1

Vegetation ecology – an overview

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1.1 Vegetation ecology, vegetation and plant community

1.1.1 Vegetation, phytocoenose, plant community

Vegetation ecology, the study of the plant cover and its relationships with the environment, also called synecology, is a complex scientific undertaking, both regarding the overwhelming variation of its object of study in space and time, and its intricate interactions with abiotic and biotic factors. It is also a very modern science with important applications in well-known social activities, notably nature management, in particular the preservation of biodiversity, sustainable use of natural resources, and detecting 'global change' in the plant cover of the Earth.

Vegetation, the central object of study in vegetation ecology, can be loosely defined as a system of largely spontaneously growing plants. Not all growing plants form vegetation; for instance, a sown corn field or a flowerbed in a garden do not. But the weeds surrounding such plants do form vegetation. A pine plantation will become vegetation after some years of spontaneous growth of the pine trees and the subsequent development of an understorey.

From the early 19th century on, vegetation scientists have studied pieces of vegetation which they considered samples of a plant community (see Mueller-Dombois & Ellenberg 1974; Allen & Hoekstra 1992). Intuitively, and later on explicitly, such stands were selected on the basis of uniformity and discreteness. The vegetation included in the sample should look uniform and should be discernable from surrounding vegetation. From early on, plant communities have been discussed as possibly or certainly integrated units which can be studied as such and classified.

In order to elucidate these points a distinction is necessary between concrete stands of vegetation and the abstract concept of the plant community, a distinction not explicitly found in the works of most early European and American vegetation scientists, but characteristic of the Braun-Blanquet approach, i.e. phytosociology as it was developed in Central Europe, notably by J. Braun-Blanquet, with a strong emphasis on typology, the establishment of plant community types based on descriptions of stands (called *relevés*).

Westhoff & van der Maarel (1978) proposed to reserve the term 'phytocoenose' for the concrete stand of vegetation; their definition may be reformulated as 'a piece of vegetation in a uniform environment with a relatively uniform floristic composition and structure that is distinct from the surrounding vegetation'. The corresponding definition of the abstract plant community or phytocoenon is a type of phytocoenose derived from the characterization of a group of phytocoenoses corresponding with each other in all characters that are considered typologically relevant. A plant community can be conveniently studied while separated from its abiotic and biotic environment with which it forms an ecosystem, even if this separation is artificial. Conceptually this can be solved by extrapolating a phytocoenose to a biocoenose by including all other organisms interacting with the above-ground and below-ground parts of the phytocoenose. For a community of birds, insects, molluscs or any other taxonomic group under study (see Barkman 1978) we adopt the term taxocoenosis and for all organisms included in a part of the ecosystem, e.g. all on a certain trophic level or in one layer of vegetation, the term merocoenose can be used (Westhoff & van der Maarel 1978).

As follows from the definition, the delimitation in the field of phytocoenoses is based on distinctiveness and uniformity. Distinctiveness of a stand has been much discussed and interpreted. Distinctiveness implies discontinuity towards the surrounding vegetation. This can be environmentally obvious, for example in the case of a depression in a dry area, or, in a man-made landscape, roadside vegetation between the road and a ditch. However, more usually the distribution of the local plant populations should be checked. This has been actual since H.A. Gleason (e.g. 1926) observed that species are 'individualistically' distributed along omni-present environmental gradients and thus cannot form bounded communities (Nicholson & McIntosh 2002). Note that this observation referred to stands of vegetation, even if the word 'community' was used! The wealth of literature on ordination (see Chapter 2) offered ample proof of the 'continuum concept of vegetation' (McIntosh, see Nicholson & McIntosh 2002).

Gleason and many of his adherers were of the opinion that plant species could not form integrated communities because of their individualistic behaviour and criticized the community concept of F.E. Clements (e.g. 1916; see also Mueller-Dombois & Ellenberg 1974), the pioneer in succession theory, who compared the community with an organism and, apparently, recognized plant community units in the field. However, this 'holistic approach' to the plant community had little to do with the recognition of phytocoenoses in the field.

Shipley & Keddy (1987) simplified the controversy by reducing it to the occurrence of different boundary patterns in the field. They devised a field method to test the 'individualistic and community-unit concepts as falsifiable hypotheses'. They detected the concentration of species distribution boundaries at certain points along environmental gradients. In their study – as in other studies – boundary clusters are found in some cases and not in others. Coincidence of distribution boundaries occur at a steep part of an environmental gradient, and at places with a sharp spatial boundary or strong fluctuations in environmental conditions.

The occurrence of different boundary situations as such is of theoretical importance. They can be linked to the two types of boundary distinguished by van C.G. van Leeuwen and put in a vegetation ecological framework by van der Maarel (e.g. 1990). The first type is the limes convergens which can be identified with ecotones s.s. or tension zones. Here species boundaries can be determined strictly by abiotic conditions, but interference between species may play a part (e.g. Shipley & Keddy 1987), and the ecotone may also be caused or sharpened by plants, the so-called vegetation switch (Wilson & Agnew 1992). The opposite type of boundary, limes divergens or ecocline, is typically what we now call a gradient situation where species reach local distribution boundaries in an 'individualistic' way (van der Maarel 1990).

Despite the general appreciation of the individualistic character of species distributions, Gleason himself has never doubted the reality of plant communities. He even used the term association – albeit in a different way from European phytosociologists. Later 'Gleasonians' also recognized that 'there is a certain pattern to the vegetation with more or less similar groups of species recurring from place to place' (Curtis 1959). This was further elucidated by R.H. Whittaker (e.g. 1978; see also Mueller-Dombois & Ellenberg 1974). It is thus quite possible to arrive at plant community types by comparing phytocoenoses which may lack sharp boundaries – or/and floristic uniformity – but which appear to be sufficiently similar. The same situation occurs in soil science.

Unlike distinctiveness, the aspect of uniformity has been more generally accepted as a prerequisite for the plant community. Most vegetation ecologists agree on a certain uniformity a phytocoenose should show in order to be included in any plant community study. A check on the uniformity would include that, at least over a certain area, the vegetation has the same appearance, physiognomy, i.e. the same height and the same plant species in a dominant position. In addition the floristic composition should not vary too much. In very few cases quantitative checks have been developed, such as in the school of Curtis (e.g. 1959) where quadrants of a stand-to-be were compared with a $\chi 2$ test for homogeneity (note that statistical homogeneity would imply a random distribution of plants over the stand and this restriction is too rigorous; therefore the term uniformity is preferred, even if its test is not quantitative). Together with the vegetation the environment is checked for obvious variation, for instance water level.

Even Gleason, although convinced of the continuity in vegetational variation (see Nicholson & McIntosh 2002), considered uniformity as essential. However, Gleason and others have also recognized that stands of vegetation are seldom uniform. Apparently a certain degree of variation within a phytocoenose is generally accepted. See further Chapter 2.

1.1.2 Plant communities: integrated, discrete units?

Within the neutral definitions of plant community and phytocoenose, quite different ideas and opinions on the essence of the plant community have been expressed since the early 20th century and the discussion is still going on. The above-mentioned controversy between Clements and Gleason has been an important element in this discussion and also a confusing one because it has not always been clear whether statements referred to the phytocoenose or the phytocoenon level. As a concluding remark on this controversy and an introduction to this section, an original interpretation of the difference between the two masters by Allen & Hoekstra (1992) and a comment on this interpretation will follow. The interpretation is based on the differences in the landscapes the two grew up in: Clements was brought up in the prairie landscape of Nebraska and viewed plant communities as units from horseback, while Gleason walked through the forest, from tree to tree, aware of the small-scale differences within the community. Thus, the different environments may have had a decisive influence on their 'perspective'.

However, two outstanding European contemporaries of Clements and Gleason do not fit this interpretation at all! The Russian plant ecologist G.I. Ramenskiy, who is generally considered the father of ordination and who was a Gleasonian *avant la lettre*, demonstrated the individuality of species distributions along gradients with meadow vegetation. On the other hand, the Finnish forest ecologist A.K. Cajander developed an authoritative typology of Finnish forests (e.g. Trass & Malmer 1978). Apparently, emphasizing continuities or rather discontinuities can be done in any plant community type and this has to do with intellectual attitude rather than upbringing and field experience.

The ideas of Clements and Gleason can be seen as different concepts of the plant community. Westhoff & van der Maarel (1978) distinguished them from each other as 'organismal concept' and 'individualistic concept', respectively, and from two other concepts: the 'social structure' concept and the 'population structure' concept. The concept of social structure goes back to J.K. Paczoski (see Braun-Blanquet 1932) and early Russian authors, who recognized the multitude of interactions between species, such as competition, symbiosis and saprophytism. The population structure was highlighted by R.H. Whittaker (e.g. Whittaker 1975; White 1985). It added to the community concept that the properties of each participating plant species are not only determined by interactions between species but also within species.

More recently, ecologists became interested in the possibility (for others the necessity) that a plant community has (must have) 'emergent properties', causing the whole to be more than the sum of its parts. One of the few properties investigated with this idea in mind was the development of dominance and diversity. Wilson *et al.* (1998) considered that relative abundance distributions are 'an important feature of community structure', and Wilson (1999a) discussed different types of assembly rule for plant communities, based on (i) the performance of individual species, (ii) species numbers, (iii) plant characters (traits) and (iv) species abundance relations, while emphasizing the need to compare actual community properties with a null model assuming the absence of such rules. Weiher & Keddy (1999) highlighted the relevance of constraints in the representation of traits in relation to environmental variation and suggested that traits related to the availability of mineral resources, such as maximum biomass and leaf shape, are more tightly constrained as soil fertility increases. They proposed the term 'assembly rules' as a key concept. They suggest that the plant community needs more structure, 'order', if more energy flows through the system. Finally, Grime (2001) paid attention to the mechanisms of plant community assembly. He concentrated on dominance-diversity relations while dividing the participating species into dominant, subordinate and transient, and taking into account the different plant functional types which play a part. When we look at the plant community as a component of an ecosystem, overall community characteristics such as a certain level of evapotranspiration and biomass production are considered emergent properties as well (Chapter 3).

One or more of these different plant community concepts are reflected in the many plant community definitions available. The definition by Westhoff & van der Maarel (1978) is representative of phytosociology as it was developed in Central Europe, notably by J. Braun-Blanquet, and in Northern Europe by G.E. Du Rietz. However, it also reflects ideas from early Anglo-American plant ecology, both in Great Britain (A.G. Tansley) and the USA (F.E. Clements), notably the emphasis on the interrelations between community and environment and on species interactions. The definition is in fact a double one because of the separation between concrete and abstract units (see above). The concrete phytocoenose is defined as 'a part of a vegetation consisting of interacting populations growing in a uniform environment and showing a floristic composition and structure that is relatively uniform and distinct from the surrounding vegetation'.

Several later definitions of the plant community reflected the outcome of the more recent debates on the holistic and individualistic concepts, and on the reality of emergent properties. Looijen & van Andel (1999) reviewed some community definitions (but not the above-mentioned one) and focused on problems of ambiguity and distinctiveness. They tried to cope with this problem by redefining the community as 'a set of individuals that occur in the intersection of the areas occupied by populations of these species'. The attempt to spatially delimit a community in this way is theoretically possible but in practice it will fail; also, the delimitation of population boundaries is dependent on the scale of observation (Parker 2001). Parker developed a 'focal-individual model' of a community, which is based on a web of interactions between individuals. According to this model the plant community has no fixed boundaries, neither in space nor in time. The 'phenomenological' definition by Grootjans *et al.* (1996) tries to avoid any element of discussion but maintains the need for a spatial limit. They add a time dimension because of the changes over time of a community which is not necessarily undergoing succession: 'largely spontaneously growing plant individuals which are present within a distinguishable space-time unit'.

In view of these comments, the 1978 definition should be adapted. First, in extreme environments, the representatives of one taxonomical group under study, for instance vascular plants, may belong to only one species, for instance *Salicornia europaea* in European low salt marshes or *Ipomoea pes-caprae* on tropical beaches. So we had better delete the implicit assumption that at least two species are involved. Second, it may be realistic to avoid a discussion on whether the boundary of a phytocoenosis coincides with the formal or actual boundary of the populations of participating species. Third, it may not be necessary to include interactions. For most of us these are obvious and universal, but theoretical cases of plants growing together without interactions should not be excluded a priori. In conclusion the following definition may be presented:

> a phytocoenosis is a piece of vegetation in a uniform environment with a relatively uniform floristic composition and structure that is distinct from the surrounding vegetation.

1.1.3 Plant communities and plant community types

From the phytocoenosis to the plant community is not only moving from analysis to typology and from the concrete to the abstract, it is also changing the perspective from a neutral description of the local plant cover to a certain conception of the community.

Plant community types must be based on characteristics analysed in phytocoenoses. Naturally, these are derived from the plant species present. Originally, the decisive characteristic was the physiognomy, i.e. the dominance of certain growth forms such as trees, shrubs and grasses. The different physiognomic types were called formations and were usually described for large areas by plant geographers, such as E. Warming (see Mueller-Dombois & Ellenberg 1974). Later on the combination of plant species, the floristic composition, became decisive, albeit in combination with physiognomy (implicitly or explicitly). For this community type the term association became standard under the definition adopted at the 1910 Botanical Congress (see section 1.1.1): 'A plant community of definitive floristic composition, presenting a uniform physiognomy, and growing in uniform habitat conditions. The association is the fundamental unit of synecology' (see Westhoff & van der Maarel 1978).

The idea of a community type can be conceived irrespective of boundaries, either between phytocoenoses in the field or between phytocoena in environmental or ordination space. R. Tüxen considered a type as an ideal concept – in line with German philosophers – which could empirically be recognized as a 'correlation concentrate'. Tüxen's idea was elaborated by H. von Glahn who distinguished three steps in classification: (i) identification, through reconnaissance and comparison; (ii) elaboration of a maximal correlative concentration, i.e. first of vegetation, second of environmental characteristics, through tabular treatment (and nowadays multivariate methods); and (iii) systematic categorization, i.e. arranging the type in a system of plant communities (see Westhoff & van der Maarel 1978). The concise description of the classification process by Whittaker (e.g. 1978) came very close to this European approach. See further Chapter 4.

1.1.4 Above-ground and below-ground components of the plant community

Vegetation studies are usually restricted to the above-ground components, even if it is known long since (see, e.g. Braun-Blanquet 1932) that the below-ground components are of decisive importance for the anchoring of plants, the uptake of water and nutrients, and the storage of photosynthates. Most of the large biomass is made up by roots (including storage organs such as corms, bulbs, tubers and crowns, showing stratification and occurring in various growth forms) (e.g. McMichael & Persson 1991), rhizomes (horizontal stems sending out shoots upward and roots downward) and seeds. It would be logical, although technically complicated and inevitably semi-destructive, to include below-ground components in the definition and description of plant communities. Nevertheless this has not become common practice, not even for the soil seed bank (see, however, Chapter 6).

