.4	plantlets (pseudovivipary)				
				1.1.5	plant fragments of stem origin				
				1.1.6	budding plants				
		1.2	CGO of root-origin: root tubers at or above soil surface						
			1.3	CGO of leaf-origin: buds on leaves (gemmae)					
		2	CGO below soil surface	2.1	CGO of stem-origin	2.1.1	stems	2.1.1.1	epigeogenous stems
								2.1.1.2	hypogeogenous stems
2.1.2	tuber-splitters								
2.2	CGO of root-origin			2.2.1	root-splitters				
				2.2.2	adventitious buds on roots				
2.2.3	root tubers below-ground								
3	spacers above and renewal buds below soil surface: offspring tubers at distal end of above-ground stems								

An example for species *Potentilla anserina* (it combines 3 types of CGO):

CGO1	CGO2	CGO3	CGO4
2.1.1.1.	2.2.2.	1.	

Note that

CGO1	CGO2	CGO3	CGO4
2.1.	1.		

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

Special cases

Development of some detachable vegetative units is usually strongly seasonal. Therefore, a single examination need not be sufficient for some plants. For example, aquatic plants form turions only in autumn, pseudovivipary can be observed only on flowering stems, short-lived

below-ground structures are best developed in the end of a season, as they decay in winter. Root tubers usually complete their development in summer, requiring long days, while stem tubers complete their development in autumn, when days are short.

Data structure

Type of variable: nominal

Obligatory fields to be filled in for every source:

Clonal_growth_organ

Detailed comments on identification of CGO categories

Clonal growth present/absent

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

Trees grow clonally if they sprout from roots (many species) or produce rhizomes (few species) (Del Tredici 2001). Root-sprouting trees are usually surrounded by saplings of root origin. Their below-ground root connection to parent plants indicates that these are not seedlings established from generative propagules. The saplings are distributed around the trunk but sometimes they occur beneath the whole tree crown. Spacer connecting the offspring with the parent tree is sometimes situated deep in the soil but it is usually not necessary to dig out the whole spacer because morphology of the below-ground organs indicates offspring origin. If the below-ground axis is segmented, consisting of nodes bearing scale leaves, roots and buds, and internodes, i.e., it is formed by a stem, and not by a root, offspring is of vegetative origin (Fig. 4.4). Other traits discriminating saplings of root and seed origin are visible above ground. While shaded saplings originated from seeds have about constant annual increments, vegetatively originated saplings have markedly longer first annual increments and then their growth rate slows down. They may finally develop into mature trees, but only if their parent tree dies or is heavily injured (Del Tredici 2001).

In small trees and shrubby woody plants descendants of clonal origin may reach about the same size as parent plants and they usually form clones in the form of a thicket (*Prunus spinosa*) or small wood (*Rhus typhina*, *Robinia pseudacacea*). In this case we have to find whether young shoots situated at thicket margin are linked with other shoots or not. Trees occurring closely to the border of their distribution limit grow clonally more often than in the centre of their distributional area (Koop 1987). In perennial herbs with spacer between parent and offspring plants persisting over a short period, offspring could be misidentified for seedlings. Thus, it is necessary to look at overall morphology of such seedling-like plants in detail. An example of a seedling-like root-sprouting plant *Diplotaxis muralis* is presented in figure 4.4a. Similarly, adventitious buds on leaves of *Cardamine pratensis*, plantlets produced in axils of rosette leaves of *Pinguicula* species, plantlets arising from small offspring bulbs of many bulbous species are sometimes confused with seedlings.

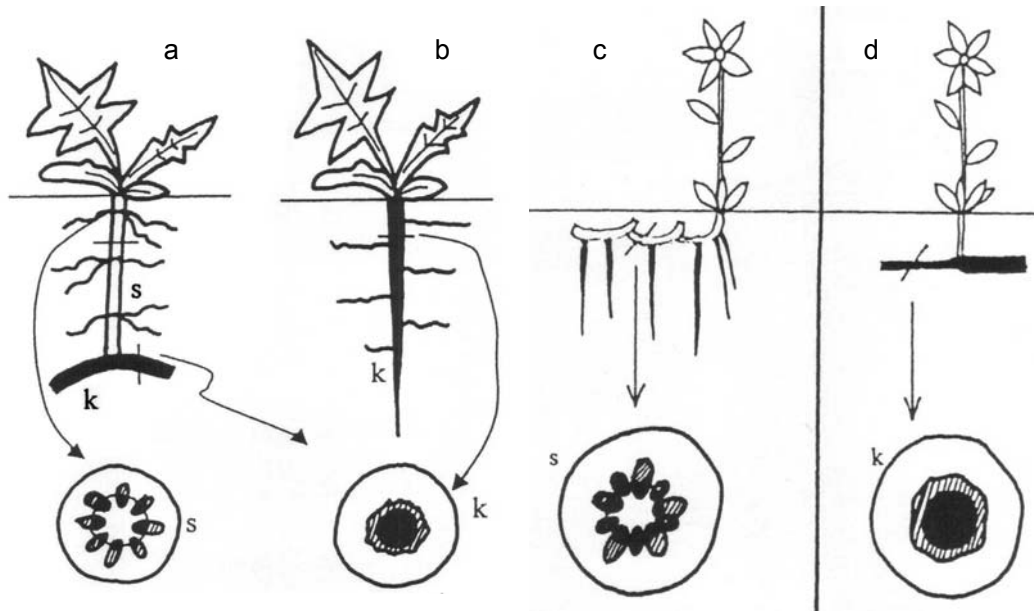


Figure 4.4. Differences between adventitious shoot (a) and seedling (b) of *Diplotaxis muralis* and the differences between the junction of a vertical leafy shoot, horizontal stem (rhizome) and adventitious roots (c) and a junction of a horizontal root and adventitious shoot (d). The arrows point to cross-sections of secondarily thickened shoot and root; full = xylem; hatched = phloem; white = parenchyma with k = root; s = shoot.

Perennial herbs and shrubs with penetrating main root and without adventitious roots are usually not considered as clonal. However, if they reach sufficient age, their main root may split into several independent fragments (root-splitters). Similar effect may be observed in plants with perennial tuber (tuber-splitters) (Lukasiewicz 1962, Schenk 1999).

Clonal growth of short-lived plants is also often overlooked. Among aquatic plants we can find several annuals which grow clonally (*Trapa natans*; Groth *et al.* 1996). Some terrestrial short-lived plants, such as *Barbarea vulgaris* or *Rorippa palustris*, may grow clonally if their habitat is neither disturbed, nor overgrown by perennials (Klimešová 2003).

Origin of CGO: stem/root/leaf

Most CGOs are of stem origin. The stem forms a natural axis of the whole plants and other organs are initiated on it. At nodes it produces leaves, buds and sometimes also roots. From the viewpoint of clonal growth the buds are crucial because all shoots (offspring produced by clonal growth, ramets) originate as buds. Roots and leaves may also serve as CGOs, if buds are formed on them adventitiously (Holm 1925, Rauh 1937).

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

In unclear cases anatomical structure should be assessed to decide the origin of the below-ground organ (Fig. 4.4b). On cross-section of a root vascular bundle is in the centre, whereas

in stems, vascular tissue forms a hollow cylinder. Root tubers differ from stem tubers by the absence of nodes and internodes. Stem tubers may bear remains of leaves or leaf scales and bud is usually at terminal position. Root tubers are usually smooth, often branched, and their bud need not be terminal. In the case of small organs, tuber anatomy should be examined on cross-sections using a microscope. On stem tubers we can find a central cylinder, the tissue of a bud at the tip of the tuber is not separated from the tissue of the tuber. On cross-sections of root tubers we do not see the central cylinder, the tissue of the bud at the tip of the tuber is clearly separated from the tissue of the tuber. If the main storage tissue is formed by scale leaves of the bud, rather than by a root or stem, then we call this vegetative diaspore a bulbil; we put it to CGOs of stem origin (Troll 1937-1941, Wagenitz 1996).

Leaves may serve as CGOs if they form adventitious buds (*Drosera rotundifolia* - Domin 1925; *Cardamine pratensis* - Hansen 1881) or if they transform into a stem (*Utricularia* sp. div.; Arber 1920). These cases are often not readily observable in the field because they appear transiently or are induced by injury. Therefore, it is desirable to pay attention to the surrounding of the target plants, and to ground and fallen leaves.

4.4. ROLE OF CGO IN PLANT GROWTH

Introduction

Some plants require some CGOs for their survival; such CGOs are necessary. An additive CGO is initiated by some environmental conditions, such as high nutrient availability or low competition strength. A CGO which is formed after an injury only and does not occur on intact plants, is regenerative. This classification was developed by Wittrock (1884), who used it to classify root-sprouting plants. Knowledge of the role of CGO in plant growth is useful when predicting behaviour of plants in stressful and disturbed environments. For example, plants of *Achillea millefolium* producing long hypogeogenous rhizomes in abandoned meadows do not develop them in regularly mown meadows and produces epigeogenous rhizomes only. These are less efficient in horizontal spreading. Other species sprout from roots in special conditions only or after being injured (Rauh 1937). This trait characterises individual CGO. In clonal plants utilising a single mode of clonal growth it is applicable to species as well.

How to collect?

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

Data structure

Type of variable: nominal

Obligatory fields to be filled in for every source:

CGO_role

Input data

- none,
- regenerative,
- additive,
- necessary.

References

Wittrock 1884; Rauh 1937

4.5. LIFE-SPAN OF A SHOOT (SHOOT CYCLICITY)

Introduction

This corresponds to the traditional distinction between monocyclic, dicyclic and polycyclic shoots. We define the life-span of a shoot as a duration of a small life-cycle sensu Rabotnov, i.e. from sprouting of a bud, through the growth, flowering and fruiting of the shoot, until its death. This trait is relatively easily applicable on sympodially growing and root-sprouting plants. In monopodial plants the apical shoot is vegetative and potentially immortal. Lateral shoots may flower, however, in some cases they are formed by a single flower so that it has little sense to consider their life-span.

Life-span of a shoot may differ between individual CGO. Some types of clonal growth result in offspring shoots which are considerably smaller in comparison with the parent shoot. Therefore, their development is slower and longer until first flowering. For example, branching of *Dentaria bulbifera* rhizomes results in offspring shoots capable of flowering in the first year of their life, if environmental conditions are favourable. In contrast, offspring shoots originated from bulbils on stems of parent plants are similar to seedlings in size and require several years before they flower.

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

How to collect?

Observation of marked shoots over their life-span is the best and most reliable source of information about shoot cyclicity. In some cases indirect evidence can be utilised: If a clonal fragment bears both sterile and fertile shoots then its shoots are usually di- or polycyclic. If all shoots are of the same size and developmental stage, and there is a larger renewed bud on the perennating organ, the shoots are usually monocyclic.

Special cases

There are plants with all shoots at the same developmental stage not only within a plant individual, but even in the whole population or across distributional area. Still, they do not have monocyclic shoots; their shoots are polycyclic, synchronised in their development.

Data structure

Type of variable: ordinal

Obligatory fields to be filled in for every source:

Shoot_cyclicity

Input data

- 1 year (monocyclic),
- >1 year (dicyclic and polycyclic).

4.6. PERSISTENCE OF CONNECTION BETWEEN PARENT AND OFFSPRING SHOOTS

Introduction

Individual clonal growth organs may differ in persistence of spacers connecting parent and offspring ramets (Jónsdóttir & Watson 1997, Oborny *et al.* 2000). They either split into physically and physiologically independent units after a short time (splitters) or remain inter-connected for a long time (integrators). For example, offspring plants developed on stolons of *Fragaria vesca* separate from the parent plant after first season already, however, offspring plants initiated by branching of rhizome of the same plant remain inter-connected for many years. This trait indicates for which time are offspring ramets potentially supported by resources from their parent ramet and for which time spreading of systemic enemies through the inter-connected clonal system is possible (Jónsdóttir & Watson 1997). The shorter

persistence of the interconnection is, the lower is the amount of storage for initiation of its growth and the slower is the initial growth of the offspring ramet (Klimeš & Klimešová 1999b). The three categories which we suggest separate (1) ephemeral connection between e.g. bulbils and parent plant, (2) offspring plants developed on stolons which remain inter-connected with the parent plant for one to two seasons, and (3) pairs of parent and offspring ramets inter-connected for a longer period, often up to several decades. This trait characterises individual CGO. In clonal plants utilising a single mode of clonal growth it is applicable to species as well.

How to collect?

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

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

Special cases

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

Data structure

Type of variable: ordinal

Obligatory fields to be filled in for every source:

Persistence_connection

Input data

- <1 year
- 1-2 years
- >2 years

4.7. NUMBER OF OFFSPRING SHOOTS/PARENT SHOOT/YEAR

Introduction

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

How to collect?

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

Special cases

In sympodially growing plants which branch after flowering, the parent shoot is regularly replaced by an offspring shoot. This process does not result in multiplication. In contrast, in monopodially growing shoots, branching implies multiplication, as parent shoots may survive and continue their growth. It follows from this difference that, if the number of offspring per parent shoot per year of a monopodially growing plant is <1 , numerous descendant may arise in the course of several years.

Data structure

Type of variable: ordinal

Obligatory fields to be filled in for every source:

Offspring

Input data

... are coded by 1 to 4:

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

4.8. LATERAL SPREAD/YEAR

Introduction

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

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

How to collect?

Annual increments of a plant are often recognizable as repeating structures along a horizontal stem. For example, in plants which flower every year, remains of flowering shoots may mark annual increments. In monopodially growing epigeogenous stems, thicker parts are produced in summer and thinner ones in spring and autumn (*Rumex alpinus*, *Alchemilla monticola*). In sympodially growing plants with perennial rhizome and one generation of shoots per season, annual increments can be estimated by measuring the length of a horizontal shoot increment (*Polygonatum multiflorum*). If several values are at disposal for a given species and locality, modal value should be used as input data.

Special cases

In some pseudo-annuals and plants with short-lived above-ground horizontal stems this trait can be evaluated during a short time period only because after offspring is established the parent plant dies and the spacer between them eventually decays as well. Difficulties arise when evaluating lateral spread of root-sprouting plants. Adventitious shoots can easily be

established on older roots and annual increments cannot be easily evaluated on roots. Moreover, after an initial expansion of the root system perennial root-sprouters start to produce shoots from the base of established shoots and stop their lateral spreading. In this case we recommend to find remnants of this-year and last-year adventitious shoots and to measure distance between them.

This trait should not be confused with the distance between offspring ramets or the distance between parent and offspring ramets.

Data structure

Type of variable: ordinal

Obligatory fields to be filled in for every source:

Lateral_spread

Input data

- <0.01 m,
- 0.01–0.25 m,
- >0.25 m,
- dispersable diaspores (covered within dispersability traits)

5. SEED TRAITS

The seed traits included in the LEDA Traitbase are seed number per shoot (including seed production and shedding period), seed weight, seed shape, and seed longevity.

5.1. SEED NUMBER PER SHOOT

Introduction

Seed number is an important functional trait in understanding regeneration strategies, abundance and dynamics of plant species after for instance disturbance and is often correlated with other traits such as seed size and seedling size (Shipley & Dion 1992). The existence of trade-offs between seed number and seed size for a given reproduction allocation was examined by Leishman (2001). Seed production is a highly variable trait and is very sensitive to, for instance site and climatic conditions or predators (Aksoy *et al.* 1998, Salisbury 1942, Harper 1977, Weiner 1988, Lovett Doust & Lovett Doust 1988, Kelly & Sork 2002). The seed production of a species also varies with the different life stages (Harper 1977, Begon 1993). The mean seed number per ramet increased with the ramet biomass (Escarre & Thompson 1991) and also increased within the same species with the plant size (Niklas 1994). Additionally, seed production may exhibit periodic cycles, for example the mast years of some tree species, which may be an endogenous fixed phenomenon (Silvertown & Lovett Doust 1993; see also Period of seed production).

Seed densities (and as far as known spore densities) are highest in frequently disturbed habitats such as arable fields, and lowest in primary forest (Silvertown & Lovett Doust 1993). In the case of aggressive invaders after disturbance the relationship between seed (or spore) production and vegetative reproduction depends on the stage of succession (i.e. *Pteridium aquilinum*; Korpelainen 1995). To estimate the potential of seed production you need the optimal species-species conditions in the field.

Trait definition

Seed number: Is defined as the total seed (or spore) production (filled and unfilled seeds) per ramet/shoot of a species.

In the LEDA Traitbase the seed (or spore) number is measured per shoot⁸ or ramet. Weiher *et al.* (1999) defined a ramet as an iteration of the basic form of a plant with obvious

⁸ = In the cases of clonal species shoot is defined as the same as ramet (Kleyer 1995).

connections to other ramets that would clearly unify the parts into one iteration. With this definition we should be able to identify the following examples as individuals:

1. Multiple stemmed shrubs and trees (e.g. *Vaccinium corymbosum*, *Erica tetralix*; Fig. 5.1)
2. Ramets of clonal species with stolons (e.g. *Agrostis stolonifera*, *Carex arenaria* (Fig. 5.1), *Glechoma hederacea*) or rhizomes (e.g. *Typha latifolia*)
3. Ramets of clonal species with root sprouting ability (e.g. *Robinia pseudacacia*, *Prunus spinosa*).
4. Ramets of tussock-forming graminoids (e.g. *Dactylis glomerata*, but also perennial *Juncus* spec. with pectinate-forming tussocks) pose somewhat of a problem in that the tussock acts as a functional unit in terms of holding space (see Eriksson & Jakobsson 1998).



Figure 5.1. Two examples of seed number one for multiple shoots (*Erica tetralix*; a), and one for clonal species (*Carex arenaria*; b).

What and how to collect

In general three levels of seed/ spore number are used:

- Per inflorescence or per fertile frond (in the case of horsetails per fertile shoot/stem)
- Per ramet or shoot
- Per square metre (only useful in relation to plant population biology)

For the LEDA Traitbase only the seed number per shoot (ramet) will be measured, but seed number per inflorescence or per square metre obtained from published sources will be accepted as optional measurements.

In agreement to the upper definitions of “ramet” and “individual” three levels on sampling focuses decided: For non-clonal plants the individual (= the genet) is appropriate; for clonal plants, ramets are probably most appropriate; and in the case of tussock plants, whole tussock may be most appropriate to be sampled (see Fig. 5.2). In total a minimum of 10 inflorescences per species should be collected at a sample site, with as a collecting rule, one inflorescence per shoot from a representative randomly selected healthy individual. When multiple inflorescences are present on the sampled shoot, the total number of inflorescences of that shoot should be counted to be able to determine (or estimate) the total seed number per shoot (see Measurements). Note that measurements of seed production the sampling should take place under optimal species-specific habitat conditions, for instance, shade tolerant species should not be collected from sunny places. In case of rare species in Northwest Europe a minimum of 3 inflorescences should be selected per defined search area. Note that for orchids only published data sets will be used in the LEDA Traitbase.

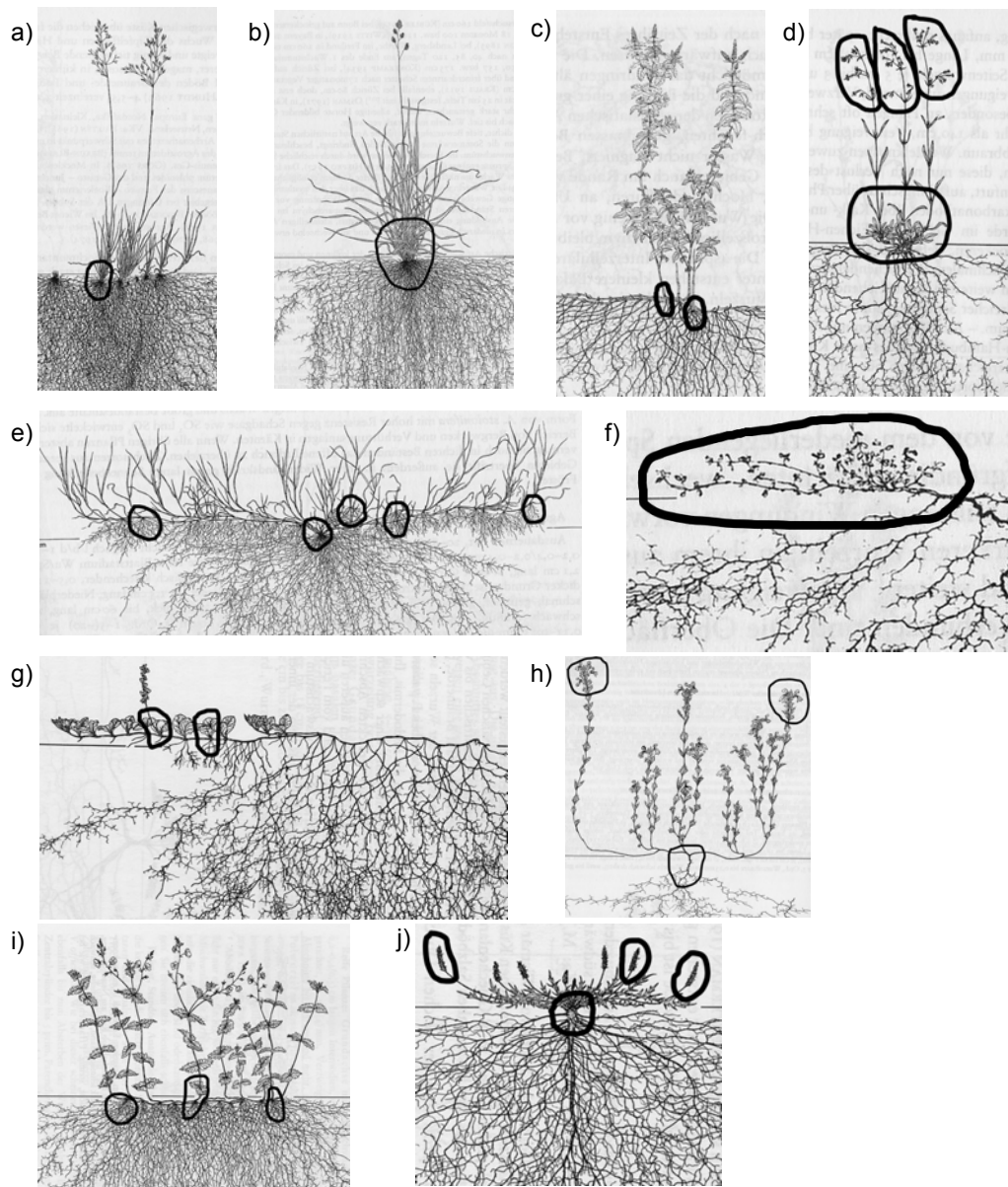


Figure 5.2. What to collect for seed number per shoot or ramet. Black circles in drawings of different species mark the functional unit (i.e. individual) to be collected for seed number (the inflorescences marked are to distinguish between seed number per inflorescence and seed number per ramet/shoot). Examples of different shoots are: (a) *Agrostis tenuis* with loosely short below-ground stem, (b) *Dactylis glomerata* is very compact ramet group (often with many inflorescences) that is defined as one functional unit, (c) *Mentha longifolia* a clonal species with clearly defined shoots, (d) *Silene nutans* a semi-rosette plant with a branched shoot and one main root, which is defined as one functional unit with several inflorescences (e) *Agrostis stolonifera* with large expanded lateral above-ground stems (5 ramets marked) and different root points. (f) *Thymus pulegioides* a prostrate branched dwarf shrub with one central root, (f) *Veronica officinalis* a perennial herb with large expanded lateral above-ground stems and different root points, (g) *Euphrasia nemorosa* a branched annual hemiparasit with many inflorescence stems and one central root (seasonal ecotypes are typical for this genus), (h) *Veronica chamaedrys* a perennial herb with a loosely below-ground stem and clear defined shoots (i) *Plantago coronopus* a rosette plant with many inflorescences and one central root. (Kutschera & Lichtenegger 1982, 1992, modified by Kunzmann).

Storing and processing

Each collected inflorescence should be put into a separate dry paper bag and stored dry at room temperature. When using a 'seed counting machine' the seeds should be cleaned, e.g. by using a seed-cleaning machine to separate the seeds from the awns, pappus or adnate fruit bodies.

