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Vegetation Ecology: Historical Notes and Outline

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1.1 Vegetation ecology at the community level

1.1.1 Vegetation and plant community

Vegetation ecology, the study of the plant cover and its relationships with the environment, is a complex scientific undertaking, regarding the overwhelming variation of its object of study, both in space and in time, as well as its intricate interactions with abiotic and biotic factors. It is also a very modern science with important applications in well-known socio-economic 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 onwards, vegetation scientists have studied stands (small areas) 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. Most early European and American vegetation scientists did not explicitly make a distinction between actual stands of vegetation and the abstract concept of the plant community. This distinction was more

important in the 'Braun-Blanquet approach' (Westhoff & van der Maarel 1978). This approach, usually called **phytosociology**, was developed in Central Europe in the early decades of the 20th century, notably by J. Braun-Blanquet from Zürich, and later from Montpellier. The Braun-Blanquet approach, also known as the Zürich–Montpellier school, became the leading approach in vegetation science. It has a strong emphasis on the typology of plant communities based on descriptions of stands, called relevés. This can be understood because of its practical use (see also Chapter 2). However, Braun-Blanquet (1932, 1964) paid much attention to the relations of plant communities with the environment and the interactions within communities (see Section 1.1.2), which is now incorporated in the concept of ecosystem.

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. In a similar way, a community of birds, insects, molluscs or any other taxonomic group under study, including mosses and lichens, can be studied separately as well (see Barkman 1978). One can also describe a biotic community, i.e. the combination of a plant community and several animal groups (Westhoff & van der Maarel 1978).

Uniformity and distinctiveness. As mentioned above, the delimitation of stands of vegetation in the field is based on an internal characteristic, i.e. **uniformity**, and an external one, i.e. **distinctiveness**. Distinctiveness of a stand has been much discussed and interpreted. Distinctiveness implies discontinuity with surrounding vegetation. This is sometimes very obviously environmentally determined, for example in the case of a depression in a dry area, or the roadside vegetation between the road and a ditch in an artificial landscape. However, more usually the distribution of the local plant populations is decisive. This has been the case since H.A. Gleason (e.g. 1926) observed that species are 'individualistically' distributed along omnipresent environmental gradients and thus cannot form bounded communities. Note that this observation referred to stands of vegetation, even if the word community was used! The wealth of literature on ordination (see also Chapter 3) offers ample evidence of the 'continuum concept of vegetation' (McIntosh 1986).

Gleason and many of his adherers criticized the community concept of F.E. Clements (e.g. 1916), 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 plant communities in the field.

Shipley & Keddy (1987) simplified the controversy by reducing it to the recognition 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 (see also Chapter 3).

The occurrence of different boundary situations as such is of theoretical importance. They can be linked to the two types of boundary distinguished by C.G. van Leeuwen and put in a vegetation ecological framework (see Westhoff & van der Maarel 1978; van der Maarel 1990). The first type is the *limes convergens* which can be identified with an **ecotone** *sensu stricto* or tension zone. Here species boundaries can be determined strictly by abiotic conditions, which shift abruptly, in space and/or in time, although interference between species may play a part (e.g. Shipley & Keddy 1987); 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 where species reach local distribution boundaries in an 'individualistic' way along gradually changing environmental conditions (van der Maarel 1990).

Despite the general appreciation of the individualistic character of species distributions, it has been 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). Indeed, the individualistic and community concepts are now generally integrated (e.g. van der Maarel 2005).

1.1.2 Plant communities: integrated, discrete units or a convenient tool

Concepts. Within the neutral definitions of plant community quite different ideas and opinions on the nature of the plant community have been expressed since the early 20th century and the discussion is still going on. The controversy between Clements and Gleason has been an important element in this discussion. Allen & Hoekstra (1992) posited that the contrasting viewpoints of the two masters were influenced by the differences in the landscapes where they grew up. 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. 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 that 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. Westhoff & van der Maarel (1978) considered that the 'organismal concept' of Clements versus the 'individualistic concept' of Gleason, can rather be interpreted as the 'social structure' concept and the 'population structure' concept, respectively (see van der Maarel 2005).

Definitions. 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: '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. They may emphasize the co-occurrence of populations (Looijen & van Andel 1999), interactions between individuals (Parker 2001), or the 'phenomenological' coincidence (Grootjans *et al.* 1996). '**Emergent properties**' are causing the whole to be more than the sum of its parts, such as dominance–diversity relations (Whittaker 1965; Wilson *et al.* 1998). Weiher & Keddy (1999) proposed the term 'assembly rules'. Grime (2001) paid attention to the mechanisms of plant community assembly. Details and more literature on aspects of integration are found in van der Maarel (2005).

In conclusion, a plant community is generally recognized as a relatively uniform piece of vegetation in a uniform environment, with a recognizable floristic composition and structure, that is relatively distinct from the surrounding vegetation. Even if the populations of the participating species are usually distributed individualistically in the landscape, they may well interact within the community and build up an integrated unit with emergent properties. At the same time, plant communities can be convenient units for conveying information about vegetation and its environment.