Also, root-related phenomena such as nitrogen-fixing and and mycorrhizal symbioses are well known as important but they were only recently included in vegetation studies (see Chapter 11). Evidently, the dense contacts between roots, biological turnover (through biomass consumption and decomposition, humus formation and partial re-use of mineralized components) and nutrient cycling are convincing contributions to the notion of the integrated plant community.

1.1.5 Vegetation observed at different spatial and temporal scales and levels of integration

The plant community as defined above is a realistic concept only at a certain scale of observation, i.e. the scale at which it is possible to judge the relative uniformity and distinctness. This 'community scale' will vary with the structure of the community, from some m^2 for short grassland to several thousand m^2 in giant forest. Within the relative uniformity many plant communities show differentiation, both vertically and horizontally. The vertical differentiation is most pronounced in woody vegetation where the different layers – tree, shrub, herb and moss layers – are usually described separately. Particularly in Fennoscandia such layers were found to occur independently of each other, for instance a moss layer of a certain composition could occur both in heathland and pine forest. Horizontal differentiation arises through animal excrements, bark formation on trees, fallen trees, dead shrubs and grasses. For these partial phytocoenoses and other microcommunities of other organisms than vascular plants, mosses and lichens (as usually included in vegetation studies), the term *synusia* (plural *synusiae*) has come into existence, largely through the work of H. Gams (see Barkman 1978). Such microcommunities are dependent on the phytocoenosis they form part of – and are therefore also indicated as dependent communities – but are units in their own right. An example is the work of J.J. Barkman on microcommunities within juniper scrub, formally described as *Dicrano-Juniperetum*, which differ in floristic composition and particularly in microclimate (Stoutjesdijk & Barkman 1992).

Many of these synusiae have been subjected to formal classification and environmental characterization (Westhoff & van der Maarel 1978). Many microcommunities result from internal changes in the community, including the natural death of plants, animal activities and other disturbances.

Plant communities are also part of larger units. In the usual hierarchy the next higher unit above the community is the ecosystem, which in its turn is part of a **biome**, a formation together with its fauna and environment. In vegetation ecology communities are rather considered as components of landscape units (**ecotopes**). Mueller-Dombois & Ellenberg (1974) distinguish four types of community complex:

1 *Mosaic complex*, such as the hummock-hollow complex in bogs;
2 *Zonation complex* along a local gradient, e.g. a lake shore;
3 *Vegetation region*, roughly equivalent to a formation;
4 *Vegetation belt*, a zonation complex along an elevational gradient, *inter alia* a mountain.

In the Braun-Blanquet approach a formal typology of such units has been developed by R. Tüxen, based on the analysis of the occurrence of associations and other syntaxa and distinguishing characteristic syntaxon combinations, so-called **sigma-syntaxa** or **sigmeta**. Such vegetation complexes are united into **geosigmeta**, being the phytosociological characterization of larger landscape types (see Schwabe 1989; Dierschke 1994).

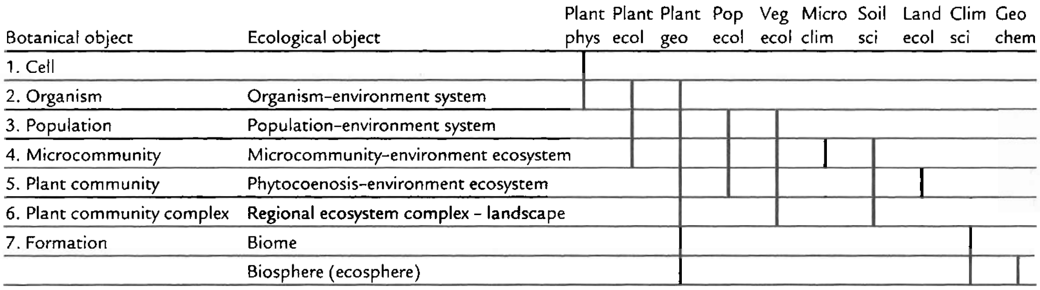

Fig. 1.1 Objects of botanical, ecological and environmental studies – plant physiology; plant ecology; plant geography; population ecology; microclimate studies; vegetation ecology; soil science; landscape ecology; climatology; geochemistry – at different levels of organization and different scales of observations.

Textbooks usually present 'levels of organization': for instance Allen & Hoekstra (1992): 1. Cell ς, 2. Organism ς, 3. Population ς, 4. Community ς, 5. Ecosystem ς, 6. Landscape ς, 7. Biome ς, 8. Biosphere. However, the objects of study arranged in such sequences are not all comparable. Even if plant organisms and populations appear as community constituents in many community definitions, they are not organizational subunits of ecosystems.

We should in fact distinguish two sequences (Fig. 1.1). Moreover, as Allen & Hoekstra (1992) made clear, there is some confusion between level of organization and scale of observation which run parallel, but only to a certain extent. They give the (slightly exaggerated) example of moss populations (level 3) on a dead tree (level 2) in a forest (4) which occur in a moss community complex (6) while the organisms in the rotting log form an ecosystem (5). What they mean is that at one scale of observation quite different levels of organization are studied. Conversely, different scales of observation can be included at one level of organization. A vegetation ecologist may study quadrats of 1 m^2 in short grassland or moss communities and plots of 10^4 m^2 in rain forest. Detailed vegetation maps have been made of only 10^{-2} km^2 while the phytosociological vegetation map of Europe covers *c.* 10^7 km^2.

Finally, as also indicated in Fig. 1.1, each discipline or approach involved in the study of plants and ecosystems, respectively, usually extends beyond its 'central' level of organization. The intricate relations between organization and scale are extended by including temporal scales (section 1.7). A summary of these considerations is presented in Fig. 1.2, which combines a scheme relating levels of organization to temporal scales of vegetation dynamics with a scheme relating spatial to temporal research scales. Essential elements in the hierarchical approach of organization levels and scales are the recognition of (i) mosaic structures, with elements of a mosaic of a smaller grain size being mosaics of their own at a larger grain size; (ii) different processes governing patterns at different scales; and (iii) different degrees of correlation between vegetational and environmental variables at different grain sizes.

	Fluctuation	Gap, patch dynamics	Cyclic succession	Secondary succession	Primary succession	Secular succession
Organism–environment	10^{-1}–1 yr 10^{-2}–10 m	1–10 yr 10^{-2}–10 m				
Population–environment	1 yr 1–10 m	1–10 yr 10–10^{2} m	1–10^{2} yr 10–10^{2} m	10–10^{2} yr 10–10^{2} m	10–10^{3} yr 10–10^{2} m	
Microcommunity–environment	1 yr 1–10 m	1–10 yr 10–10^{2} m				
Phytocoenosis–environment	1 yr 1–10 m	1–10 yr 10–10^{2} m	1–10^{2} yr 10–10^{2} m	10–10^{2} yr 10–10^{2} m	10–10^{3} yr 10–10^{2} m	
Regional landscape				10^{0}–10^{2} yr 10^{2}–10^{4} m	10^{2}–10^{3} yr 10^{2}–10^{4} m	10^{2}–10^{4} yr 10^{2}–10^{4} m
Biome						10^{3}–10^{6} yr 10^{4}–10^{6} m
Biosphere						10^{6}–10^{7} yr

Fig. 1.2 Spatial scales (m) and temporal scales (yr) of studies of ecological objects and their dynamics, based on adapted schemes of van der Maarel (1988) and Gurevitch *et al.* (2002).

1.1.6 Vegetation survey and sampling

Whatever our aim, approach and scale of observation, vegetation, whether loosely defined or approached as a phytocoenosis or a unit on a higher level of integration, should be described and measured. Vegetation characteristics are either derived from plant morphological characters, usually called **structure**, or from the plant species recognized, the **floristic composition**. Our description or analysis will only include a relatively small piece of vegetation which is considered representative of a larger unit. This leads to the issue of **sampling**.

In statistics the members of the universe can usually be identified without problems, e.g. the individuals of a crop and the trees in a plantation. In vegetation ecology this is much less simple. Moreover, the variables we measure and compare are partly composite and difficult to measure, notably the species composition, or only measurable through destructive sampling, notably above-ground biomass (and most below-ground characteristics as well).

Our universe to be sampled is the total area occupied by a certain type of vegetation. However, (i) it is difficult to identify this type, even if we have some previous knowledge about it; and (ii) this total area can be too large to be encompassed in one sampling. The first problem can be approached as follows – partly following the classical textbook by Cain & Castro (1959): sampling is preceded by **reconnaissance,** an inspection of a local area where the vegetation pattern with its dominant species and species combinations is recognized and related to topography and other apparent environmental conditions. The second problem can be solved by restricting ourselves to a 'local universe'.

The reconnaissance is followed by a **primary survey,** including a brief description of the dominant vegetation types. Of course the areal extent and amount of detail will depend on the specific objective of the study. Amongst the many different objectives four common ones are:

1 Phytosociological, with the intention to analyse phytocoenoses for a subsequent community classification, either of one particular type, or, preferably, of the all the types locally recognized;

2 Ecological, with the intention to correlate the local variation in vegetation composition with variation in environmental factors; ideally ecological and phytosociological sampling are integrated;

3 Dynamical, with the intention to establish or revisit pieces of vegetation for describing vegetation changes;

4 Applied, for instance to investigate the effect of a management measure.

The next phase in the analysis is an **intensive survey**, usually including a more complete description and measurement of the structure and species composition of the vegetation, and analysis of soil and microclimate characteristics.

In any case a unit of investigation has to be located and delimited. Since this is usually a well-delineated piece of vegetation the indication plot or **sample plot** is obvious. Other terms in use include stand, site and **quadrat**, a sample area within a frame, usually a square. For time series of observations the terms **permanent plot** or **permanent quadrat** are in use. Often terms for the analysis of the plot – analysis itself, sample, record, relevé – are used as equivalent to the sample plot. We better stick to the terms **plot** and **sample**, while adding the term **relevé** (French for record) for the special case it was originally meant for: a phytosociological record of a phytocoenosis for classification purposes.

As to the phytosociological sampling objective, the Braun-Blanquet approach has often been criticized (e.g. by Mueller-Dombois & Ellenberg 1974) for a neglect of the primary survey and a 'subjective' selection of sample plots which are recognized as representative stands of a plant community type from which relevés have been taken elsewhere. The problem with selective sampling is not so much that the sample is not representative but rather that other, related stands of vegetation are not sampled. However, the personal bias of phytosociologists and the lack of representative samples will be compensated for if larger numbers of samples of a certain type are available. This is the case in most European countries. For example, the survey of British plant communities (Rodwell 1991–2000) was based on 35,000 samples. In the survey of plant communities of The Netherlands (Schaminée *et al.* 1995–1999) lower units are documented by up to several hundreds of relevés, and higher units by several thousands. The database behind this survey, which is still growing, contained 350,000 samples (relevés) in 2001, and software to handle such huge data sets has been developed (Hennekens & Schaminée 2001).

If vegetation analysis proceeds on the basis of sample plots the plot is usually analysed completely, at least regarding species composition ('**single-plot analysis**'). In certain cases and in certain traditions **multiple-plot analysis** is preferred on the basis of systematically or randomly located small squares.

In cases where the delineation of a sample plot is not possible – or not desired – so-called **plotless sampling** can be applied (see Mueller-Dombois & Ellenberg 1974). This proceeds along lines where contacts with vegetation are recorded at regular distances, or with networks of points, or with small quadrats. Lines, points or quadrats can be laid out at random, in a systematical way, or in a combination (stratified random sampling). The formerly practised vegetation analysis in Northern Europe (e.g. by Du Rietz 1931; see also Trass & Malmer 1978) can be considered as a transition between multiple-plot analysis s.s. and plotless sampling.

1.1.7 Size of the sample plot; minimal area

When an intensive survey is carried out in a sample plot the size of this plot has to be determined. Usually the entire local phytocoenosis (according to its definition) is inspected as to uniform environment, floristic composition and structure, as distinct from the surrounding vegetation. Depending on the type of vegetation the area covered may vary from a few m^2 to several ha. If species composition is one of the descriptors, the sample plot should not be too small because only a few species would then be included. This leads to a discussion of the concept of minimal area, defined (Westhoff & van der Maarel 1978) as a 'representative area, as an adequate sample of species of regular occurrence', which is related to the total number of species in the stand. A definition such as that of Mueller-Dombois & Ellenberg (1974): 'the smallest area on which the species composition of the community in question is adequately represented' is what Westhoff & van der Maarel called a 'synthetic minimal area'. Such an area cannot be determined without previous knowledge of the community sampled; this can have been acquainted during the successive approximation.

To this end the determination of a species-area relationship has been recommended, both in classical phytosociology (Braun-Blanquet 1932) and in Anglo-American textbooks of vegetation analysis (Cain & Castro 1959). The usual way of determining this relation is to start with a very small quadrat, count the number of species, enlarge the quadrat, usually with a factor 2, count the number of additional species, etc. until the boundaries of the local stand are reached. Instead of such a series of nested plots randomly located plots of increasing size are theoretically preferred and, still better, several such series should be analysed (see Dietvorst *et al.* 1982 for references). The species-area relation is usually plotted as number of species against area. The resulting curve is quasi-asymptotic and the suggestion was to consider as minimal area an area beyond which the curve levels off.

Although this procedure has been long criticized as it is subjective, i.e. dependent on the choice of the ratio of the *y*-axis to the *x*-axis, it has remained standard practice in phytosociology, partly under the influence of Tüxen (1970) who collected many species-area curves from the literature and spoke of a '**saturated community**' if the minimal area had been reached. It is curious that the decisive arguments against this approach had already been provided by the Swedes O. Arrhenius, L.G. Romell and H. Kylin before Braun-Blanquet had published the first edition of his textbook. They had developed three models of species-area relationships, in graphical terms the log-log, the linear-log and the linear-linear relation, respectively. The third relation, the real saturation curve was only found in species-poor communities, while the first was fully developed by Preston (1962) and the second is well-known as the basis for the α-diversity of Fisher, as elaborated by Williams (1964). Braun-Blanquet (1932) mentioned these models but he was only vaguely aware of the repercussions for the minimal area approach by confirming that Kylin's model of a linear-linear species-area relation was appropriate for the minimal area approach but by not realizing that the other two models, which are much more commonly applicable to natural communities, question the validity of the species-area based determination of the minimal area (see Westhoff & van der Maarel 1978).

While these considerations on minimal area refer to numbers of species represented, the area to be sampled should also be large enough to represent the abundance relations of the participating species. This idea was expressed for the first time by E. Meijer Drees in 1954, who distinguished between qualitative (species-area-based) and quantitative minimal area. In his case the latter concept referred to the area where most of the timber species in tropical rain forest stands were represented with trees of more than 100 cm circumference.