How to measure

In general there are several methods used to determine the seed number:

1. *Counting method*: In this method the seed number of all inflorescence present on the shoot/ramet are counted (most exact method, but time consuming).
2. *Counting and estimation method*: This method is used when only one inflorescence is collected per shoot. After the seeds of the collected inflorescence are counted, the number of seed per shoot/ramet is estimated by multiplying the seed number per inflorescence with the number of total inflorescences counted per shoot. For example to determine the seed production of tussock grasses (e.g. *Festuca ovina* s.l.) 3-5 inflorescences per tussock (and count the total number of inflorescences) should be collected and the seeds counted after which seed production is extrapolated to the whole tussock. Five replicates are used to compare the range between tussocks. For special cases as *Agrostis stolonifera* all inflorescences in 1 square metre are collected with 3 replicates at least (s. measuring) as an option, for replication standards (see also Shipley & Dion 1992).
3. *Counting and weighing method*: This method of seed number estimation is often used by forestry ecologists, agricultural scientists and plant population biologists. This method uses the value of the total weight of a counted number of seeds (e.g. 50, 100 seeds per batch, $N=5$), divided by the number of weighed seeds to estimate the seed production of the whole plant.
4. *Total weight of seed production*: Forestry scientists to estimate the crop of forest trees often used this method. It is easy, to get published data of seed mass or weight and the number of seeds per tree. The mean seed weight value was used to get a seed number of total weight of seed production.

To save time it is helpful to use a seed counting machine, note, however, that the seeds have to be cleaned thoroughly before the machine is able to count the seeds. For very small seeds a stereoscope with counting grid ocular should be used (method 1 and 2). In the case of number of spores LEDA will use only published data (see also Special cases).

Special cases and sampling methodology

In several cases extrapolated data are necessary, because the measurement of seed/spore production is more complicated, often with more time exposure:

- *Tussock grasses*: These produce a lot of tillers with inflorescences - use method 2.
- *Mature trees and shrubs ≥ 4 m*: For high trees or shrubs with bigger diaspores another method is used. The seed production is calculated per seed or fruit number lying upon the soil surface under the tree crown. Finely woven gauze is put underneath the tree as a 'seed trap' and all diaspores that fall down are caught in the seed collecting net (e.g. *Fraxinus excelsior*; Gardner 1977). The cover from a crown of the tree is calculated in m^2 and the sum of seed production per shoot is estimated (Note that some tree species (e.g. *Quercus*) have periodic mast years with various periodicity). Old individuals of *Quercus robur* produced up to 90.000 acorns per shoot (50.000 acorns in average) in mast years (Jones 1959, Crawley & Long 1995). The estimation of seed production of higher trees (i.e. *Populus*, *Salix*) with wind-dispersed many-seeded capsules is much more difficult. In this case, collect three twigs/branches and count the seeds of ten catkins from each twig. On the next step count the number of catkins of each twig and estimate the seed production per twig. At last count the twigs of an individual and estimate the seed production per tree. For each species estimate 3-5 random selected mature trees per defined search area.

- *Mature trees and shrubs < 4 m*: The same method as used for the higher trees can be used. There are more effective methods to count trees or shrubs with fruits (e.g. *Sambucus nigra*, Atkinson & Atkinson 2002). For instance by calculating the weight of 10 diaspores of 5-10 different individuals (=bush/tree) per species. For example *Sambucus nigra* will have one seed per fruit, but in the case of *Vaccinium myrtillus* on average 25 seeds per berry can be found (Eriksson & Fröberg 1996). The total harvested fruit crop per bush or tree will be weighed and the seed number estimated per bush or tree by calculating the mean weight of fruits. For each species estimate 5-10 randomly selected mature shrubs or trees per defined search area.
- *Spore number of ferns, clubmosses or horsetails*: In the case of Pteridophyta (ferns, clubmosses or horsetails) only published data sets will be used. When raw data of spore numbers would be available, the following standardised approach should be followed: Collect 3-5 fertile fronds with spores or other spore-bearing structures, per shoot per defined search area. It is helpful to put the frond with spores on a bigger dry filter paper for some hours. In this time, the frond has died out and the spores are dispersed on paper. To count the spore production of ferns a microscope is needed due to spore size ($\leq 30 \mu\text{m}$), and the counting is more difficult as many are produced (e.g. *Pteridium aquilinum* - 300.000.000 spores/single frond; Cody & Crompton 1975). When counting use a spore number use filter paper with a grid and count the number per cm^2 (5 replicates) and then estimate the production for the whole frond. In most cases Pteridophytes have single shoots/stems/fronds and often extensively rhizomes or grow as a rosette hemicryptophyte with several leaves/fronds and a short rhizome. The spore number of horsetails (*Equisetum*) is count by spore number per shoot (sporophyte). In this case it is the same as spore number by inflorescence, because there is only one cone per sterile stem. Normally, horsetails have extensive rhizomes with many shoots. In the same way ferns are estimated (e.g. *Pteridium aquilinum*, *Polypodium*, *Cystopteris*) because the fertile frond grows as a single shoot from the larger rhizome. Count the spore number of heterosporous quillwort (genus *Isoetes*), an underwater rosette hemicryptophyte, as spore number per shoot. Many ferns are rosette hemicryptophytes with several (sterile and/or fertile) fronds per shoot (short rhizome) (i.e. *Dryopteris*, *Polystichum*, *Matteuccia*). So you can distinguish between counting the spore number per fertile frond and the spore number per shoot.

It should be noted that the methods of seed number counting/estimation mentioned in this section are a choice of species-specific examples. As seed size, seed morphology, and dispersal mechanism between plant species are highly various is essential to accept other species-specific methodologies to estimate the seed number in the best way (see Minimal requirements).

Minimal requirements

Seed number per shoot is obtained through measurement and/or estimation and therefore data sets from literature or other sources can not be accepted when the number of replicates and the standard deviation or standard error are not present.

If the methods used in published data are not clear, the seed production of a species can only be assigned to a minimum/maximum range or as a field observation (see General standards). Any data entry of a single observation without information of the habitat counted as a mean value. Seed number is a measured (or estimated) trait with many species-specific options for collecting, processing and measuring. Measurements (unpublished data) need to follow the standardised protocol with all described options and other species-specific methods, with mean or the median with the standard deviation or with standard error as an end result. In the case of published and unpublished data LEDA accepted the unknown of replicates or numbers of a record as a single observation, entered as a mean. The lack of information on any of the obligate points mentioned above will result in rejection of the data. For any data entered into the Traitbase it is required to record the obligate fields of the general standards on the description of the sample site (i.e. georeference, habitat, method), including the size of collecting area to estimate data quality. Data obtained from greenhouse or garden experiments are only accepted when all obligate fields can be completed.

Data structure

- To collect: 1 inflorescence of 10 different individuals = 10 inflorescences in total per species (per sample site)
- Obligate:
- Type of variable: numerical
 - Number of individuals per sample (n): 10
 - Number of replicates (N): 1
 - Unit: seed number/shoot or ramet
 - Values; N-number, min., max. median, quartile, mean, standard deviation, Standard error
 - Reproduction unit: Measured per inflorescence (= 1), per shoot or ramet (= 2), or per m² (= 3)
 - Trait specific measurements: counting (1), counting and estimation (2), counting and weighing (3), total weight of seed production (4), unknown (5)
 - Validity range: 0-500.000.000 in cases (a) and (b), 0-5.000.000.000 in case (c)
- Optional:
- o Seed viability: percentage of total seed production

5.1.1. PERIOD OF SEED PRODUCTION & SEED SHEDDING: Additional traits to seed production per shoot

For the trait seed production two obligate additional features or helper-traits are useful, namely period of seed production and seed shedding.

Additional trait definition

Period of seed production: Describes the frequency of generative reproduction cycles over time, in other words how often species produce seeds in a certain time period (= seed crop frequency; Silvertown & Lovett Doust 1993).

Seed shedding: Is the time and duration of seed releasing.

Note: Period of Seed production in this case does not mean the percentage seed set, as seed set is defined as the fraction of ovules developing into seeds.

Note: Additionally information on the seed viability could be entered as an optional choice in the Traits base. This includes additional information about the proportion of viable seeds expressed in percentage per total seed/spore production from the total seed production.

PERIOD OF SEED PRODUCTION

The period of seed production is of importance for the time in which genets are replaced within a population. The frequency of (annual or interannual) seed production of a species also determines the dispersal in space and time (e.g. to refill the seed bank). Combined with seed number, seed crop frequency could be a weighed measure for annual seed production of a species in a sample area.

The period of seed production (or seed crop frequency) is a trait of reproduction capacity, e.g. as an expression of the time ratio to allocated biomass in growth versus in reproduction (Harper 1977). Pluriennial species allocate biomass in their vegetative growth (e.g. big rosettes, long central roots) often for several years, and die after the only once reproduction at the end of their life time (e.g. *Agave*; Harper 1977).

A special case of interannual seed crop (variation) is the mast fruiting of perennial plants, especially known from trees and some shrubs. Masting is defined as (synchronous) intermittent of seed production of large crops by a population of plants (Koenig & Knops 2000). Herrera *et al.* (1998) criticised the term masting or fruiting mast, because it appeared to be too difficult to classify species as either masting or non-masting species, as well as to define mast years and non-mast years among a masting species in an objective way. However, studies of many long time datasets of trees and shrubs has shown that wind-pollinated and predator-dispersed species have a higher variation of annual seed production as biotically pollinated and fructivore-dispersal species, compared by the coefficient of variation (Herrera *et al.* 1998, Kelly & Sork 2002). Kelly & Sork (2002) understand masting as an adaptive reproductive trait overlaid on the direct influence of weather, i.e. trees in cold

climatic conditions produce high level of seed crops only between several years without or low levels of seed crops.

Another phenomenon is the seed crop frequency of annuals and perennials. Populations of *Poa annua*, a (pseudo)annual grass, produced multiple variable seed crops within different stages of their life-cycle and also in multiple plant generations within a year (Begon *et al.* 1997). Also ramets of the perennial herb *Rumex acetosella* produced flowers and seeds several times within a year (Escarre & Thompson 1991).

A combination of seed number and life span with seed crop frequency could be given the total seed production of an individual plant as also population level of each species (excl. annual variation). Period of seed production can be described in two levels, per individual and per population, sometimes with different results for the same species (see Table 4.2). An individual of a biennial species for e.g., produce only once time in his two-year life-cycle seeds. But an established population of the same biennial species produce seeds yearly, reasoned by their mixed life stages. In the rule, to understand the reproductive capacity of a species it is more important to focus the individual level. But to estimate the total seed production of a species per sample area in a year or to understand the (synchronous) mast years of trees or pluriennials, investigations of the population level are necessary.

Table 4.2. Aggregated categories to describe the seed crop frequency per species on the individual level as also on population level.

Period of seed production*	Per individual/ramet	Per population
Multiple times (1)	perennial herbs, some annuals	annuals, perennials
Annually (2)	annuals, perennials	annuals, biennials, pluriennials, perennials
Two years (incl. mast fruiting) (3)	biennials, some perennials (trees)	biennials, pluriennials, some perennials (trees)
More than two years (incl. Mast fruiting) (4)	pluriennials, some perennials (trees, shrubs, some geophytes)	pluriennials, some perennials (trees, shrubs, some geophytes)

* Note that the categories including mast fruiting do not distinguish between different levels of masting.

What to collect

Data on the period of seed production will be mainly obtained from literature and will be recorded as frequency interval (i.e. within a year). Note, that the aggregation categories in table 4.2 of the period of seed production will be used as one option output-form of the LEDA Traitbase. The 'Biological Flora of the British Isles' describes for many plant species, how often seed is set over the time. Instead of the discussion in favour or against the mast fruiting concept, the LEDA Traitbase provides information about the phenomenon masting in two columns; in the period of seed production column (1) you get information about the period of seed production within a year and/or over multiple years, and in the column mast years (2) is noted if a given species is marked as a masting species in literature.

Data structure

- Obligate:
- Type of variable: numerical (output: numerical or ordinal)
 - Unit: numbers and years
 - Trait specific method: 0 = unknown, 1 = observation per individual, 2 = observation per population
 - Masting perennial species: masting (1); non masting (2) or unknown (3), not applicable (0)
 - Differentiation between seed production per generation and per plant: Annuals with more than one generation per year (1); seasonal ecotypes with different flowering times (2); perennials with more than one flowering/fruiting time per year (3); unknown (4), not applicable for all other cases (0)

SEED SHEDDING

Seed shedding can be described as the process after seed ripening and before seed dispersed, processes that in many plant species overlap in time. Seed shedding is an

additional trait that has close functional relations to seed number, period of seed production, seed size, seed dispersal and seed bank longevity.

Seed shedding has two dimensions, defined as the time and duration of the seed releasing, i.e. which months of the year are the seeds shed (=time) and how long is the timespan of seed shedding (=duration; Harper 1977; Bonn & Poschlod 1998).

The releasing of seeds in different species can occur in a very short time span (i.e. days) up to periods of several months in low sequences (Harper 1977). The course of seed shedding is influenced by physiological processes and structural organisation of fruit ripening and seed detachment, more so than by direct environmental forces (Harper 1977, Kjellsson 1985).

What are advantages (and disadvantages) of a species-specific seed shedding season and duration in a year? For instance dispersal of certain seeds can be an advantage during high frequencies of strong winds in autumn, but also in hot summer periods with thermic events or thunderstorms (Kunzmann 2000). Early seed ripening and releasing in the year can be also an advantage to escape higher vegetation, responsible for breaking the wind in the vegetation period. The synchronous presentation of ripe fleshy-fruits within bird migration is referred to by Bonn & Poschlod (1998).

The timespan of seed shedding is also different between the species. For instance fast seed shedding can be a defence to pre-dispersal predation (Harper 1977), on the other hand other species flower and produce seeds near all the year in Britain (*Poa annua*, *Senecio vulgaris*; Harper 1977). Releasing periods in myrmecochorous guilds are restricted to the foraging season of the seed-dispersing ants, for e.g. only 2 days in *Scilla bifolia* (Fig. 5.3; Kunzmann 1993) or 11 days in *Melica uniflora* (Kjellsson 1985). One example of long-time seed shedding is the wind-dispersed Compositae *Carlina vulgaris*, where seed releasing begins in October up to April next year, almost continuous (Fig. 5.3; Kunzmann 2000). Kjellsson (1985) distinguished cumulative curve-types of quantitative seed fall over time in dependence on their dispersal type, e.g. a hyperbolic curve in case of ant-dispersed *Melica uniflora* or a linear curve in case of wind-dispersed *Luzula multiflora*.



Figure 5.3. The short-term seed-releasing species *Scilla bifolia* (a) and long-term seed-releaser *Carlina vulgaris* (b) (Photo source: see Source list).

What to collect

Seed shedding is an interval trait, expressed in the first and the last month of seed shedding. There are three different options to collect records for this trait:

1. Use of published and unpublished sources (e.g. flora's or the Biological Flora of British Isles).
2. Observations during investigations of other traits as seed number or seed size. Only the season and the time space were or will be noted.
3. Species-specific or interspecific studies of seed shedding and of primary seed fall (e.g. use records of trap experiments to investigate dispersal of diaspores).

(Note, that sometimes a secondary seed fall of a species in a trap could change the estimated record of seed shedding. It is also important to check the evidence of trap experiments, based

only on few seeds, very critical. For e.g. of long-time seed shedding species, use only the time span, in which 95 % of quantitative seed fall was found in traps, since the beginning of the individual seed shedding).

In all cases three options described above, the first and the last month of seed shedding will be noted. In general each record with an unknown number of replicates will be collected as one single observation. In the case of species-specific studies (option 3) the number of replicates is generally known. For any data entered into the Traitbase it is possible to make an obligate qualifier about the known or unknown of number of individuals and the number of samples (for e.g. to compare populations). For new measurements (option 3) the one sample per species (per sample site) is collected consisting of data of 10 individuals, with a preferred number of 30 individuals. A second important obligate qualifier is to know if the species is flowering and fruiting more than once a year (see Table 4.2). This is interesting for many perennial species, but also for annuals with seasonal ecotypes, for e.g. *Rhinanthus*, *Euphrasia* (Zopfi 1993a,b, 1997).

Note, that the duration of seed shedding per individual is in most cases much shorter than duration of seed shedding per population, depending on their local environmental conditions or to their genetic disposition (e.g. *Scilla bifolia* Kunzmann 1993; *Salix spec.* Karrenberg *et al.* 2002).

Data structure

- Obligate:
- Type of variable: numerical, interval (ranges)
 - Unit: months, numbers
 - Values: range from first to last month of seed shedding season (January = 1 - December = 12)
 - Number of individuals per population (sample size (N)): 10 (0 for unknown)
 - Number replicates (N): 1
 - Number of different flowering/fruiting times: once a year (1) or more than once a year (2), unknown (0)
 - Trait specific method: observation per individual (1), observation per population (2), unknown (0)
- Optional:
- o Real time span of seed shedding within time space, expressed in weeks, unknown (=0)
 - o Unit: weeks

5.2. SEED WEIGHT & SEED SHAPE

Introduction

A wide range of seed weight can be found across species reaching from less than 10^{-6} to more than 10^4 g (Harper 1977). Through a better provision of nutrients, large seeds are thought to have a superior chance in establishing as seedlings (Salisbury 1942, Grime *et al.* 1988). This suggestion gets support from several investigations, either from analysing correlations between seed mass and habitat conditions (Hodkinson *et al.* 1998) or from seedling experiments (e.g. Dalling & Hubbell 2002, Leishman & Westoby 1994a, 1994b, Saverimuttu & Westoby 1996, but see Paz *et al.* 1999). For a set of plants of the British flora Thompson *et al.* (1993) found that seed size does predict persistence in soil but Leishman & Westoby (1998) could not find the same results for the Australian flora. There are several ways to measure seed weight that differ in the way what to measure (the seed s. str., the reserve mass, the dispersal unit) and the method for drying the seed prior to weighing (airdried, oven dried with different temperatures and for different durations). In LEDA seed weight is the air dried weight of (preferable) 100 germinules or dispersules that were collected from 10 individual plants of a species at one site.

In the same way as seed size, seed shape is also an important predictor for seed longevity in the soil (Thompson *et al.* 1993) and one can imagine that it might also be important for the ability of a seed to swim or to get dispersed by the wind. An easily obtainable measure for

seed shape is the one proposed by Thompson et al. (1993). The shape (V_s) is captured by dividing length, width and height of a seed separately by length and then calculating the variance of the three values: $V_s = \Sigma (x - \bar{x})^2/n$ with $n = 3$ and $x = \text{length}/\text{length}; \text{height}/\text{length}; \text{width}/\text{length}$. The minimum value of V_s is 0 in perfectly spherical seeds and the maximum values range between 0.2 and 0.3 in needle- or disc-shaped seeds.

Trait definition

Seed weight: Is the air dried weight of (preferable) 100 germinules or dispersules.

Seed shape: Is the variance of the three dimensions length, width and height, dividing each dimension by length so that length is unity.

What and how to collect

A number of 100 seeds collected from 10 different plants is the preferred standard for collecting seeds for seed weight and shape (see also Fig. 5.4). If this is not feasible, e.g. because the sampled species is scarce, at least 25 seeds from 5 different individual plants of a species are collected. It might be necessary to extend the number of seeds when species tend to have very small seeds (e.g. Orchids). When heteromorphism (see below) occurs 100 seeds have to be collected for each heteromorphic class.

The best time for collection of the seeds is obviously the time of seed maturity. In several cases this point of time might be difficult to define. Clues are attributes like the colour of the seeds or the capsules containing the seeds, the strength of the attachment of the seeds or capsules to the plant and developmental stages of additional seed structures (e.g. pappus).

Date and location of the collection has to be noted with each population sampled and the sample of each plant is kept separately. Each sample can thus be attached to a corresponding individual and the individuals to the corresponding population.

Although it is quite a subjective decision, average sized seeds of a plant should be collected rather than very small and very big ones (Cornelissen et al. 2003). Also one should be careful that no parts of the seeds that belong to the dispersule get lost while collecting because this would avoid to measure the proper unit. The collected seeds of each plant are kept in dry paper bags. Because it is necessary to weigh the mass including appendages it is not recommended to put the seeds into a seed cleaning machine in general.

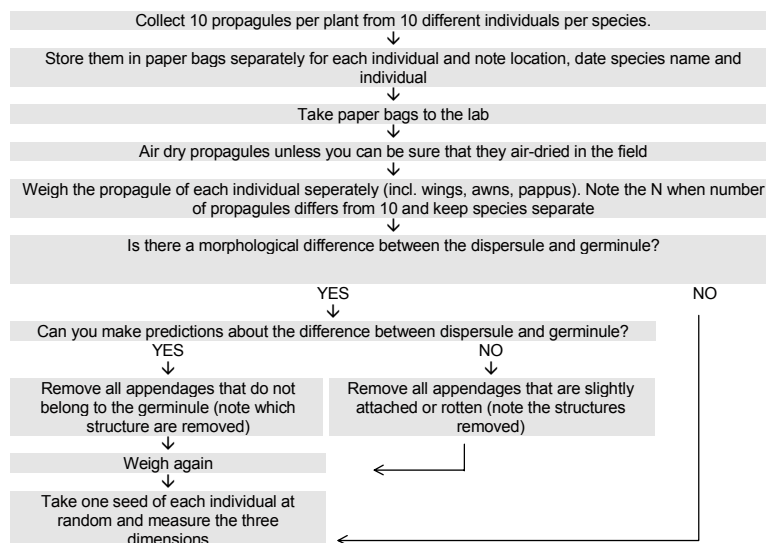


Figure 5.4. Work procedure to be followed for accurate data measurements of seed weight and shape.

What to measure

Seed weight

If seeds were collected in natural populations both dispersules and germinules are measured following the subsequent procedure:

1. Collected seeds are air dried prior to the measurements.
2. Weigh 10 dispersules of each individual separately including appendage(s). If the number of dispersules differs from 10 note N. Make sure to keep the dispersules separated per individual after weighing!
3. Remove all structures that do not belong to the germinule, i.e. all parts that easily fall off or are likely to decay (Keep in mind that the germinule is the unit that enters the soil). If there are no morphological differences between dispersule and germinule directly proceed to measure length, height and width.
4. Note the structures that have been removed according to the categorisation.
5. Weigh again and still keep the seeds separated per individual for measuring seed shape.

The measured unit is milligrams (mg) and the used scales have to display at least three decimal digits.

Seed shape

For each dimension the mean of 5 seeds is noted to calculate the shape index. If possible these 5 seeds are drawn by chance from the same seeds that were used to measure seed weight, each seed from one single individual.

The shape (V_s) is captured by dividing length, width and height of a seed separately by length and then calculating the variance of the three values: $V_s = \sum (x - \bar{x})^2 / n$ with $n = 3$ and $x = \text{length/length}; \text{height/length}; \text{width/length}$. The minimum value of V_s is 0 in perfectly spherical seeds and the maximum values range between 0.2 and 0.3 in needle- or disc-shaped seeds.

The length of a seed is regarded as the longest dimension, no matter if it is equivalent to the morphological length. For instance the propagules in some *Caryophyllaceae* are described as wider than long in identification keys but length should be measured on what is here regarded as width, i.e. the longest axis that can be found in the seed.

The width is defined as the widest axis perpendicular to the length axis. Height (sometimes regarded as thickness) is the shortest axis perpendicular to the length axis and perpendicular to the width axis. The unit for all of the three measured dimensions is millimetres (mm).

Further remarks on the measuring of seed length, width and height were made by Otto (2002) when drawing up the BIOLFLOR database; In trigonous seeds (e.g. *Carex* and *Polygonum* species) the widest of the three sides is taken into account for the width value while the mean of the remaining two sides are considered as height. Width axis and height axis are not perpendicular in such seeds.

Appendages extending from the seed in a direction more or less parallel to the length axis are taken into consideration when measuring the length but the same appendages do not contribute to the width (e.g. perigone of *Scabiosa*) while hairs and spines clearly sticking out are added to the width.



Figure 5.5. Trigonous seed of *Persicaria hydropiper* (source Bioimages 2003)

For small seeds a binocular microscope with a measuring ocular is used so that the number of decimal digits can be maximised. Length, width and height can also be measured with a calliper rule but not with normal rulers because the latter do not make it possible to obtain decimal digits.

As for the removal of structures before weighting the seeds it is necessary to record information on the structures that were removed after measuring the dispersule to measure the germinule.

Special cases

When seeds can not be collected in natural habitats, e.g. because the species is very scarce, collection of seed material follows the subsequent priority:

1. Mature seeds of natural origin from seed lists of botanical gardens
2. Mature seeds from wild plants grown in cultivation (seed commerces)
3. Mature seeds of unknown origin from seed lists of botanical gardens or seed commerces

Seeds from botanical gardens and seed commerces mostly can not be assigned to individual plants and thus all seeds must be weighed at once and be divided by the total number of the seeds to obtain the mean weight. The sample size thus becomes 100 in such cases.

When deriving data for seed weight and seed shape from published literature some further problems might occur. In most cases no means for different individuals are given and sometimes even no sample size. Also it is possible that only a range is given by a maximum and a minimum value.