1.1.3   Vegetation survey and sampling

Whatever our aim, approach and scale of observation, vegetation – whether loosely defined or approached as a plant community, or as a unit in a higher level of integration – should be described and analysed. Vegetation characteristics are either derived from plant morphological characters, usually called *structure*, or from the plant species recognized, the *floristic composition*. In Chapter 2, R.K. Peet & D.W. Roberts present a detailed account of community description. Amongst the many different objectives, there are four common ones:

1 phytosociological: community classification and survey, dealt with in Chapter 2;
2 ecological: correlation of the variation in vegetation composition with variation in environmental factors, dealt within Chapter 3;
3 dynamical: study of vegetation changes; see Chapter 4;
4 applied: nature conservation and management, the subject of Chapter 14.

Size of the sample plot; minimal area. A contemporary approach to the selection of plot size and shape for vegetation sampling is discussed in Chapter 2, while only a brief history of the development of the minimal area concept is provided here. The size of a sample plot will depend on the type of vegetation and may vary from a few square metres to several hectares. **Minimal area** is defined here (in line with Mueller-Dombois & Ellenberg 1974 and Westhoff & van der Maarel 1978) as a 'representative area on which the species of regular occurrence are found'. In various schools (Braun-Blanquet 1932; Cain & Castro 1959) determination of a species–area relationship has been recommended as a way to identify minimum area, on the assumption that the curve would reach an asymptote at which a '*saturated community*' (Tüxen 1970) would be reached. However, in practice this occurs only in species-poor communities whereas in communities richer in species a semi-logarithmical or a log–log function is found; see Chapter 11 on Diversity for more on functions.

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. For further information see van der Maarel (2005), who has also summarized minimal area data for 38 community types. These data are summarized in Chapter 2.

Vegetation characteristics. Vegetation structure and floristic composition are usually measured or estimated on a plant community basis. *Structure* includes: **stratification**, the arrangement of phytomass in layers; **cover**, as percentage of the surface area of the sample plot; **phytomass**, expressed as dry-weight g/m^2, kg/m^2 or t/ha ($1\,t/ha = 10\,kg/m^2$), or as productivity in $g/m^2/yr$; and **leaf area index**, LAI, and its derivate specific leaf area. These elements appear particularly in Chapters 10–12, and see, for example, Mueller-Dombois & Ellenberg (1974). 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 (see also Chapter 12). Structural analysis of above-ground plant parts should be (but is seldom) completed with an analysis of the below-ground parts, as stimulated by Braun-Blanquet (1932, 1964; Dierschke 1994). Species data should not only be collected above-ground but also below-ground. 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** for 19 species in steppe vegetation based on percentage dry weight contributions of species to green phytomass and below-ground organs are quite different.

Species composition includes a list of species for the sample plot (usually vascular plants only), with expressions of their quantitative occurrence, usually broadly called **abundance**. This comprises: (1) *abundance* proper, 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; (2) *frequency*, the number of times a species occurs in subplots within the sample; (3) *cover* of individual species is usually estimated along a cover scale – many scales have been proposed, the most current of which are described in Chapter 2; (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 is analogous to the *importance value* developed by Curtis (1959) – the product of density, frequency and cover – which has been popular in the USA for some decades. Several proponents of a combined cover–abundance estimation have nevertheless found it necessary to convert the abundance categories from the combined scale into approximate cover values. Two combined scales still in use are the Domin or Domin-Krajina scale (see Chapter 2) and the most frequently used Braun-Blanquet scale which, in several variants, has been in use since the 1920s. Van der Maarel (1979) suggested an 'ordinal transform' scale replacing the modern nine-point Braun-Blanquet scale by the values 1–9. This scale was also included in Westhoff & van der Maarel (1978) and has found wide acceptance. Van der Maarel (2007) also suggested a cover-based interpretation of this scale by transforming the abundance categories so that they approximate a ratio scale, where the means of the cover classes form a geometrical (×2) series (see Table 1.1). Peet & Roberts (Chapter 2) concentrate on cover values, but emphasize that cover intervals should confirm to the Braun-Blanquet scale, which the geometrical-ordinal scale does.

1.1.4   Plant communities and plant community types

Typology and syntaxonomy. When plant communities are described in the field by means of relevés (or other types of analysis), they can be compared with each other and an abstract typology can be developed. Plant community types must

Table 1.1   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. See also van der Maarel (2007).

Braun-Blanquet	Abundance category	Cover: interpreted interval	OTV cover interval	OTV
r	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

be based on characteristics analysed in the field. 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 and Chapter 15). Later the floristic composition became decisive. For this community type the term association became standard under the definition adopted at the 1910 Botanical Congress (see also Chapter 2).

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: (1) identification, through reconnaissance and comparison; (2) elaboration of a maximal correlative concentration, i.e. first of vegetation, second of environmental characteristics, through tabular treatment (and nowadays multivariate methods); (3) systematic categorization, i.e. arranging the type in a system of plant communities (Westhoff & van der Maarel 1978).