Another quantitative approach had already been proposed by G.E. Du Rietz in the 1920s: the frequency of species in series of quadrats of increasing size is determined and the number of 'constant' species (with frequency of at least 90%) is plotted against area. M. Gounot, C. Roux and other French investigators calculated the floristic similarity between quadrats of increasing size. However, none of these more sophisticated methods produced saturation curves in most cases. Dietvorst *et al.* (1982; also for references) elaborated the similarity approach by comparing values with the maximum similarity values obtained in models with 5000 cells with varying numbers of species and mean cover. Critical quantitative similarity levels varied from more than 90% in salt marsh to 50–80% in open sand dune vegetation; qualitative levels from 50% in *Calluna* heath to 80% in salt marsh. The highest of the two corresponding minimal area levels was chosen as minimal area. These values were within the range indicated by Westhoff & van der Maarel (1978). It was also shown that the sizes of the two minimal areas are related to species richness and amount of dominance (Table 1.1).

Barkman (1989) advocated an additional method by plotting the increase in species number against log area (based on large numbers of replicates). If the increase is zero over short trajectories this would be an indication that the size of some within-community pattern is exceeded. Following E. Meijer Drees and others, he also emphasized the concept of '**biological minimal area**', the area needed for a local phytocoenosis to maintain itself, including patch dynamics. For forests this area

Table 1.1 Relation between the size of the qualitative (MA_{qual}) and quantitative (MA_{quan}) minimal area in relation to species richness and mean species dominance. Based on Dietvorst *et al.* (1982). Reproduced by permission of Kluwer Academic Publishers.

		Mean species dominance	
		High	Low
Species richness	High	MA_{quan} small $MA_{qual} >> MA_{quan}$	MA_{quan} large MA_{qual} large
	Low	MA_{quan} small MA_{qual} small	MA_{quan} large $MA_{qual} < MA_{quan}$

could be several ha. The species richness of the total vegetation stand is the same as what nowadays is called the community species pool (Zobel *et al.* 1998).

In conclusion, a 'minimal area' to be sampled, related to species richness, canopy height and species dominance relations, remains difficult to determine. Instead a 'representative' sampling area should be selected the size of which can be chosen on the basis of field experience with different vegetation types as represented in various textbooks. Table 1.2 presents size intervals for representative sample plots.

Table 1.2 Minimal area values (m^2) for various plant communities, largely according to Westhoff & van der Maarel (1978) with additions, partly following Knapp (1984) and Dierschke (1994). Nomenclature largely according to Rodwell *et al.* (2002). In case of mosaic complexes, e.g. in heathland, bog and forest, intervals refer to the elements of the complex and not to the complex as a whole.

Epiphytic moss and lichen communities		0.1–0.4
Terrestrial moss and lichen communities		1–2
Free-floating aquatic communities (*Lemnetea*)		2–5
Hygrophilous pioneer communitie (*Isoeto-Nanojuncetea*)		2–5
Vegetation of trampled habitats (*Polygono-Poetea annuae*)		2–5
Lower salt marshes (*Thero-Salicornietea*)		4–10
Open dune and sand grasslands (*Koelerio-Corynephoretea*)		4–10
(Sub-)Mediterranean therophyte communities (*Helianthemetea guttati*)		4–10
Heavily managed grasslands (*Cynosurion cristati*)		4–10
Upper salt marshes (*Juncetea maritimi*)		10–25
Rooted floating aquatic communities (*Potametea*)		10–25
Temperate pastures and meadows (*Molinio-Arrhenatheretea*)		10–25
Basiphilous grasslands (*Festuco-Brometea*)		10–25
Ombrotrophic bog vegetation (*Oxycocco-Sphagnetea*)		10–25
Bog-pool and mire vegetation (*Scheuchzerio-Caricetea fuscae*)		10–25
Steppes (*Festuco-Brometea*)		20–50
(Sub-)Alpine calcareous grasslands (*Elyno-Seslerietea*)		20–50
Coastal yellow dune communities (*Ammophiletea*)		20–50
Tall swamp vegetation (*Phragmito-Magnocaricetea*)		20–50
Heathlands (*Calluno-Ulicetea*)		20–50
Weed communities (*Stellarietea mediae*)		40–100
Woodland fringe and gap vegetation		40–100
Perennial ruderal vegetation (*Artemisietea vulgaris*)		40–100
Temperate scrub (*Rhamno-Prunetea*)		40–100
Mediterranean maquis (*Quercetea ilicis*), chaparral		40–100
Mediterranean low scrub (*Cisto-Lavanduletea*)		40–100
Willow and poplar scrub and woodland (*Salicetea purpureae*)		100–250
Fynbos		100–250
Deciduous forest on rich soils in Europe (*Querco-Fagetea*):	herb layer	100–250
Swamp woodland (*Alnetea glutinosae*)		100–250
Coniferous forest (*Vaccinio-Piceetea*)		200–500
Managed deciduous forest on rich soils in Europe (*Querco-Fagetea*):	canopy	200–500
Mature deciduous forest on rich soils in Europe (*Querco-Fagetea*):	canopy	400–1000
Ibid. in North America:	canopy	400–1000
Desert vegetation		400–1000
(Sub-)Tropical dry forest	canopy	400–1000
Tropical secondary forest	canopy	2000–5000
Tropical rain forest	canopy	4000–10,000

1.1.8 Sampling of vegetation characteristics

Vegetation structure and floristic composition are usually measured or estimated on a plant community basis. Barkman (1979) distinguished between **texture**, the composition of morphological elements, and **structure s.s.**, the spatial arrangement of these elements – the temporal arrangement, including **phenology** (see, *inter alia* Mueller-Dombois & Ellenberg 1974; Dierschke 1994), can be included here. However, most ecologists still use structure as a general term.

Four overall measurements, some of them more widely used than others, may be mentioned:

1 **Stratification**, the arrangement of phytomass in layers. Usually a tall tree, low tree, tall shrub, low shrub, dwarf-shrub, tall herb, low herb and moss layer are distinguished if separated from each other. See further, *inter alia*, Mueller-Dombois & Ellenberg (1974).

2 **Cover.** Percentage cover is the relative area occupied by the vertical projection of all aerial parts of plants, as a percentage of the surface area of the sample plot. This can be determined for the vegetation as a whole or for separate layers. Cover is usually estimated by eye, but can also be determined more accurately through the line-intercept method – in sparse vegetation – where contacts between the line and plant parts are counted, or the point-intercept method – in dense short vegetation – where contacts with a cross-wire grid are counted, or the cover pin frame – in dense taller vegetation – where pins are moved vertically downwards and contacts with plant parts are counted (because pins can hit plants at several heights total cover can exceed 100%).

3 **Phytomass.** Total phytomass (= plant biomass) in the plant community, is expressed as dry-weight $g \cdot m^2$, $kg \cdot m^2$ or $t \cdot ha$ ($t \cdot ha^{-1} = 10\ kg \cdot m^2$). Phytomass is usually determined by removing the **standing crop**, the above-ground phytomass during the period of maximal development. The standing crop is related to, but by no means identical to, what is produced during the growing season – which varies from weeks in arctic to 12 months in moist tropical environments. Plant production, i.e. production by **autotrophic plants**, also called **primary production** – to distinguish it from secondary production, which is the transformation of phytomass by heterotrophic organisms, animals and saprobes – is usually expressed in terms of **productivity**, production per time unit, usually $g \cdot m^2 \cdot yr$ (see Chapter 3). The destructive sampling necessary for phytomass measurements usually requires an adapted sampling scheme so that a sufficient area of the same vegetation remains undisturbed.

Phytomass can be determined per layer so that a vertical phytomass profile can be obtained and interpreted in terms of species interactions and light climate (e.g. Fliervoet 1985). Barkman (1988) developed a method and apparatus to determine **phytomass denseness**, and its horizontal and vertical distribution. This method is also destructive, but only small sections of plant mass are cut. Such profiles can be fruitfully linked to measurements of microclimate (Stoutjesdijk & Barkman 1992).

4 **Leaf area index**. The total area of leaf surface (actually photosynthetic surface) expressed in m^2 per m^2 surface area is known as **leaf area index**, LAI; it can be determined per layer and can thus also be used for a refined description of the architecture of vegetation. A derivate characteristic is **specific leaf area**, SLA = leaf (lamina) area

per unit leaf (lamina) dry mass. LAI and cover are related, but no studies of the correlation between the two characteristics for individual species are known to the author.

Next, structural-physiognomic characteristics can be determined. Typical textural characters, as mentioned by Barkman (1979), are leaf size, leaf consistency, leaf orientation, leaf longevity and plant growth form. The consistent analysis (rather the detailed description) of such characters as developed by P. Dansereau, F.R. Fosberg and A.W. Küchler, and life-form categories based on, or elaborated from, C. Raunkiær's system – and summarized by Mueller-Dombois & Ellenberg (1974), Kent & Coker (1992) and Dierschke (1994) – is usually related to the respective classification systems developed. The description of the characteristics and spatial position of organs, as in textural descriptions, including drawings of vegetation profiles, has not become a standard procedure. Structural research rather proceeds via the species composition combined with the allocation of species to life form or other categories.

Structural analysis of above-ground plant parts should be (but is seldom) completed with an analysis of the below-ground parts. For instance, Dierschke (1994) presented examples of root stratification.

1.1.9 Sampling of species characteristics

The species composition of a plant community, the key element in its definition, is described in its simplest form by a list of species occurring in the sample plot. The list is mostly restricted to vascular plants, and almost always to their above-ground parts; often easily recognizable mosses, liverworts and lichens are included. The quantity a species attains can be called its **performance**, but often the term abundance is used, even if this is only one of the following quantitative measures:

1 **Abundance**, the number of individuals on the sample plot. Because individuality in many (clonal) plant species is difficult to determine (see Chapter 5), the concept of **plant unit**, a plant or part of a plant (notably a shoot) behaving like an individual, is needed, if only for a quantitative approach of species diversity based on the distribution of plant units over species (Williams 1964). **Density** is a derivate variable, being the abundance per unit area.

2 **Frequency** is the number of times a species occurs in subplots within the sample plot – or within an undelimited phytocoenosis (formally plottless sampling).

3 **Cover** can be measured species-wise (see section 1.1.8); it is usually estimated along a cover scale. Many scales have been proposed (van der Maarel 1979), some of which more or less linear (e.g. with 10% intervals), some geometrical, e.g. the still-used five-point geometrical Hult–Sernander–Du Rietz scale (after R. Hult, R. Sernander and G.E. Du Rietz) developed during the 1910s by the so-called Uppsala school (see Trass & Malmer 1978).

4 **Cover-abundance** is a combined parameter of cover – in case the cover exceeds a certain level, e.g. 5% – and abundance. This 'total estimate' (Braun-Blanquet 1932) has been both criticized as a wrong combination of two independently varying parameters and praised as a brilliant integrative approach. It reminds us of the **importance value** developed by Curtis (1959), the product of density, frequency and cover, which has been popular in the US for some decades. Several proponents of a combined

cover-abundance estimation have nevertheless found it realistic to convert the abundance categories in the combined scale into approximate cover values. The two combined scales still in use are the Domin or Domin–Krajina scale (after the Czech ecologists K. Domin and V.J. Krajina; see Mueller-Dombois & Ellenberg 1974) and the Braun-Blanquet scale which, in several variants, has been in use since the 1920s. Van der Maarel (1979) suggested an 'ordinal transform' (OTV) scale replacing the modern nine-point Braun-Blanquet scale by the values 1–9, which could be used, if not as arithmetic at least as ordinal values. This scale was also included in Westhoff & van der Maarel (1978) and has found wide acceptance.

Van der Maarel (in Fresco *et al.* 2001) suggested a cover-based interpretation of this scale by replacing the original abundance categories 1–4 by mean cover % values and by interpreting the high ordinal transform values (OTVs) 8 and 9 as corresponding to in reality much higher cover % values than those indicated by the Braun-Blanquet scale, in fact > 100% – because in dense vegetation the dominant species develop phytomass in several vegetation layers (as is in fact measured with the vertical pin method mentioned in section 1.1.8). We can then draw a regression line (as was in fact suggested by Jongman *et al.* 1995) and obtain the equation

$$\mathrm{OTV} = 1.415 \ln C + 2 \tag{1.1}$$

where C the cover value in %. Herewith we would have a fair approximation to a ratio scale, where the means of the cover classes form a geometrical (× 2) series. See Table 1.3.

5 Basal area, the area outline of a plant near the surface, is of particular interest for trees and can be used for tree volume estimations (see Mueller-Dombois & Ellenberg 1974). A related measure is tree diameter at breast height (DBH; at 1.30 m), which is more often used in standard forest descriptions.

6 Phytomass can be measured per species, even if this is a very tedious work. These data can be used to accurately relate species performances to each other and to follow species performances in time series of observations and experiments.

Table 1.3 Extended Braun-Blanquet cover-abundance scale and ordinal transform values (OTV) according to van der Maarel (1979) with interpreted cover value intervals for low cover values. From Fresco *et al.* (2001). Reproduced by permission of the publisher.

Braun-Blanquet	Abundance category	Cover: interpreted interval	OTV cover interval	OTV
	1–3 Individuals	$c \leq 5\%$		1
+	Few individuals	$c \leq 5\%$	$0.5 < c \leq 1.5\%$	2
1	Abundant	$c \leq 5\%$	$1.5 < c \leq 3\%$	3
2m	Very abundant	$c \leq 5\%$	$3 < c \leq 5\%$	4
2a	Irrelevant	$5 < c \leq 12.5\%$		5
2b		$12.5 < c \leq 25\%$		6
3		$25 < c \leq 50\%$		7
4		$50 < c \leq 75\%$		8
5		$c > 75\%$		9

7 **Sociability**, the gregariousness of plant units of a species, has been a standard parameter included in phytosociological relevés (Braun-Blanquet 1932). Five degrees are distinguished, varying from 1 = plant units growing singly to 5 = growing in great crowds over most of the sample plot. However, this parameter has seldom been used in the comparison of relevés, mainly because sociability is species-specific for many species and also because there is no numerical way to treat the data. See also section 1.1.10.

Species data should not only be collected above-ground but also below-ground. Dierschke (1994) presented examples of root:shoot ratio differentiation within a plant community. Titlyanova *et al.* (1999) showed how in steppes the below-ground phytomass (which can store 70% of the net primary production) is more homogeneously distributed, both over the area and over the species. The dominance-diversity curves of 19 species in steppe vegetation based on percentage dry weight contributions of species to green phytomass and below-ground organs are quite different. Where in both cases the top species are *Stipa krylovii* and *Potentilla acaulis*, the other species have different sequences and the below-ground curve is much less steep.