Data structure

To collect: 10 seeds of 10 different individuals = 100 seeds in total per species (per site)

- Obligate:
- Type of variable: numerical, integer, decimal
 - Sample size (n): 10
 - Number of replicates (N): 10
 - Unit: mg (weight), mm (length, width, height), unitless (shape)
 - Values: mean, standard variation, standard error
 - Validity ranges: 10^{-6} - 10^4 (weight), 0.1-100 (length, width, height), 0.001-0.3 (shape)
 - Collection date: day/month/year (dd.mm.yy)
 - Reference system: see general standards

5.3. SEED LONGEVITY

Introduction

Buried viable seed banks are a fundamental aspect of seed plant biology. They play an important role in the conservation and restoration of plant communities (Bakker 1989), and are important predictors of plant response to changing land use and climate (Hodgson & Grime 1990). However, the information on seed/germinule/dispersule/fruit survival in the soil is scattered and for many plant species still unknown. The LEDA project will make an attempt to fill the gaps in this knowledge by means of recent literature compilation (after 1992), field experiments and through the use of correlations with other seed attributes in this database like seed weight and shape).

LEDA adopted three types of soil seed banks (Thompson et al. 1997, Thompson 1993, Poschlod & Jackel 1993, Thompson 1992, Bakker et al. 1991, Bakker 1989), namely:

- Transient: species with seeds that persist in the soil for less than one year, often much less
- Short-term persistent: species with seeds that persist in the soil for at least one year, but less than five years
- Long-term persistent: species with seeds that persist in the soil for at least five years

Formalised classification can be achieved by application of the key to seed bank types (Figure 5.6). The key applies only to naturally buried seeds and to data of the most common type, that is, an enumeration of seeds in soil sampled on a single occasion. The key uses both direct and indirect evidence of longevity, but gives priority to direct evidence. The key

deals with the small quantity of incompletely or inadequately described vegetation by assuming that all species in the seed bank are also present in the vegetation. Any species in the vegetation but not detected in the seed bank is considered to be transient.

When using seasonal sampling without subdivision by depth, the key is incapable of distinguishing short-term from long-term persistent, and all persistent species will be allocated to the short-term persistent category. The same is true for sampling in frequently disturbed areas such as agricultural fields or urban areas, even when different layers are sampled. Due to this disturbance the depth distribution of the seeds is disturbed and the 'general rule' that deeper buried seeds are older, can not be applied. Only with additional information on management (i.e. when last disturbed) and the vegetation history of the site, the species can be distinguished between short- and long-term persistence. For example, when a species is found in the soil seed bank that is absent from the vegetation for over 4 years, it can be assumed to be long-term persistent. Or when an agricultural field is not ploughed for over four years, it can be assumed that the viable seeds found in the deeper layers are long-term persistent. When information on management and /or the vegetation is absent, the solution is to allocate all persistent species to the short-term persistent category. The guiding principle in dealing with all data sources is to use the data if at all possible, while making the fewest assumptions and using the 'present' category only as a last resort.

Data collection and admissibility

In all data sets that have attributed one or two buried seeds will be excluded (possible consequences of contamination or recent dispersal). In order to apply this criterion we had to know exactly how many seeds of each species were actually recovered. The most frequent single reason for rejecting data was an inability to discover this information, usually because it was impossible to work out the actual area sampled. Some classic papers had to be omitted on account of this problem (e.g. Milton 1948).

Other frequent causes of rejection were: burial experiments conducted for too short a period (often measured only in months); data for two or more sites, treatments or taxa pooled; data presented only as frequencies or graphs; species identification poor, e.g. only to genus. For example the classic paper of Van Altena and Minderhoud (1972), describing the established vegetation and seed bank of over 70 meadows, could not be used since all data were condensed to frequencies.

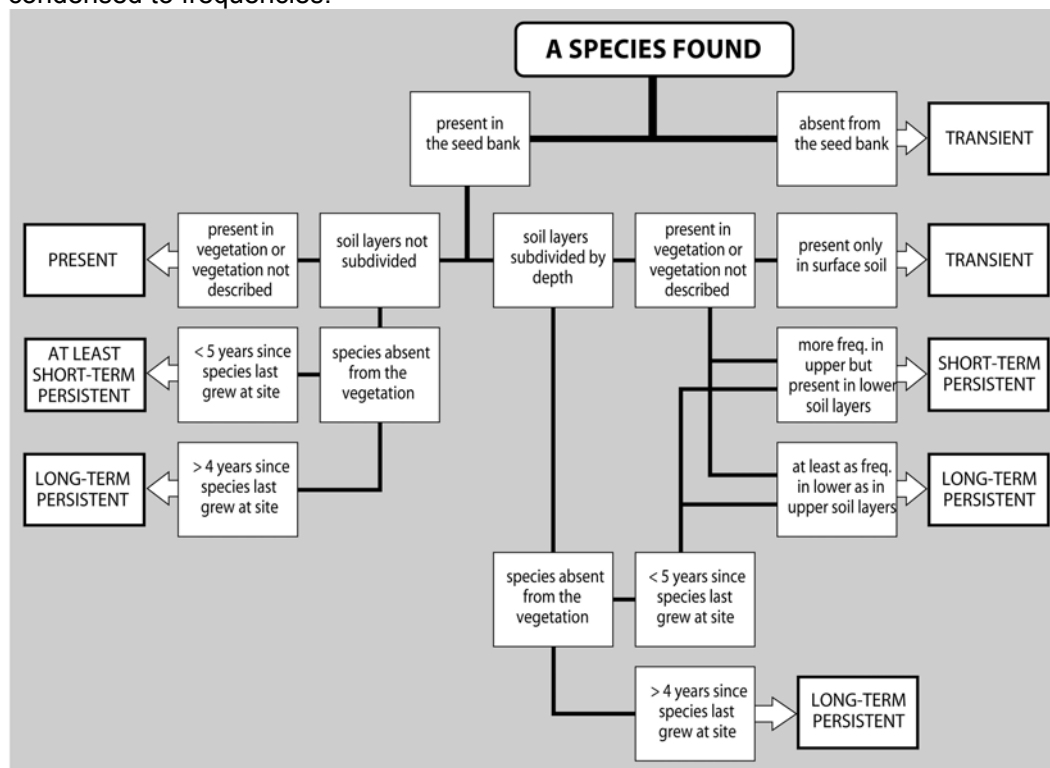


Figure 5.6. Key to allocate species a seed bank classification (Thompson *et al.* 1997).

The second most frequent cause of rejection was that no attempt was made to determine the viability of seeds extracted from soil. Much has been written on the relative merits of extraction or germination of seeds from soil samples (e.g. Gross 1990), but germination has the undeniable advantage of guaranteeing that the seeds recovered are alive. Symonides (1978) found that fewer than 10% of seeds of some species extracted from the seed bank were capable of germination. It therefore seemed prudent to reject data where no effort was made to determine if seeds extracted from the soil were viable. Germination, staining with tetrazolium and a firm or white embryo is all accepted as evidence of viability. Some of the problems we encountered are a consequence of the inevitable condensation of large amounts of data necessary to meet the demands of journal editors. A further difficulty we encountered was inconsistency between methods and results. For every source we attempted to work out if the methods as described could have produced the stated results. To give a simplified and hypothetical example, if a total area of 0.1 m² of soil was sampled, and the data expressed on an m⁻² basis, then (a) the minimum possible density was 10, and (b) all densities should be multiples of 10. Surprisingly frequently, calculations of this sort revealed data which could not have been obtained from the methods as described. Wherever possible, we tried to correct methodological problems or abbreviated data by contacting the authors. Following up publications in this way sometimes led us to useful unpublished data. Inevitably, however, some problems remained unresolved and the sources had to be rejected.

Minimal requirements

<i>Trail number</i>	Every separate sample, in a particular reference for which separate information is provided, is given a number. Hence the trail number is each separate experiment or site or individual on which different replicate measurements are performed. This can be, for example, samples from separate sites or the same site where on more than one occasion the seed bank was sampled. The trial number is the key identifier between the reference and the data in the database and is obligatory information.
<i>Seed bank method</i>	The method used to sample the seed bank is obligatory information. In the LEDA Traitbase seven categories of seed bank sample method can be chosen: 1. Seeds deliberately buried in a garden plot without subsequent disturbance 2. Seeds deliberately buried in a garden plot with subsequent disturbance 3. Seeds deliberately buried in the field 4. Soil sample from natural vegetation, seeds extracted and germination or viability tested (includes methods involving any reduction of sample volume, other than just discarding part of sample) 5. Soil sample from natural vegetation, seeds germinated without extraction or sample reduction 6. Same as 5, but germination in the field (e.g. first season after sod-cutting or topsoil removal, only individuals with cotyledons) 7. Sequential sampling of natural seed banks on at least 6 occasions per year. (If <6, each sampling date is treated like a separate trail, add details in comments column) NOTE: Data from experiments that extract seeds from soil but do not assess germinability or viability should be <u>ignored</u>.
<i>Area unit</i>	Is the unit in which the data is expressed. The categories for the unit expression are: 1. inch² 2. M² 3. acre 4. foot² 5. cm² 6. hectare (ha)
<i>Area expressed</i>	Is the component in which the data actually expressed with the actual volume that is sampled per sample core (e.g. 0.2m ² or 722 cm ²) and is expressed as a number with 4 decimals (expressed in the area unit).
<i>N</i>	Number of cores sampled per within one trial (i.e. 10 cores are seen as 10 replicate for that particular trail).
<i>Area sampled</i>	Is the total area that is sampled per trail - For example in a site 60 cores are taken using a core of 8.55 cm², resulting in a total of 513.179cm² soil sampled. NOTE: If area sampled is not given or cannot be calculated, the data should be ignored.
<i>Sample depth</i>	Is the total sampling depth cm, and expressed as a number with 1 decimal.
<i>Number of layers</i>	This is number of separate layers for which data are reported, not necessarily the number actually examined, i.e. the number of separate layers tested for seeds, expressed as integer.
<i>Thickness top layer</i>	Thickness of top layer, including litter (if any) in cm. expressed as a number with 1 decimal. This is top layer as actually analysed and ideally the top layer should be as close as possible to 5 cm. Therefore it may actually be two layers combined.
<i>Sample month</i>	For seasonal sampling expressed as a number (Month 1-12), with the value 0 if no seasonal information is given. NOTE: The months are numbered July-June in Southern hemisphere.
<i>Duration</i>	Length of time (in months) for which germination of buried seeds is continued, expressed as number of months.

<i>Actual density</i>	Seed density expressed as the actual seed numbers found (i.e. as given in the reference). The species where only one or two seeds were found will be omitted as being a possible consequence of contamination or recent dispersal. Expressed as a number with 1 decimal.
<i>Density per m2</i>	Density (re)calculated into seed number per square meter (i.e. density), using the entries in density, area unit, area expressed and area sampled. An algorithm needs to calculate this and store this information in the database. This information will be used for output and higher aggregation levels. Seed density per square meter will be expressed in a rounded number (no decimals).
<i>Max longevity</i>	This is the maximum length of time (in years) that the species has survived in the soil. This field is employed when the seeds are definitely known not to have survived any longer, i.e. in burial experiments where the seeds did not survive as long as the experiment (< 1 year is 0). Expressed as the number of years (integer).
<i>Max possible longevity</i>	This field is employed where the conditions above do not apply, i.e. the remaining data from artificial burial experiments, plus all longevity data from naturally buried seeds. Expressed as text, i.e. >2, >5 in years (> + integer).
<i>Seed bank present</i>	Are seeds of species present in soil? 1. Yes 0. No NOTE: In general avoid data where vegetation is not described, however if it is not known, we assume it is.
<i>Layer distribution</i>	1. At least as frequent in lower soil layers as in upper layers 2. More frequent in upper soil layers but present in lower layers 3. Present only in upper soil layers NOTE: This is question 4 in the seed bank key (see figure 2.1) where the upper soil layers refers to top 5cm or the nearest practical approximation). For example: A seed bank is sampled in three layers; 0-2cm, 2-4cm and 4-6cm. In this case the upper layer will be the combination of the first 2 sampled layers (0-2 and 2-4 cm). For the sake of comparison of densities the data of 4-6cm layer were multiplied by two thus becoming the deeper layer.
<i>Vegetation present</i>	Is species present in vegetation? 1. Yes 0. No
<i>Last occurrence</i>	When was the species last seen in the vegetation? 1. > four years since species last grew at site 0. < five years since species last grew at site, or time since species last grew at site unknown NOTE: This is question 5 in the seed bank key of figure 2.1.
<i>Seed bank type</i>	Is the conclusion of the key in Figure 2.1: 1. transient 2. short-term persistent 3. long-term persistent 4. present (this category represents low quality data and is not included in higher aggregation levels!)
<i>Comments</i>	Space to add treatments, age of a site, differences between trials etc. as a text of maximal 100 characters

Soil seed bank sampling protocol

A summarised protocol of seed bank sampling largely follows the points mentioned by Ter Heerdt et al. (1996), who used a combined method of concentrating soil samples and germination in the glasshouse. Depending on the aim of the study one should take the following points into account:

1. Use a preliminary study of the vegetation and soil seed bank to get an impression of the composition of the seed bank and to learn to identify the seedlings as soon as possible. This study should also provide insights into the abundance, distribution and patchiness of the species present. The space needed in the glasshouse can be estimated at this stage. Favourable germination conditions of many species can be derived from the literature. (see Hodgson et al. 1995, Baskin & Baskin 1998).
2. Deciding whether the species found are persistent or transient is much simpler if at least two layers of soil are sampled separately.
3. To avoid stratification problems, collect soil samples in early spring. Natural stratification has already taken place in the field.
4. Wash the soil samples with water on a coarse sieve to remove roots, pebbles etc., and on a fine sieve to remove all clay and silt. A mesh size of 0.2 mm will retain seeds of most species.
5. Spread the concentrated sample on a sterilised medium in a layer as thin as possible, and certainly not thicker than 5 mm. Preferably add on top of the medium a thin layer of sterile white sand to mark the border between medium and sample, to be able to sort the remainder of the sample after germination has stopped.
6. If germination is carried out in a glasshouse or open cage, prepare control trays to record contamination by wind-borne seeds (see Fig. 5.7).
7. Remove emerging seedlings as soon as possible. When germination has stopped, we recommend further disturbance of the sample to enable seeds deeper in the sample to germinate. Keep a careful watch for signs of herbivore activity and take appropriate action if any are seen.
8. Presence of remaining seeds should be checked with a seed separation method followed by hand-sorting (see 5 also).
9. Try to give a complete description of the vegetation where the soil samples were taken.
10. Adequate replication is essential in order to be able to perform any statistics on the data. Degree of replication will depend on the density and patchiness of the seed bank. Pooling of small individual cores into larger samples is advocated both for statistical reasons and for ease of handling. Small cores are often easier if the soil is stony.



Figure 5.7. Sample equipment used for soil seed bank sampling (a, b) and seedling emergence of seed bank samples in the greenhouse (c).

Preferred field sampling protocol:

Select ten squares of homogeneous vegetation (at least 2x2 m each, preferably 5x5m). Remove the litter layer. Sample ten cores to a depth of 10cm from each square and subdivide each core in a 0-5 cm and 5-10 cm layer (corer 4 cm, diameter). Pool each of ten samples per square per layer. Concentrate samples on a sieve of 0.2 mm and analyse samples according to the seedling emergence method under standard conditions with plenty of light and water. Include control trays to monitor contamination. Sort (part) of the remainder

after germination has stopped for ungerminated seed. Provide a vegetation description of each of the ten plots to enable seed bank classification.

Data structure

Data characteristic	Format	Unit	Validity range	Level
Trail number	number	-	1-99	obligate
Method	category (number)	-		obligate
Area unit	category (number)			obligate
Area expressed	number	cm ² , m ² ... (matching area unit)		obligate
Area sampled	number	cm ² , m ² ... (matching area unit)		obligate
Sample depth	number	cm	1-100	obligate
Number of layers	number	-	0-20	obligate
Thickness top layer	number	cm	0-20	obligate
Sample month	number	-	0-12	obligate
Duration	number	months	1-36	obligate
Actual density	number		0-10 ⁶	obligate
Density/m ²	number	Seeds/m ²	0-10 ⁶	obligate
Max longevity	number	Years	1-200	obligate
Max possible longevity	text	Years		obligate
Seed bank present	category (number)			obligate
Layer distribution	category (number)			obligate
Vegetation present	category (number)			obligate
Last occurrence	category (number)			obligate
Seed bank type	category (number)			obligate

5.4. MORPHOLOGY DISPERSAL UNIT

Introduction

Seed dispersal influences many key aspects of the biology of plants, including spread of invasive species, metapopulation dynamics, and diversity and dynamics in plant communities, but is inherently hard to measure (Cain *et al.* 2000). The morphology of the dispersal unit can be in this perspective be of importance as the dispersal mode(s) of species can often be recognized by morphological characteristics of fruits and seeds. For example, wings or panicles for wind dispersal, release mechanisms for explosive dispersal, sweet or nutritive fruit pulp for dispersal by frugivorous animals, nutritive nuts for dispersal by granivorous animals, adhesive structures for dispersal in furs, and airy tissues for dispersal by water (see Fig. 5.8; Van der Pijl 1982).

Trait definition

Morphology dispersal unit: Defined by the assignment to one or more of the following categories: nutrient rich appendages or structures (subcategories elaiosome, aril, pulp), elongated appendages (subcategories hairs, pappus, prickles and thorns, hooks, awns), plain appendages, balloon structures, no obvious appendages.

How and what to collect

Because morphology of dispersal unit is an observational trait no strict instructions for collecting are made. In general the dispersules that are checked for their morphological structures should be the same that were collected for one of the measured seed traits. These dispersules have to be checked for their morphology anyway because the structures that the dispersule was weighed with have to be defined.

What to measure

The morphology of the seeds will be recorded from literature sources or from observations. For the LEDA project 6 seed morphology categories, with several sub-categories, will be used (see also Fig. 5.8):

Morphological type categories	Sub-categories
1	Nutrient rich structures

	a	elaiosome			
	b	aril			
	c	pulp			
2	Elongated appendages	a ₁₋₃ hooky b ₁₋₃ stiff structures c ₁₋₃ long structures d ₁₋₃ many structures	or	non-hooky smooth structures short structures few structures	unknown unknown unknown unknown
3	Flat appendages	a large structures b small structures			
4	Balloon structures	a +/- closed structures b +/- open structures			
5	No appendages	a diaspores with structured surface b diaspores with smooth surface			
6	Other specialisations				

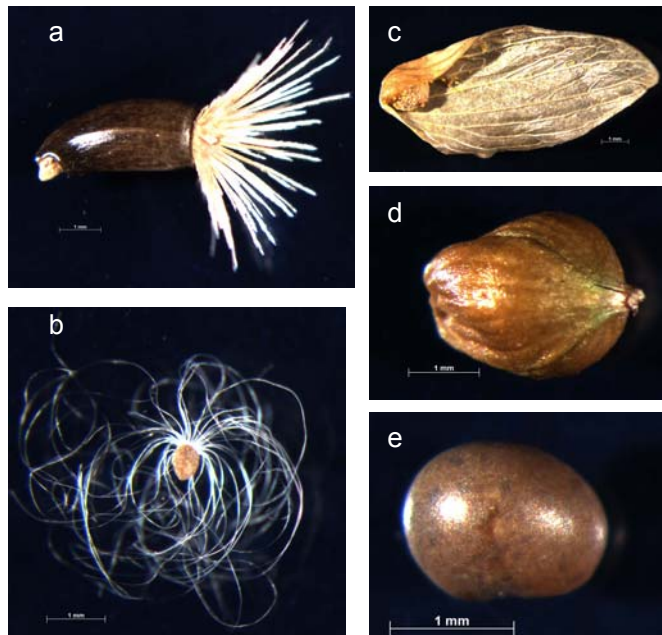


Figure 5.8. Some examples of the different seed morphology categories are (a) *Centaurea scabiosa* (pappus- bristles), (b) *Epilobium tetragonum* (long hairs), (c) *Humulus lupulus* (flat appendage), (d) *Carex alba* (balloon structure), and (e) *Lotus corniculatus* (no specialised structures) (Photo's: UREG).

Special cases

In some species, the intra-individual variation, often occurring within the same infructescence, is tremendous and different types (or morphs) of seeds or fruits can be defined (Table 5.1). This variation is associated with heteromorphism, which is an example of phenotypic variation as it refers to within-individual variation. Therefore, seed heteromorphism can be defined as the production of different types of seeds by one single individual (Imbert 2002). For most species classified as seed heteromorphic, the differentiation among morphs is obvious. For instance, the variation of achene shape in *Calendula* sp. is a well-known example of heterocarpy, and in many *Calendula* species (*C. arvensis*, *C. stellata* for instance), three or four achene morphs are present (Heyn et al. 1974). However, plant species commonly show intra-individual variation in seed size, either mass or length. This variation can also be observed for other structures as pappus or wing. Therefore, the distinction between continuous variation and heteromorphism can be difficult.

Table 5.1. Systematic repartition of heterocarpic species (Mabberley 1997 from Imbert 2002).

Family ¹	No. species	No. genera	Species example
Apiaceae	3	3	<i>Torilis nodosa</i>
Asteraceae	138	52	<i>Senecio jacobaea</i> , <i>Tragopogon dubius</i>
Brassicaceae	12	8	<i>Cakile maritima</i> , <i>Sinapis alba</i>
Carvophyllaceae	11	2	<i>Spergularia marina</i> , <i>Spergularia echinosperma</i>
Chenopodiaceae	18	10	<i>Atriplex patula</i> , <i>Salicornia europaea</i>
Cistaceae	4	1	<i>Cistus creticus</i>
Commelinaceae	1	1	<i>Commelina benghalensis</i>
Euphorbiaceae	1	1	<i>Croton setigerus</i>
Fabaceae	5	5	<i>Pisum fulvum</i> , <i>Vicia sativa</i> subsp. <i>amphicarpa</i>
Eumariaceae	1	1	<i>Ceratocarpus heterocarpus</i>
Nyctaginaceae	9	1	<i>Abronia latifolia</i>
Papaveraceae	2	2	<i>Glaucium flavum</i> , <i>Platystemon californicus</i>
Plantaginaceae	1	1	<i>Plantago coronopus</i>
Poaceae	7	7	<i>Agrostis hyemalis</i> , <i>Echinochloa crus-galli</i>
Polygonaceae	1	1	<i>Emex spinosa</i>
Rubiaceae	1	1	<i>Asperula arvensis</i>
Thymelaceae	1	1	<i>Thymelea velutina</i>
Valerianaceae	2	1	<i>Fedia cornucopiae</i>
TOTAL	218	99	

¹ A detailed list of heteromorphous species from the families can be found in the appendix of Imbert (2002).

For LEDA the seed heteromorphism categories are derived from Otto (2002) and consist of a combination of heteromorphism type (A to L) and class within the heteromorphism type (1 to 4). For instance the species *Atriplex sagittata* can have seeds with the heteromorphism type G with class 1, 2, 3 or 4, which will place them in the category G1, G2, G3 and G4.

Type	Class 1	Class 2	Class 3	Class 4	Example species
A	Fruit: middle or disc of the infructescence	Fruit: edge of the infructescence			<i>Bidens cernua</i>
B	Upper (part of) fruit	Lower (part of) fruit			<i>Rapistrum perenne</i>
C	Seed without wings	Seed with wings			
D	Flat or biconvex germinule	Triangular germinule			<i>Persicaria hydropiper</i>
E	Eruciform fruit with wings	Eurciform fruits without wings	Fruit with hook	Cymbocarpous or fruit with flying device	<i>Calendula arvensis</i>
F	Black seed	Brown seed			<i>Chenopodium album</i>
G	Black germinule / ~ with perigone	Black germinule / ~ with prophyll	Red-brownish or smaller brown germinule / ~ with prophyll	Yellow-brownish or bigger brown germinule / ~ with prophyll	<i>Atriplex sagittata</i>
H	Glume fruit	Part of infructescence			<i>Bromus tectorum</i>
I	Glume fruit with long awn	Glume fruit with short awn			<i>Bromus japonicus</i>
J	Calyx bidentate	Calyx tridentate			<i>Eryngium campestre</i>
K	Early formed black seed/fruit	Late formed yellow-brownish seed/fruit			-
L	No information on type depending metric data				-
X	Not heteromorphous				<i>Holcus mollis</i>

6. DISPERSABILITY TRAITS

General introduction

Seed dispersal, or the transport of seeds away from a parent plant, is an important process in the regeneration of most of the higher plants. Its evolutionary importance is illustrated by the mechanisms and structures of plants that promote seed dispersal. Seed dispersal is advantageous to plants when it enhances seed survival and increases reproductive success, and it may do so in various ways. First, dispersal reduces the risk of distance- or density-dependent mortality. Second, seed dispersal theoretically enhances a plant's chance to place seeds in suitable establishment sites. Third, dispersal may improve germination when it involves passage through the gut of animals. Other possible advantages of seed dispersal are colonization, area extension, and gene flow.