The Braun-Blanquet approach developed a hierarchical system of plant community types which resembles the taxonomy of organisms. Each syntaxon is defined by a characteristic species combination, a group of **diagnostic taxa** which may include **character** ('faithful') **taxa**, **differential taxa** and **companions**. The confinement of taxa to syntaxa is seldom absolute and degrees of **fidelity** have been recognized. 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. This has been elucidated by Westhoff & van der Maarel (1978) and particularly Dierschke (1994). Other challenges arise. At what level in the syntaxonomical hierarchy should a newly described syntaxon be placed? Syntaxa of a lower rank often show floristic similarities to syntaxa from different classes. These and other problems were discussed by Westhoff & van der Maarel (1978); see also van der Maarel (2005) and Chapter 2. After this system has long been distrusted and left aside in Anglo-American ecology, the concise description of vegetation classification by Robert H. Whittaker (e.g. 1978) came close to the European approach and stimulated worldwide interest.

Numerical classification. The development of numerical methods for the classification – as well as the ordination – of plant community samples started after the Second World War in various countries, e.g. Th. Sørensen in Denmark, D.M. de Vries in the Netherlands, J.T. Curtis in the USA and W.T. Williams in the UK (see Westhoff & van der Maarel 1978). Application of these methods on a larger scale was initiated in 1969 by the Working Group for Data-Processing of the International Association of Vegetation Science. The aim of this group was first of all to build up a database of phytosociological relevés. This implied the unification of the identity and nomenclature of the plant species involved and the development of a coding system. Numerical clustering and table arrangement programmes were developed, two of which received much attention and application.

TABORD (van der Maarel *et al*. 1978) is an agglomerative method based on a similarity analysis and subsequent fusion of relevés and clusters and

a subsequent arrangement of clusters in an ordered phytosociological table. A chi-square analysis was implemented to indicate the fidelity of species to clusters. The elaborated version FLEXCLUS by O. van Tongeren (in Jongman *et al*. 1995) is searching for a cluster structure on an optimal level of similarity and an ordination, so that the structure is reticulate rather than hierarchical.

TWINSPAN (Hill 1979), a divisive method on the basis of the position of relevés along axes of a correspondence analysis ordination and a subsequent tabular ordering, is by far the most popular method and its popularity has grown since it was incorporated in the program TurboVeg for phytosociological classification of very large data sets (Hennekens & Schaminée 2001). Attractions of the latter 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 problems with correspondence analysis, which are discussed in Chapter 3. Numerical classification is treated extensively in Chapter 2.

Classification of natural and semi-natural vegetation. Under this denominator, R.K. Peet and D.W. Roberts in Chapter 2 present a comprehensive and sophisticated guide to conceptual and methodological issues in the development, interpretation and use of modern vegetation classifications based on large-scale surveys. Vegetation description and classification are integral to contemporary planning, management and monitoring for conservation of natural communities. Chapter 2 examines several large-scale national and multinational classification systems and finds that standardization of methods and nomenclature are attributes of successful classification systems. Peet and Roberts outline all components of vegetation classification: planning and data acquisition; numerical classification or other approaches to creating vegetation classes or entities (entitation); community characterization, determination (assigning new observations to classes), integration and documentation. Numerical classification typically involves calculating distance or similarity measures from community composition data and then applying some sort of clustering or partitioning algorithm. Chapter 2 outlines the variety of methods currently applied to the vegetation classification problem and their relative merits for use with ecological community data.

1.1.5   Vegetation and environment: discontinuities and continuities

M.P. Austin, in Chapter 3, treats vegetation and environment in a coherent way, indeed as **vegetation ecology**. This term was coined by Mueller-Dombois & Ellenberg (1974), both of whom were educated in Germany in the tradition of continental-European phytosociology. Anglo-American vegetation ecology has its roots in plant ecology – and is usually called so. However, the study of plant communities in the UK with A.G. Tansley, in the USA with Cowles, F.E. Clements and later R.H. Whittaker, and in continental Europe with J. Braun-Blanquet and H. Ellenberg, has always been an ecological rather than a botanical undertaking, despite the differences in approach (McIntosh 1986).

Community and continuum. Austin (Chapter 3) 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. He shows how three key *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.

Measuring the environment. Austin (Chapter 3) emphasizes the importance of a framework of 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 an order of impact (van der Maarel 2005; see also Chapter 14).

   A useful distinction within the environmental factors is between (i) indirect, distal factors, notably altitude, topography and landform, and (ii) direct factors such as temperature, groundwater level and pH – which are determined by indirect factors, and resource factors such as water availability and nutrients. Generally, vegetation ecology is more meaningful when the environmental factors available for vegetation–environment studies are more physiologically relevant. Austin also re-introduces the concept of scalars, major integrated environmental complexes, once introduced by Loucks (1962) in an ordination study of forests, but largely neglected afterwards.