The main use of data on species characteristics is in the classification and ecology of communities, but these data also form the basis for the analysis of vegetation dynamics. For this purpose permanent sample plots can be established which are regularly, preferably annually, investigated. In order to interpret changes in species characteristics the data should be more accurate than in a spatial context. In relevés of permanent plots and in the analysis of chronosequences (section 1.7) a more detailed cover scale can be used. However, to reduce the effects of subjectivity more exact data, notably on phytomass, are preferred.

1.1.10 Standardized phytosociological relevé

In the framework of the European Vegetation Survey a template for common data standards for phytosociological relevés has been proposed (Mucina *et al.* 2000), including area and form of plot, exact location, distinction of vegetation layers, and use of any scale for species quantities which can be converted to the ordinal transform scale.

1.1.11 Spatial pattern analysis

The notion of **pattern** in vegetation has become standard since Watt's (1947) paper on pattern and process in the plant community. The basic idea is that in many communities many plant species occur in **patches** which occur in **mosaics** and that these patches 'are dynamically related to each other'. The occurrence of patches is one of three ways plant units of a species can be located: the clumped or underdispersed distribution. In the opposite case the dispersion is regular (overdispersion). The intermediate situation is a random dispersion – note that in a perfectly homogeneous community all species should have such a dispersion.

There exists a wide variety of methods of pattern detection. Dale (1999) treated most of them.

In one group of methods, presence-absence data of one (or more) plant species are collected in small quadrats, usually located in transects – a line-intercept approach is also possible. The selected size of the quadrats is dependent on the structure of vegetation. In each quadrat the presence, or a quantitative measure, e.g. cover degree, is recorded and the variance of the distribution calculated. Next quadrats are lumped in blocks (pairs, quadruples, etc.) and each time variance is calculated again. The graph of variance against block size may reveal patterns. This method was developed by P. Greig-Smith and K.A. Kershaw in the 1950s. Several statistically elaborated variants have been developed and of which three-term local quadrat variance is recommended by Dale (1999). Here the mean variance between the variance of a block and the sum of two adjacent blocks on either side is calculated.

In another group of methods dating from the 1970s, plants are replaced by a point and the distances of plant points to each other, or to nearest neighbours, or to fixed reference points are determined. The frequency distribution of the distances can reveal patterns. One of the popular statistics is Ripley's *K*, called after the statistician B.D. Ripley (e.g. Haase 1995). This type of method is effective when plant units (notably trees) or patches (in desert vegetation) can be easily individualized; data may be obtained from remote sensing and then large-scale patterns can be detected.

New variants and new methods are regularly being published. As an example of a new method, Dai & van der Maarel (1997) suggested patch-size frequency analysis as an easy, straightforward – but statistically complicated – approach based on presence (or cover) records in transects of small quadrats. Patterns may occur in a hierarchical way: a species may occur in patches of a given size, where the patches may have a clumped dispersion. Also, the size of gaps between patches may show a pattern. Patterns of correlated species dispersions may also be detected. Finally, the pattern of abiotic or biotic parameters possibly show interference with the plant pattern. For example, Dai & van der Maarel found that the plant species *Filipendula vulgaris* showed patches of occurrence with ≥ 5% cover with the same size (*c*. 50 cm diameter) as patches of cow dung in the grazed limestone grassland this species is characteristic of.

1.2 Vegetation and environment: discontinuities and continuities

1.2.1 European and Anglo-American development of vegetation ecology

In Chapter 2 Austin treats vegetation and environment in a coherent way, indeed as vegetation ecology. This term was coined by Mueller-Dombois & Ellenberg (1974) who both were educated in Germany in the ecological tradition of continental-European phytosociology. Anglo-American vegetation ecology has its roots in plant ecology – and is usually called so. Despite this and earlier textbooks, including that of Braun-Blanquet (1932), Anglo-American plant ecology has for some time identified European phytosociology with the mere description of plant communities. This was in the 1940s and 1950s when the 'Braun-Blanquet system' of plant communities became fully developed. Extensive surveys were published in the newly established journal *Vegetatio* and nomenclature rules were discussed. Possibly Anglo-American readers may have concluded that phytosociology was synonymous with rigid community typology. The confusion has since long been resolved. Continental-European vegetation ecology has developed in many directions (e.g. Ellenberg 1988).

Community typology is still important, but nowadays particularly as a pragmatic tool in communication, both between ecologists and between ecology and society. Simultaneously, plant community description has become an appreciated branch of ecology in Anglo-American ecology. In Europe the European Vegetation Survey project, initiated by S. Pignatti, is well under way. It was the obvious next step in 'phytosociological systematics' developed by R. Tüxen and stimulated during many symposia led by him (see Dierschke 1994). The importance of such surveys for society has always been pointed out by Tüxen, who was the father of applied phytosociology. And society is increasingly aware of this importance. For instance, the European project has recently resulted in a very useful and sponsored survey of plant communities each with an English name referring to the type of habitat and distribution area (Rodwell *et al.* 2002).

1.2.2 Discontinuities and continuities; classification and ordination

Austin makes clear that both vegetation and environment are characterized by discontinuities and continuities and that their interrelationships should be described by multivariate methods of ordination and classification. It shows how mainly three paradigms have emerged during the history of vegetation ecology, which we can conveniently label 'association', 'indirect gradient' and 'direct gradient'; the differences between the paradigms are smaller than is often believed and vegetation ecology can further develop when a synthesis of the three paradigms is developed.

The concept of environmental gradient plays a central part here. Where vegetation varies continuously in relation to environmental variation a series of communities would form a **coenocline** (see Westhoff & van der Maarel 1978). The description of clinal variation and particularly the choice of proper ordination methods can be optimized by finding a realistic model of plant species behaviour along the underlying environmental gradients. Where vegetation shows more abrupt transitions numerical classification is appropriate, but again the application of methods can be optimized by adopting a proper species model. In this respect, the concept of **compositional turnover**, i.e. the coming and going of plant species along a gradient, may be mentioned. Through a measure of this turnover the length of a gradient can be estimated. Økland (1990) presented a summary and recommended SD, the number of mean standard deviations of species occurring along the gradient. Formally this measure can only be used if all species are distributed according to a Gaussian response curve, which, as Austin shows, they are not.

As to numerical ordination, Austin treats two methods as representative for the plethora of methods, Correspondence Analysis (CA) and its derivate Canonical Correspondence Analysis (CCA), and Non-metric Multidimensional Scaling (NMDS). CA-CCA has become the standard ordination approach, even if it is based on assumptions which are not often met. It has certainly become so popular because of the effective computer program available. The scaling methods are computationally more complicated, but theoretically to be preferred.

As to numerical classification, Austin treats again two methods, the divisive method TWINSPAN and the agglomerative method UPGMA. Basically both approaches achieve a hierarchical structure, graphically shown as a dendrogram. TWINSPAN is by far the most popular method and its popularity has only grown since it was incorporated in the program TURBOVEG for phytosociological classification of very large data sets (Hennekens & Schaminée 2001). Attractions of these programs are the capacity and speed and the relatively low number of options one has to consider, but this has distracted the attention from their weaknesses: the strictly hierarchical approach and the fact that it is based on Correspondence Analysis, with its problems.

UPGMA and some related methods have been used both for obtaining groups of similar species and groups of similar sample plots. Program TABORD by E. van der Maarel *et al.* and its elaborated version FLEXCLUS by O. van Tongeren (see Jongman *et al.* 1995) are in a way a combination of clustering and ordination with the result presented in an ordered phytosociological table. Essential here is that a cluster structure is searched for on an optimal level of similarity and then ordered, so that the approach is reticulate rather than hierarchical. This is considered a more realistic phytosociological approach and at the same time a step towards the paradigm synthesis advocated by Austin.

1.2.3 Ideas of environment

Under this heading Austin emphasizes the importance of a framework of 'broad environmental factors' which should be developed for any study of vegetation and environment. The special attention paid to climatic and derivate microclimatic factors leads to the notion of the hierarchy of spheres influencing vegetation in this order of impact (see also Chapter 12):

Atmosphere	> Lithosphere	> Hydrosphere	> Pedosphere	> Biosphere
Climate	Bedrock	Groundwater	Soil factors	Fauna
temperature, precipitation				

A useful distinction within the environmental factors is between (i) indirect factors, notably altitude, topography and landform; (ii) direct factors such as temperature, groundwater level and pH – which are determined by indirect factors; and (iii) resource factors such as water availability and nutrients, which are determined by indirect and direct factors. Another distinction is between distal and proximal factors, where the proximal factors are operating directly on the plant. Generally, vegetation ecology is more meaningful if the environmental factors available for vegetation – environment studies are more physiologically relevant.

1.2.4 Ecological characterization of communities by means of indicator values

An additional way of characterizing the environment of a plant community is to use indicator values assigned to the participating plant species. The best known system of values is that of H. Ellenberg (Ellenberg *et al.* 1992), with indicator values for most of the Central European vascular plant species regarding moisture, soil nitrogen status, soil reaction (acidity/lime content), soil chloride concentration, light regime, temperature and continentality. The values generally follow a, typically ordinal, nine-point scale, based on field experience and some measurements. They reflect, as Austin describes it, the ecological behaviour of species, their realized niche. Even if these values are typically a 'distant' approach of the environment, they have been used abundantly, also in north-west Europe. Using them to calculate (weighted) mean values for plots and communities is a calibration problem, discussed by ter Braak (see Jongman *et al.* 1995).

1.3 Vegetation and ecosystems

Leuschner, in Chapter 3 on ecosystems, concentrates his essay on trophic levels between which matter and energy is exchanged. Elaborations of this theme are found particularly in Chapters 10 on plant–herbivore relations and 11 on interactions between plants and soil-dwelling organisms. It is also worth repeating the message on the importance of the below-ground parts of the plant which are parts of the plant community but also the physical link between the biotic and abiotic parts of the ecosystems.

An important part of the primary production ends up in the below-ground plant parts. Here both decomposition and humus formation take place. In an ecosystem in steady state there is a balance between net primary production and organic matter decomposition. This balance is reached in later stages of succession. As Leuschner states, after perturbation an ecosystem can often rapidly regain certain structural properties. As an example, Titlyanova & Mironycheva-Tokareva (1990) described the building up of the below-ground structure during secondary succession in just a few years. On the other hand, the re-development of a steady state in steppe grassland may take 200 yr. This also relates to the actual discussion on the relation between diversity and ecosystem function (Chapter 8).

It is interesting that ecosystem ecologists have no doubt about the reality of emergent properties. It is as if these properties appear clearer, the higher the level of integration is at which we are looking at ecosystems. Ultimately we are facing clear aspects of regulation at the 'Gaia' level of the global ecosystem.

Leuschner finishes his chapter with a treatment of four biogeochemical cycles, of carbon, nitrogen, phosphorus and water. These cycles are studied on the global level and these processes on this level return in Chapter 14.

1.4 Vegetation types and their broad-scale distribution

1.4.1 Physiognomic-ecological classification; formations

In Chapter 4, Box & Fujiwara treat vegetation typology mainly in relation to the broad-scale distribution of vegetation types. On a world scale types have largely been

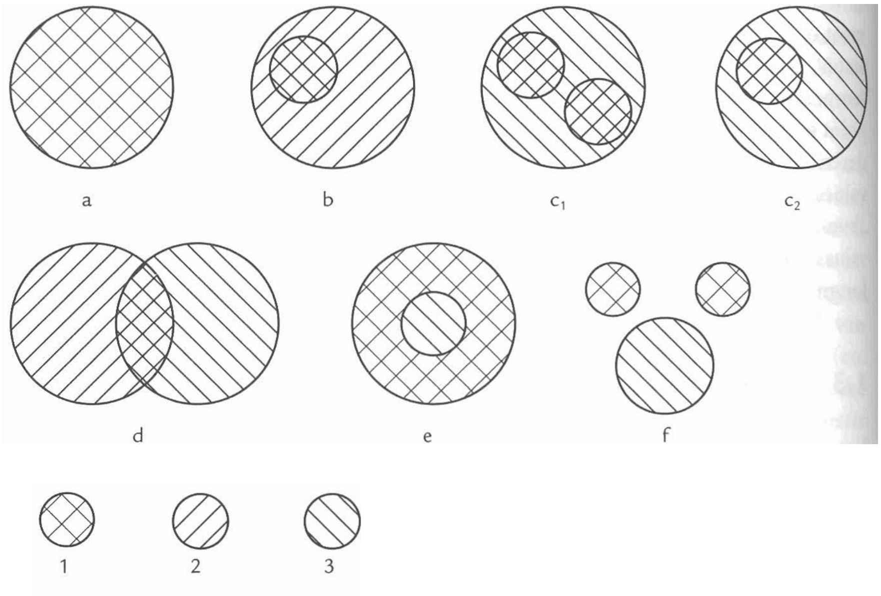

Fig. 1.3 Different types of character taxa (CT) based on the relation between the distribution area of a taxon (A_t) and that of a syntaxon (A_s) it should be characteristic of. **a.** General CT: $A_t \approx A_s$; **b.** Local CT: $A_t < A_s$ and included in A_s; **c.** Regional (superregional) CT: $A_t > A_s$; also CT in other syntaxa (c_1) or diffuse behaviour outside syntaxon and then rather CT of a higher-rank syntaxon (c_2); **d.** Local CT: A_t and A_s different but with overlap; **e.** Regional CT: A_t and A_s overlap but taxon is genetically and ecologically more variable in the centre of A_t and only CT in the periphery of A_s; **f.** Differential CT: $A_t >> A_s$ while locally present in some syntaxa and absent in others. Figure from Dierschke (1994), text based on Westhoff & van der Maarel (1978). Reproduced by permission of the publisher.

defined physiognomically, in the beginning (early 19th century) by plant geographers, including A. Grisebach, who, as early as 1838, coined the term formation. Some readers may share the author's memory of the famous world map of formations by H. Brockmann-Jerosch & E. Rübel decorating the main lecture hall of many botanical institutes. Box & Fujiwora emphasize the ecological context in which these physiognomic systems were developed. In fact, the English term plant ecology was coined in the translation of the book on ecological plant geography by Warming (1909).

1.4.2 Plant community classification; the Braun-Blanquet approach

Plant community classifications have now been developed to the extent that they can be used in broad-scale distribution studies and mapping projects. Some further essentials may be added. This undoubtedly most influential community classification system, called **syntaxonomical system**, is hierarchical and resembles the taxonomy of plants (and animals). The association – although originally given a wider definition (section 1.1.2) – is the central community type; similar associations are united in **alliances**, alliances in **orders**, and orders in **classes.** As in the case of species with subspecies, associations may be differentiated into **subassociations**. During the development of syntaxonomy various intermediate ranks have been introduced, but the four levels mentioned here remain the most important ones. Each syntaxon is defined by a characteristic species combination, a group of **diagnostic taxa** which may include **character taxa, differential taxa** and **companions**. The degree of differentiation within the taxon is usually the species, but in regions with detailed floras subspecies and varieties are also used, while in certain cases (see below) genera may appear. Character species are ideally confined to one syntaxon **S** – but need not occur there in all or most of the relevés assigned to **S**; differential species occur in **S** but not in syntaxa within the next higher rank, while again in other syntaxa; companions occur in most relevés of **S** but also in other syntaxa. As a further parallel to the taxonomy of plants a syntaxonomical nomenclature has been formalized (Weber *et al.* 2000).