Plant species often have more than one dispersal mode and seeds of all species might be dispersed by all kinds of dispersal vectors. Conventional classification systems use only binary assignment schemes classifying each species as either being dispersed by means of a certain dispersal vector or not. However, for ecological questions it is important to know (i) if the dispersal vector is capable of long-distance dispersal, and (ii) how efficiently the species is dispersed by this vector. In LEDA, gradual differences in the dispersability of plant species will be expressed by dispersal potentials. Dispersal potentials will be estimated from the literature for anemochory (dispersal by wind), hydrochory (dispersal by water), epizoochory (adhesive dispersal), endozoochory (internal animal dispersal), hemerochory (dispersal by man) and scatter hoarding. The attachment capacity, survival rate after digestion, buoyancy and terminal velocity will be measured as indicator parameters for the dispersal types epizoochory, endozoochory hydrochory and anemochory, respectively. For the final trait analysis, own measurements will be combined with those from the literature

6.1. SEED RELEASING HEIGHT

Introduction

The significance of seed releasing height is particularly obvious for wind dispersal, the effectiveness of which is largely determined by two plant traits – seed releasing height and terminal velocity of the diaspore (Tackenberg 2003). The potential for effective wind dispersal is greatest in species with a large releasing height and a low terminal velocity. However, these two traits do not act independently; the lower the heights of release, the more seeds are dependent on a low terminal velocity to achieve effective dispersal. Conversely, tall plants (e.g. trees) may achieve significant wind dispersal with only a moderately low terminal velocity (Nathan *et al.* 2002). Releasing height is also important for ectozoochory – the height at which ripe diaspores are presented will strongly influence the type of animals that might disperse them (Fischer *et al.* 1996). Indeed, the low probability of tree seeds encountering most mammals has been suggested as the reason for the scarcity of seeds with specific adaptations for ectozoochory among plants > 2 m tall (Hughes *et al.* 1994). Arboreal mammals may make poor dispersal vectors on account of their ability rapidly to remove adhesive seeds.

Trait definition

For the great majority of plants the seed releasing height = plant height, i.e. the highest point of the plant is a flower, and subsequently seeds or fruit. Therefore for many plants, although certainly not all, seed releasing height may be greater than canopy height. It cannot automatically be assumed that seed releasing height = flower height (see special cases below).

How to measure

Releasing height should be measured near the end of the growing season, and should be measured as the difference between the elevation of the highest fruit or seed and the base of the plant.

The same type of individuals as for canopy height should be sampled (see Chapter 1, Section1), i.e. healthy, adult plants that have their foliage exposed to full sunlight (or otherwise plants with the strongest light exposure for that species). However, because

releasing height is much more variable than some of the leaf traits, measurements are taken preferably on at least 25 individuals per species.

The height to be measured is the height of the inflorescence (or seeds, fruits), which frequently projects above the foliage. Measure releasing height preferably towards the end of the growing season (but during any period in the non-seasonal Tropics), as the shortest distance between the highest seed or fruit and ground level.

For estimating the height of tall trees there are several options:

1. A telescopic stick with metre marks
2. Measuring the horizontal distance from the tree to the observation point (d) and the angles between the horizontal plane and the tree top (α) and between the horizontal plane and the tree base (β). The tree height (H) is then calculated as: $H = d \times [\tan(\alpha) + \tan(\beta)]$. This method is appropriate in flat areas
3. Measuring the following 3 angles: (1) between the horizontal plane and the tree top (α); between the horizontal plane and the top of an object of known height (h ; e.g. a pole or person) that is positioned vertically next to the trunk of the tree (β); and (3) between the horizontal plane and the tree base (which is the same as the base of the object or person) (γ). The tree height (H) is then calculated as: $H = h \times [\tan(\alpha) - \tan(\gamma)] / [\tan(\beta) - \tan(\gamma)]$. This method is appropriate on slopes

Special cases

- In herbaceous species, 'stretched length' (see canopy height) does not apply: **releasing height is always height of the ripe seeds from the ground.**
- In some cases, releasing height is less than plant or canopy height, e.g. some shrubs with major extension growth of stems after flowering, some *Carex* tussocks. Also in some herbs (e.g. *Cyclamen* spp.), the flowering stem normally bends or collapses after flowering; here the seed releasing height may be much less than the flowering height.
- In the case of epiphytes or certain hemi-parasites (which penetrate tree or shrub branches with their haustoria), releasing height is defined as the shortest distance between the highest fruit and centre of their basal point of attachment. Record releasing height for species that use external support, i.e. twines, vines and lianas, as distance from the ground.
- The seed releasing height for water plants is measured as the distance between the highest point of inflorescence and the water surface.
- For small populations or rare species a minimum of 3 replicates (instead of 25 replicates) is accepted.

Minimal requirements

To estimate releasing height BIOPOP1 used drawings from the German flora (see also Canopy height, Chapter 1). These data will be incorporated into the LEDA Traitbase, however note that the statistical quality of this method is low, because the ranges of minimum and maximum height are only field observations with an unknown number of replicates.

To obtain the releasing height of the species missing from the BIOPOP list, the standardised measuring protocol of releasing height (as described above) should be used.

When in any published source the "seed releasing height" is a real measurement (i.e. not derived from drawings), information on the number of replicates, mean or median with the standard deviation or standard error is obligatory. Missing information on one of the above mentioned criteria will result in rejection of the data.

For any data entered into the Traitbase, record the obligate fields of the general standards on the description of the sample site (i.e. georeference, habitat, and method), including the size of collecting area to estimate data quality. For releasing height field data are preferred, but data from garden experiments are accepted with additional information about the sample site (see general standards). In the LEDA Traitbase the seed releasing height will be expressed in metres, but data expressed in other units will be accepted and converted to metres.

Unless otherwise stated, 'plant height' in floras can be assumed to be (maximum) releasing height. For example, in the standard British flora (Stace 1997), the height of *Digitalis purpurea* is given as 'up to 2 m', and *Hypochaeris radicata* as 'up to 60 cm'.

Data structure

- To collect: 1 height measurement of 25 different individuals per species (per site) = 25 heights in total per species
- Obligate:
- Type of variable: Numerical
 - Sample size: 25
 - Number of replicates: 1
 - Units: m
 - Values: N, mean, median, standard deviation, standard error
 - Method used: 1 - Obtained by measurements (standardised protocol), 2 - Obtained from published data, 3 - Estimated from drawings
 - Validity range: 0-70 (for European plants)
 - Support structure: yes = 1 or no = 2
 - Collecting date: day/month/year (dd.mm.yy)

6.2. TERMINAL VELOCITY

Introduction

If a seed is dropped from some height it acquires a "terminal" velocity, this is an important characteristics in wind dispersal of diaspores (Augsburger 1986).

The pull of gravity on any object is a constant value, but the effect of air resistance depends on the object's size, density and shape. These three factors determine the rate of fall through still air.

Theoretically the object or particle will start falling at a slow rate but will accelerate until it reaches its maximum rate of fall, which we call its "terminal velocity". Air movement also affects the rate of fall, and if the airflow is upward, it can oppose gravity, thus reducing the rate of fall. If the air velocity equals the "terminal velocity" of the seed, the seed will float, but if the air velocity exceeds the "terminal velocity", it will lift the seed. Where seeds have different "terminal velocities" (due to different size, density or shape), some will fall while smaller, lighter and/or "wingier" seeds will be lifted by the air stream (Kice 2002). This 'uplifting' is of great significance for dispersal of seeds by wind; long-distance dispersal by wind is only likely to be achieved by seeds that are uplifted (Nathan *et al.* 2002; Tackenberg 2003).

This theory shows the importance of the wings and plumes of diaspores is to delay the fall, for as long as it is in the air the wind can act upon it. This is the reason that the wings are often found to be oblique, causing the fruit to rotate under the wind, which carries it a further distance before it reaches the ground. The longer it takes to reach the ground and remains under the influence of the wind, the further a seed or fruit can be dispersed (Ridley 1930). Note that structures that slow the rate of all of seeds (e.g. wings or pappus) do not usually impart any horizontal velocity themselves.

Trait definition

Terminal velocity is the maximum rate of fall in still air, i.e. the rate of fall when the effects of gravity are balanced by air resistance.

How and what to collect

Measurements should be conducted on the dispersule, i.e. on the seed or fruit with all its normal attached structures, e.g. pappus, wing(s), awn(s). If there is any doubt about which structures should be included, measure terminal velocity both with and without. Species with fleshy fruits – measure the isolated seed only, without the fleshy part.

What to measure

Ideally, freshly-collected air-dry seeds should be measured, but older stored seeds may have to be measured in some cases. It is important that dispersal structures (esp. pappus) are undamaged. It is impossible to specify exact methods for measurement of terminal velocity, since there are at least two fundamentally different approaches. First, measurements of actual rate of fall in still air (e.g. Askew *et al.* 1996). Secondly, measurements of air speed when the seed is suspended in a vertical air flow (e.g. Jongejans & Schippers 1999). Generally the two methods give similar results (Jongejans & Schippers 1999). The latter method automatically measures terminal velocity, but the former will only measure terminal velocity if the seed is allowed to complete its acceleration before velocity is measured. Heavy seeds may need to fall several metres before they achieve terminal velocity, but the errors potentially involved are of little ecological significance – seeds that fall at $> 2 \text{ m sec}^{-1}$ are very unlikely to be effectively dispersed by wind (Tackenberg *et al.* 2003). The overriding concern will be that the LEDA Editorial Board is satisfied that the method is accurate enough to provide measurements to at least one decimal place.



Figure 6.1. Machine for measuring terminal velocity (Photo: K. Thompson).

Minimal requirements

For any data entered into the Traitbase it is obligatory to record the obligate fields of the general standards on the description of the sample site (i.e. georeference, habitat, method), including the size of collecting area to estimate data quality. Data obtained from diaspores originating from greenhouse or garden experiments are only accepted when all obligate fields can be completed.

Data structure

- To collect: 10 intact dispersules per species
(Note that one measurement on one seed is a single observation, and therefore N is the number of seeds measured (the individual measurements are not reported))
- Obligate:
- Type of variable: Numerical
 - Sample size: 10
 - Number of replicates: 1
 - Unit: m s^{-1}
 - Values: N, mean, median, minimum, maximum, standard deviation, standard error
 - Method: 1 - Obtained by measurements (standardised protocol), 2 - from published data
 - Validity range: 0.01 – 10
 - Collecting date: day/month/year (dd.mm.yy)

6.3. BUOYANCY

Introduction

The trait buoyancy (floating capacity) is an indicator parameter for the potential of a species to get dispersed by water. The longer the seeds of a species can float on water, the further they can get dispersed, though it is also dependent on the flow velocity (lakes, ditches, rivers). However, not only the maximum floating time but also the proportion of seeds floating for certain time period is an important parameter related to the dispersal potential by water.

Trait definition

Buoyancy: A measure of the floating capacity of diaspores on water, indicating a certain dispersal potential.

Floating capacity potential: Indication given to species to indicate their potential to be dispersed via water.

How and what to collect/ measure

Measurements should be conducted on the dispersule, i.e. on the seed or fruit with all its normal attached structures, e.g. pappus, wing(s), awn(s). If there is any doubt about which structures should be included or if a species has heteromorphic diaspores, buoyancy is measured on all diaspore types. For species with fleshy fruits both the whole fruit and the isolated seeds only (without the fleshy part) should be measured.

To measure floating capacity, two seed sets of each 100 seeds per species (= 200 seeds in total per species) need to be collected, if possible from plants growing in their typical habitats and from different individuals

Floating capacity is given as the proportion of seeds still floating after a defined time period. The floating capacity will be measured with 100 seeds per species and two replicates as Bill (2000) has shown a low variability in the results in similar experiments about buoyancy. The seeds are gently put in glass beakers (10 cm width, 12 cm height; volume: 600 ml) filled with about 300 ml distilled water. The beakers are placed on a "shaking" machine (Fig. 6.2) which gently moves with a frequency of 100/minute and an amplitude of about 1 cm. According to Van Diggelen & Boedeltje (pers. comm.), differences observed between the species are already steady after 1 week, largest changes occur within the first day. Therefore, the observations what proportion of seeds is still floating will be carried out at the following intervals:

Floating time intervals	T0	= right after the start
	T1	= 0.0035 days (5 min)
	T2	= 0.042 days (1 hour)
	T3	= 0.083 days (2 hours)
	T4	= 0.25 days (6 hours)
	T5	= 1 day
	T6	= 7 days



Figure 6.2. Measurement of the floating capacity of seeds using a shaking machine.

The data sheet for the input of measured data (see data structure) will comprise the mean and median floating capacity, N (number of replicates), the standard deviation, the standard error, the minimum and the maximum, the time step as well as information about the examined dispersal unit (according to the trait “morphology of dispersal unit”; see Section 5.1).

Generally, the entries for the field “time step” do not need to be in accordance with these data standards. For data comprising only T_{50} or T_{90} (time ‘T’ when 50% or 90% of the seeds have sunken), the mean floating capacity is 50 % (or 10%), the time interval is the given value in days. For example *Carex hirta*:

Data set 1: mean floating capacity = 50 % Time step = 20.25 days.

Data set 2: mean floating capacity = 10 % Time step = 112 days.

→ T_{50} = 486 hours (or 20.25 days) and T_{90} = 112 days

Minimal requirements

For any data entered into the Traitbase it is obligatory to record the obligate fields of the general standards (see Section 2) on the description of the sample site (i.e. georeference, habitat, method), to estimate data quality.

The mean, N (number of replicates), the minimum and maximum are required. Furthermore, information about the measured dispersal unit (seed or diaspore) is obligate information.

If less seeds than 200 are available, the experiment can exceptionally be conducted with less seeds per replicate

Data structure

Data field	Scale	Valid data entries
Species name	Nominal	Categories from species list
Mean floating capacity (%)	Metric	$0 \leq \text{mean} \leq 100$
Median floating capacity (%)	Metric	$0 \leq \text{median} \leq 100$
N	Metric	≥ 1 , whole numbers
Minimum floating capacity (%)	Metric	$0 \leq \text{min} \leq 100$
Maximum floating capacity (%)	Metric	$0 \leq \text{max} \leq 100$
Standard deviation	Metric	Positive value
Standard error	Metric	Positive value
Time step [in days]	Metric	≥ 0
Dispersal vector	Nominal	Categories from Table D2 “Dispersal vectors”
Floating capacity potential	Ordinal [algorithm]	Calculated from mean floating capacity - turning mean floating percentage to one of three floating capacity potential categories (algorithm to be defined): 1 = low floating capacity, 2 = medium floating capacity, 3 = high floating capacity
Seed structure [to be linked to the trait morphology of dispersal unit]	Nominal	Categories used for the trait “morphology of dispersal unit”
Diaspore type	Nominal	Categories used for the trait “morphology of dispersal unit”
Comment	Nominal	Text

6.4. EXTERNAL ANIMAL DISPERSAL (EPIZOOCHORY)

Introduction

Dispersal systems such as passive animal dispersal may play important roles in seed dispersal. The dispersal in which seeds are carried away from parent plants by attachment to the surface of animals is called ectozoochory, epizoochory or external animal dispersal.

The trait attachment capacity is an indicator for epizoochory; it shows how long a seed keeps attached to the fur, i.e. how far it is dispersed by animals.

Trait definition

External animal dispersal:	Is the dispersal of diaspores by means of attachment to the fur, hooves etc. of animals. Also known as ecto or epizoochory.
Attachment capacity:	A measure to indicate how well diaspores can be dispersed via ectozoochory.

How and what to collect/ measure

Measurements should be conducted on the dispersule, i.e. on the seed or fruit with all its normal attached structures, e.g. pappus, wing(s), awn(s). If there is any doubt about which structures should be included or if a species has heteromorphic diaspores, attachment capacity is measured on all diaspore types. For species with fleshy fruits both the whole fruit and the isolated seeds only (without the fleshy part) should be measured. For the trait attachment capacity, six seed sets of each 100 seeds per species (= 600 seeds in total per species) need to be collected, if possible from plants growing under natural conditions and from different individuals.

Attachment capacity is measured as the proportion of seeds still attached in the fur of a jiggled animal fur. It is measured by using the jiggling machine ("Rüttelmaschine", Fig. 6.3) according to the methods described in Talmon (2002). The experiments are carried out on sheep and on cattle fur. The fur (fur size of about 30 x 50 cm, nailed on a wooden board of 30 x 50 cm) is homogenised using a special "comb" (board with wooden pins). Per species 100 seeds (with all appendages) are combed into the fur, after which the fur pieces are installed at the sides of the machine. The value "attachment capacity" refers to the percentage of seeds still attached to the fur after 2400 jiggles (equivalent to 1 hour when jiggling with 40 hubs/ minute). The experiments are carried out on 3 replicates each for sheep and cattle fur.



Figure 6.3. The jiggling machine ("Rüttelmaschine"); it can be used to measure attachment capacity. The comb is used to homogenise the fur and to comb the seeds into the fur.

The data sheet for the input of measured data (see data structure) will comprise the mean and median percentage attachment capacity, the dispersal vector, N (number of replicates), the standard deviation, the standard error, the minimum and the maximum as well as information about the examined dispersal unit (according to the categories of the trait "morphology of dispersal unit"). Further columns conform to general data standards described in Section 2 (methods, country, study area (here: including origin of material), UTM, altitude).

Minimal requirements

The mean of the replicate measurements, N (number of replicates), the standard deviation, the minimum and the maximum are given. Other obligate information concerns the method used and the dispersal unit stage.

If less seeds than 600 are available, the experiment can exceptionally be conducted with less seeds per replicate.

Data structure

Parameter	Scale	Valid data entries
Species name	Nominal	Categories from species list
Mean attachment capacity (%)	Metric	$0 \leq \text{mean} \leq 100$
Median attachment capacity (%)	Metric	$0 \leq \text{median} \leq 100$
N	Metric	≥ 1 , whole numbers
Minimum attachment capacity (%)	Metric	$0 \leq \text{min} \leq 100$
Maximum attachment capacity (%)	Metric	$0 \leq \text{max} \leq 100$
Standard deviation	Metric	Positive value
Standard error	Metric	Positive value
Dispersal vector	Nominal	Categories from Table 6.1 Dispersal vectors
Attachment capacity potential	Ordinal [algorithm]	Calculated from mean attachment capacity - turning mean attachment capacity to one of three attachment capacity potential categories (algorithm to be defined): 1 = low attachment capacity, 2 = medium attachment capacity, 3 = high attachment capacity
Seed structure [to be linked to the trait morphology of dispersal unit]	Nominal	Categories used for the trait "morphology of dispersal unit"
Diaspore type	Nominal	Categories used for the trait "morphology of dispersal unit"
Comment	Nominal	Text

6.5. INTERNAL ANIMAL DISPERSAL (ENDOZOOCHORY)

Introduction

Endozoochory, the interaction between diaspores and the animals that ingest and disperse their seeds, has been the subject of many ecological studies (e.g. Janzen 1984, Clausen et al. 2002). In many vegetation types, mammals and birds are attracted to and disperse seeds because of the reward provided by edible parts of the fruits or seeds. Herbivores are often used for the management of heathlands and species rich grasslands. The land use of these large grazers for a very large degree determines the dispersal of plant diaspores as many seeds are eaten by herbivores that survive digestion.

The "survival rate after digestion" indicates how efficiently a species is dispersed via the animals gut. In the traitbase, the survival rate is given as the mean percentage seeds having survived simulated digestion in comparison to the control.

Trait definition

Internal animal dispersal: Is the dispersal of diaspores by means of the digestive system of animals. Also known as endozoochory.

Survival capacity: An measure to indicate how well a diaspore can survive the digestive tract to be able to be dispersed via endozoochory.

How and what to measure

The (relative) survival rate after digestion is measured as the proportion of viable seeds after an experimentally simulated digestion in relation to the viability of an untreated control. Measurements should be conducted on the apparently viable dispersule, i.e. on the seed or fruit with all its normal attached structures, e.g. pappus, wing(s), awn(s). If there is any doubt about which structures should be included, measure survival of digestion both with and without. Species with fleshy fruits – measure the isolated seed only, without the fleshy part.

For the trait survival rate after digestion, 10 seed sets of each 150 seeds per species (= 1500 seeds in total per species) need to be collected if possible from plants growing under natural conditions and from different individuals. Seeds used for the experiment should not be dormant.

According to the method of Bonn (in prep.), the simulation of ingestion and digestion includes a mechanical treatment representing chewing and a chemical treatment standing for seed digestion in the abomasus.

For both control and simulation of digestion, five replicate seed sets of each 150 seeds per species are used. The seeds are filled in plastic lids („Schnappdeckel“, 75mm x 28 mm) which are attached to a wooden board. The seeds should completely cover the bottom of the lid (single layer); if seeds are too large, several lids are used. An iron stick („chewing stick“, 1.3 m long) which is fitting exactly in the plastic lids (contact area 2 cm², end padded with a thin layer of technical fleece and covered with masking tape) is loaded with body weight (~70 kg) and moved 90° laterally twice (Fig. 6.4).

Figure 6.4. Simulation of chewing: mechanical treatment of seeds (in plastic lids attached to a wooden board) using a “chewing stick”

Afterwards, the “chewed” seeds are placed in small glass tubes filled with HCl (0.1M) for eight hours and washed with distilled water on a porcelain filter afterwards.

The survival rates are examined by comparing the germination rates of treated versus untreated seeds (simulation vs. control). For both the simulation and the control, five sets of 150 seeds each are put on two filter paper circles of 90 mm in diameter in transparent plastic dishes. They are watered with distilled water and closed with parafilm-laboratory film. The dishes are placed in a growth chamber with a 14 h light/22°C, 10 h darkness/12°C climate regime for six weeks with seedlings being counted and removed once a week. Viability of the remaining seeds is tested by pressing the seeds with a needle to test if the embryo is firm (Bakker et al., 1996).

The data sheet for the input of measured data (see data structure) will comprise the mean and median percentage survival rate, the dispersal vector, N (number of replicates), the standard deviation, the standard error, the minimum and the maximum as well as information about the examined dispersal unit (according to the categories of the trait “morphology of dispersal unit”; here: ruminants). Further columns conform to general data standards (i.e. methods, country, study area (here: including origin of material), UTM, altitude).

Minimal requirements

The mean of the five replicate measurements, N (number of replicates), the standard deviation, the minimum and the maximum are given. Other obligate information concerns the state of the examined dispersal unit (seed or diaspore).

If less seeds than 1500 are available, the experiment can exceptionally be conducted with less seeds per replicate or with only 3 replicates.

Data structure

Parameter	Scale	Valid data entries
Species name	Nominal	Categories from species list
Mean survival rate (%)	Metric	$0 \leq \text{mean} \leq 100$
Median survival rate (%)	Metric	$0 \leq \text{median} \leq 100$
N	Metric	≥ 1 , whole numbers
Minimum survival rate (%)	Metric	$0 \leq \text{min} \leq 100$
Maximum survival rate (%)	Metric	$0 \leq \text{max} \leq 100$
Standard deviation	Metric	Positive value
Standard error	Metric	Positive value
Dispersal vector	Nominal	Categories from Table 6.1 Dispersal vectors
Survival rate potential	Ordinal [algorithm]	Calculated from mean survival rate - turning mean floating percentage to one of three survival rate potential categories (algorithm to be defined): 1 = low survival rate, 2 = medium survival rate, 3 = high survival rate
Seed structure*	Nominal	Categories used for the trait "morphology of dispersal unit"
Diaspore type	Nominal	Categories used for the trait "morphology of dispersal unit"
Comment	Nominal	Text

* To be linked to the trait morphology of dispersal unit.

6.6. DISPERSAL DATA OBTAINED FROM LITERATURE

Seeds of most species are dispersed by means of different dispersal vectors. In the literature, general information about the dispersal types as well as more specific information about the dispersal vectors are given and can be included in the Traitbase. For ecological questions it is not only essential to know in which way species are dispersed, but if they can be dispersed over long distances by the dispersal type or vector. Hence, in the traitbase, every dispersal type and vector is classified as being capable of long-distance dispersal or not. Adding new dispersal vectors, additional information about the capability of long-distance dispersal is requested. Hence water and wind dispersal in a broad sense can not be accepted as valid data entries, because they include dispersal types capable of long distance dispersal (meteorochory, nautochory) as well as dispersal types capable of short distance dispersal only (boleochory, ombrochory; see Table 6.1, 6.2 for further details).

Generally, further information has to be linked to the data fields "dispersal type" (Table 6.1) and "dispersal vector" (Table 6.2) as every dispersal type or vector has to be described and assigned to the main dispersal type and to its capability of long-distance dispersal (LDD).

If possible, the dispersal potential (1 = low; 2 = medium, 3 = high) can be defined per plant species, dispersal type and vector. Independent of the vectors' capability of long-distance dispersal, the dispersal potential demonstrates how well a species is dispersed by the relevant vector. Other data fields are in accordance to the general standards.