   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 and West European vascular plant species regarding moisture, soil nitrogen status, soil reaction (acidity/lime content), soil chloride concentration, light regime, temperature and continentality. The system is also mentioned in Chapter 12. The values generally follow a (typically ordinal) 9- or 10-point scale, based on field experience and some measurements. They are used to calculate (weighted) mean values for plots and communities, which is a calibration problem, discussed by ter Braak (in Jongman *et al*. 1995).

Indirect ordination, direct ordination. Austin (Chapter 3) explains how **indirect ordination** determines environmental gradients on the basis of the variation in the vegetation data, while **direct ordination** starts from the variation in environmental factors and then determines the distribution of plant species along these environmental gradients. Indirect ordination is numerically developed in many different methods, of which correspondence analysis, and its derivate canonical correspondence analysis and non-metric multidimensional scaling are treated in detail by Austin, while relating the appropriateness of these methods to the character of the distribution of species along environmental gradients.

Classification and ordination as complementary approaches. From Chapters 2 and 3 it becomes clear that classification and ordination are both useful and can usually be profitably integrated in plant community studies. In this connection, an old approach may be mentioned, based on the observation that in coarse-grained relatively dynamic and homogeneous ecotone environments, plant communities are relatively poor in species and simply structured, whereas fine-grained relative constant and divergent ecocline environments, plant communities are richer in species, more structured and integrated. 'Ecotone communities' can be more easily classified and be included in a hierarchy, while 'ecocline communities' cannot be easily classified and are more liable to be ordinated together with related communities. A framework for combining both numerical approaches is presented in Fig. 1.1. As a 'golden mean' it was recommended to apply both approaches, with an optimally effective syntaxonomy on the alliance/order level (van der Maarel unpublished).

1.1.6   Vegetation dynamics

In Chapter 4, S.T.A. Pickett, M.L. Cadenasso and S.J. Meiners adopt the vision that vegetation dynamics is governed by three general processes: differential **site**
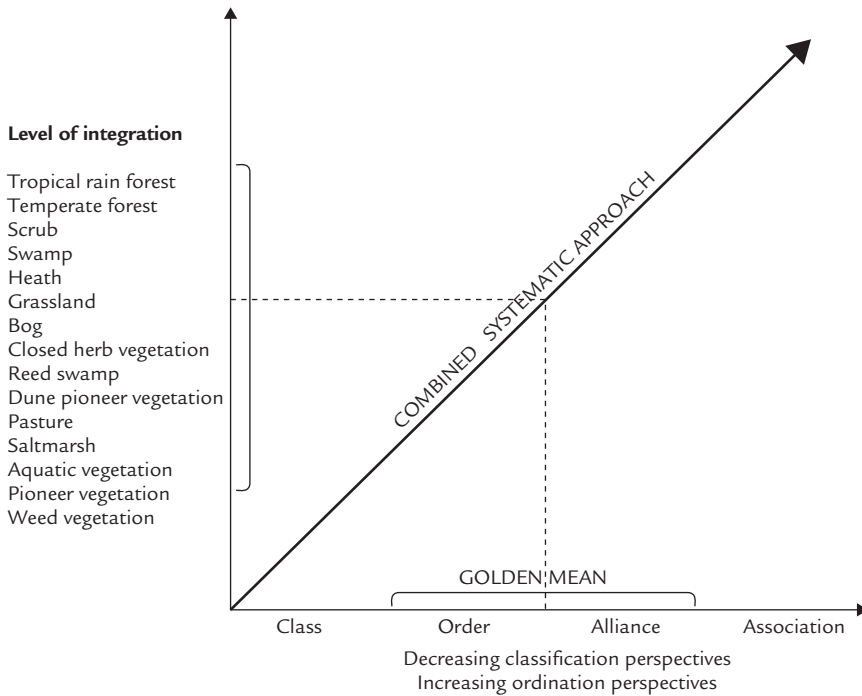

Fig. 1.1   Relation between the level-of-integration in vegetation and the relative success of classification vs ordination in a 'combined systematic approach'. (Based on a figure designed by E. van der Maarel in consultation with V. Westhoff & C.G. van Leeuwen, and presented in a lecture at the International Botanical Congress in Edinburgh, 1964.)

availability, differential **species availability** and differential **species performance**. If a site becomes differentially available, species are differentially available at that site, and/or species perform differentially at that site. As a result the composition and/or structure of vegetation will change.

Analytical methods. The two main methods for analysing vegetation dynamics are the repeated description of **permanent plots** and the description of sites of different ages, forming a **chronosequence** ('space-for-time substitution'). 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). Nowadays thousands of such plots are under regular survey, many surveyed initially to help solve management problems (Chapter 12).

Types of disturbance and types of vegetation dynamics. As Pickett *et al*. (1987) explained and Chapter 4 discusses further, site availability is largely the result of a disturbance; differential species availability is a matter of dispersal (Chapter 6); and differential species performance is based on the differences in ecophysiology and life history (Chapter 12), which is the outcome of species interactions (Chapters 7 and 9) and herbivory (Chapter 8). Chapter 4 also elucidates how vegetation dynamics are increasingly affected by human activities (see also Chapter 14).