The confinement of taxa to syntaxa is seldom absolute and degrees of **fidelity** have been recognized. The classical fidelity degrees (Braun-Blanquet 1932) are seldom seriously applied. Szafer & Pawlowsky (see Dierschke 1994) proposed a refined scale – which does not seem to be applied either. The main problem is that the distribution area of characteristic species seldom coincide with that of their syntaxon: they can be much wider, but also smaller, or overlap only partly. Westhoff & van der Maarel (1978) and particularly Dierschke (1994) have discussed this (including some ideas of J. Barkman) and distinguished local, regional, superregional and absolute character species (Fig. 1.3). In practice a syntaxon is often quite loosely defined by a species combination which is more or less characteristic.

Equally little discussion has been published on the decision whether syntaxa of a given lower rank shall be united with a syntaxon of the next highest rank – or maybe the next highest rank still. Now syntaxonomy is carried out numerically (Mucina & Dale 1989) it is obvious to link syntaxonomical ranks to levels of similarity, as has already been initiated by Westhoff & van der Maarel (1978), but which was surprisingly not developed any further.

Another major problem, related to the former two problems – which is hardly investigated – is the imperfectness of the hierarchy. Syntaxa of a lower rank often show floristic similarities to syntaxa from different classes, and many character species of a given syntaxon show a low degree of fidelity. Obviously problems of fidelity and hierarchy will only get worse when phytosociological surveys are extended over large areas. The crucial question is not whether a syntaxonomical hierarchy can be maintained and extended, but whether it will work.

1.4.3 Plant community classification; large-scale approaches

Extension of phytosociological surveys over large areas is both a great perspective and a formidable challenge, not only scientifically, also organisationally. Box & Fujiwara mention the examples of Japan, Europe and the USA. The European Vegetation Survey has recently resulted in a survey of 928 phytosociological alliances in 80 classes, each with an English name referring to the physiognomy, type of habitat and distribution area (Rodwell *et al.* 2002). The classes are grouped into 15 formations. A similar project was initiated in North America. Notably, the Federal Geographic

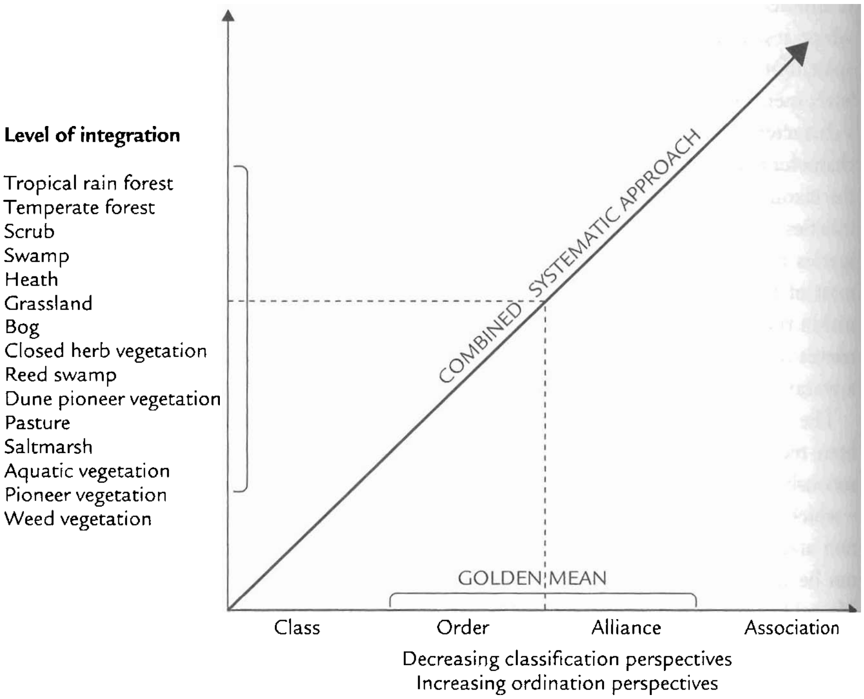

Fig. 1.4 Relation between the level of integration in vegetation and the relative success of classification versus ordination in a 'combined systematic approach'. (Slightly changed after van der Maarel 1979, following an idea of E. van der Maarel, V. Westhoff & C.G. van Leeuwen.)

Data Committee of the US Geological Survey developed a classification with a hierarchy of higher-level physiognomic units and two lower-level floristic units, associations and superimposed alliances. US vegetation ecologists have been linked to this project under the auspices of the Ecological Society of America and have developed standards for the description of the floristic units (Jennings *et al.* 2002). In this project, the association is defined as a physiognomically uniform group of vegetation stands that share one or more diagnostic (dominant, differential, indicator or character) species. The alliance is a physiognomically uniform group of associations sharing one or more diagnostic (dominant, differential, indicator or character) species which, as a rule, are found in the uppermost stratum of the vegetation. These units should occur as repeatable patterns of assemblages across the landscape, and are generally found under similar habitat conditions (Grossman *et al.* 1998). Note that uniform physiognomy is emphasized more than in the European Vegetation Survey. In the preliminary survey 4657 associations have been listed, nested within 1522 alliances. The number of alliances compares well with the above-mentioned number for Europe.

It is clear from this short description that there is a growing interest in subordinating floristic units to physiognomic ones. This is also directly relevant for vegetation mapping. The integrated physiognomic-floristic approach has indeed been proven to be effective since its apparently first attempt by van der Maarel & Westhoff in the 1960s (see van Dorp *et al.* 1985).

1.4.4 Potential natural vegetation, biomes and ecosystems

Box & Fujiwara pay some attention to the problem met with in the mapping of vegetation of larger areas which have lost most of their original vegetation due to human land use and to the development of the concept of **potential natural vegetation** for large-scale vegetation mapping. Reconstruction of vegetation types developing as new climax after human impact would have stopped is of course difficult and can proceed in different ways (see Bredenkamp *et al.* 1998 for different possibilities and an example map of Ireland by J.R. Cross with only 19 units).

Formations can be extended to biomes by including the characteristic fauna of the regions involved and to ecosystems by including global climate and soil characteristics. Distribution patterns can be better understood by means of a plant functional approach – a development in which Box has been directly involved.

1.4.5 Classification and ordination as complementary approaches in phytosociology

The broad-scale vegetation surveys in Europe and the USA consider the alliance as a sort of central unit – doubtless mainly for practical reasons. There was a similar focus on the alliance level from a theoretical viewpoint A cross-section of NW European vegetation types was arranged according to their environment, ranging from coarse-grained relatively dynamic and homogeneous to fine-grained relative constant and divergent environments (Fig. 1.4), or ecotone versus ecocline environments (van der Maarel 1990). The hypothesis was that with increasing environmental complexity classification becomes less and ordination becomes more effective. As a 'golden mean' it was recommended to apply both techniques while approaching the syntaxonomy on the alliance/order level (van der Maarel 1979). The confusing complication is that the most integrated communities are the most difficult to discern and classify. Anyway, the combined approach suggested 40 years ago is in the same spirit as the conclusion by Austin in Chapter 2.

1.5 Clonal growth of plants in the community

Svensson, Rydin & Carlsson give a clear account on the ways and ecological significances of vegetative spread by clonal plants, and there is little to add to that from a vegetation ecology viewpoint. They make clear that clonal spread is a form of dispersal – even if (diaspore) dispersal as discussed in Chapter 6 will be seen as dispersal proper. An important source of variation is in the length of stolons and runners and the speed with which these are formed. The distinction between 'phalanx' and 'guerilla' behaviour of species, as endpoints along this line of variation, is real but it is curious that other terms seem never to have been proposed. Apart from the mental hesitation one should have to consider plants as warriors, the two strategies can hardly be compared in terms of history and number of 'genets' involved. The description of the types in Chapter 5 makes clear how little the behaviour of clonal plants resembles military strategies, particularly 'guerilla' (even the spelling of the word causes confusion; one should properly stick to the Spanish 'guerrilla'). The form of extension with a dense network of short, slowly growing clones may simply be called 'frontal', while plants with rapidly growing loose, long internodes have an 'errant' extension. The latter terms characterize clonal extension more realistically.

Of special interest for vegetation ecology is the characterization of vegetation types regarding the relative importance of clonal species and their role in patch dynamics (section 1.15).

1.6 Dispersal

As Chapter 5, which deals with clonal dispersal, Chapter 6 on diaspore dispersal by Poschlod, Tackenberg & Bonn is a well-defined contribution to which little needs to be added from a vegetation ecology viewpoint. Nevertheless there are important links to other chapters, first of all the next two chapters 7 and 8.

As to vegetation succession, the availability of diaspores is one of the major characteristics of secondary (post-agricultural and post-disturbance) succession, versus the lack of diaspores on the virginal substrates of a primary succession. On a smaller temporal and spatial scale the mobility of plants through clonal and diaspore dispersal is a driving force in 'pattern and process' in the plant community. Fine-scale mobility of plants as described in the carousel model and similar contexts is very much a matter of dispersal to open space becoming available.

Poschlod *et al.* make clear that dispersal is one of the essential factors which determine the composition of the species pool of a plant community (Zobel *et al.* 1998, who consider species reservoir a better, i.e. a more appropriate term). The community reservoir is supplied through dispersion from the local reservoir around the community, which in its turn is supplied by the regional reservoir through migration and speciation (for a different species pool approach see Chapter 9).

This chapter is also a natural place to treat the soil seed bank – which, as Poschlod *et al.* also state, would better be called diaspore bank. Zobel *et al.* (1998) suggested inclusion of the diaspore bank in the community pool, thus including the so-called persistent diaspores. It is a matter of discussion whether to also include species that never germinate in the target community – because they do not fit the environment. However, there are many examples of species apparently not fitting an environment and nevertheless occurring there, if only ephemerally. This is usually a matter of 'mass effect', the availability of numerous diaspores meeting favourable conditions for germination. This has long been recognized in phytosociology as vicinism (van der Maarel 1995).

1.7 Vegetation succession

1.7.1 Analysis of vegetation dynamics

In Chapter 7, Pickett & Cadenasso present results from analyses of both **chronosequences** ('space-for-time substitutions') and **permanent plots** and they indicate how the long-term, ideally yearly, analysis of permanently marked plots is gaining importance. There is a long tradition of permanent plot studies in Europe, starting in 1856 with the Park Grass Experiment at Rothamsted near London (mentioned in Bakker *et al.* 1996). Phytosociological studies of permanent plots started in the 1930s and there are now thousands of such plots under regular survey, many of them in the first place to help in solving management problems (Chapter 12). Bakker *et al.* (1996), who summarized this development, mention as perspectives of permanent plot studies the monitoring of changes, separating fluctuations from successional trends, and enabling extrapolations both in time and space.

Two parallel time series of great use in vegetation succession are first of all the census of individual plants. Mapping and counting plants in permanent plots started in the early 1900s (White 1985). A more recent time series is that of remote sensing data. If such data are accurate enough and can be phytosociologically interpreted after field work both short-term and long-term changes on the landscape level can be followed. Van Dorp *et al.* (1985) described the succession (largely a primary one) of a young dune landscape over 50 yr through interpretation of five aerial photos and two phytosociological maps of the area.

1.7.2 Causes of vegetation dynamics

Pickett & Cadenasso start by drawing a parallel to the theory of natural selection and a theory of vegetation dynamics and making an 'if then' statement: if a site becomes available, species are differentially available at that site, and/or species perform differentially at that site, then the composition and/or structure of vegetation will change. Succession is a special form of vegetation dynamics with a discrete starting point, a directional trajectory, and an unambiguous end. As Pickett *et al.* (1987; see also Glenn-Lewin & van der Maarel 1992) explained, site availability is largely the result of a disturbance, differential species availability is a matter of dispersal (see Chapter 6), and differential species performance is based on the differences in ecophysiology and life history, the outcome of species interactions (see Chapters 9 and 11) and herbivory (see Chapter 10).

1.7.3 Types of disturbance and types of vegetation dynamics

One of the interesting consequences of this approach is that the classical distinction between primary and secondary succession disappears. The two decisive factors, disturbance and dispersal, vary gradually. At one extreme the disturbance is intensive and/or coarse-scale and the newly available site is really virginal, e.g. the island

Surtsey which arose after a volcanic eruption. In the beginning there was no community pool and no local species pool and dispersal was a limiting factor. Here we have a primary succession s.s. At the other extreme a disturbance may leave part of the substrate and the local species pool in tact and a regeneration succession will result which is hardly a secondary succession in the usual sense. This is an example of the 'fine-scale dynamics' Pickett & Cadenasso describe. The chapter gives several other examples of within-community processes.

Since disturbance is the major trigger of vegetation dynamics, some disturbance typology is useful. Following Grubb (1985), White & Pickett (1985) and Glenn-Lewin & van der Maarel (1992) we can distinguish between extent, time (frequency) and magnitude (intensity) of a disturbance. Pickett & Cadenasso give examples of how these aspects can vary – while presenting details on the relatively unknown dynamics of riparian wetlands. Vegetation change after a disturbance will vary in the time period needed to reach a new stable state. Fig. 1.2 indicates how we can distinguish between fluctuation (on the population level), patch dynamics, secondary succession, primary succession, and secular succession, long-term vegetation change in response to (global) changes in climate (see Chapter 14), and how the time scale varies from less than a year to thousands of years. Dynamic studies of plant populations, expecially clonal plants, may vary from 10 to 10^3 yr (examples in White 1985). Cyclic successions may take only some years in grasslands rich in short-lived species (e.g. van der Maarel & Sykes 1993), 30–40 yr in heathlands (e.g. Gimingham 1988) and 50–500 yr in forests (e.g. Veblen 1992). The duration of successional stages at the plant community level ranges from less than a year in early secondary stages in the tropics to up to 1000 yr in late temperate forest stages. Finally, long-term succession in relation to global climate change may take a hundred to a million years (e.g. Prentice 1992).

1.7.4 Development of vegetation and soil

Pickett & Cadenasso point to the fact that in between disturbances biomass will accumulate. More generally, succession is a process of building up biomass and structure, both above-ground in the form of vegetation development, and below-ground in the form of soil building. Odum (1969) in his classical paper on ecosystem development was one of the first to present an overall scheme of gradual asymptotic biomass accumulation and a peak in gross production in the 'building phase' of a succession. This scheme was refined and extended to soil development by Peet (1992) and others.