Minimal requirements

The method has to be given as it indicates the data quality ("unknown" as least reliable method).

Data structure

Parameter	Scale	Valid data entries
Species name	Nominal	Categories from species list
Dispersal type	Nominal	Categories from table 6.1: dispersal types- explanation table (linked to table 6.1)
Dispersal vector	Nominal	Categories from table 6.2: dispersal vectors and their categorisation (linked to table 6.2)
Dispersal potential	Ordinal	Estimates how well the species is dispersed by the respective vector: 1 = low dispersal potential, 2 = medium dispersal potential, 3 = high dispersal potential

Seed structure *	Nominal	Categories used for the trait "morphology of dispersal unit"
Diaspore type	Nominal	Categories used for the trait "morphology of dispersal unit"
Comment	Nominal	Text

* To be linked to the trait morphology of dispersal unit.

Table 6.1. Dispersal types- explanation table

Dispersal type	Main dispersal type	LDD*	explanation
autochor	autochor	no	Self dispersal
ballochor	autochor	no	Explosive mechanisms
blastochor	autochor	no	Autonomous placement of seeds or daughter plant away from mother plant
chamaechor	chamaechor	(yes)	Tumbleweeds; dispersal unit rolling over the soil surface; caused by wind
agochor	hemerochor	yes	Unintended dispersal by man
ethelochor	hemerochor	yes	Dispersal by trading of plants or seeds
hemerochor	hemerochor	yes	Dispersal by man
speirochor	hemerochor	yes	Dispersal with seeds of agricultural species
meteorochor	anemochor	yes	Dispersal by wind (Note: flyers only, no tumbleweeds or wind-ballistics)
nautochor	nautochor	yes	Dispersal by surface currents of water
ombrochor	ombrochor	no	"raindrop-ballistics": raindrops triggering ballistic seed dispersal
dysochor	zoochor	yes	Dispersal by scatter-hoarding animals
endozoochor	zoochor	yes	Dispersal after digestion
epizoochor	zoochor	yes	Adhesive dispersal
zoochor	zoochor	yes	Dispersal by animals
... to be continued			

* LDD: Long distance dispersal.

Table 6.2. Dispersal vectors and their categorisation into capability of long-distance dispersal (LDD).

Dispersal vector	LDD	Dispersal vector	LDD
Ants	no	Man	yes
Birds	yes	Manure	yes
Cattle	yes	Marmot	no
Chamois	yes	Mouse	no
Commerce	yes	Ornamental plant	yes
Corn contamination	yes	Rabbit	yes
Deer	yes	Roe	yes
Earthworms	no	Ruminants	yes
Fish	yes	Shaken fresh water (lab experiments)	yes
Flowing fresh water	yes	Shaken fresh water with detergents (lab experiments)	yes
Flowing salt water	yes	Sheep	Yes
Goats	yes	Squirrel	yes
Hay transport	yes	Standing fresh water	Yes
Horses	yes	Standing salt water	yes
Liquid manure	yes	Wild boar	yes
Litter transport	yes	...	
Mammals	yes		

SECTION 4. REFERENCES

1. LITERATURE REFERENCES

- Aksoy, A., Dixon, J.M. & Hale, W.H.G. (1998) Biological Flora of the British Isles: *Capsella bursa-pastoris* (L.) Medikus (*Thlaspi bursa-pastoris* L., *Bursa bursa-pastoris* (L.) Shull, *Bursa pastoris* (L.) Weber). *Journal of Ecology*, 86, 171-186.
- Arber, A. (1920) *Water plants. A study of aquatic angiosperms*. Cambridge University Press.
- Askew, A.P., Corker, D., Hodgkinson, D.J. & Thompson, K. (1996) A new apparatus to measure the rate of fall of seeds. *Functional Ecology*, 11, 121-125.
- Atkinson, M.D. & Atkinson, E. (2002) Biological Flora of the British Isles: *Sambucus nigra* L. *Journal of Ecology*, 90, 895-923.
- Augspurger, C.K. (1986) Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany*, 73(3), 353-363.
- Bakker JP (1987) Restoration of species-rich grasslands after a period of fertiliser application. In: Van Andel, J, Bakker, JP & Snaydon, RW (eds) *Disturbance in Grasslands*, pp.185-200. Junk Publishers, Dordrecht.
- Bakker, J.P. (1989) *Nature Management by Grazing and Cutting*. Kluwer, Dordrecht.
- Bakker, J.P., Bos, A.F., Hoogveld, J. & Muller, H.J. (1991) The role of the seed bank in restoration management of semi-natural grasslands. In: *Terrestrial and aquatic ecosystems; perturbation and recovery* (ed. O. Ravera), pp. 449-455. Ellis Horwood.
- Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. & Thompson, K. (1996) Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica*, 45: 461-490
- Bakker, J.P., Elzinga, J.A., & De Vries, Y. (2002) Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. *Applied Vegetation Science* 5:107-120.
- Barkman, J. (1988) New Systems of Plant growth forms and phenological plant types. In: *Plant form and vegetation structure* (eds M.J.A. Werger P.J.M Van der Aart, H.J. During, J.T.A. Verhoeven), pp. 9-44.
- Baskin C.C. & Baskin, J.M. (1998) *Seeds - Ecology, Biogeography and Evolution of Dormancy and Germination*. San Diego, California. Academic Press.
- Begon, M, Mortimer, M. & Thompson, D. J. (1997) *Populationsbiologie*, Heidelberg, Berlin, Oxford Spektrum, Akad. Verlag.
- Bell, A.D. (1991) *An Illustrated Guide to Flowering Plant Morphology*. Oxford University Press.
- Bellingham, P. J. & Sparrow, A. D. (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* 89, 409-416.
- Bill, H-C. (2000) *Besiedlungsdynamik und Populationsbiologie charakteristischer Pionierpflanzenarten nordalpiner Wildflüsse*. Wissenschaft in Dissertationen Band 557, Görich & Weiershäuser GmbH, Marburg.
- Biological Flora of the British Isles. *Journal of Ecology* series. See URL: <http://www.britishecologicalsociety.org/articles/publications/journals/ecology/content/biologicalflora>.
- Böcker R, Kowarik I, Bornkamm R(1983) Untersuchungen zur Anwendung der Zeigerwerte nach Ellenberg. *Verh. Ges. Ökol.* 11, 35-56.
- Bonn & Poschlod (1998): *Ausbreitungsbiologie*.
- Bonn, S. (in prep.) Assessment of endozoochorous dispersal potential in plant species - a methodological approach.
- Brack, L. & Wood, G.B. (1997) Forest mensuration. URL: <http://sres.anu.edu.au/associated/mensuration/> BrackandWood1998/.
- Burns, I.G. (1991) Short- and long-term effects of a change in the spatial distribution of nitrate in the root zone on N uptake, growth and root development of young lettuce plants. *Plant, Cell & Environment*, 14, 21-33.
- Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany*, 87,1217-1227.
- Caldwell, M.M., Manwaring J.H. & Durham, S.L. (1991a) The microscale distribution of neighbouring plant roots in fertile soil microsites. *Functional Ecology*, 5, 765-772.
- Caldwell, M.M., Manwaring, J.H. & Jackson, R.B. (1991b) Exploitation of phosphate from fertile soil microsites by three Great Basin perennials when in competition. *Functional Ecology*, 5, 757-764.

- Castro-Díez, P., Puyravaud, J.P., Cornelissen, J.H.C. & Villar-Salvador, P. (1998) Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. *Oecologia*, 116, 57-66.
- Chapman, D. (ed.) (1996) *Water quality assessments, a guide to the use of biota, sediments and water in environmental monitoring*. Chapman & Hall, London.
- Clausen, P., Nolet, B.A., Fox, A.D. & Klaassen, M. (2002) Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in Northern Europe – a critical review of possibilities and limitations. *Acta Oecologica*, 23, 191-203.
- Cody, W.J. & Crompton, C.W. (1975) The Biology of Canadian weeds : 15. *Pteridium aquilinum* (L.) Kuhn. *Canadian Journal of Plant Science*, 55, 1059-1072.
- Cole CV, Innis GS, Stewart JWB (1977) Simulation of phosphorus cycling in semi-arid grassland. *Ecology* 58, 1-15.
- Cook, C.D.K. (1987) Vegetative growth and genetic mobility in some aquatic weeds. *Differentiation patterns in higher plants* (ed K.M. Urbanska), pp. 217–225. Academic Press, London.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van der Heijden, M.G.A., Pausas, J.G. and Poorter, H. (2003) Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335-380.
- Crawley, M.J. & Long, C.R. (1995) Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *Journal of Ecology*, 83, 683-696.
- Dalling, J.W. & Hubbell, S.P. (2002) Seed size, growth rate and gap micro-site conditions as determinants of recruitment success for pioneer species. *Journal of Ecology*, 90, 557-568.
- Del Tredici, P. (2001) Sprouting in temperate trees: a morphological and ecological review. *Botanical Review*, 67, 121-140.
- Den Hartog, C. & Segal, S. (1964) A new classification of the water plant communities. *Acta Botanica Neerlandica*, 13, 367-393.
- Diekmann, M. (1995) Use and improvement of Ellenberg's indicator values in deciduous forests of the Boreo-nemoral zone in Sweden. *Ecography* 18, 178-189.
- Diggle, P.K. (1997) Extreme preformation in alpine *Polygonum viviparum*: An architectural and developmental analysis. *American Journal of Botany* 84, 154-169.
- Domin, K. (1925) *Rostlinné tvarosloví. Základy srovnávací a popisné morfologie rostlin*. Československá Botanická společnost v Praze.
- Drew, M.C., Saker, L.R. & Ashley, T.W. (1973) Nutrient supply and the growth of the seminal root system in barley. I. The effect of nitrate concentration on the growth of axes and laterals. *Journal of Experimental Botany*, 24, 1189-1202.
- EEA (2002) EUNIS habitat classification. Version 2.3. URL: <http://mrw.wallonie.be/dgrne/sibw/EUNIS/home.html>
- Ellenberg H, Weber HE, Dull R, Wirth V, Werner W, Paulissen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18, 1-248.
- Enquist, B.J., West, G.B., Charnov, E.L. & Brown, J.H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature*, 401, 907-911.
- Eriksson, O. & Fröborg, H. (1996) Windows of opportunity for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. *Canadian Journal of Botany*, 74, 1369-1374.
- Eriksson, O. & Jakobsson, A. (1998) Abundance, distribution and life histories of grassland plants: a comparative study of 81 species. *Journal of Ecology*, 86, 922-933.
- Escarre, J. and J. D. Thompson (1991) The effects of successional habitat variation and time of flowering on seed production in *Rumex acetosella*. *Journal of Ecology* 79, 1099-1112.
- EUNIS (2002) EUNIS Habitat classification glossary. URL: <http://mrw.wallonie.be/dgrne/sibw/EUNIS/eunis.gloss.html>.
- FAO (1998) *World Reference Base for Soil Resources*. World Soil Resources Reports 84. Rome.
- Fernández-Santos, B., Gómez-Gutiérrez, J.M. & Moreno-Marcos, G. (1999) Effects of disturbance caused by traditional Spanish rural land use on the regeneration of *Cytisus multiflorus*. *Applied Vegetation Science*, 2, 239-250.
- Fischer, S.F., Poschlod, P., & Beinlich, B. (1996) Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology*, 33, 1206-1222.
- Fitter, A.H. & Peat, H.J. (1994) The Ecological Flora Database. *Journal of Ecology*, 82, 415-425.
- Fonseca, C.R., Overton, J.M., Collins, B. & Westoby, M. (2000) Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology*, 88, 964-977.
- Gardner, G. (1977) The reproductive capacity of *Fraxinus excelsior* on the Derbyshire Limestone. *Journal of Ecology*, 65, 107-118.

- Garnier, E. & Laurent, G. (1994) Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. *New Phytologist*, 128, 725-736.
- Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., Roumet, C. & Navas, M.L. (2001) Consistency of species rankings based on functional leaf traits. *New Phytologist*, 152, 69-83.
- Garnier, E., Shipley, B., Roumet, C. & Laurent, G. (2001) A standardised protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology*, 15, 688-695.
- Gartner, B. L. (1995) Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. Gartner, B. L. (ed) (1995) *Plant stems: Physiology and Functional Morphology*, Academic Press, San Diego, 125-150.
- Gartner, B. L. (edit) (1995) *Plant stems: Physiology and Functional Morphology*, Academic Press, San Diego.
- Givnish, T. J. (1995) Plant stems: Biomechanical adaptation for energy capture and Influence on species distributions. Gartner, B. L. (edit) (1995) *Plant stems: Physiology and Functional Morphology*, Academic Press, San Diego, 3-50.
- Givnish, T.J. (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist*, 106, 131-160.
- Golterman, H.L. (ed.) (1969) *Methods for chemical analysis of fresh waters*. International Biological Program Handbook 8. Blackwell, Oxford.
- Goodwin MJ, Parkinson RJ, Williams END, Tallwin JRB (1998) Soil phosphorus extractability and uptake in a *Cirsium molinietum* fen-meadow and an adjacent *Holcus lanatus* pasture on the culm measures. *Agriculture, Ecosystems and Environment* 70, 169-179.
- Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology*. Unwin Hyman, London.
- Grissino-Mayer HD (1999) *Introduction to Soil Science*. URL: www.valdosta.edu/~grissino/geol3710/soil14.htm
- Gross, K.L. (1990) A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology*, 78, 1079-1093.
- Groth, A.T., Lovett-Doust, L. & Lovett-Doust, J. (1996) Population density and module demography in *Trapa natans* (Trapaceae), an annual, clonal aquatic macrophyte. *American Journal of Botany*, 83, 1406-1415.
- Hacke, U.G., Sperry, J.S. & Pitterman, J. (2000) Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology*, 1, 31-41.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloh, K.A. (2001): Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, 126, 457-461.
- Hamdoun, A.M. (1972) Regenerative capacity of root fragments of *Cirsium arvense* (L.) SCOP. *Weed Research*, 12, 128-136.
- Hansen, A. (1881) *Vergleichende Untersuchungen über Adventivbildungen bei den Pflanzen*. Christian Winter Ver., Frankfurt am Mein.
- Harper, J. L. (1977) *Population Biology of Plants*, Academic Press, New York.
- Harper, J.L. (1981) The population biology of modular organisms. *Theoretical ecology* (ed. R. May) pp.53-77. Blackwell, Oxford.
- Haslam, S.M. (1972) *Phragmites communis* Trin. *Journal of Ecology*, 60, 585-610.
- Hawkes JC, Pyatt DG, White IMS (1997) Using Ellenberg indicator values to assess soil quality in British forests from ground vegetation: a pilot study. *Journal of Applied Ecology*, 34, 375-387.
- Hegi, G. (1998). *Illustrierte Flora von Mitteleuropa*; I 3. Berlin, Hamburg, Verlag Paul Parey.
- Herrera, C. M., Jordano, P., Guitian, J. & A. Traveset (1998) Annual Variability in Seed production by Woody Plants and the Masting Concept: Reassessment of Principles and Relationship to Pollination and Seed Dispersal. *American Naturalist*, 152, 576-594.
- Heyn, C.C., Dagan, O. & Nachman, B. (1974) The annual *Calendula* species, taxonomy and relationships. *Israel Journal of Botany*, 23, 169-201.
- Hill, M.O. & Carey, P.D. (1997) Prediction of yield in the Rothamstead Park grass experiment by Ellenberg indicator values. *Journal of Vegetation Science*, 8, 579-586.
- Hodgson, J.G. & Grime, J.P. (1990) The role of dispersal mechanisms, regeneration strategies and seed banks in the vegetation dynamics of the British landscape. In: *Species dispersal in Agricultural Habitats* (eds R.G.H. Bunce & D.C. Howard). Belhaven Press, London.
- Hodgson, J.G., Grime, J.P., Hunt, R. & Thompson, K. (1995) *The Electronic Comparative Plant Ecology*. Chapman and Hall, London.
- Hodkinson, D.J., Askew, A.P., Thompson, K., Hodgson, J.G., Bakker, J.P., & Bekker, R.M. (1998) Ecological correlates of seed size in the British flora. *Functional Ecology*, 12, 762-766.
- Holm, T. (1925) On the development of buds upon roots and leaves. *Annals of Botany* 39, 867-881.

- Horvath, D.P. & Anderson, J.V. (2002) A molecular approach to understanding root bud dormancy in leafy spurge. *Weed Science*, 50, 227-231.
- 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 Physiology*, 128, 1439-1446.
- Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgeron, L., & Westoby, M. (1994) Predicting dispersal spectra - a minimal set of hypotheses based on plant attributes. *Journal of Ecology*, 82, 933-950.
- 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 Ecology*, 166, 49-61.
- Imbert, I. (2002) Ecological consequences and ontogeny of seed heteromorphism. *Perspectives in Plant Ecology, Evolution and Systematics*, 5, 13-36.
- Irmisch, T. (1850) *Zur Morphologie der monokotylyschen Knollen- und Zwiebelgewächse*. G. Reimer Verlag, Berlin.
- Iwasa, Y. and Kubo, T. (1997) Optimal size of storage for recovery after unpredictable disturbances. *Evolutionary Ecology*, 11, 41-65.
- Jackson, R.B. & Caldwell, M.M. (1993) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* 74, 612-614.
- Jäger, E.J. & K. Werner (2000): *Rothmaler Exkursionsflora von Deutschland*. Gefäßpflanzen: Atlasband. Jena, Fischer.
- Jäger, E.J. & Werner, K. (eds.) (2002) *Exkursionsflora von Deutschland. Band 4. Gefäßpflanzen: Kritischer Band*. Spektrum Akademischer Verlag Heidelberg.
- Janzen, D.H. (1984) Dispersal of small seeds by big herbivores: foliage is the fruit; *American Naturalist*, 123, 338-353.
- Jones, E. W. (1959) Biological Flora of the British Isles: *Quercus* (L.). *Journal of Ecology*, 47, 169-222.
- Jongejans, E. & Schippers, P. (1999) Modelling seed dispersal by wind in herbaceous species. *Oikos*, 87, 362-272.
- Jongejans, E. & Telenius, A. (2001) Field experiments on seed dispersal by wind in ten umbelliferous species (Apiaceae). *Plant Ecology*, 152, 67-78.
- Jónsdóttir, I.S. & Watson, M.A. (1997) Extensive physiological integration: An adaptive trait in resource-poor environments? *The ecology and evolution of clonal plants* (eds. H. de Kroon & J. van Groenendael) pp. 109-136. Backhuys Publishers, Leiden, the Netherlands.
- Karrenberg, S., P. J. Edwards & J. Kollmann (2002). "The life history of Salicaceae living in the active zone of floodplains." *Freshwater Biology* 47: 733-748.
- Kelly, D. (1994) The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* 9, 465-470.
- Kelly, D. and V. L. Sork (2002) "Mast seeding in perennial plants: why, how, where?" *Annual Review of Ecology and Systematics* 33: 427-447.
- Kice (2002) What is terminal velocity? URL: <http://www.kice.com/multi-aspirator-background.htm>.
- Kjellsson, G. (1985) "Seed fall and phenological overlap in a guild of ant-dispersed herbs." *Oecologia* 68: 140-146.
- Klapp E (1965) *Grünlandvegetation und Standort*. Parey, Berlin.
- Kleyer, M. (1995) *Biological traits of vascular plants - a database*. University of Stuttgart, Arbeitsberichte, N.F. 2, Stuttgart, 23 p.
- Klimeš, L., Klimešová, J., Hendriks, R. & van Groenendael, J. (1997) Clonal plant architectures: a comparative analysis of form and function. *The ecology and evolution of clonal plants*. (eds. H. de Kroon & J. van Groenendael) pp. 1-29, Backhuys Publishers, Leiden.
- Klimeš, L. & Klimešová, J. (1999a) CLO-PLA2 - A database of clonal plants in central Europe. *Plant Ecology*, 141, 9-19.
- Klimeš, L. & Klimešová, J. (1999b) Root sprouting in *Rumex acetosella* under different nutrient levels. *Plant Ecology*, 141, 33-39.
- 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? *Evolutionary Ecology*, 15, 363-382.
- 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. Root sprouting plants in central Europe. In prep.
- Klimešová, J. & Martínková, J. Intermediate growth forms as a model for study of plant clonality functioning: an example with root sprouters. In prep.
- Klimešová, J. (2001) Adventivní odnožování - přehlížená vlastnost kořenů rostlin. *Zprávy České Botanické Společnosti, Praha, Materiály*, 18, 63-72.

- Klimešová, J. (2003) Monokarpické rostliny schopné přežít silnou disturbanci (Monocarpic plants surviving severe disturbance). *Zprávy České Botanické Společnosti, Praha, Materiály*, in press.
- Klotz, S., Kühn, I. & Durka, W. (2002) BIOFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. - *Schriftenreihe für Vegetationskunde*, 38, 1-334.
- Koenig, W.D. & Knops, J.M.H. (2000) Patterns of annual seed production by northern hemisphere trees: a global perspective. *American Naturalist*, 155, 59-69.
- Koop, H. (1987) Vegetative reproduction of trees in some European natural forests. *Vegetatio*, 72, 103-110.
- Korpelainen, H. (1995) Mating system and distribution of enzyme genetic-variation in Bracken (*Pteridium aquilinum*). *Canadian Journal of Botany*, 73, 1611-1617.
- Korsmo, E. (1930) *Unkräuter im Ackerbau der Neuzeit*. Verlag von Julius Springer, Berlin.
- Kranz, O. (2000) Böden und Landnutzung auf Mauritius - Aspekte einer geoökologischen Detailuntersuchung mit Hilfe Geographischer Informationssysteme, Diplomarbeit am Fachbereich Geographie, Marburg. URL: <http://137.248.191.13/Excursions/SAcd/Referate/Boden%20Maskarenen/Allin1.htm>.
- Kruijne, A.A., De Vries, D.M. & Mooi, H. (1967) Bijdrage tot de oecologie van Nederlandse graslandplanten. *Verslagen Landbouwkundige Onderzoeken* 696. Pudoc, Wageningen.
- Krumbiegel, A. (2001) Vegetative reproduction strategies of pseudo-annual plants in central Europe. *Beiträge zur Biologie der Pflanzen*, 72, 287-313.
- Kulak (2003) Katholieke Universiteit Leuven, biologie. URL: <http://www.kulak.ac.be/facult/wet/biologie/pb/kulakbiocampus/lage%20planten/Orobanche%20hederiae%20-20Klimopbremraap/klimopbremraap.htm>.
- Kunzmann, D. (1993) *Vegetationskundliche und populationsbiologische Untersuchungen zum Blaustern (Scilla bifolia L.) am Oberrhein*. Diplomarbeit am Lehrstuhl für Geobotanik, Freiburg i. Br.
- Kunzmann, D. (2000) *Untersuchungen zur Diasporenbank und des Samenflugs trocken-magerer Standorte als Beitrag zur Definition biotischer Entwicklungspotentiale*. Dissertationes Botanicae Band 326, Gebrüder Borntraeger, Berlin, Stuttgart.
- Kutschera, L. & Lichtenegger, E. (1992) *Wurzelatlas mitteleuropäischer Grünlandpflanzen. Band 2. Pteridophyta und Dicotyledonae (Magnolipsida)*. Teil 1. Stuttgart, Fischer.
- Landolt E (1977) Ökologische Zeigerwerte zur Schweizer Flora. Veröffentlichungen des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel, Zürich 64, 5-208.
- Lehsen, V. (2002) Lafore - Leaf area for everyone. URL: <http://www.uni-oldenburg.de/landeco/Download/Software/Laforem/Lafore.html>.
- Leishman, M. R. (2001). Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93: 294-302.
- Leishman, M.R. & Westoby, M. (1994a) The role of seed size in seedling establishment in dry soil conditions - experimental evidence from semi-arid species. *Journal of Ecology*, 82, 249-258.
- Leishman, M.R. & Westoby, M. (1994b) The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology*, 8, 205-214.
- Leishman, M.R. & Westoby, M. (1998) Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Functional Ecology*, 12, 480-485.
- Lovett Doust, J. & Lovett Doust, L. (1988) *Plant Reproductive Ecology: Patterns and Strategies*. Oxford University Press, New York.
- Lukasiewicz, A. (1962) Morphologic development types of perennials. *The Poznan Society of Friends of Science, Department of Mathematical and Natural Sciences, Publication of the Section of Biology*, 27, 1-398. [in Polish]
- Lyon de, M.J.H. & Roelofs, J.G.M. (1986) *Waterplanten in relatie tot waterkwaliteit en bodemgesteldheid, deel 1 & deel 2*. Report of the department of Aquatic Ecology, University of Nijmegen, Nijmegen.
- Mabberley, D.J. (1997) *The Plant Book*. Cambridge University Press, Cambridge.
- Martínková, J., Klimešová, J. & Mihulka, S. (2004a) Resprouting after disturbance: an experimental study with short-lived monocarpic herbs. *Folia Geobotanica*, in press
- Martínková, J., Kočvarová, M. & Klimešová, J. (2004b) Resprouting after disturbance in the short-lived herb *Rorippa palustris* (Brassicaceae): an experiment with juveniles. *Acta Oecologica*, in press.
- Milton, W.E.J. (1948) The buried viable-seed content of upland soils in Montgomeryshire. *Empire Journal of Experimental Agriculture*, 16, 163-177.
- Morton A. (2003) DMAP - Distribution mapping software. URL: <http://www.dmap.co.uk/>.
- Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., Pacala, S.W., & Levin, S.A. (2002) Mechanisms of long-distance dispersal of seeds by wind. *Nature*, 418, 409-413.