One of the interesting consequences of the primate of disturbance is that primary sites are more carefully analysed and mostly seem to have at least some legacy. So, the classical distinction between primary and secondary succession is replaced by a gradient between two extremes. After a disturbance, the time needed for the vegetation to reach a new stable state will vary. Fig. 1.2 indicates how we can distinguish between fluctuation (on the population level), patch dynamics, secondary succession, primary succession, secular succession and

	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 similar schemes in van der Maarel 1988 and Gurevitch *et al*. 2002.)

long-term vegetation change in response to (global) changes in climate (see Chapter 17), and how the time scale varies from less than a year to thousands of years. Dynamic studies of plant populations, especially clonal plants, may vary from 10 to 10^3 yr (examples in White 1985). Cyclic successions may take only a few 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).

Development of vegetation and soil. In Chapter 4, Pickett *et al.* 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.

The contribution to these developments by individual species varies with the type of succession and the successional phase. The old phytosociological literature already described 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. 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.

1.1.7   Pattern and process in the plant community

The phrase '**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 plant community, which is in a steady state, changes may occur patchwise as a result of local disturbance (exogenous factors) or plant senescence (endogenous factors); in the gaps formed, regeneration will occur that will initially lead to a patch of vegetation which is different from its surroundings. These processes are 'fine-scale vegetation dynamics' (Chapter 4) within a community, rather than of the community as a whole or of larger units.

Spatial pattern analysis. Spatial patterns of plant units of particular species comprise the development of patches, that may form a clumped distribution, regular (overdispersed) dispersion and homogeneous (random) distribution. The statistical analysis of these patterns was introduced in plant ecology by Greig-Smith (1957) and Kershaw (1964), who were particularly interested in the causes of patch formation. Kershaw distinguished between morphological, environmental and sociological patterns. Morphological patterns arise from the growth-form

of plants, in particular clonal plants (see Chapter 5). Environmental patterns are related to spatial variation in environmental factors (see Chapter 3), for instance soil depth. Sociological patterns result from species interactions (see Chapter 7) and temporal changes in the behaviour of plants.

The development of analytical methods has proceeded and has been regularly reviewed (e.g. Dale 1999; Fortin & Dale 2005; Franklin 2010), but the ecological application of these methods has remained limited and will not be treated further in this book.

Patch dynamics. On the other hand, the study of patch dynamics in relation to internal environmental dynamics has continued and has found a place in Chapter 4 by Pickett *et al*. Within-community patch development as linked to disturbance, particularly gap formation, started in the 1920s in forests by R. Sernander in Sweden and A.S. Watt in Great Britain (Hytteborn & Verwijst 2011). When the investigated forest plots and the gaps are large, the dynamics are considered a regeneration succession (see Chapter 4) and the succession stages have been described as their own plant communities. In the European syntaxonomical system, these stages have remote positions, being different classes (e.g. Rodwell *et al*. 2002).

Watt (1947) described similar patch dynamics in bogs (where he had studied the work of the Swede H. Osvald from 1923), heathlands and grasslands (see also van der Maarel 1996). In bogs the well-known mosaic of hollows and hummocks appeared to be dynamically related and was described as a '**regeneration complex**'. Watt considered the different stages as seral and also as separate communities, involved in a **cyclic succession**. Whether or not to call these cyclical processes 'succession' is a matter of definition and of scale (e.g. Glenn-Lewin & van der Maarel 1992). An alternative term *Mosaik-Zyklus* has been proposed by the German animal ecologist H. Remmert (Remmert 1991: '*mosaic-cycle*'). A mosaic-cycle is a special case of patch dynamics where the changes are triggered largely by endogenous factors, in particular plant senescence. Exogenous factors generally also play some part (Burrows 1990).

Regeneration niche and the carousel model. 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, through the death or partial destruction of plant units, the 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. In grazed grasslands, local removal of plant parts, trampling and deposition of dung are additional causes of gaps, often large ones.

Where gaps arise more or less continuously in grasslands and plant species become not only locally extirpated because of disturbances and/or death but also have continuous opportunities to re-establish, species may show a high fine-scale mobility. At the same time, patch dynamics can contribute considerably to the co-occurrence of many plant species on small areas of grassland. The limestone grassland on the alvars of southern Öland (Sweden), which is rich in annuals, as a whole appeared to be remarkably constant in floristic composition, while
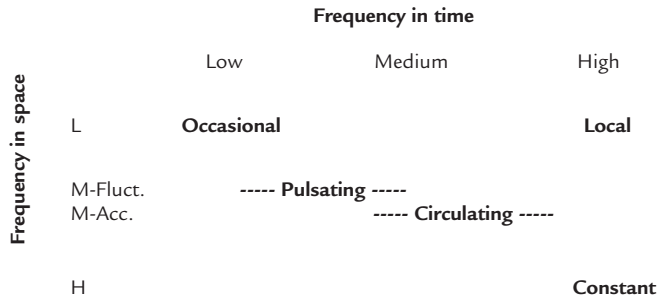
Frequency in time

	Low	Medium	High
L	**Occasional**		**Local**
M-Fluct.	----- **Pulsating** -----		
M-Acc.		----- **Circulating** -----	
H			**Constant**