The contribution to these developments by individual species varies with the type of succession and the successional phase. The old phytosociological literature paid attention to different types of species while emphasizing the 'constructive species', i.e. the species with a high biomass production which build up the vegetation (Braun-Blanquet 1932). Russian ecologists have used the term edificator for this type of species (see, e.g. J. White 1985). Usually these species are dominants. Grime (2001) summarized the conditions for the development of dominance and mentioned maximum plant height, plant morphology, relative growth rate and accumulation of litter as important traits for dominants.

1.8 Diversity and ecosystem function

1.8.1 Different aspects of diversity

Chapter 8 by Lepš is on diversity or biodiversity as it is called nowadays. It starts with a brief treatment of some diversity indices. These are all concerned with species diversity, or rather taxon diversity, the variation in taxa. In addition to α-diversity within-taxon or genetic diversity is mentioned and β- (between-community) diversity is briefly treated. The β-index presented, i.e. Whittaker's, has also been recommended by Magurran (1988) and Fresco *et al.* (2001). It is related to measure of compositional turnover along gradients discussed in section 1.2.2.

At the landscape level, γ-diversity, some combination of α- and β-diversity, can be used, but no special measure has been proposed according to Fresco *et al.* (2001) in their survey of diversity indices. Its simplest form should be $\alpha \times \beta$. In practice it is the total number of species in a landscape unit (community complex).

In a review of biodiversity aspects by van der Maarel (1996) some forms of distinctiveness are also considered aspects of biodiversity: **phylogenetic distinctiveness**, based on taxonomic distinctiveness, **numerical distinctiveness**, based on the rarity of occurrence, and **distributional distinctiveness**, i.e. endemism of taxa. Lepš makes the point that the diversity of a community is largely a function of the species pool and the forms of distinctiveness can indeed be determined in the species pool.

1.8.2 Measures of α-diversity

Two different approaches for the determination of species diversity are distinguished, both based on the relationships between the quantities with which the different species occur. One approach describes the way in which species number increases with increasing sample size; the other calculates some index of diversity based on relative quantities of species. In the first approach diversity indices are derived from models about the distribution of plant units (section 1.1.9), with α the parameter of the log series distribution (see Williams 1964) being the best known index. The second basic approach makes use of the distribution of species quantities over the species without assuming any particular distribution model. Indices of this type, the Shannon index being the best known, are, as it were, parameter-free diversity measurements (van der Maarel 1996).

As Lepš makes clear, diversity has both an aspect of species **richness**, i.e. the number of species, and of **evenness**, the way species quantities are distributed. These two aspects are more related than is generally recognized by users of diversity indices. According to the relation between the various diversity indices described by M.O. Hill (equation 8.3, p. 201) the well-known indices of Simpson and Shannon are similar – which almost all studies using both indices have demonstrated – in that the most abundant species determines, to some extent, the diversity, but Simpson does this more than Shannon. If species proportions are relative biomass or cover values, even the Shannon index would indicate the non-evenness rather than the richness. Since the ordinal transform scale may be considered an approximative geometric cover scale (section 1.1.9) ordinal transformation of cover-abundance values – or logarithmic transformation of biomass values – before applying the Shannon index would give more realistic results.

1.8.3 Diversity and function

Chapter 8 was planned as a contribution to diversity but developed into an essay on the relation beween diversity and ecosystem function. Much research – and speculation – has been triggered by the symposium volume by that name edited by Schulze & Mooney (1994). As Lepš elucidates, biotic diversity can be better understood if it can be divided into functional components. If we manage to distinguish such types and allocate each species to a type, diversity – i.e. species richness – can then be approached as the number of functional types multiplied by the mean number of species per type.

1.9 Species interactions structuring plant communities

The concise chapter on species interactions by van Andel gives a survey of the different types of interaction and then pays attention to the following types of interaction: competition, allelopathy, parasitism, facilitation and mutualism. Interestingly the attention for competition, the classical main type of interaction, is no longer predominant. Competition as a mechanism to arrange species packing along gradients (see Chapter 2) remains important, particularly for vegetation ecologists (e.g. Mueller-Dombois & Ellenberg 1974). Still, the typically community-structuring force of facilitation is a more fascinating topic in vegetation ecology – compare, for instance, its place in Chapter 9 with that in the recent but more autecologically oriented textbook by Crawley (1997). Facilitation, in particular, nursery effects has been described for almost all plant community types where one or more environmental factors (nutrient shortage, drought, temperature) could be critical for some plants but not for others. On the other hand, succession may be hampered by processes of inhibition.

Another important community-structuring interaction type with a rapidly growing body of literature devoted to it is mycorrhiza. Van Andel treats it as an important aspect of mutualism, but it forms also part of the topic ‘interactions between higher plants and soil-dwelling organisms’, elaborated in Chapter 11.

Van Andel’s chapter is one of the few where bryophytes are treated in some detail. In addition to his description of bryophyte pattern formation the review paper by Rydin (1997) can be mentioned, which shows how, despite the generally low resource levels bryophytes have available, they can compete intensively. Zamfir & Goldberg (2000) described experiments showing how competition between mosses on the community level can be different from competition on the individual level (and also described the difference between the two approaches).

1.10 Plant–herbivore interactions

In Chapter 10 Sankaran & McNaughton present an integrative account on herbivory, linking up with Chapters 3, 7, 8, 9 and 12. In view of the broad spectrum of plant types and plant parts being eaten and the equally broad spectrum of eating animals, as well as the often intricate mutual adaptations between plants and animals in each case of interaction, the idea of co-evolution comes into mind (e.g. Howe & Westley 1988).

Plants deal with herbivory by avoidance or tolerance, i.e. compensation for damage; a range of compensatory responses is discussed. Another interesting range is discussed between symbiotic and parasitic aspects of grazing. Finally an actual twofold theme is treated: effects of herbivores on plant diversity and effects of herbivore diversity.

Chapter 7 discusses another aspect of herbivory, its contribution to pattern formation. This aspect has been looked upon from another angle by Olff & Ritchie (mentioned in Chapter 10) who relate the impact of herbivores to species diversity in relation to productivity and palatability along gradients of soil fertility and precipitation. These authors continued to elaborate on the relation between plant species diversity and environmental conditions (Olff *et al.* 2002) and particularly the significance of variation in herbivore size (Haskell *et al.* 2002).

1.11 Interaction between higher plants and soil-dwelling organisms

Kuyper & de Goede concentrate in Chapter 11 on the interactions between plants and soil organisms occurring around and in the roots. Naturally, their topic shows overlaps with the two preceding chapters. The three major processes described are nitrogen fixation by bacteria, mycorrhizae with fungi and root-feeding by invertebrates. As in the previous chapter the gradual transition and alteration between symbiotic and antagonistic aspects is emphasized. It is in the context of the environmental conditions how costs and benefits of symbioses affect plants. There is also a large variation in the degree of specificity regarding the interaction. Both plants and mutualistic and antagonistic soil organisms show different degrees of specificity or selectivity. Both private and shared associations could amplify or reduce the differences in competitive abilities between plant species. As a consequence, there is no one-to-one relationship between the below-ground mechanisms and processes, and the effects on plant species richness in vegetation.

There is an interesting link to Chapter 13 on plant invasion in that exotic plants, introduced in another region where some of the accompanying soil-dwelling organisms do not occur, may behave quite differently. A link with Chapter 7 follows from the elucidation of the two hypotheses as to the driving force of succession. If mycorrhizal fungi are causes of plant dynamics (driver hypothesis), the presence of specific mycorrhizal fungi is required for the growth of specific plants. If soil organisms are merely passive followers of plant species dynamics (passenger hypothesis), specific plants are required to stimulate the growth of specific mycorrhizal fungi.

1.12 Vegetation conservation, management and restoration

The chapter on management by Bakker is ample proof of the profit made by conservation, management and restoration ecology of the development of vegetation ecology, at least in Europe and Japan (Chapter 4). Phytosociological classification facilitates communication over national boundaries on target plant communities; vegetation mapping can be used for land use planning. Still more importantly, ecological theory regarding the behaviour of plant species along gradients, ecological indicator values, diaspore dispersal, species pool, seed bank dynamics and succession has been developed (see Chapters 2, 6, 7 and 8). The development of ecohydrology as a basis for the restoration of nutrient-poor wetlands is particularly impressive.

Most of Bakker's examples of successful management projects are from Western Europe where indeed both theory and practice have been developed constantly. For a world perspective, see Perrow & Davy (2002).

1.13 Invasive species and invasibility of plant communities

Chapter 13 by M. Rejmánek, D.M. Richardson & P. Pyšek deals with the main characteristics of invasive species; main pathways of migration of invasive species and characteristics of environments and plant communities open to invasions. Of special interest are the relations between invasive and local native species and the often different behaviour of invasive species in their new, alien environment. An interesting suggestion is that invasibility of plant communities by exotics is mainly caused by fluctuations in resource availability (cf. Grime 2001).

Only few invasive species become dominant in new environments and act as a 'transformer species'. They have major effects on the biodiversity of the local native community. They all transform the environment and different ways of transformation are treated. Useful information is provided on the perspectives of eradication of invasive species. As a rule of thumb, species which have invaded an alien area for more than 1 ha can hardly be eradicated.

A very interesting and important conclusion which is emerging is that stable environments with little anthropogenic disturbance tend to be less open to invasive species.

1.14 Vegetation ecology and global change

Chapter 14 by B. Huntley & R. Baxter deals with global pollution problems, notably eutrophication, increasing CO_2 concentration and sea-level rise, but particularly global warming. Of interest in this connection are models to help understand and predict future changes of some main ecosystem types, and problems of species to cope with changes and of dispersing to newly available suitable environments.

Studies on effects of global changes rely heavily on palaeo-ecological studies. In a way these studies are extrapolations into the future of the processes of secular succession, already mentioned in section 1.7. Secular succession, also called vegetation history (Huntley & Webb 1988), was already recognized in early phytosociology, e.g. by Braun-Blanquet (1932) under the name synchronology, as the ultimate vegetation succession.

A major problem in global change studies is that communities subjected to the impact of global changes can be in the process of long-term responses to disturbances which happened long ago. As an example the case of the Fiby forest near Uppsala can be mentioned. Palaeo-ecological research by R. Bradshaw & G. Hannon and gap-dynamical studies by I.C. Prentice and H. Hytteborn *et al.* (review in Engelmark & Hytteborn 1999) showed how more than 400 yr ago *Picea abies* entered the forest upon the termination of the domestic grazing of the mixed *Quercus robur* forest, and how 200 yr ago the *P. abies* stage was largely destroyed by a gale, upon which *Populus tremula* took over. This is still present with trees originating from that period in the now regenerated *Picea* forest, which still has some isolated broad-leaved *Quercus* and *Tilia* trees. It will be very difficult here to separate possible trends following global warming from further changes resulting from the two major historical 'disturbances'.

Models – which are continuously developed but do not play a major part in Chapter 14 – suffer from the uncertainty regarding estimations of crucial parameters, leading to an often broad range of the parameter predicted. Moreover, it may appear that essential parameters have been overlooked. Nevertheless, the further development of predictive models must be encouraged.

1.15 Pattern and process in the plant community

1.15.1 Patch dynamics, cyclic succession and mosaic cycle

In various chapters elements of pattern and elements of process have been put forward. In this section spatial and temporal aspects of vegetation dynamics within the plant community will be discussed. The word combination pattern and process has become a standard feature of community ecology since A.S. Watt published his seminal paper (Watt 1947). The basic idea is that within a phytocoenosis which is in a steady state on the community level, changes may occur patchwise as a result of local disturbance (exogenous factors) or plant senescence (endogenous factors); in the gaps formed regeneration will occur which will in the first instance lead to a patch of vegetation which is different from its surroundings. It should be noted that 'pattern' as an object of pattern analysis (section 1.1.11) may have different causes. With Kershaw (see Kershaw & Looney 1985) we may distinguish between morphological, environmental and sociological pattern. Morphological pattern arises from the growth form of plants, in particular clonal plants (Chapter 5). Environmental pattern is related to spatial variation in environmental factors, for instance soil depth. Sociological pattern results from species interactions and temporal changes in the behaviour of plants and should be the 'pattern' in Watt's pattern and process.

The phenomenon of patch dynamics has been discovered and described in woodland and forest by Watt since the 1920s, and by R. Sernander in Sweden some years earlier (van der Maarel 1996). They observed that gaps arise in the forest through disturbance of some kind and that vegetation regenerates via herb, shrub and low tree stages. If such gaps are large enough, the various stages of this regeneration succession (see Chapter 7) can be described as own plant communities. In the European syntaxonomical system (section 1.4.2) the various regeneration succession stages and the mature forest parts are placed in different classes (e.g. Rodwell *et al.* 2002), but only in ecological surveys (e.g. Ellenberg 1988) is the successional coherence clear. If the gaps are large, as with hurricanes and fire, the following succession proceeds as it were on the community level and is called secondary succession (Chapter 7).

Watt described similar patch dynamics in bogs (where he had studied the work of H. Osvald from 1923), heathlands and grasslands. In bogs the well-known mosaic of hollows and hummocks appeared to be dynamically related and was described as a 'regeneration complex'. As Watt described it: 'each patch in this space-time mosaic is dependent on its neighbours and develops under conditions partly imposed by them'. He adds that the different stages were considered seral and also as separate communities. That is why the term cyclic succession was coined for the complex. However, for Watt it was just one community with a homogeneous substrate.

The case of heathland, which was elaborated by Ph. Stoutjesdijk in The Netherlands (see Stoutjesdijk & Barkman 1992) and particularly in Scotland by C.H. Gimingham (e.g. 1988), concentrated on the population dynamics of the dominant species *Calluna vulgaris*. *Calluna* heath is a model community where four stages – in this case at the same time growth phases of the species – can be distinguished: pioneer (establishment of *Calluna*, up to 6 yr), building (development of hemispherical bushes up to 50 cm height, cover up to 100%, up to 15 yr), mature (lichens on old stems, mosses under the canopy, up to 25 yr) and degenerate (central branches dying, establishment of grasses, up to 40 yr). During the first two, 'upgrade' phases there is a net gain in biomass, during the second two, 'downgrade' there is a net loss. In the case of *Calluna* it is largely the growth and later senescence of the dominant species which determines the cycle. Because the stages are related to individual *Calluna* bushes and the dominant species is always present, they are not recognized as separate communities.

Whether or not to call these cyclical processes succession is a matter of definition and of scale. When the stages have a relatively large spatial extent and are recognized as communities the term cyclic succession is appropriate. See, e.g. Glenn-Lewin & van der Maarel (1992) for exceptions (e.g. *Calluna* heath does not always show this cyclic process) and other examples. An alternative term *Mosaik-Zyklus* has been proposed by the German animal ecologist H. Remmert; this term was introduced in the English literature as mosaic-cycle (Remmert 1991). A mosaic-cycle is a special case of patch dynamics where the changes are triggered largely by endogenous factors, in particular plant senescence. The bogs and heathlands of Watt may fulfil this criterion, although exogenous factors may play some part here as well (Burrows 1990).