- Niklas, K.J. & Enquist, B.J. (2002) On the vegetative biomass partitioning of seed plant leaves, stems, and roots. *The American Naturalist*, 159, 482-497.
- Niklas, K.J. (1994) *Plant allometry: the scaling of form and process*. The University of Chicago Press, Chicago.
- Oborny, B., Kun, A., Czarán, T. & Bokros, S. (2000) The effect of clonal integration on plant competition for mosaic habitat space. *Ecology*, 81, 3291-3304.
- Otto, B. (2002) Merkmale von Samen, Früchten, generativen Germinulen und generativen Diasporen. In: *BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland* (eds S. Klotz, I. Kühn, W. Durka). *Schriftenreihe für Vegetationskunde*, 38, 177-196. Bundesamt für Naturschutz, Bonn- Bad Godesberg.
- Otto, B. (2002) Merkmale von Samen, Früchten, generativen Germinulen und generativen Diasporen. *BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland* (eds. Klotz S., Kühn I., Durka W.). *Schriftenreihe für Vegetationskunde* 38, 177-196. Bundesamt für Naturschutz, Bonn- Bad Godesberg.
- Page, C.N. (1982) *The ferns of Britain and Ireland*. Cambridge University Press.
- Page, C.N. (1988) *Ferns. Their habitats in the British and Irish landscape*. London, Collins.
- Pakeman, R.J., Digneffe, G. & Small, J.L. (2002) Ecological correlates of endozoochory by herbivores. *Functional Ecology*, 16, 296-304.
- Parkhurst, D.F. & Loucks, O.L. (1972) Optimal leaf size in relation to environment. *Journal of Ecology*, 60, 505-537.
- Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. (1999) Alvar grasslands in Estonia: variation in species composition and community structure. *Journal of Vegetation Science*, 10, 561-570.
- Pärtel M, Zobel M, Zobel K, Van der Maarel E (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, 75, 111-117.
- Passioura, J.B. (1988) Water transport in and to roots. *Annual Review of Plant Physiology and Plant Molecular Biology*, 39, 245-265.
- Pavlu, V., Hejzman, M. Pavlu, L. & Gaisler, J. (2003) Effect of rotational and continuous grazing on vegetation of an upland grassland in the Jizerské Hory Mts., Czech Republic. *Folia Geobotanica*, 38, 21-34.
- Paz, H., Mazer, S.J. & Martinez-Ramos, M. (1999) Seed mass, seedling emergence, and environmental factors in seven rain forest *Psychotria* (Rubiaceae). *Ecology*, 80, 1594-1606.
- Peterson, R.L. (1975) The initiation and development of root buds. *The development and function of roots*. (eds. Torrey, J.G. & Clarkson, D.T.) pp. 125-161, Academic Press, London.
- Piqueras, J. & Klimeš, L. (1998) Clonal growth and population dynamics in the pseudo-annual plant *Trifolium europaeum* L. *Plant Ecology*, 136, 213-227.
- Plant Dictionary (2003) Plant biology - Ohio state university. URL: <http://www.hcs.ohio-state.edu/hort/biology/Lab/growthform.html>.
- Poschlod, P. & Jackel, A.-K. (1993) Untersuchungen zur Dynamik von generativen Diasporenbanken von Samenpflanzen in Kalkmagerrasen. I. Jahreszeitliche Dynamik des Diasporenregens und der Diasporenbank auf zwei Kalkmagerrasenstandorten der Schwäbischen Alb. *Flora*, 188, 49-71.
- Poschlod, P., Kleyer, M. & Tackenberg, O. (2000) Databases on life history traits as a tool for risk assessment in plant species. *Zeitschrift für Ökologie und Naturschutz*, 9, 3-18.
- Poschlod, P., Kleyer, M., Jackel, A.-K., Dannemann, A. & Tackenberg, O. (2003) BIOPOP – a database of plant traits and internet application for nature conservation. *Folia Geobotanica*, 38, 263-271.
- Pyankov, V. I., Kondratschuk, A.V. & Shipley, B. (1999) Leaf structure and specific leaf mass: the alpine desert plants of the Eastern Pamirs, Tadjikistan. *New Phytologist*, 143, 131-142.
- Rauh, W. (1937) Die Bildung von Hypocotyl- und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. *Acta Nova Leopoldina, Halle*, 4/24, 395-555.
- Raunkiaer, C. (1934) *The Life Forms of Plants and Statistical Plant Geography*. Clarendon, Oxford.
- Reyes, G., Brown, S., Chapman, J. and Lugo, A. E. (1992): Wood densities of tropical tree species. General Technical Report SO-88, US-Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, USA.
- Richards, J.H. & Caldwell, M.M. (1985) Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: A field study with *Agropyron* species. *Journal of Applied Ecology*, 22, 907-920.
- Ridley, H. (1930) *The Dispersal of Plants throughout the World*. L. Reeve & Co. Ltd., Kent.
- Roderick, M.L. (2000) On the measurement of growth with applications to the modelling and analysis of plant growth. *Functional Ecology*, 14, 244-251.

- Roo-Zielinska, E. & Solon, J. (1998) Phytosociological typology and bioindicator values of plant communities, as exemplified by meadows in the Nina valley, Southern Poland. *Doc. Phytosociol.*, 11, 543-554.
- Rothmaler, W. (2000) *Exkursionsflora von Deutschland*. Spektrum, Heidelberg, Berlin.
- Russell EW (1973) *Soil Conditions and Plant Growth*. 10th Edition. Longman, London.
- Ryser, P. (1996) The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology*, 10, 717-723.
- Salisbury, E.J. (1942) *The reproductive capacity of plants*. Bells, London. 244 p.
- Sammul, M., Kull, K. & Tamm, A. (2003) Clonal growth in a species-rich grassland: Results of a 20-year fertilization experiment. *Folia Geobotanica*, 38, 1-20.
- Saverimuttu, T. & Westoby, M. (1996) Seedling longevity under deep shade in relation to seed size. *Journal of Ecology*, 84, 681-689.
- Schaffers, A.P. & Šykora, K.V. (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science* 11, 225-244.
- Schaffers AP, Šykora KV (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science*, 11, 225 - 244.
- Schenk, H.J. (1999) Clonal splitting in desert shrubs. *Plant Ecology* 141: 41-52.
- Sculthorpe, C.D. (1967) *The Biology of Aquatic Vascular Plants*. London.
- Shipley, B. & Dion, J. (1992) The Allometry of seed production in herbaceous angiosperms. *The American Naturalist*, 139, 467-483.
- Shipley, B. & Vu, T.T. (2002) Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytologist*, 153, 359-364.
- Silvertown JW, Lovett Doust (1993). *Introduction to plant population biology*. Oxford, London, Blackwell Scientific Publications, 210 p.
- Sperry, J. S. (1995) Limitations on Stem Water Transport and their consequences. Gartner, B. L. (edit) (1995) *Plant stems: Physiology and Functional Morphology*, Academic Press, San Diego, 105-125.
- Stace, C.A. (1997) *New Flora of the British Isles*. 2nd edition. Cambridge University Press, Cambridge.
- Strøm (2000). URL: http://www.toyen.uio.no/botanisk/nbf/plantefoto/Petasites_hybridus.htm.
- Symonides, E. (1978) Numbers, distribution and specific composition of diaspores in the soils of the plant association Spargulo-Corynephorum. *Ekologia Polska*, 26, 11-122.
- Tackenberg, O. (2003) Modeling long-distance dispersal of plant diaspores by wind. *Ecological Monographs*, 73, 173-189.
- Tackenberg, O., Poschlod, P., & Bonn, S. (2003) Assessment of wind dispersal potential in plant species. *Ecological Monographs*, 73, 191-205.
- Tallowin, J.R.B. & Smith, R.E.N. (2001) Restoration of a Cirsio-Molinietum fen meadow on an agriculturally improved pasture. *Restoration Ecology*, 9, 167-178.
- Talmon (2002) Ausbreitung von Pflanzenarten-Modellierung der Ausbreitung von Pflanzenarten in Trockenstandorten. In: MOSAIK-Projekt: Halboffene Weide- und Felsgraslandschaften als alternative Leitbilder für die Pflege von Trockenstandorten und ihre Konsequenzen für das Überleben von Flora und Fauna, Zwischenbericht 2002, BMBF, 55-64.
- Tamm, A., Kull, K. & Sammul, M. (2001) Classifying clonal growth forms based on vegetative mobility and ramet longevity: a whole community analysis. *Evolutionary Ecology*, 15, 383-401.
- Ter Braak CJF, Gremmen NJM (1987) Ecological amplitudes of plant species and the internal consistency of Ellenberg's indicator values for moisture. *Vegetatio* 69, 79-87.
- Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. (1996) An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology*, 10, 144-151.
- Thimonier A, Dupouey JL, Bost F, Becker M (1994) Simultaneous eutrophication and acidification of a forest ecosystem in North-East France. *New Phytologist* 126, 533-539.
- Thompson, K. (1992) The functional ecology of seed banks. In *Seeds: the Ecology of Regeneration in Plant Communities*. (ed. M Fenner) pp. 231-258. CAB International, Wallingford, UK.
- Thompson, K. & Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, 67, 893-921.
- Thompson, K., Band, S.R. & Hodgson, J.G. (1993) Seed size and shape predict persistence in soil. *Journal of Ecology*, 7, 236-241.
- Thompson, K., Bakker, J.P. & Bekker, R.M. (1997) *The soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press.
- Troll, W. (1935) *Vergleichende Morphologie der höheren Pflanzen: Vegetationsorgane*. Erster Band Teil 1, Berlin.

- Troll, W. (1935) Vergleichende Morphologie der höheren Pflanzen: Vegetationsorgane. Erster Band Teil 1, Berlin.
- Troll, W. (1937-1941) *Vergleichende Morphologie der höheren Pflanzen. Band 1 - Vegetationsorgane*. Verlag von Gebrüder Borntraeger, Berlin - Zahlendorf.
- USDA (1993) Soil Survey Staff, Natural Resource Conservation Service, Soil Survey Manual, United States Department of Agriculture, Handbook No. 18. URL: <http://www.vdh.state.va.us/onsite/regulations/Appendix-F.pdf>
- Van Altena, S.C. & Minderhoud, J.W. (1972) Keimfähige Samen von Gräsern und Kräutern in der Narbeschicht der Niederländischen Weiden. *Zeitschrift für Acker- und Pflanzenbau*, 136, 95-109.
- Van der Maarel E (1993) Relations between sociological-ecological species groups and Ellenberg indicator values. *Phytocoenologia* 23, 277-289.
- Van der Maarel E, Boot R, Van Dorp D, Rijntjes J (1985) Vegetation succession on the dunes near Oostvoorne, The Netherlands; a comparison of the vegetation in 1959 and 1980. *Vegetatio* 58, 137-187.
- Van Diggelen R, Boedeltje G. (unpubl.) Protocol buoyancy experiment. Unpublished report.
- Verburg, R.G. (1998) The witch at the forest floor. Reproductive allocation and clonal diversity in the pseudo-annual *Circaea lutetiana* L. - PhD thesis. Utrecht University, Utrecht.
- Vevle, O. & Aase, K. (1980) On the use of ecological factor numbers in Norwegian forest communities. *K. Nor. Vidensk. Selsk. Mus. Rapp. Bot. Ser.*, 5, 178-201.
- Vickery, J.A., Tallwin, J.R.B., Ferber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. & Brown, V.K. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, 38, 647-664.
- Wagenitz, G. (1996) *Wörterbuch der Botanik*. Gustav Fisher, Jena.
- Waller, D. M. & Steingraeber, D. A. (1995) Opportunities and Constraints in the Placement of Flowers and Fruits in the placement of Flowers and Fruits. In *Plant stems: Physiology and Functional Morphology*. Gartner, B. L. (ed.), Academic Press, San Diego, 51-74.
- Wehsarg, O. (1954) *Biologie der Ackerunkräuter*. Akademie - Verlag GmbH., Berlin.
- 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 of Vegetation Science*, 10, 609-620.
- Weiner, J. (1988) The Influence of Competition on Plant Reproduction. In: Lovett Doust J, L Lovett Doust (eds.); *Plant Reproductive Ecology: Patterns and Strategies*. New York (Oxford University Press), 228-245.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199, 213-227.
- Wetzel, R.G. (2001) *Limnology, lake and river ecosystems*. Academic Press, New York.
- Wilson, B. F. (1995) Shrub stems: Form and function. In *Plant stems: Physiology and Functional Morphology*. Gartner, B. L. (ed.), Academic Press, San Diego, 91-102.
- Wilson, P.J., Thompson, K. & Hodgson, J.G. (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, 143, 155-162.
- Wittrock, V.B. (1884) Ueber Wurzelsprossen bei krautigarten Gewächsen, mit besonderer Rücksicht auf ihre verschiedene biologische Bedeutung. *Botanisches Centralblatt* 17 (8, 9), 227-232 and 257-264.
- Wright, I.J., Westoby, M. & Reich, P.B. (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology*, 90, 534-543.
- Ziegenspeck, H. (1936) Orchidaceae. *Lebensgeschichte der Blütenpflanzen Mitteleuropas*. (eds. O. Kirschner, E. Loew & C. Schröter) pp. 1-840. Stuttgart: Eugen Ulmer Verlag.
- Zobler L (1986) *A world soil file for global climate modelling*. NASA TM-87802. National Aeronautics and Space Administration. Washington.
- Zophi, H-J. (1993a) Ecotypic variation in *Rhinanthus alectorolophus* (Scopoli) Pollich (Scrophulariaceae) in relation to grassland management I. Morphological delimitation's and habitats of seasonal ecotypes. *Flora*, 188, 15-39.
- Zophi, H-J. (1993b) Ecotypic variation in *Rhinanthus alectorolophus* (Scopoli) Pollich (Scrophulariaceae) in relation to grassland management II. The genotypic basis of seasonal ecotypes. *Flora*, 188, 153-173.
- Zophi, H-J. (1997) Ecotypic variation of *Euphrasia rostkoviana* Hayne (Scrophulariaceae) in relation to grassland management II. The genotypic basis of seasonal ecotypes. *Flora*, 192, 279-295.

2. SOURCE REFERENCES

- Carex arenaria* (http://erick.dronnet.free.fr/belles_fleurs_de_france/carex_arenaria.htm)
- Carlina vulgaris* (<http://www.habitas.org.uk/flora/photo.asp?item=4478>)
- Centaurea scabiosa* (<http://www.beenthere-donethat.org.uk/hampshire/winchester40big.html>)
- Chondrilla juncea* (<http://www.gut-im-bild.at/pages/Chondrilla-juncea.htm>)
- Chondrilla juncea* (<http://www.gut-im-bild.at/pages/Chondrilla-juncea.htm>)
- Daphne mezereum* (http://www.giftpflanzen.com/daphne_mezereum.html)
- Daphne mezereum* (http://www.giftpflanzen.com/daphne_mezereum.html)
- Erica tetralix* (<http://www.isleoflismore.com/florafauna/flowers.htm>)
- Helianthus tuberosus* (<http://www.mpiz-koeln.mpg.de/pr/garten/schau/HelianthustuberosusL/Topinambur.html>)
- Lemna minor* (<http://www.ulsamer.at/fo1/lemna-minor-1.htm>)
- Orobanche hederæ* (KULAK 2003)
- Persicaria hydropiper* (<http://www.bioimages.org.uk/HTML/P143750.HTM>)
- Phyllitis scolopendrium* (<http://hem.spray.se/saxifraga/ormbunkar.htm>)
- Pimpinella saxifraga* (<http://tomclothier.hort.net/album/pimpinel.htm>)
- Ranunculus ficaria* (<http://www.kulak.ac.be/facult/wet/biologie/pb/kulakbiocampus/images/lage%20planten/Ranunculus%20ficaria%20bulbosus%20-%20Gewoon%20speenkruid/>)
- Scilla bifolia* (http://www.boga.ruhr-uni-bochum.de/html/Scilla_bifolia_Foto.html)

SECTION 5. APPENDIX

Appendix 1	ISO Country codes with English and French country names (Sorted alphabetical by English country name)
Appendix 2	Second and third level of habitat classification of EUNIS
Appendix 3	Glossary
Appendix 4	Indicator values aquatic plants

Appendix 1. Official ISO 3166-1 country codes (ordered by English name). Some country code elements may become obsolete and therefore the ISO 3166-1 list will be regularly updated. See for further details <http://www.iso.ch/iso/en/prods-services/iso3166ma/02iso-3166-code-lists/list-en1.html>).

English Name	French Name	Code
Afghanistan	Afghanistan	AF
Albania	Albanie	AL
Algeria	Algérie	DZ
American Samoa	Samoa Américaines	AS
Andorra	Andorre	AD
Angola	Angola	AO
Anguilla	Anguilla	AI
Antarctica	Antarctique	AQ
Antigua and Barbuda	Antigua-Et-Barbuda	AG
Argentina	Argentine	AR
Armenia	Arménie	AM
Aruba	Aruba	AW
Australia	Australie	AU
Austria	Autriche	AT
Azerbaijan	Azerbaïdjan	AZ
Bahamas	Bahamas	BS
Bahrain	Bahreïn	BH
Bangladesh	Bangladesh	BD
Barbados	Barbade	BB
Belarus	Bélarus	BY
Belgium	Belgique	BE
Belize	Belize	BZ
Benin	Bénin	BJ
Bermuda	Bermudes	BM
Bhutan	Bhoutan	BT
Bolivia	Bolivie	BO
Bosnia and Herzegovina	Bosnie-Herzégovine	BA
Botswana	Botswana	BW
Bouvet Island	Bouvet, Île	BV
Brazil	Brésil	BR
British Indian Ocean Territory	Océan Indien, Territoire Britannique De L'	IO
Brunei Darussalam	Brunéi Darussalam	BN
Bulgaria	Bulgarie	BG
Burkina Faso	Burkina Faso	BF
Burundi	Burundi	BI
Cambodia	Cambodge	KH
Cameroon	Cameroun	CM
Canada	Canada	CA
Cape Verde	Cap-Vert	CV
Cayman Islands	Caïmanes, Îles	KY
Central African Republic	Centrafricaine, République	CF
Chad	Tchad	TD
Chile	Chili	CL
China	Chine	CN
Christmas Island	Christmas, Île	CX
Cocos (Keeling) Islands	Cocos (Keeling), Îles	CC
Colombia	Colombie	CO
Comoros	Comores	KM
Congo	Congo	CG
Congo, The Democratic Republic of The	Congo, La République Démocratique Du	CD
Cook Islands	Cook, Îles	CK
Costa Rica	Costa Rica	CR
Côte D'Ivoire	Côte D'Ivoire	CI
Croatia	Croatie	HR
Cuba	Cuba	CU
Cyprus	Chypre	CY
Czech Republic	Tchèque, République	CZ
Denmark	Danemark	DK
Djibouti	Dsjibouti	DJ
Dominica	Dominique	DM
Dominican Republic	Dominicaine, République	DO
Ecuador	Équateur	EC
Egypt	Égypte	EG
El Salvador	El Salvador	SV
Equatorial Guinea	Guinée Équatoriale	GQ

Appendix 1. Continued

English Name	French Name	Code
Eritrea	Érythrée	ER
Estonia	Estonie	EE
Ethiopia	Éthiopie	ET
Falkland Islands (Malvinas)	Falkland, Îles (Malvinas)	FK
Faroe Islands	Féroé, Îles	FO
Fiji	Fidji	FJ
Finland	Finlande	FI
France	France	FR
French Guiana	Guyane Française	GF
French Polynesia	Polynésie Française	PF
French Southern Territories	Terres Australes Françaises	TF
Gabon	Gabon	GA
Gambia	Gambie	GM
Georgia	Géorgie	GE
Germany	Allemagne	DE
Ghana	Ghana	GH
Gibraltar	Gibraltar	GI
Greece	Grèce	GR
Greenland	Groenland	GL
Grenada	Grenade	GD
Guadeloupe	Guadeloupe	GP
Guam	Guam	GU
Guatemala	Guatemala	GT
Guinea	Guinée	GN
Guinea-Bissau	Guinée-Bissau	GW
Guyana	Guyana	GY
Haiti	Haïti	HT
Heard Island and McDonald Islands	Heard, Île Et McDonald, Îles	HM
Holy See (Vatican City State)	Saint-Siège (État De La Cité Du Vatican)	VA
Honduras	Honduras	HN
Hong Kong	Hong-Kong	HK
Hungary	Hongrie	HU
Iceland	Islande	IS
India	Inde	IN
Indonesia	Indonésie	ID
Iran, Islamic Republic of	Iran, République Islamique D'	IR
Iraq	Iraq	IQ
Ireland	Irlande	IE
Israel	Israël	IL
Italy	Italie	IT
Jamaica	Jamaïque	JM
Japan	Japon	JP
Jordan	Jordanie	JO
Kazakhstan	Kazakhstan	KZ
Kenya	Kenya	KE
Kiribati	Kiribati	KI
Korea, Democratic People's Republic of	Corée, République Populaire	KP
Korea, Republic of	Corée, République De	KR
Kuwait	Koweït	KW
Kyrgyzstan	Kirghizistan	KG
Lao People's Democratic Republic	Lao, République Démocratique Populaire	LA
Latvia	Lettonie	LV
Lebanon	Liban	LB
Lesotho	Lesotho	LS
Liberia	Libéria	LR
Libyan Arab Jamahiriya	Libyenne, Jamahiriya Arabe	LY
Liechtenstein	Liechtenstein	LI
Lithuania	Lituanie	LT
Luxembourg	Luxembourg	LU
Macao	Macao	MO
Macedonia, The Former Yugoslav Republic of	Macédoine, L'ex-République Yougoslave	MK
Madagascar	Madagascar	MG
Malawi	Malawi	MW
Malaysia	Malaisie	MY
Maldives	Maldives	MV
Mali	Mali	ML
Malta	Malte	MT
Marshall Islands	Marshall, Îles	MH
Martinique	Martinique	MQ

Appendix 1. Continued

English Name	French Name	Code
Mauritania	Mauritanie	MR
Mauritius	Maurice	MU
Mayotte	Mayotte	YT
Mexico	Mexique	MX
Micronesia, Federated States of	Micronésie, États Fédérés De	FM
Moldova, Republic of	Moldova, République De	MD
Monaco	Monaco	MC
Mongolia	Mongolie	MN
Montserrat	Montserrat	MS
Morocco	Maroc	MA
Mozambique	Mozambique	MZ
Myanmar	Myanmar	MM
Namibia	Namibie	NA
Nauru	Nauru	NR
Nepal	Népal	NP
Netherlands	Pays-Bas	NL
Netherlands Antilles	Antilles Néerlandaises	AN
New Caledonia	Nouvelle-Calédonie	NC
New Zealand	Nouvelle-Zélande	NZ
Nicaragua	Nicaragua	NI
Niger	Niger	NE
Nigeria	Nigéria	NG
Niue	Niue	NU
Norfolk Island	Norfolk, Île	NF
Northern Mariana Islands	Mariannes Du Nord, Îles	MP
Norway	Norvège	NO
Oman	Oman	OM
Pakistan	Pakistan	PK
Palau	Palaos	PW
Palestinian Territory, Occupied	Palestinien Occupé, Territoire	PS
Panama	Panama	PA
Papua New Guinea	Papouasie-Nouvelle-Guinée	PG
Paraguay	Paraguay	PY
Peru	Pérou	PE
Philippines	Philippines	PH
Pitcairn	Pitcairn	PN
Poland	Pologne	PL
Portugal	Portugal	PT
Puerto Rico	Porto Rico	PR
Qatar	Qatar	QA
Réunion	Réunion	RE
Romania	Roumanie	RO
Russian Federation	Russie, Fédération De	RU
Rwanda	Rwanda	RW
Saint Helena	Sainte-Hélène	SH
Saint Kitts and Nevis	Saint-Kitts-Et-Nevis	KN
Saint Lucia	Sainte-Lucie	LC
Saint Pierre and Miquelon	Saint-Pierre-Et-Miquelon	PM
Saint Vincent and The Grenadines	Saint-Vincent-Et-Les Grenadines	VC
Samoa	Samoa	WS
San Marino	Saint-Marin	SM
Sao Tome and Principe	Sao Tomé-Et-Principe	ST
Saudi Arabia	Arabie Saoudite	SA
Senegal	Sénégal	SN
Seychelles	Seychelles	SC
Sierra Leone	Sierra Leone	SL
Singapore	Singapour	SG
Slovakia	Slovaquie	SK
Slovenia	Slovénie	SI
Solomon Islands	Salomon, Îles	SB
Somalia	Somalie	SO
South Africa	Afrique Du Sud	ZA
South Georgia and The South Sandwich Islands	Géorgie Du Sud Et Les Îles Sandwich Du	GS
Spain	Espagne	ES
Sri Lanka	Sri Lanka	LK
Sudan	Soudan	SD
Suriname	Suriname	SR
Svalbard and Jan Mayen	Svalbard Et Île Jan Mayen	SJ
Swaziland	Swaziland	SZ

Appendix 1. Continued

English Name	French Name	Code
Sweden	Suède	SE
Switzerland	Suisse	CH
Syrian Arab Republic	Syrienne, République Arabe	SY
Taiwan, Province of China	Taiwan, Province De Chine	TW
Tajikistan	Tadjikistan	TJ
Tanzania, United Republic of	Tanzanie, République-Unie De	TZ
Thailand	Thaïlande	TH
Timor-Leste	Timor-Leste	TL
Togo	Togo	TG
Tokelau	Tokelau	TK
Tonga	Tonga	TO
Trinidad and Tobago	Trinité-Et-Tobago	TT
Tunisia	Tunisie	TN
Turkey	Turquie	TR
Turkmenistan	Turkménistan	TM
Turks and Caicos Islands	Turks Et Caïques, Îles	TC
Tuvalu	Tuvalu	TV
Uganda	Ouganda	UG
Ukraine	Ukraine	UA
United Arab Emirates	Émirats Arabes Unis	AE
United Kingdom	Royaume-Uni	GB
United States	États-Unis	US
United States Minor Outlying Islands	Îles Mineures Éloignées Des États-Unis	UM
Uruguay	Uruguay	UY
Uzbekistan	Ouzbékistan	UZ
Vanuatu	Vanuatu	VU
Venezuela	Venezuela	VE
Viet Nam	Viet Nam	VN
Virgin Islands, British	Îles Vierges Britanniques	VG
Virgin Islands, U.S.	Îles Vierges Des États-Unis	VI
Wallis and Futuna	Wallis Et Futuna	WF
Western Sahara	Sahara Occidental	EH
Yemen	Yémen	YE
Yugoslavia	Yougoslavie	YU
Zambia	Zambie	ZM
Zimbabwe	Zimbabwe	ZW

Appendix 2. First three hierarchical levels of the EUNIS Habitat classification (EEA 2002).