Frequency in space (vertical axis label)

Fig. 1.3 Types of within-community plant species mobility based on frequency in space and time in 10 × 10 cm subplots in limestone grassland during 1986–1994. Mean spatial frequency values divided into high, >75% (H), medium, 35–75% (M; M-Fluc., 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.)

the species composition on subplots from 10 to 100 cm² changed from year to year. Van der Maarel & Sykes (1993) quantified this mobility as (1) cumulative frequency, i.e. the cumulative number of subplots a species is observed in over the years and (2) cumulative species richness, i.e. the mean number of species that is observed in a subplot over the years. A 'carousel model' was suggested to characterize this '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. Several types of mobility could be distinguished, mainly based on mean frequency and mean cumulative frequency (Fig. 1.3). Lepš (Chapter 11) discusses these aspects of regeneration as contribution to the species richness in communities.

1.2   Internal organization of plant communities

1.2.1   Clonality in the plant community

In Chapter 5, B. Svensson, H. Rydin & B. Carlsson give an account of the processes and ecological significance of vegetative spread by clonal plants. 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. Clonality is largely an internal community process, but it may link a community to neighbouring communities, or still further away, as the chapter describes. Neighbour effects have long been recognized in phytosociology as vicinism (van der Maarel 1995). See also Section 1.3.2. Important sources of clonal variation include the length of the ramets formed (notably rhizomes, stolons and runners) and the speed with which these are formed.

Svensson *et al.* pay attention to the distinction between 'phalanx' and 'guerilla' forms of vegetative reproduction of species, which they consider as

endpoints on a continuum variation. Ecologists may resist the metaphor of plants as warriors, and are confused about the spelling of guerilla (the correct spelling of the originally Spanish word being guerrilla). Moreover, the two strategies do not seem to even resemble the two types of warfare involved. Nevertheless the distinction between the two types is useful.

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 1.1.7; Chapter 4), the relation between clonality and competition and co-existence (Chapters 7 and 11) and the relation between clonality and herbivory (Chapter 8).

1.2.2   Seed ecology and assembly rules in plant communities

This title for Chapter 6 by P. Poschlod *et al.* suggests that the original focus on diaspore dispersal in the first edition of this book has now been broadened towards the ecology of diaspores and their dispersal and germination, in relation to community assembly. The following Chapters 7 on species interactions and 11 on diversity further discuss assembly rules while Chapter 6 is now also linked to Chapter 4 on vegetation dynamics. 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 as it becomes 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, incidentally, consider species reservoir a better – i.e. a more appropriate – term than species pool). 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. This chapter is also a natural place to treat the soil seed bank, which – as Poschlod *et al.* state – is in fact rather a diaspore bank. Zobel *et al.* (1998) suggested including the diaspore bank in the community pool, thus including the so-called persistent diaspores. It is debatable whether species that never germinate should also be included in the target community – because the environment may not be suitable for them. However, there are many examples of species apparently not being suitable for 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 just outside the mother community, also known as **vicinism** (van der Maarel 1995).

1.2.3   Species interactions structuring plant communities

The concise chapter on species interactions by J. van Andel, Chapter 7, gives a survey of the different types of species interaction and then pays attention to

the following types of interaction: competition, allelopathy, parasitism, facilitation and mutualism. The focus on competition, the classical main type of interaction, is no longer predominant in this edition, even though competition as a mechanism to arrange species packing along gradients (see Chapter 2) remains important in vegetation ecology. The typically community-structuring force of facilitation is now a more fascinating topic in vegetation ecology. 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, while it also forms part of the topic 'interactions between higher plants and soil-dwelling organisms', elaborated in Chapter 9.

Van Andel's chapter is one of the few where bryophytes are treated in some detail. In addition, the review paper by Rydin (1997) and the detailed competition study by Zamfir & Goldberg (2000) can be mentioned.

1.2.4   Terrestrial plant–herbivore interactions

In Chapter 8, M. Sankaran & S.J. McNaughton present an integrative account on herbivory, with links to Chapters 4, 6, 7, 11 and 14. The idea of co-evolution comes to mind (e.g. Howe & Westley 1988) in view of the broad spectrum of plant types and plant parts being eaten and the equally broad spectrum of herbivores, as well as the often intricate mutual adaptations between plants and animals in each type of interaction.

Plants deal with herbivory by avoidance or tolerance (i.e. compensation for damage), and a range of compensatory responses is discussed. There is a range from symbiotic to parasitic aspects of grazing. Finally, herbivores and herbivore diversity have major effects on plant diversity and pattern formation.

1.2.5   Interaction between higher plants and soil-dwelling organisms

In Chapter 9, T.W. Kuyper & R.G.M. de Goede concentrate on the interactions between plants and soil organisms that occur around and in roots. The three major processes described are N-fixation by bacteria, mycorrhiza with fungi and root-feeding by invertebrates. The gradual transition and alteration between symbiotic and antagonistic aspects is related to the ranges of interactions described in the two preceding chapters.