1.15.2 Patch dynamics in forest

Although gap regeneration in temperate (beech) forest was Watt's first example of pattern and process, and Sernander had studied regeneration in Swedish boreal forest, the first impact of Watt's 1947 paper was on heathland and grassland ecologists – partly because he was working and publishing on these systems after 1947, and, for a different reason, that forest ecologists, particularly in North America were preoccupied with secondary, old-field succession, which took place over large areas in a spectacular way. The scheme of 'ecosystem development' (section 1.7.4) by Odum

(1969), which had a considerable impact on succession theory, was based on old-field succession. During the 1970s interest in forest dynamics became broadened. The review by White (1979) and the book by White & Pickett (1985) put disturbance and patch dynamics in the focus of forest dynamics (see Chapter 7). As to gap dynamics, points of special interest are the influence of the size, form and orientation of gaps on regeneration and the differences in gap light climate dependent on latitude, tree replacement series, the release of suppressed shade-tolerant mature tree species when light becomes available in the gap (see, e.g. Burrows 1990; Veblen 1992). In temperate and particularly boreal forest not only regeneration after windthrow but also after fire is of particular concern (e.g. Engelmark *et al.* 2000).

1.15.3 Patch dynamics in grassland

The work by Watt on grasslands inspired P.J. Grubb, one of his pupils, to elaborate the concept of regeneration niche in a paper as influential as Watt's (Grubb 1977). The essence of this concept is that gaps arise everywhere, every time through the death or partial destruction of plant units through natural death of short-lived species and all sorts of animal activities, and the open space can be occupied by a germinating seed or by a runner of a clonal plant. The concept was found especially useful in grasslands where many such gaps are so small that they are hardly noticed. In grazed grasslands local removal of plant parts, trampling and deposition of dung are additional causes of gaps, often larger ones. An example of an intricate relation between the availability of microsites and the activities of voles (*Microtus arvalis*) in grassland was given by Gigon & Leutert (1996). See Fig. 1.5.

Grasslands are expecially suited for the study of patch dynamics because the gaps – microsites – are small, can be easily manipulated and the appearance and disappearance of plant units, particularly seedlings, can be accurately followed. An example of manipulation with fire and soil disturbance is the work of Collins (e.g. 1989), who found that spatial heterogeneity is created under such circumstances.

1.15.4 The carousel model

Where gaps arise more or less continuously in grasslands and plant species both become locally extinct because of disturbances and/or death, but also get continuous opportunities to re-establish, species may show a high fine-scale mobility. At the same time, as in the example of Fig. 1.6, patch dynamics can contribute considerably to the co-existence – albeit co-occurrence in many cases – of many plant species on small areas of grassland. During the careful observation over several years of hundreds of very small subplots in plots of limestone grassland on the alvars of southern Öland the impression arose that the grassland community as a whole, described as *Veronica spicata-Avenula pratensis* association was remarkably constant in floristic composition, while the species lists on subplots of 10 cm^2 and 100 cm^2 seemed to change from year to year. Van der Maarel & Sykes (1993) quantified this mobility in two ways, species-wise and subplot-wise: (1) cumulative frequency, i.e. the cumulative number of subplots a species is observed in over the years; (2) cumulative species richness, i.e. the mean number of species that is observed in a subplot over the

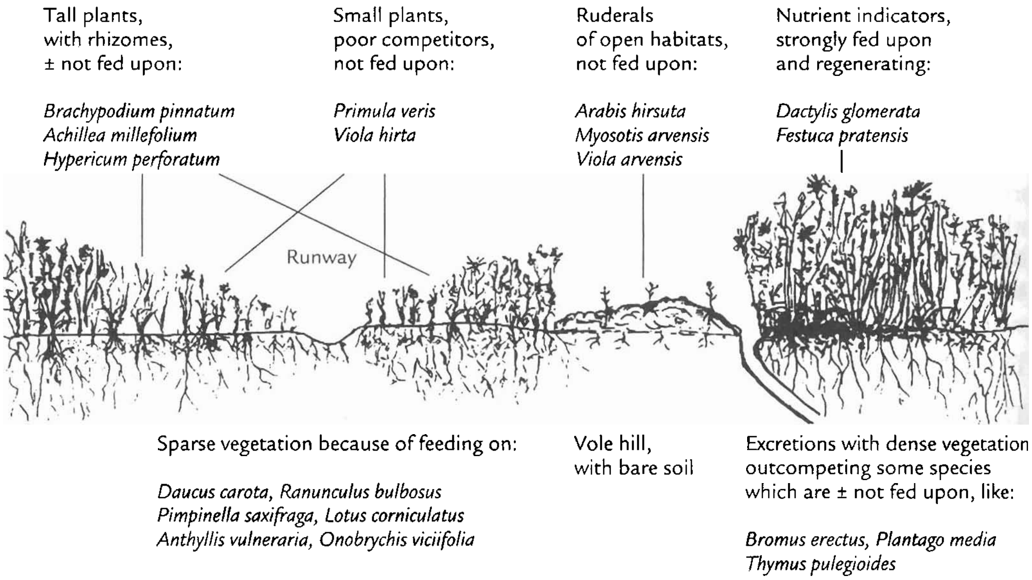

Fig. 1.5 Fine-scale vegetation pattern related to a pattern of microsites in limestone grassland created by *Microtus arvalis*. Reproduced by permission of the publisher. Gigon & Leutert (1996). From Scale not indicated; width of the figure represents *c.* 13 cm.

years. Indeed, many species appeared in many new subplots, which led to the suggestion of a carousel with a 'merry-go-round' of most species. In this short, open grassland on summer-dry soil many short-lived species are involved and germination is a main process in (re-)establishment of species. Simultaneously Herben *et al.* (1993) described fine-scale mobility in a mountain grassland and used persistence as their measure, i.e. the tendency of a species to remain in the subplot where it occurs, as the complement of mobility. Here the mobility of clonal plants (see Chapter 5) was in the focus of interest.

Amongst the comments on the carousel model were the lack of a null model of mobility. Van der Maarel & Sykes (1997) showed how observed mobility can be compared with a model of random allocation of species over subplots taking their frequencies into account, upon a comment by J.B. Wilson in line with his null model for species richness variance (Wilson *et al.* 1995). Also a minimum mobility model was suggested where species occurrences were allocated as far as possible to the same subplots where they occurred earlier – so persistence was maximized. Both cumulative species richness and cumulative frequency were compared with values obtained with the random and the minimum model. Fig. 1.7 shows an example of an increase in cumulative richness – considerable in itself – which is approximately intermediate between the 'minima' and the 'random' accumulation. As to the cumulative frequency, a species mobility index was proposed:

$$\mathrm{MR} = (cf_{\mathrm{obs}} - f_{\mathrm{min}})/cf_{\mathrm{R}} \qquad (1.2)$$

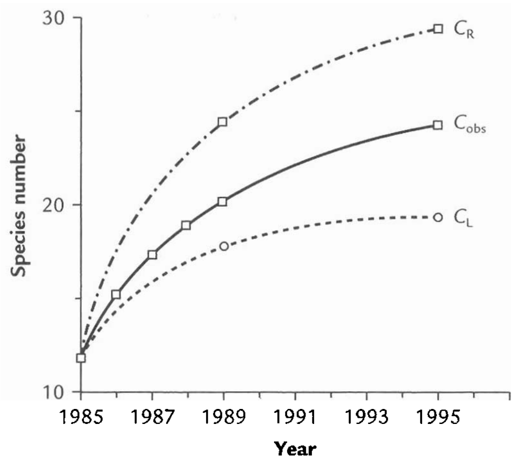

Fig. 1.6 Average species accumulation over 10 yr in 10 cm × 10 cm subplots in a limestone grassland permanent plot. C_{obs} is the observed number; C_R is the accumulation according to a random mobility model; C_L is the accumulation according to a minimum mobility model. Note that in 10 yr mean accumulating number of species increased from *c.* 12 to *c.* 24. After van der Maarel & Sykes (1997).

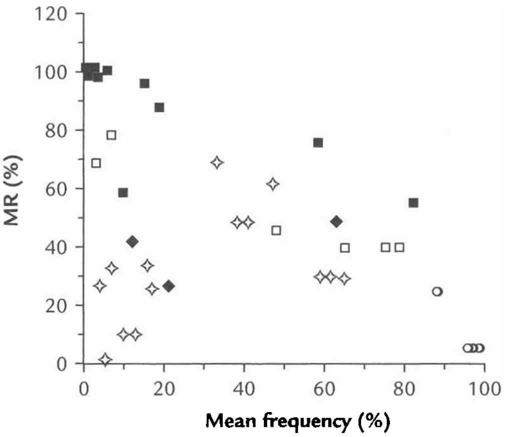

Fig. 1.7 Mobility rate (MR) of plant species in limestone grassland plots in relation to their mean frequency in 10 cm × 10 cm subplots. ○ = constant species; □ = species cumulative frequency not significantly different from random (black: annuals); ✧ = species cumulative frequency significantly lower than random (black: short-lived perennials). After van der Maarel & Sykes (1997). Reproduced by permission of the publisher.

where cf_{obs} is the observed cumulative frequency, in this case over a 10-yr period in the same grassland as mentioned above, f_{min} is the lowest annual frequency observed during the period of observation, and cf_R is the expected frequency according to the random model. Fig. 1.7 shows how this index is related to the mean frequency of

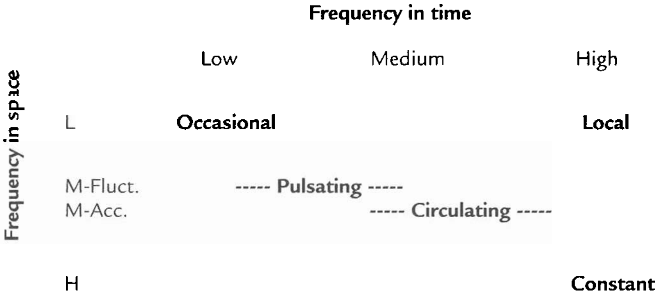

Fig. 1.8 Types of within-community plant species mobility based on frequency in space and time in 10 cm × 10 cm subplots in limestone grassland during 1986–94. Mean spatial frequency values divided into high, > 75% (H), medium, 35–75% (M; M-Fluct. = with large between-year differences; M-Acc = accumulating frequency) and low, < 25% (L). Temporal frequency values divided into H (occurring in > 66% of the years), M (33–66%) and L (< 33%). After van der Maarel (1996). Reproduced by permission of the publisher.

species, in such a way that, naturally, a high mean frequency prevents a species from being mobile. It also indicates that most species with a natural mobility near to the random model are annuals or short-lived perennials. This picture was elaborated as in Fig. 1.8 (van der Maarel 1996) into a division into five categories (van der Maarel & Sykes 1997) with 'local' species (with low mean and low cumulative frequency) at one end, followed by 'occasional species' (with low mean frequency and relatively high cumulative frequency), 'pulsating' species (with medium mean frequency, but low frequency in at least one year, and high cumulative frequency), 'circulating species' (with relatively constant medium mean frequency and high cumulative frequency) and 'constant species' (with high mean frequency).

The carousel model has helped to discover species mobility in several other grasslands and also in woodlands, where, as was expected, mobility is low for most species and different forest patches may have own carousels (Maslov & van der Maarel 2000). This was also concluded by Palmer & Rusch (2001), who at the same time tried to find solutions for some shortcomings in the carousel model. They focused on species mobility and stated first that this was not only a matter of appearance in new microsites, 'immigration', with immigration rate i being the probability of occupying an empty plot per year, but also of disappearance in old microsites, 'extinction', with extinction rate e being the probability of an occupied plot becoming empty per year. Palmer & Rusch also introduced an equilibrium frequency p where immigration and extinction are in balance, and where the three parameters are related as follows:

$$p = i/(i + e) \tag{1.3}$$

They made clear that turnover rate can be defined as the reciprocal of residence time and this is equal to the extinction rate. They also showed that persistence V (e.g. Herben *et al.* 1995) is related to i and e in a simple way:

$$V = 1 - e - i \qquad (1.4)$$

The turn-around time of a species, the carousel time, CT, follows from

$$\mathrm{CT} = (-\log N - \log(1 - P_0))/\log(1 - i) \qquad (1.5)$$

where N is the number of plots and P_0 is the initial frequency of the species. Note that carousel time is dependent on the initial frequency of the species and on the number of plots, the number of 'seats in the carousel'.

Palmer & Rusch also make some remarks on the reality of random models and show that for the random model of van der Maarel & Sykes (considered less realistic) RCT can be related to CT under the random model and an index 'relative carousel time' can be derived which is simply:

$$\mathrm{RCT} = \log(1 - p)/\log(1 - i) \qquad (1.6)$$

They then present some results based on (only) four years of observation and find carousel times for the largest plots (1 m^2) from 13 to > 4000 yr. They wonder whether this parameter is useful for explaining species co-existence on a short time scale. One may agree with this, but one can also comment that part of the high mobility in the grassland is caused by pulsating and occasional species and it may need a longer series of observations to include 'top years' for certain species. Finally, Palmer & Rusch comment that the number of plots and their size are decisive for the value of CT. Therefore it may be better to use RCT as defined above. Indeed, results presented by Palmer & Rusch show that RCT values are more constant across subplot size and differences between species are large enough to compare species and hypothesize about the differences.

1.16 Plant functional types, life-form types and plant strategy types

1.16.1 Plant functional types and guilds

Plant functional type (PFT) is a group of plant species sharing certain morphological-functional characteristics. PFTs are in the first place used in ecological studies, but they are also important in plant geography (see Chapter 4). The use of plant function seems to go back to Knight & Loucks (1969) who related plant function and morphology to environmental gradients, and Box (1981) who correlated 'ecophysiognomic' plant types with climatic factors, and used climatic envelopes for selected sites to predict the combination of forms (Chapter 4) – Peters (1991) mentioned this study with its validated global model as a good example (one of the few) of predictive ecology. Smith & Huston (1989) stated that the PFT concept is analogous to the (zoological) concept of guild' and described it as a group of species that 'use the same type of resources in more or less the same way'. Indeed botanical guild systems have been developed (see Semenova & van der Maarel 2000). Wilson (1999b) considered

Table 1.4 Some classical life-form systems of vascular plants. **A.** Main life-form groups according to Du Rietz (1931). **B.** Growth forms according to Warming (1909); only main groups distinguished. **C.** Main terrestrial life forms according to Raunkiær (1934), largely following Braun-Blanquet (1964). **D.** Hydrotype groups according to Iversen (1936).