Code	Hierarchical level 1	Code	Hierarchical level 2	Code	Hierarchical level 3
A	Marine habitats	A1	Littoral rock and other hard substrata	A1.1	Littoral rock very exposed to wave action
				A1.2	Littoral rock moderately exposed to wave action
				A1.3	Littoral rock sheltered from wave action
				A1.4	Rock habitats exposed by action of wind (e.g. hydrolittoral)
				A1.5	Rockpools
				A1.6	Littoral caves and overhangs
		A2	Littoral sediments	A2.1	Littoral gravels and coarse sands
				A2.2	Littoral sands and muddy sands
				A2.3	Littoral muds
				A2.4	Littoral mixed sediments
				A2.5	Habitats with sediments exposed by action of wind (e.g. hydrolittoral)
				A2.6	Coastal saltmarshes and saline reedbeds
		A3	Sublittoral rock and other hard	A2.7	Littoral sediments dominated by aquatic angiosperms
				A3.1	Infralittoral rock very exposed to wave action and/or currents and tidal streams
				A3.2	Infralittoral rock moderately exposed to wave action and/or currents and tidal streams
				A3.3	Infralittoral rock sheltered from wave action and currents and tidal streams
				A3.4	Caves, overhangs and surge gullies in the infralittoral zone
				A3.5	Circalittoral rock very exposed to wave action or currents and tidal streams
				A3.6	Circalittoral rock moderately exposed to wave action or currents and tidal streams
				A3.7	Circalittoral rock sheltered from wave action and currents including tidal streams
				A3.8	Caves and overhangs in the circalittoral zone
				A3.9	Deep circalittoral rock habitats
				A3.A	Vents and seeps in sublittoral rock
		A4	Sublittoral sediments	A4.1	Sublittoral mobile cobbles, gravels and coarse sands
				A4.2	Sublittoral sands and muddy sands
				A4.3	Sublittoral muds
				A4.4	Sublittoral mixed sediments
				A4.5	Shallow-water sediments dominated by angiosperms (other than [Posidonia])
				A4.6	[Posidonia] beds
		A5	Bathyal zone	A4.7	Deep circalittoral sediment habitats
				A4.8	Seeps and vents in sublittoral sediments
				A5.1	Bathyal zone hard substrates
				A5.2	Bathyal zone mixed substrates
				A5.3	Bathyal zone sand
				A5.4	Bathyal zone muddy sand
		A6	Abyssal zone	A5.5	Bathyal zone mud
				A5.6	Seeps in the bathyal zone
				A5.7	Caves in the bathyal zone
				A6.1	Hard substrates on the abyssal plain
				A6.2	Soft substrates on the abyssal plain
				A6.3	Tectonic ridges
				A6.4	Seamounts
				A6.5	Abyssal hills
				A6.6	Hadal zone (deep ocean trenches)
				A6.7	Caves in the abyssal zone
				A6.8	Anoxic deep seabed habitats below anoxic water
		A7	Pelagic water column	A7.1	Enclosed coastal saline or brackish water
				A7.2	Partially enclosed coastal water
				A7.3	Unenclosed mixed shallow water
				A7.4	Unenclosed seasonally stratified coastal water
				A7.5	Euphotic zone in non-coastal water
				A7.6	Reduced-salinity water below the euphotic zone
				A7.7	Water over continental shelf below euphotic zone
				A7.8	Water below euphotic zone over seabed beyond continental slope break
				A7.9	Ice-dominated marine habitats
				A7.A	Open ocean habitats with currents and eddies
				A7.B	Anoxic water column
B	Coastal habitats	B1	Coastal dune and sand habitats	B1.1	Angiosperm communities of sand beach driftlines
				B1.2	Sand beaches above the driftline
				B1.3	Shifting coastal dunes
				B1.4	Coastal stable dune grassland (grey dunes)
				B1.5	Coastal dune heaths
				B1.6	Coastal dune scrub
				B1.7	Coastal dune woods
				B1.8	Moist and wet dune slacks
				B1.9	Machair

Appendix 2. Continued.

Code	Hierarchical level 1	Code	Hierarchical level 2	Code	Hierarchical level 3		
C	Inland surface water habitats	B2	Coastal shingle habitats	B2.1	Shingle beach driftline habitats		
		B3	Rock cliffs, ledges and shores, including the supralittoral	B2.2	Unvegetated mobile shingle beaches above the driftline		
				B2.3	Upper shingle beaches with open vegetation		
				B2.4	Fixed shingle beaches, with herbaceous vegetation		
				B2.5	Shingle and gravel beaches with scrub vegetation		
				B2.6	Shingle and gravel beach woodland		
				B3.1	Supralittoral rock (lichen or splash zone)		
		C1	Surface standing waters	B3.2	Unvegetated rock cliffs, ledges, shores and islets		
				B3.3	Rock cliffs, ledges and shores, with halophytic angiosperms		
				B3.4	Soft sea-cliffs, often vegetated		
				C1.1	Permanent oligotrophic lakes, ponds and pools		
				C1.2	Permanent mesotrophic lakes, ponds and pools		
				C1.3	Permanent eutrophic lakes, ponds and pools		
		C2	Surface running waters	C1.4	Permanent dystrophic lakes, ponds and pools		
				C1.5	Permanent inland saline and brackish lakes, ponds and pools		
				C1.6	Temporary lakes, ponds and pools (wet phase)		
				C2			
				C2.1	Springs, spring brooks and geysers		
				C2.2	Permanent non-tidal, fast, turbulent watercourses		
		C3	Littoral zone of inland surface waterbodies	C2.3	Permanent non-tidal, slow, smooth-flowing watercourses		
				C2.4	Tidal rivers, upstream from the estuary		
				C2.5	Temporary running waters (wet phase)		
				C2.6	Films of water flowing over rocky watercourse margins		
				C3			
				C3.1	Species-rich helophyte beds		
				C3.2	Water-fringing reedbeds and tall helophytes other than canes		
				C3.3	Water-fringing beds of tall canes		
				C3.4	Species-poor beds of low-growing water-fringing or amphibious vegetation		
C3.5	Pioneer and ephemeral vegetation of periodically inundated shores						
C3.6	Unvegetated or sparsely vegetated shores with soft or mobile sediments						
C3.7	Unvegetated or sparsely vegetated shores with non-mobile substrates						
C3.8	Inland spray- and steam-dependent habitats						
D	Mire, bog and fen habitats			D1	Raised and blanket bogs		
				D2	Valley mires, poor fens and transition mires	D1.1	Raised bogs
						D1.2	Blanket bogs
		D3	Aapa, palsa and polygon mires	D2.1	Valley mires		
				D2.2	Poor fens		
		D4	Base-rich fens	D2.3	Transition mires and quaking bogs		
				D3.1	Palsa mires		
		D5	Sedge and reedbeds, normally without free-standing water	D3.2	Aapa mires		
				D3.3	Polygon mires		
				D4.1	Rich fens, including eutrophic tall-herb fens and calcareous flushes and soaks		
				D4.2	Basic mountain flushes and streamsides, with a rich arctic-montane flora		
		E	Grassland and tall forb habitats	E1	Dry grasslands	D5.1	Reedbeds normally without free-standing water
D5.2	Beds of large sedges normally without free-standing water						
D5.3	Swamps and marshes dominated by [Juncus effusus] or other large [Juncus] spp.						
D6.1	Inland saltmarshes						
D6.2	Inland saline or brackish species-poor helophyte beds normally without free-standing water						
E1.1	Open thermophile pioneer vegetation of sandy or detritic ground						
E2	Mesic grasslands			E1.2	Perennial calcareous grassland and basic steppes		
				E1.3	Mediterranean xeric grassland		
				E1.4	Mediterranean tall-grass and [Artemisia] steppes		
				E1.5	Mediterraneo-montane grassland		
		E1.6	Subnitrophilous grassland				
		E1.7	Non-Mediterranean dry acid and neutral closed grassland				
				E1.8	Mediterranean dry acid and neutral closed grassland		
				E1.9	Dry, open perennial and annual siliceous grassland, including inland dune grassland		
				E1.A	Mediterranean dry acid and neutral open grassland		
				E1.B	Heavy-metal grassland		
				E2.1	Permanent mesotrophic pastures and aftermath-grazed meadows		
				E2.2	Coarse permanent grassland and tall herbs, usually mown but little grazed		
				E2.3	Mountain hay meadows		
				E2.4	Iberian summer pastures (vallicares)		
				E2.5	Meadows of the steppe zone		
				E2.6	Agriculturally-improved, re-seeded and heavily fertilized grassland, including sports fields and grass lawns		

Appendix 2. Continued.

Code	Hierarchical level 1	Code	Hierarchical level 2	Code	Hierarchical level 3
F	Heathland, scrub and tundra habitats	E3	Seasonally wet and wet grasslands	E3.1	Mediterranean tall humid grassland
		E4	Valley mires, poor fens and transition mires	E3.2	Mediterranean short humid grassland
				E3.3	Sub-mediterranean humid meadows
				E3.4	Moist or wet eutrophic and mesotrophic grassland
				E3.5	Moist or wet oligotrophic grassland
				E4.1	Snow-patch grassland
		E5	Woodland fringes and clearings and tall forb habitats	E4.2	Moss and lichen dominated mountain summits, ridges and exposed slopes
				E4.3	Acid alpine and subalpine grassland
				E4.4	Calciphilous alpine and subalpine grassland
				E4.5	Alpine and subalpine enriched grassland
				E5.1	Over-grazed arid Mediterranean garrigues (ermes)
				E5.2	Thermophile woodland fringes
				E5.3	[Pteridium aquilinum] fields
				E5.4	Moist or wet tall-herb and fern fringes and meadows
				E5.5	Subalpine moist or wet tall-herb and fern habitats
				E5.6	Lowland habitats colonised by tall nitrophilous herbs
		E6	Inland saline grass and herb-dominated habitats	E6.1	Mediterranean inland saline grass and herb-dominated habitats
		F	Tundra	E6.2	Continental inland saline grass and herb-dominated habitats
				F1.1	Shrub tundra
		F2	Arctic, alpine and subalpine scrub habitats	F1.2	Moss and lichen tundra
				F2.1	Snow-patch dwarf willow scrub
				F2.2	Evergreen alpine and subalpine heath and scrub
				F2.3	Subalpine deciduous scrub
		F3	Temperate and mediterraneo-montane scrub habitats	F2.4	[Pinus mugo] scrub
				F3.1	Temperate thickets and scrub
				F3.2	Mediterraneo-montane broadleaved deciduous thickets
		F4	Temperate shrub heathland	F4.1	Wet heaths
				F4.2	Dry heaths
				F4.3	Macaronesian heaths
		F5	Maquis, matorral and thermo-Mediterranean brushes	F5.1	Arborescent matorral
				F5.2	Maquis
				F5.3	Pseudomaquis
				F5.4	[Spartium junceum] fields
		F6	Garrigue	F5.5	Thermo-Mediterranean shrub habitats
				F6.1	Western garrigues
				F6.2	Eastern garrigues
				F6.3	Illyrian garrigues
				F6.4	Black Sea garrigues
				F6.5	Macaronesian garrigues
				F6.6	Supra-Mediterranean garrigues
				F6.7	Mediterranean gypsum scrubs
				F6.8	Xero-halophile scrubs
				F7.1	West Mediterranean spiny heaths
		F7	Spiny Mediterranean heaths (phrygana, hedgehog-heaths and related coastal cliff vegetation)	F7.2	Central Mediterranean spiny heaths
				F7.3	East Mediterranean phrygana
				F7.4	Hedgehog-heaths
				F8.1	Canarian xerophytic habitats
		F8	Thermo-Atlantic xerophytic habitats	F8.2	Madeiran xerophytic habitats
		F9	Riverine and fen scrubs	F9.1	Riverine and lakeshore [Salix] scrub
				F9.2	[Salix] carr and fen scrub
				F9.3	Southern riparian galleries and thickets
		FA	Hedgerows	FA.1	Hedgerows of exotic species
				FA.2	Highly-managed hedgerows of native species
				FA.3	Species-rich hedgerows of native species
				FA.4	Species-poor hedgerows of native species
		FB	Shrub plantations	FB.1	Shrub plantations for whole-plant harvesting
				FB.2	Shrub plantations for leaf or branch harvest
				FB.3	Shrub plantations for flowers or fruit, other than vineyards
G	Woodland and forest habitats and other wooded land	G1	Broadleaved deciduous woodland	FB.4	Vineyards
				G1.1	Riparian [Salix], [Alnus] and [Betula] woodland
				G1.2	Fluvial [Fraxinus] - [Alnus] and [Quercus] - [Ulmus] - [Fraxinus] woodland
				G1.3	Mediterranean [Populus], [Fraxinus], [Ulmus] and related riparian woodland
				G1.4	Broadleaved swamp woodland not on acid peat
				G1.5	Broadleaved swamp woodland on acid peat
				G1.6	[Fagus] woodland
				G1.7	Thermophilous deciduous woodland
				G1.8	Acidophilous [Quercus]-dominated woodland
				G1.9	Non-riverine woodland with [Betula], [Populus tremula], [Sorbus aucuparia] or [Corylus avellana]
				G1.A	Meso- and eutrophic [Quercus], [Carpinus], [Fraxinus], [Acer], [Tilia], [Ulmus] and related woodland
				G1.B	Non-riverine [Alnus] woodland
				G1.C	Highly artificial broadleaved deciduous forestry plantations
				G1.D	Fruit and nut tree orchards

Appendix 2. Continued.

Code	Hierarchical level 1	Code	Hierarchical level 2	Code	Hierarchical level 3
H	Inland unvegetated or sparsely vegetated habitats	G2	Broadleaved evergreen woodland	G2.1	Mediterranean evergreen [Quercus] woodland
		G3	Coniferous woodland	G2.2	Eurasian continental sclerophyllous woodland
				G2.3	Macaronesian [Laurus] woodland
				G2.4	[Olea europaea] - [Ceratonia siliqua] woodland
				G2.5	[Phoenix] groves
				G2.6	[Ilex aquifolium] woods
				G2.7	Canarian heath woodland
				G2.8	Highly artificial broadleaved evergreen forestry plantations
				G2.9	Evergreen orchards and groves
				G3.1	[Abies] and [Picea] woodland
				G3.2	Alpine [Larix] - [Pinus cembra] woodland
				G3.3	[Pinus uncinata] woodland
				G3.4	[Pinus sylvestris] woodland south of the taiga
				G3.5	[Pinus nigra] woodland
				G3.6	Subalpine mediterranean [Pinus] woodland
				G3.7	Lowland to montane mediterranean [Pinus] woodland (excluding [Pinus nigra])
				G3.8	Canary Island [Pinus canariensis] woodland
				G3.9	Coniferous woodland dominated by [Cupressaceae] or [Taxaceae]
				G3.A	[Picea] taiga woodland
				G3.B	[Pinus] taiga woodland
				G3.C	[Larix] taiga woodland
				G3.D	Boreal bog conifer woodland
				G3.E	Nemoral bog conifer woodland
				G3.F	Highly artificial coniferous plantations
		G4	Mixed deciduous and coniferous woodland	G4.1	Mixed swamp woodland
				G4.2	Mixed taiga woodland with [Betula]
				G4.3	Mixed sub-taiga woodland with acidophilous [Quercus]
				G4.4	Mixed [Pinus sylvestris] - [Betula] woodland
				G4.5	Mixed [Pinus sylvestris] - [Fagus] woodland
				G4.6	Mixed [Abies] - [Picea] - [Fagus] woodland
				G4.7	Mixed [Pinus sylvestris] - acidophilous [Quercus] woodland
				G4.8	Mixed non-riverine deciduous and coniferous woodland
				G4.9	Mixed deciduous woodland with [Cupressaceae] or [Taxaceae]
				G4.A	Mixed woodland with [Cupressaceae], [Taxaceae] and evergreen oak
				G4.B	Mixed mediterranean [Pinus] - thermophilous [Quercus] woodland
				G4.C	Mixed [Pinus sylvestris] - thermophilous [Quercus] woodland
		G5	Lines of trees. small anthropogenic woodlands. recently felled woodland. early-stage woodland and coppice	G4.D	Mixed [Pinus nigra] - evergreen [Quercus] woodland
				G4.E	Mixed mediterranean pine - evergreen oak woodland
				G4.F	Mixed forestry plantations
				G5.1	Lines of trees
				G5.2	Small broadleaved deciduous anthropogenic woodlands
				G5.3	Small broadleaved evergreen anthropogenic woodlands
				G5.4	Small coniferous anthropogenic woodlands
				G5.5	Small mixed broadleaved and coniferous anthropogenic woodlands
				G5.6	Early-stage natural and semi-natural woodlands and regrowth
				G5.7	Coppice and early-stage plantations
		H1	Terrestrial underground caves. cave systems. passages and waterbodies	G5.8	Recently felled areas
				H1.1	Cave entrances
				H1.2	Cave interiors
				H1.3	Dark underground passages
				H1.4	Lava tubes
				H1.5	Underground standing waterbodies
				H1.6	Underground running waterbodies
				H1.7	Disused underground mines and tunnels
		H2	Screes	H2.1	Boreal siliceous screes
				H2.2	Boreal limestone screes
				H2.3	Temperate-montane acid siliceous screes
				H2.4	Temperate-montane calcareous and ultra-basic screes
				H2.5	Acid siliceous screes of warm exposures
				H2.6	Calcareous and ultra-basic screes of warm exposures
		H3	Inland cliffs. rock pavements and outcrops	H3.1	Acid siliceous inland cliffs
				H3.2	Basic and ultra-basic inland cliffs
				H3.3	Macaronesian inland cliffs
				H3.4	Wet inland cliffs
				H3.5	Almost bare rock pavements. including limestone pavements
				H3.6	Weathered rock and outcrop habitats
		H4	Snow or ice-dominated habitats	H4.1	Snow packs
				H4.2	Glaciers
		H5	Miscellaneous inland habitats with very sparse or no vegetation	H5.1	Fjell fields and other freeze-thaw features with very sparse or no vegetation
				H5.2	Glacial moraines with very sparse or no vegetation
				H5.3	Clay. silt. sand and gravel habitats with very sparse or no vegetation

Appendix 2. Continued.

Appendix 2: Continued.

Code	Hierarchical level 1	Code	Hierarchical level 2	Code	Hierarchical level 3
I	Regularly or recently cultivated agricultural, horticultural and domestic habitats	H6	Recent volcanic features	H5.4	Dry organic substrates with very sparse or no vegetation
				H5.5	Burnt areas with very sparse or no vegetation
				H5.6	Trampled areas
				H5.7	Boulder fields
				H6.1	Sparsely vegetated volcanic mountain summits, lava and ash fields
				H6.2	Unvegetated lava and ash fields
		I1	Arable land and market gardens	H6.3	Fumaroles, solfataras and mofettes
				I1.1	Intensive unmixed crops
				I1.2	Mixed crops of market gardens and horticulture
				I1.3	Arable land with unmixed crops grown by low-intensity agricultural methods
				I1.4	Inundated or inundatable croplands, including rice fields
				I1.5	Bare tilled, fallow or recently abandoned arable land
J	Constructed, industrial and other artificial habitats	I2	Cultivated areas of gardens and parks	I2.1	Large-scale ornamental garden areas
				I2.2	Small-scale ornamental and domestic garden areas
		J1	Buildings of cities, towns and villages	I2.3	Weed communities of recently abandoned garden areas
				J1.1	Residential buildings of city and town centres
				J1.2	Residential buildings of villages and urban peripheries
				J1.3	Urban and suburban public buildings
				J1.4	Urban and suburban industrial and commercial sites still in active use
				J1.5	Disused constructions of cities, towns and villages
				J1.6	Urban and suburban construction and demolition sites
		J2	Low density buildings	J2.1	Scattered residential buildings
				J2.2	Rural public buildings
				J2.3	Rural industrial and commercial sites still in active use
				J2.4	Agricultural constructions
				J2.5	Constructed field boundaries
				J2.6	Disused rural constructions
				J2.7	Rural construction and demolition sites
		J3	Extractive industrial sites	J3.1	Active underground mines
				J3.2	Active opencast mineral extraction sites, including quarries
				J3.3	Recently abandoned above-ground spaces of extractive industrial sites
		J4	Transport networks and other constructed hard-surfaced areas	J4.1	Weed communities of transport networks and other constructed hard-surfaced areas
				J4.2	Road networks
				J4.3	Rail networks
				J4.4	Airport runways and aprons
				J4.5	Hard-surfaced areas of ports
				J4.6	Pavements and recreation areas
				J4.7	Constructed parts of cemeteries
		J5	Highly artificial saline and brackish standing waters and associated structures	J5.1	Highly artificial saline and brackish standing waters
				J5.2	Highly artificial saline and brackish running waters
				J5.3	Highly artificial non-saline standing waters
				J5.4	Highly artificial non-saline running waters
				J5.5	Highly artificial non-saline fountains and cascades
		J6	Waste deposits	J6.1	Weed communities of waste deposits
				J6.2	Household waste and landfill sites
				J6.3	Non-agricultural organic waste
				J6.4	Agricultural and horticultural waste
				J6.5	Industrial waste
				J6.6	Waste resulting from building construction or demolition