A link to Chapter 13 on plant invasions is the often noticed difference in behaviour of invasive plants in their new regions compared to their old, which is related to the difference in accompanying soil-dwelling organisms. A link to Chapter 4 follows from the elucidation of the two hypotheses about 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.

1.3   Structure and function in plant communities and ecosystems

1.3.1   Vegetation and ecosystem

The plant community together with the animals within, the soil underneath and the environment around is now generally considered an integrated unit, the ecosystem. Nevertheless, most vegetation studies are restricted to the above-ground plants, even if it is long since known (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 of roots and seeds.

Root-related phenomena such as nitrogen-fixation and mycorrhiza are now being included in vegetation studies (Chapter 9). 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 integrated ecosystems.

Chr. Leuschner, in Chapter 10, focuses on trophic levels between which matter and energy are exchanged. An important part of the primary production ends up in the below-ground plant parts. Here 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 recovery to 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 11).

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: carbon, nitrogen, phosphorus and water. These cycles are studied on the global level and these processes at this level return in Chapter 17.

1.3.2   Diversity and ecosystem function

Chapter 11 by J. Lepš is on diversity or **biodiversity** as it is called nowadays. It starts with a brief treatment of some diversity indices: α or **within-community**, β or **between-community** and γ or **within-landscape** diversity, basically a product of α and β. These are all concerned with species diversity, or rather taxon diversity, the variation in taxa. In addition, within-taxon or (phylo-)genetic diversity is receiving increasing attention. Relatively new aspects of biodiversity are **phylogenetic distinctiveness**, based on taxonomic distinctiveness, **numerical**

distinctiveness, based on the rarity of occurrence, and **distributional distinctiveness**, i.e. endemism of taxa (van der Maarel 2005). 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.

As Lepš confirms, 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, the well-known indices of Simpson and Shannon are similar in that the most abundant species to some extent determines the diversity, but Simpson does this more than Shannon.

Chapter 11 emphasizes the relation between diversity and ecosystem function. Much research 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. Important contemporary studies of biodiversity are concerned with productivity, disturbance, co-existence and stability in the plant community.

1.3.3 Plant functional types and traits at the community, ecosystem and world level

Chapter 12 by A.N. Gillison treats the characteristics and function of life-forms and growth-forms in a contemporary fashion under the denominator of plant functional types. As in the previous chapter, such a treatment has to exceed the level of integration of the plant community, and is indeed relevant up to the global level, where it relates to Chapter 15. A **plant functional type** (PFT) is a group of plant species sharing certain morphological–functional characteristics. The notion 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 (see also Chapter 15). Peters (1991) mentioned this study with its validated global model as a good example (one of the few) of predictive ecology.

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 1.2; see also Table 15.2). Environmental adaptation is most obvious in the life-form system of Raunkiær.

Table 1.2   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 acording 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 unfavourable 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)

(*Continued*)

Table 1.2 (*Continued*)

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

Plant strategy is a concept more recent than life-form that is also closely related to PFT. The best known system of plant strategies is that by Grime (2001; earlier publications cited there), with competitors (C) 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. Strategies are 'groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology'. Such 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 predominantly used. These concepts and their use are all discussed by Gillison in Chapter 12.

The three strategy types proposed by Grime have been maintained virtually unchanged, even if the system has been regularly criticized. 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 (Rabotnov 1975), which are astonishingly similar to the CSR types (Onipchenko *et al*. 1998; Grime 2001). 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 – typology.

1.4   Human impact on plant communities

This section comprises two topics which are almost entirely concerned with human impact on plant communities. Several other chapters also provide information on human impacts, notably Chapter 4 on disturbance, Chapter 6 on

diversity, Chapter 8 on grazing, Chapter 11 on diversity and Chapter 17 on global change.

1.4.1   Plant invasions and invasibility of plant communities

In the new edition of Chapter 13, M. Rejmánek, D.M. Richardson and P. Pyšek consider the burgeoning literature on biological invasions, a research focus motivated by the need to understand why a small percentage of introduced plants become invasive with significant environmental and economic impacts. Chapter 13 presents the characteristics of invasive species, the pathways of migration of invasive species, the characteristics of environments and plant communities open to invasion and the main impacts of invaders. 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). Other factors affecting community invasibility, reviewed in Chapter 13, include functional type diversity, spatial heterogeneity of the environment and the disturbance responses and life-history traits of resident species. 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.

   Invasion is a function of the interaction of a compatible habitat for invaders with propagule pressure. 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. As the authors conclude, plant invasions as 'natural' community experiments actually provide important opportunities to study basic ecological and evolutionary processes as well as address important applied research problems.

1.4.2   Vegetation conservation, management and restoration

Chapter 14 by J.P. Bakker is ample proof of the profit made by conservation, management and restoration ecology of the development of vegetation ecology. Phytosociological classification facilitates communication over national boundaries on target plant communities and vegetation mapping can be used for land use planning. Still more importantly, ecological theory regarding the behaviour of plant species along gradients (Chapter 3), succession (Chapter 4), diaspore dispersal, species pool and seed bank dynamics (Chapter 6) and diversity (Chapter 11) has been developed and applied in these chapters. The development of ecohydrology as a basis for the restoration of nutrient-poor wetlands is particularly impressive.