A.	
Physiognomic forms	Based on general appearance at full development
Growth forms	Largely based on shoot formation (*sensu* Warming)
Periodicity-based life forms	Based on seasonal physiognomic differences
Bud height-based life forms	Based on height of buds in the unfavourabler season (*sensu* Raunkiær)
Bud type-based life forms	Based on differences in type and structure of buds
Leave-based life forms	Based on form, size, duration of the leaves
B.	
Hapaxanthic (monocarpic) plants	Plants which reproduce only once and then die; including annuals, biennials and certain perennials, e.g. *Agave*
Pollakanthic (polycarpic) plants	Plants which reproduce repeatedly
Sedentary generative	Primary root or corm long-lived, with only generative reproduction
Sedentary vegetative	Primary root short-lived, with both generative and some vegetative reproduction
Mobile stoloniferous	Creeping above-ground with stolons which develop rootlets
Mobile rhizomatous	Extending below-ground with rhizomes
Mobile aquatic	Free-floating aquatic plants
C.	
Phanerophytes (P)	Perennial plants with perennating organs (buds) at heights > 50 cm Tree P; Shrub P; Tall herb P; Tall stem succulent P.
Chamaephytes (Ch)	Perennial plants with perennating organs at heights < 50 cm Woody (frutescent) dwarf-shrub Ch; Semi-woody (suffrutescent) dwarf-shrub Ch; herbaceous Ch, low succulent Ch, pulvinate Ch
Hemicryptophytes (H)	Perennial plants with periodically dying shoots and perennating organs near the ground Rosette H; Caespitose H; Reptant H
Geophytes (Cryptophytes) (G)	Perennials loosing above-ground parts and surviving below-ground during the unfavourable period Root-budding G; Bulbous G; Rhizome G; Helophyte G
Therophytes (T)	Annuals, completing their life cycle within one favourable growing period, surviving during the unfavourable period as seed or young plant near the ground Ephemeral T (completing cycle several times per growing period); Spring-green T; Summer-green T; Rain-green T; Hibernating green T (green almost all year).
D.	
Terriphytes	Terrestrial plants without aerenchyma
Seasonal xerophytes	
Euxerophytes	
Hemixerophytes	
Mesophytes	
Hygrophytes	
Telmatophytes	Paludal plants (growing in swamps and marshes) with aerenchyma
Amphiphytes	Aquatic plants with both aquatic and terrestrial growth forms
Limnophytes	Aquatic plants in a strict sense

guilds and PFTs as synonyms and preferred the older term guild. Nevertheless, PFT became the dominant term and was redefined as a grouping 'of species which perform similarly in an ecosystem based on a set of common biological attributes' (Gitay & Noble 1997).

During the 1990s PFT systems were particularly used in relation to climate (hence the interest in the typology of Box 1981), and more particularly climate change (e.g. Woodward & Cramer 1996), and to disturbance (Lavorel & Cramer 1999).

In a way, the abundant use of PFTs is a revival of the attention paid to **life forms** during the period 1900–1930. Life forms were seen as types of adaptation to environmental conditions, first of all by E. Warming who spoke of epharmonic convergence after the term **epharmony** = 'the state of the adapted plant', coined as early as 1882 by J. Vesque. Life-form systems from this early period include those of E. Warming from 1895, C. Raunkiær from 1907, G.E. Du Rietz from 1931 and J. Iversen from 1936 (Table 1.4). Environmental adaptation is most obvious in the life form system of Raunkiær. Modern, extended versions of this system, e.g. by Braun-Blanquet (1964), Dierschke (1994) and particularly Mueller-Dombois & Ellenberg (1974) give subdivisions of the main Raunkiær types according to differentiation into growth form and plant height.

1.16.2 Plant strategy types

A concept more recent than life form which is also closely related to PFT is **plant strategy.** The best known system of plant strategies is that by Grime (2001; earlier publications cited there). A special introduction in this book is devoted to PFTs, where he treats the two concepts as equivalent, if not synonymous, but maintains the term strategy in the rest of the book. However, there is a simple difference: strategies, 'groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology' (Grime) are the combined characteristics of a PFT. These characteristics have also been called **attributes**, e.g. the '**vital attributes**' of Noble & Slatyer (1980), used in relation to community changes caused by disturbances. However, nowadays the term **trait** (probably borrowed from genetics) is used, while attribute is now also used for the different expressions of a trait, which should rather be called states (see further Semenova & van der Maarel 2000).

The three strategy types proposed by Grime have been maintained virtually unchanged, even if the system has been regularly criticized. They enable plants to cope with environmental constraints of two kinds, **stress**, 'external constraints which limit the rate of dry matter production', and **disturbance**, 'destruction of plant biomass arising from outside abiotic, biotic and human impact'. The constraints leading to stress can be both shortages and excesses in the supply of resources, but in practice the focus is on shortages.

Plants in the adult stage have developed three types of strategy. **Competitors** (C) are adapted to environments with low levels of stress and disturbance; **stress-tolerators** (S) to high stress and low disturbance, and **ruderals** (R) to low stress and high disturbance. No plants have developed a 'viable strategy' for the combination of high stress and high disturbance. By distinguishing intermediate levels of stress

Table 1.5 Some adaptations of stress-tolerant, competitive and ruderal plants, selected from the list presented by Grime (2001).

	Stress-tolerant	**Competitive**	**Ruderal**
Life form	Herbs, shrubs, trees	Herbs, shrubs, trees	Herbs
Shoots	Wide range of growth forms	Dense leaf canopy Wide lateral spread	Small stature Little lateral spread
Leaves	Small, leathery or needle-like	Robust, mesomorphic	Various, often mesomorphic
Maximum potential growth	Slow	Rapid	Rapid
Response to stress	Responses slow and minor	Maximizing vegetative growth	Less vegetative growth, flowering
Acclimation of photosynthesis and mineral nutrition to seasonal changes in resources	Strongly developed	Weakly developed	Weakly developed
Storage of photosynthates and mineral nutrients	In leaves, stems and/or roots	Rapidly incorporated into vegetative structures, partly stored	In seeds
Longevity of established phase	Long to very long	Long or relatively short	Very short
Longevity of leaves and roots	Long	Relatively short	Short
Leaf phenology	Evergreen; various patterns of leaf production	Peaks of leaf production in periods of maximum	Short phase of leaf production
Perennation	Stress-tolerant leaves and roots	Dormant buds and seeds	Dormant seeds

and disturbance intermediate (so-called secondary) strategy types are distinguished: **competitive ruderals** (C-R) adapted to low stress and moderate disturbance; **stress-tolerant ruderals** (S-R) adapted to high stress and moderate disturbance; **stress-tolerant competitors** (S-C) adapted to moderate stress and low disturbance; and **C-S-R strategists** adapted to moderate stress and moderate disturbance. Table 1.5 presents some traits in which the three main strategy types differ. Obviously, competitors and ruderals are quite similar, apparently because of their link to 'low stress', which means soil fertility (see also Chapter 5).

CSR theory has some predecessors, mentioned by Grime (2001). The most interesting is the theory of L.G. Ramenskiy, who distinguished three types of life-history strategies which are astonishingly similar to the CSR types, as concluded by Grime (2001). The first introduction to Ramenskiy's work in English (mediated by D. Mueller-Dombois) was by Rabotnov (1975), who spoke of 'phytocoenotypes'. His

Table 1.6 Some adaptations of persistent ('P'), vigorous ('V') and exploiting ('E') plant populations based on Onipchenko *et al.* (1998).

Type	Persistent (P)	Vigorous (V)	Exploiting (E)
Synonym Rabotnov	Patient	Violent	Explerent
Synonym Onipchenko *et al.*	Endurant	Dominant	Explorative
Equivalent Grime	Stress-tolerating	Competitive	Ruderal
Resource capture	Low requirement	High when resources available	High when resources available
Stage with high tolerance	Juvenile	Adult	Dormant
Conditions of occurrence	Abiotic and biotic stress	Productive conditions – large biomass production	Productive conditions – moderate biomass production
Response to biomass removal	Negative	Negative	Weak
Response to disturbance s.l.	Negative	Negative, dependent on intensity	Positive
Response to resource availability	Slow	Positive	Positive and rapid
Seed production	High; small seeds	High; large seeds	Intermediate; small seeds
Persistent seed bank	Small	No	Large
Flexibility of leaf longevity	Low	Low (seedling); high (adult)	High
Change in rate of gas exchange per unit leaf area	Low	Low	High

pupil V.G. Onipchenko used Ramenskiy's ideas in combination with ideas by Yu.E. Romanovskiy on two ways a population can succeed in the competition for limiting resources, i.e. reducing the equilibrium resource requirement R* (Tilman 1982) and developing a high resource capture capacity and a high population growth rate when the resource is available. Onipchenko *et al.* (1998) elucidated the 'RRR', Ramenskiy/Rabotnov/Romanovskiy, approach in a functional study of alpine plant communities. Table 1.6 presents some main differences and similarities between the three strategies, which are here called **persistent, vigorous** and **exploiting** strategies. Onipchenko *et al.* (1998) measured nine characteristics, both vegetative and generative, of 42 alpine species of environments strongly varying in fertility, stress and disturbance, ordinated the species on the basis of these characteristics and concluded that differences in seed and seed bank characteristics were more informative than the two parameters according to which the Grime triangle is filled, i.e. the morphology index M (biomass velopment) and relative growth rate, RGR. It was also concluded that there is a continuous variation between extreme combinations of characteristics – as Grime in fact also demonstrates – which leads to a preference for indicating degrees of persistence, vigour and exploitation rather than speak of persistent, vigorous and exploiting species and intermediate types.

1.16.3 On disturbance and stress

A more direct criticism of the Grime triangle was presented by Grubb (1985): 'stress' is a complex phenomenon which, in addition to shortage of nutrients, water and light, includes seasonal drought, high salt concentration, waterlogging, frost and heat. Grubb also differentiated 'disturbance' according to frequency, extent and intensity, and considered the division between continual and periodic disturbance as basic, connected to entirely different adaptations. Based on work by S.D. Fretwell and L. Oksanen, Oksanen & Ranta (1992) emphasized the role of grazing, the most important continual disturbance, in many plant communities and made clear that grazing has no proper place in the CSR system; they suggested to differentiate between frequency and intensity of disturbance; grazing is a form of disturbance with high frequency but low intensity, which indeed occurs in many stressful (nutrient-poor) environments. Their alternative triangle includes the well-known *r*- and *K*-selection mechanisms and '*g*-selection', which operates under high-frequency but low-intensity disturbance.

Grubb (1998) distinguished three adaptations to resource shortage instead of one: (i) 'low flexibility' strategy, with long-lived leaves, low maximum relative growth rate and no changes in form and gas exchange rate when the shortage is relieved; (ii) 'switching' strategy, with low flexibility in the juvenile stage but changing form, particularly specific leaf area (SLA) and growth rate when resources become available in the adult stage; (iii) 'gearing down' strategy, involving strong reduction in respiration rate, both in the juvenile and adult stages, when a resource becomes scarce (Table 1.7).

As remarked above, stress resulting from resource excess has so far hardly been considered, although Grubb (1985) mentioned several forms of excess stress. Yet,

Table 1.7 Some characteristics of stress-tolerant species with low flexibility, switching and gearing-down specialization, according to Grubb (1998).

Type	Switching	Gearing down	Flexibility
RGR_{max} of seedling relative to seed mass	Low	Low	Low to high
RGR_{max} of adult	Low	High	Low to high
Flexibility of SLA in response to relief of shortage	Low	Low (seedling); high (adult)	High
Flexibility of leaf longevity	Low	Low (seedling); high (adult)	High
Change in rate of gas exchange per unit leaf area	Low	Low	High

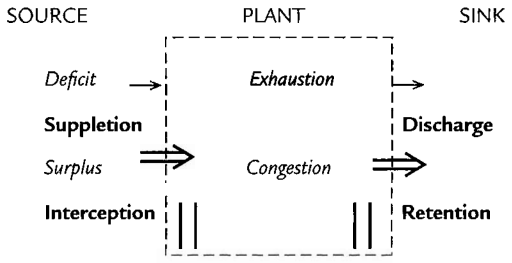

Fig. 1.9 Stress situations (italics) and adaptation mechanisms (bold) of plants, based on a model for ecosystems by G. van Wirdum & C.G. van Leeuwen as rephrased by van der Maarel (1980).

Shelford's 'law of tolerance' from 1913 (e.g. Kent & Coker 1992; Fresco *et al.* 2001) is based on a species-response curve showing two zones of stress for any relevant environmental factor: a minimum level needed and a maximum level tolerated. This double stress situation has been elaborated in a more strategic way by using a model for optimal matter and energy flow in an ecosystem where the plant is seen as a link in a source-sink system (Fig. 1.9).

1 There can be a deficit of a necessary resource – Grime's stress situation – leading to exhaustion which can be coped with in two ways: suppletion and retention. Suppletion can be achieved, for instance by extension of the root system in dry soil, foraging for water; retention for instance by storing nutrients in plants in a nutrient-poor environment.

2 There can also be a surplus of a resource, leading to congestion which can be compensated for by interception, as in the case of a coastal cliff plant under salt spray adopting a prostrate growth form and increased leaf hairiness, or by discharge, for instance salt exudation by a salt-marsh species.

Finally, a pragmatic alternative was proposed by Westoby (1998), avoiding the controversies around the concepts in Grime's system and easily applicable outside the flora of north-west Europe. Three traits are used as axes in a three-dimensional scheme: specific leaf area, plant height at maturity, and seed mass. These traits are said to vary largely independently. SLA and plant height are related to Grime's RGR and morphology index M, respectively.

1.17 Epilogue

Vegetation ecology has grown tremendously since its first textbook appeared (Mueller-Dombois & Ellenberg 1974). and since then, many thousands of papers have been published in international journals. Although only a small minority of them have been cited in this book, it is hoped that the growth of the science, both in depth and in breadth, will become clear from the 13 chapters that follow. The growing breadth is also expressed in the involvement of scientists from other disciplines in vegetation ecology, notably population ecology, ecophysiology, microbiology, soil biology, entomology, animal ecology, physical geography, geology and climatology.

It is encouraging that the international cooperation between plant ecologists all over the world has grown impressively as well. The authorship of this book includes colleagues from Africa, Asia, Australia, Europe and the USA.

Several chapters conclude with a summary of achievements, others offer perspectives for the future of our science. Let us hope that the book will indeed contribute to the further development of vegetation ecology.

Acknowledgements

I thank Mike P. Austin, Jan P. Bakker, Thom Kuyper, Marcel Rejmánek, Mahesh Sankaran, Brita Svensson and Jelte van Andel for comments on earlier versions of this chapter; Dick Visser at the Biological Centre of the University of Groningen and Joost van der Maarel of Opulus Press for drawing some figures; and last but not least Marijke van der Maarel for both reviewing and copy-editing this chapter.

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