Appendix 3. Glossary

Term	Definition
Accessory bud:	Buds which are at or near the nodes but not in the axils of the leaves
Acrisol:	Acid soil type with clay-enriched lower horizon, low CEC, and low saturation of bases
Age at first flowering:	This is the earliest age at which a plant can flower in the field
Agochory:	Unintended dispersal by man
Alisol:	Acid soil type with clay-enriched lower horizon, high CEC, but low saturation of bases
Andosol:	Soil type composed of volcanic materials, usually dark coloured
Anemochory:	Diaspore dispersal by wind
Annual:	Plants that die back after seed production - hence completes its entire life cycle within one year
Anthrosol:	Soil type dominated by human activities
Arenosol:	Soil type with a sandy or loamy sand texture
Autochory:	Self dispersal
Axillary bud:	Buds situated in an axil (i.e. the angle formed by a leaf or branch with the stem)
Axillary buds:	Buds situated on stems in axils of leaves; they develop exogenously during a normal ontogeny of shoots at the shoot apex
Ballochory:	Seed dispersal by an explosive mechanisms
Biennial:	Any plant needing two seasons of growth (with a dormant period between growth stages) to complete its life cycle, from seed to seed. In the first year, plants form vegetative growth, and in the second year they flower
Biomass:	The total mass of all living organisms in a given area
Blade:	Is usually the flat part of the leaf, excluding the petiole
Blastochory:	Autonomous placement of seeds or daughter plant away from mother plant
Boulders:	Sub-category of the substrate properties rocky including all stones from >600 mm in diameter
Bud bank:	All viable axillary and adventitious buds which are present or on a plant and are at disposal for spring re-growth, 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
Bud:	Points of growth on a stem (or rhizome) from which new shoots develop (rudimentary state of a stem)
Bulb:	A storage organ consisting of storage leaves and a shortened stem base; it may growth monopodially or sympodially; the bulb is formed by organs produced during a single season or in the course of several seasons, therefore in plants with sympodial growth they belong to different shoot generations
Buoyancy:	Floating capacity of diaspores on water
Calcisol:	Soil type dominated by calcium carbonate as powdery lime or concretions
Calyx:	
Cambisol:	Soil type with moderately developed soils with lower horizons having colour or structure changes from the parent material which permit the identification of a cambic B horizon
Canopy height:	The distance between the highest photosynthetic tissue and the base of the plant
Chamaechory:	Tumbleweeds; dispersal unit rolling over the soil surface caused by wind
Chamaephyte:	Woody or herbaceous evergreen perennial from 10 to 20 inches tall or whose shoots die back periodically. These plants are small shrubs covered by snow in the winter
Chernozem:	Soil type with a dark colour, deep soils in organic matter, calcareous lower in profile, also typical of grass steppe/prairie
Clonal growth organ:	CGO - A morphological unit of a plant, which bears a bud-bank and provides vascular connections between shoots.
Clonal plant fragment:	All physically inter-connected parts of a clonal plant
Cobbles:	Sub-category of the substrate properties rocky including all stones from 75-250 mm in diameter
Compound leaf:	Compound leaves are built from several small leaves (= leaflets) or from pinnations that sit in a regular organisation at the undivided or branched rachis
Cotyledon:	One of the first leaves to appear after germination (there may be one, two, or more); the foliar portion of the embryo as found in the seed
Daughter shoot:	daughter shoot: shoot which may be traced as a descendant of another shoot (mother shoot)
Diaspore:	Reproductive portions of a plant such as a seed or buds that are dispersed and may give rise to a new plant (see also disseminule and dispersule)
Dispersal:	Process of spreading out from point of origin
Dispersion:	Pattern resulting from dispersal
Dispersule:	Every morphological part of a plant that serves as a unit of dispersal and becomes detached from the mother-plant to disperse. Here we only provide data for the generative dispersules, i.e. units of dispersal that contain a seeds (see also germinule)
Disseminule:	A plant part that can be easily separated from the parent plant, is dispersed, and can

	grow into a new plant (see also diaspore and dispersule)
Dysochory:	Dispersal by scatter-hoarding animals
Ectozoochory:	Dispersal of diaspores via attachment to the fur of animals (adhesive dispersal). See also endozoochory
Endozoochory:	Dispersal of a seed by an animal which carries it from one place to another in its digestive tract (Internal animal dispersal). See also ectozoochory
Epiphyte:	Epiphytes are plants which grow above the ground surface, using other plants or objects for support. They are not rooted in the soil nor are they parasitic
Epizoochory:	See ectozoochory
Errant vascular hydrophyte:	Free-moving water plant - i.e. the floating aquatic plants
Ethelochory:	Dispersal by trading of plants or seeds
Eutrophic soil:	Soils with a high nutrient content supporting a high productivity. This was originally applied to nutrient-rich waters with high primary productivity but now also applied to soils
External animal dispersal:	See ectozoochory
Ferralsol:	Soil type composed of kaolinite and quartz, enriched in Fe and Al oxides
Fluvisol:	Soil type with a soil developed on river deposits showing alluvial stratification
GCO:	See clonal growth organ
Gemma:	An asexual reproductive body that becomes detached from a parent plant
Gemmipary:	Adventitious buds on leaves formed after shedding or detaching leaves from the mother plant; on bare wet soil they develop into plantlets resembling by their size seedlings
Genet:	One individual with the same genetic material
Geophyte:	Perennial (or biennial) herbaceous plants for which the stems die back to a remnant shoot system with storage organs that are imbedded in the soil. These are the plants gardeners call bulbs (including corms, rhizomes, and tubers as well as true bulbs)
Germinule:	Unit of germination. In many cases the dispersule is not the unit that will enter the soil after dispersal and germinate and therefore differs from the dispersule. This difference is due to morphological structures, such as pappus, wings, awns or fleshy nutrient containing tissues, that get lost between the time of dispersal and the time of germination
Gleysol:	Soil type with waterlogged soils with poor drainage and anaerobic conditions
Greyzem:	Soil type with a organic rich surface horizon with uncoated sand grains, typical of grass steppe/ prairie
Ground water:	Ground water is the part of precipitation that seeps down through the soil until it reaches rock material that is saturated with water
Growth form:	Type of plants with the same growth morphology or architecture (concept is free of any hypotheses about adaptation - see also life form)
Gypsisol:	Soil type with the presence of gypsum (calcium sulphate) in crystals or concretionary layers
Habitat:	The organisms within an ecosystem form a biocenosis, their inanimate environment is called a habitat and the totality of all ecosystems on earth is called the biosphere
Hapaxanthic perennial:	Plants from which the shoot dies after flowering (opposite = pleoxanthic - shoot lives and flowers again and again)
Haustorium :	The structure by which a parasite enters and draws nutrients from a plant (in fungi - hypha; in mistletoes and similar parasites - a modified root (pl.: haustoria)
Hemerochory:	General dispersal by man (e.g. mowing machines)
Hemicryptophyte:	Perennial (or biennial) herbaceous plant in which the stems die back to a remnant shoot system that lies on the ground. These are herbaceous plants with runners along the ground
Hemi-epiphytes:	Plant uses other plant for support for part of their life - the plant germinates on other plants and then establishes soil contact or the plant that germinates on the ground but later loses contact with the soil (see also epiphyte)
Hemi-parasite:	Is a plant which is only partially parasitic, possessing its own chlorophyll (green colour) and photosynthetic ability (may be facultative or obligate) - also called semi-parasite
Heteromorphism:	Occurrence of different morphological forms of the same functional unit (e.g. seeds produced by a single individual). This is called heterocarpy when the whole fruit is concerned, heteromerocarpy when it concerns parts of a fruit serve as dispersal unit or as heterospermy when it concerns the seeds
Histosol:	Soil type with more than a defined amount of organic matter; an organic soil
Holo-parasites:	A plant which is totally parasitic, lacking chlorophyll and thus unable to synthesise organic carbon
Hydrochory:	Diaspores dispersal by means of water
Hydrophyte species:	A plant adapted to growing in water, waterlogged soil or on a substrate that becomes inundated on a regular basis
Internal animal dispersal:	See endozoochory
Kastanozem:	Soil type with calcareous soils rich in organic mater, brown colour, typical of semiarid

	climates with grasses
Lamina:	A typical leaf is organised into blade (= lamina), petiole and leaf base - The blade is usually the flat part of the leaf excluding the petiole
Latitude:	Reference lines over the earth surface (also called parallels)
Leaf:	A typical leaf is organised into lamina, petiole and leaf base - usually a flat, green structure of a plant where photosynthesis and transpiration take place and attached to a stem or branch - appears subsequent to the cotyledons
Leaflet:	The single part of a compound leaf
Leptosol:	Soil type with a weakly developed shallow soil
Liana:	High climbing woody plants that germinate on the ground and maintains soil contact while using another plant for support (also Liane)
Life form:	Types of plants that are having the same kind of morphological and/or physiological adaptation to a certain ecological factor e.g. annual plants, epiphytes, herbs/forbs, graminoid, macrophytes, perennial plants, shrubs, trees, vines
Life span:	See plant life span
Lixisol:	Soil type with clay-enriched lower horizon, low CEC, and high saturation of bases
Longitude:	Reference lines over the earth surface (also called meridians)
Long-term persistent:	Seeds that persist in the soil for at least five years
Luvisol:	Soil type with a clay-enriched lower horizon, high CEC, and high saturation of bases
Mesotrophic soil:	Soils with a moderate (or intermediate) nutrient status and primary production
Meteorochory:	Dispersal by wind; but: flyers only, no tumbleweeds or wind-ballistics
Monocarpic:	Flowering and fruiting only once before dying; such plants may take several years to reach flowering size
Nautochory:	Dispersal by surface currents of water
Necessary CGO:	Clonal growth organ which is necessary for plant to complete its lifecycle phalanx - plant shoot is surrounded by its sister shoots with a higher probability than by shoots of other plants primary shoot (=main shoot): shoot arising on shoot pole of embryo pseudo-vivipary: in some plants in some situations, meristems that would normally develop into flowers develop instead into vegetative buds usually associated with adventitious roots (Bell 1991); vegetative bud may be developed into plantlet, bulbill, root or stem tuber and may be soon detached from mother plant or whole inflorescence lay down, plantlets roots and flowering stalk break or rotted out; plants resemble seedlings in their size
Nitisol:	Soil type with deep, clay-enriched lower horizon with shiny ped surfaces
Oligotrophic soil:	Soils that are poor in nutrients, with in general a low primary production
Ombrochory:	Raindrop-ballistics - where raindrops triggering ballistic seed dispersal
Other:	In general an artificial by anthropologically influenced soil substrate where e.g. a soil layer of foreign origin was transported on (i.e. parks, gardens)
Parasite:	A plant depending on another plant for part or all of its nutrition
Peat:	Is a heterogeneous organically formed substance that results from the incomplete decomposition of plants in a wet or humid environment
Pebbles:	Sub-category of the substrate properties rocky including all stones from 2-75 mm in diameter
Perennial:	A plant that normally lives more than two growing seasons and, after an initial period, produces flowers annually
Perigone:	The floral envelope, consisting of the calyx (protective structure around flower formed by sepals collectively) and corolla (innermost whorl of petals in a flower) (when present) (synonym = perianth)
Petiole:	Leaf stalk
Petiole:	Is the stalk of a leaf that attaches to the stem (synonym = leafstalk)
pH:	Stands for potential Hydrogen (abbr. pH) - a log scale measurement of the acidity/alkalinity of a solution with 1 being extremely acidic, 10 being extremely alkaline, and 7 being neutral. The full range of the pH scale (0-14) is not used in soils, as the reaction of most soils is between 3.5 and 10
Phaeozem:	Soil type with dark coloured soils rich in organic matter, with deep leaching of carbonates, associated with forest steppe
Photosynthetic tissue:	Plant tissue that manufactures sugar through the action of sunlight
Planosol:	Soil type developed in flat areas, with seasonal saturation caused by impermeable lower horizon
Plant life span:	Life span is the average length of time adult plants remain alive under certain stated conditions
Plant:	In the strictest definition of a plant is the genetic individual with the life span as the time from zygote formation to death of the genet
Plinthisol:	Soil type with a mottled appearance that harden on exposure to atmosphere
Podzol:	Soil type with bleached, light-coloured horizon below surface, with spodic B horizon
Podzoluvisol:	Soil type with a clay-enriched lower horizon into which an albic horizon is deeply tongued

Polycarpic:	Fruiting and flowering many times - The opposite of monocarpic
Propagule:	Is any part of an organism that can be detached from the organism and disseminated that serves as a unit of reproduction
Pseudovivipary:	Is an asexual reproductive strategy exhibited by some plant species in which leafy plantlets are produced instead of seeds, with genetic conservation an advantage for stress tolerators in these nutrient-poor habitats
Rachis:	The main leafstalk of a compound leaf or the main stalk of a flower cluster - in ferns it is the continuation of the stipe (= fern stem) through a compound frond (also called Rhachis)
Ramet:	A potentially independent part of a clonal plant regenerative CGO: clonal growth organ which functions after an injury of a plant only; injury of a plant results in the initiation of adventitious buds on organs which usually do not bear them when intact or in fragmentation and initiation of adventitious roots on organs which do not fragment and root when intact
Regenerative buds:	Dormant (resting) axillary and adventitious buds which break their dormancy or adventitious buds formed de novo and substituting lost shoots after an injury; they may be located on all living plant parts, including aboveground shoots
Renewal buds:	A small proportion of buds on a plant and their location is species-specific and similar in the same CGO; their location is used in the definition of Raunkiaer's life-forms and their development is seasonal; in comparison with regenerative buds the renewal buds contain more preformed structures, such as 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 plant no sharp distinction between renewal and regenerative buds exists
Regosol:	Soil type with a weakly developed soil with texture finer than sandy loam
Releasing height:	The difference between the elevation of the highest fruit or seed and the base of the plant
Replicate:	To reproduce or make an exact copy or copies by sampling something again in exactly the same way (synonym: duplicate, copy, reproduce, repeat)
Resinous species:	Plant species that are coated with a sticky gum or resin (= secretions (often aromatic) that are insoluble in water but soluble in ether or alcohol)
Rocky:	Rock fragments are unattached pieces of rock 2 mm in diameter or larger that are described by shape (spherical class 1-4 or flat class 5-8) and size
Root tubers:	The tubers are short-lived and serve as storage and regenerative organ; the plant dies back in autumn, except for the root tuber(s) which bear just one bud each for spring regrowth; during summer old tubers decay and new ones are formed
Rosette plants:	A species that will form a cluster of leaves which grows in a circular overlapping pattern arising basally from a crown or apically from an axis
Sample:	A set of individuals or items selected from a population for analysis to yield estimates of, or to test hypotheses about, parameters of the whole population (synonym: individual, representative, specimen)
Seed coat:	The outer protective covering of a seed
Seed height:	Is the shortest axis of the seed perpendicular to the length axis and perpendicular to the width axis
Seed length:	Is the longest axis that can be found in the seed
Seed number:	Is the number of seeds produced by a plant - usually given per shoot or per inflorescence
Seed set:	To produce seeds after flowering
Seed shape:	The shape variance (Vs) is captured by dividing length, width and height of a seed separately by length and then calculating the variance of the three values (minimum value of Vs is 0 in perfectly spherical seeds and the maximum values range between 0.2 and 0.3 in needle- or disc-shaped seeds)
Seed thickness:	See seed height
Seed width:	Is the widest axis of the seed perpendicular to the length axis
Seed:	Generative unit of reproduction of the spermatophytes. Seeds contain an embryo and have an outer cover (testa). Mostly they also contain endosperm (tissue that serves as nutrition source during the germination). Beside this sensus strictus definition the term seed is often used as a collective term for the generative units of reproduction, dispersal and germination
Sessile leaf:	A leaf without a petiole
Shoot cyclicity:	Life-span of a shoot from the onset of its growth until its death after fruiting
Short-term persistent:	Seeds that persist in the soil seed bank for at least one year, but less than five years
Soil acidity:	See pH
Soil moisture:	Is water stored in soils. The level of soil moisture is often depending on the height of the ground water table
Solonchak:	Soil type where salt accumulation is the dominant process
Solonetz:	Soil type dominated by sodium salts

Specific leaf area:	SLA = The ratio of leaf area to leaf dry mass
Speirochory:	Dispersal with seeds of agricultural species
Stem density:	Is determined by dividing the dry mass of a stem segment by its fresh volume - obtained value (stem specific density) quantifies woodiness and stem water content
Stones:	Sub-category of the substrate properties rocky including all stones from 250-600 mm in diameter
Succulent species:	Plant species with thick, fleshy, water-storing leaves or stems
Terminal velocity:	The maximum rate at which an object can fall - theoretically it will start to fall at a slow rate and will accelerate until it reaches its maximum fall rate or terminal velocity
Therophyte:	Annual; or plant that dies after seed production and completes its entire life cycle within one year
Tissue density:	Is defined as the dry weight per unit volume
Transient:	Seeds that persist in the soil for less than one year, often much less
Trial:	Each separate experiment or site or individual on which different replicate measurements are performed
Turgor:	Large positive internal pressure a plant can build up in the cells. Turgor has a decisive influence on the maintenance of the rigidity and stability of plant tissues
Turion:	Detachable over-wintering bud composed by tightly arranged leaves filled by storage compounds, formed in axially or apical position by some water plants; turions usually have dormancy and need to pass through winter conditions to re-growth
Turions:	An overwintering structure that is scaley or often thick and fleshy that detaches, and then germinates or starts growth in the spring.
Tussock plant:	Plants forming mats or tufts - often refers to a short plant with many stems or branches forming a cushion-like appearance
Twines:	A climbing plant with no tendrils or suckers, in which the stem winds around other plants or objects for support
UTM:	The Universal Transverse Mercator projection is designed to provide a single grid system that can be applied to the surface of the earth. In this projection, the world is divided into 60 north-south zones, each covering a strip 6° wide in longitude. These zones are numbered consecutively beginning with Zone 1, between 180° and 174° west longitude, and progressing eastward to Zone 60, between 174° and 180° east longitude
Vascular parasite:	Non-green plant growing on living, green plants. Indian-pipe (<i>Monotropa uniflora</i>) is a good example of a vascular parasite
Vascular semi-parasite:	Green plant growing attached to other living, green plants. Many plants, such as eastern North American native gerardia (<i>Agalinis purpurea</i>), photosynthesize but also supplement their nutrients by parasitizing other plants
Vertisol:	Soil type with a clayey soil which cracks widely when dry and swells when wet
Vines:	A plant that trails, clings, or twines, and requires support to grow vertically
Xerophyte species:	Plant species adapted to live under very dry conditions
Zoochory:	General dispersal by animals

Main glossaries used:

<http://www.biologie.uni-hamburg.de/b-online>

<http://davesgarden.com>

<http://glossary.gardenweb.com/glossary>

Appendix 4. Classification of species according to their response to pH of the water column.

n = number of observations

ind = indication value: * = preferably; ** = mainly; *** = strictly in this category

gg = weighted mean

Floating and submerged aquatic species

Category		n	ind	gg
I	Soorten van zuur water:			
	Sphagnum species	29	***	4.1
	Utricularia minor	16	**	4.4
	Juncus bulbosus	73	**	4.8
	Ranunculus ololeucos	6	**	4.9
II	Soorten van overwegend zwak zuur water:			
	Hypericum elodes	19	***	5.6
	Littorella uniflora	17	**	5.8
	Luronium natans	31	*	5.8
	Sparganium minimum	9	**	5.8
	Utricularia australis	16	*	5.8
III	Soorten van zwak zuur tot circumneutraal water:			
	Peplis portula	23	**	6.2
	Pilularia globulifera	10	**	6.3
	Callitriche hamulata	25	**	6.4
	Potamogeton polygonifolius	26	***	6.4
	Scirpus fluitans	27	**	6.4
	Echinodorus repens	8	***	6.5
	Myriophyllum alterniflorum	18	***	6.8
	Nymphaea candida	19	**	6.8
	Ranunculus flammula	48	*	6.8
	Ranunculus peltatus	28	**	6.8
	Riccia fluitans	36	*	6.8
	Apium inundatum	15	**	6.9
	Nitella flexilis	12	**	6.9
	Potamogeton natans	128	*	6.9
	Hottonia palustris	52	*	7.1
	Nuphar lutea	108	*	7.1
	Callitriche platycarpa	52	*	7.2
	Eleocharis acicularis	42	*	7.2
	Potamogeton obtusifolius	24	*	7.2
IV	Soorten van circumneutraal tot alkalisch water:			
	Azolla filiculoides	24	*	7.3
	Echinodorus ranunculoides	10	**	7.3
	Elatine hexandra	7	**	7.3
	Elodea canadensis	52	*	7.4
	Potamogeton compressus	22	**	7.4
	Hydrocharis morsus-ranae	83	*	7.5
	Lemna minor	175	*	7.5
	Utricularia vulgaris	24	**	7.5
	Wolffia arrhiza	11	**	7.5
	Chara globularis	20	**	7.6
	Elodea nuttallii	156	*	7.6
	Myriophyllum verticillatum	19	**	7.6
	Potamogeton acutifolius	21	*	7.6
	Potamogeton alpinus	17	*	7.6
	Potamogeton gramineus	22	**	7.6

Floating and submerged aquatic species continued.

Category		n	ind	gg	
IV	Soorten van zuur water:				
	Sphagnum species	29	***	4.1	
	Utricularia minor	16	**	4.4	
	Juncus bulbosus	73	**	4.8	
	Ranunculus ololeucos	6	**	4.9	
	Soorten van overwegend zwak zuur water:				
	Hypericum elodes	19	***	5.6	
	Littorella uniflora	17	**	5.8	
	Luronium natans	31	*	5.8	
	Sparganium minimum	9	**	5.8	
	Utricularia australis	16	*	5.8	
	Soorten van zwak zuur tot circumneutraal water:				
	Peplis portula	23	**	6.2	
	Pilularia globulifera	10	**	6.3	
	Callitriche hamulata	25	**	6.4	
	Potamogeton polygonifolius	26	***	6.4	
	Scirpus fluitans	27	**	6.4	
	Echinodorus repens	8	***	6.5	
	Myriophyllum alterniflorum	18	***	6.8	
	Nymphaea candida	19	**	6.8	
	Ranunculus flammula	48	*	6.8	
	Ranunculus peltatus	28	**	6.8	
	Riccia fluitans	36	*	6.8	
V	Apium inundatum	15	**	6.9	
	Nitella flexilis	12	**	6.9	
	Potamogeton natans	128	*	6.9	
	Hottonia palustris	52	*	7.1	
	Nuphar lutea	108	*	7.1	
	Callitriche platycarpa	52	*	7.2	
	Eleocharis acicularis	42	*	7.2	
	Potamogeton obtusifolius	24	*	7.2	
VI	Soorten van circumneutraal tot alkalisch water:				
	Azolla filiculoides	24	*	7.3	
	Echinodorus ranunculoides	10	**	7.3	
	Elatine hexandra	7	**	7.3	
	Elodea canadensis	52	*	7.4	
	Potamogeton compressus	22	**	7.4	
	Hydrocharis morsus-ranae	83	*	7.5	
	Lemna minor	175	*	7.5	
	Utricularia vulgaris	24	**	7.5	
	Wolffia arrhiza	11	**	7.5	
	Chara globularis	20	**	7.6	
	Elodea nuttallii	156	*	7.6	
	Myriophyllum verticillatum	19	**	7.6	
	Potamogeton acutifolius	21	*	7.6	
	Potamogeton alpinus	17	*	7.6	
	Potamogeton gramineus	22	**	7.6	

Emergent aquatic species

Category

		n	ind	gg
I	Soorten van zuur water:			
	Eriophorum angustifolium	18	***	4.1
	Eleocharis multicaulis	18	**	4.5
	Carex rostrata	41	**	4.9
II	Soorten van overwegend zwak zuur water:			
	Potentilla palustris	23	**	5.2
	Hydrocotyle vulgaris	60	*	5.5
	Juncus effusus	90	*	5.6
	Menyanthes trifoliata	12	**	5.7
	Scirpus lacustris	40	**	5.7
III	Soorten van zwak zuur tot circumneutraal water:			
	Cladium mariscus	10	**	6.1
	Typha angustifolia	31	*	6.7
	Iris pseudacoris	42	*	6.9
	Acorus calamus	25	***	7.0
	Sparganium emersum	62	***	7.0
	Alisma plantago-aquatica	147	*	7.1
	Cicuta virosa	25	**	7.2
IV	Soorten van circumneutraal tot alkalisch water:			
	Eleocharis palustris	89	*	7.3
	Equisetum fluviatile	62	*	7.3
	Rumex hydrolapathum	42	*	7.3
	Mentha aquatica	66	*	7.4
	Oenanthe aquatica	30	*	7.4
	Phalaris arundinacea	33	**	7.4
	Rorippa amphibia	58	**	7.5
	Sium erectum	64	*	7.5
	Glyceria maxima	145	**	7.6
	Sium latifolium	9	***	7.6
	Butomus umbellatus	55	**	7.7
	Sagittaria sagittifolia	81	**	7.7
	Sparganium erectum	105	**	7.7
	Nasturtium microphyllum	38	**	7.8
	Oenanthe fistulosa	26	**	7.8
	Polygonum amphibium	92	**	7.8
	Ranunculus sceleratus	31	**	7.9
	Alisma lanceolatum	20	**	8.0
V	Soorten van alkalisch water:			
	Veronica catenata	20	**	8.2
	Scirpus tabernaemontani	8	***	8.5
	Scirpus maritimus	18	***	8.6
VI	Indifferente soorten:			
	Juncus articulatus	54		6.8
	Typha latifolia	63		7.0
	Phragmites australis	122		7.1