   Many 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 also Perrow & Davy (2002).

1.5   Vegetation ecology at regional to global scales

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

We introduce this group of chapters by considering scales of organization from the plant community level upward. The plant community as defined in Section 1.1 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. On the next higher ecological level plant communities are part of ecosystems, while geographically they are part of community complexes. 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, i.e. a mountain.

In practice, ecological and geographical criteria are mixed in obtaining 'levels of organization', for instance Allen & Hoekstra (1992): 1. Cell < 2. Organism < 3. Population < 4. Community < 5. Ecosystem < 6. Landscape < 7. Biome < 8. Biosphere.

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. 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 to organization levels and scales are the recognition of (1) mosaic structures, with elements of a mosaic of a smaller grain size being mosaics of their own at a larger grain size; (2) different processes governing patterns at different scales; and (3) different degrees of correlation between vegetational and environmental variables at different grain sizes.

1.5.2   Vegetation types and their broad-scale distribution

In Chapter 15, E.O. Box & K. Fujiwara treat vegetation typology mainly in relation to the broadscale distribution of vegetation types. On a world scale, vegetation types have largely been defined physiognomically, in the beginning (early 19th century) by plant geographers, including A. Grisebach, who coined the term formation as early as 1838. Several readers will share the first author's memory of the famous world map of formations by H. Brockmann-Jerosch and E. Rübel decorating the main lecture hall of many botanical institutes. Box and Fujiwara 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).

It is clear that there is a growing interest in subordinating floristic units to physiognomic ones. This is also directly relevant for vegetation mapping (Chapter 16). The integrated physiognomic–floristic approach has indeed been proven to be effective since its apparently first study and vegetation map by van der Maarel & Westhoff in the 1960s (see van Dorp *et al*. 1985).

Chapter 16 also pays attention to the problems of modelling and mapping larger areas of vegetation which have lost most of their original vegetation as a result of human land use, and to the development of the concept of *potential natural vegetation* for large-scale vegetation mapping. Reconstruction of vegetation types developing after human impact would have stopped is of course difficult.

Global vegetation distribution patterns can be better understood using a plant functional approach securely rooted in ecophysiology – an approach Box has been instrumental in developing. Chapter 15 traces the development of climate-based global vegetation models from simple but powerful mechanistic rule-based models through contemporary dynamic simulation models of the vegetation, land surface and ocean–atmosphere system. The authors emphasize the importance of understanding the role of global vegetation in the earth system for studies of global change, including – but not limited to – climate change and land use change.

1.5.3   Mapping vegetation from landscape to regional scales

Chapter 16 by J. Franklin was developed for the second edition to address recent developments in vegetation mapping at the local to regional scale that combine traditional elements of photointerpretation and field mapping with powerful new data products and tools from remote sensing and geographic information science (GISci). While contemporary vegetation mapping at landscape to regional extents shares principles and techniques with global vegetation modelling and mapping (Chapter 15), it is typically carried out at the categorical resolution of the plant community. Therefore mapping must capture community attributes of structure and composition. The availability of high-resolution digital aerial imagery has allowed image processing algorithms and geographical models to be effectively married with the expert abilities of a photointerpreter. The result is multi-attribute vegetation databases replacing conventional vegetation maps that were constrained in their information content by the limits of traditional cartography. This new generation of vegetation maps depict extents ranging from local landscapes to subcontinents, at spatial resolutions ranging from 1 km down to extremely fine. Vegetation and land cover maps are being used for purposes ranging from monitoring land use change to environmental planning and management.

1.5.4   Vegetation ecology and global change

Chapter 17 by B. Huntley and R. Baxter deals with global pollution problems including deposition of N compounds and increasing tropospheric concentrations

of various pollutants, increasing UV-B and increasing CO_2 concentration, but with particular focus on global warming (climate change). Of interest in this connection are models to help understand and predict future changes of broad ecosystem types, and problems of species to cope with changes and of dispersing to newly available suitable environments.

Studies on the effects of global changes, and especially climate, on vegetation at the broad scale rely heavily on palaeo-ecological studies. In a way these studies are extrapolations into the future of the processes of secular succession. 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.

Models that simulate ecosystem processes and vegetation dynamics in response to climatic drivers, and with feedbacks to the atmosphere, may suffer from uncertainty regarding estimation 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, from the scale of species ranges to that of global vegetation, must be encouraged.

1.6   Epilogue

Vegetation ecology has grown tremendously since its first textbook appeared (Mueller-Dombois & Ellenberg 1974). Ever since, 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 16 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, landscape ecology, physical geography, geology and climatology. The updated and new chapters in this second edition highlight developments in the field during that past 5–10 years, but retain their firm grounding in the deeper history of the development of key concepts in the classic literature.

It is encouraging that international cooperation between plant ecologists all over the world has also grown impressively. 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.

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