REVIEW

Vegetation dynamics and dynamic vegetation science*

EDDY VAN DER MAAREL

Department of Ecological Botany and Ecological Research Station Öland, Uppsala University, Villavägen 14, S-752 36 Uppsala, Sweden; Department of Plant Biology, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

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INTRODUCTION

This contribution presents a review of the development of the study of vegetation dynamics since 1979, in the framework of a jubilee meeting on progress in the study of

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Table 1. Attention paid to different branches of vegetation science as estimated from the number of papers published in *Vegetatio* 1978–87 (477) and *Journal of Vegetation Science* 1989–95 (330). Figures are percentages referring to the various periods. High figures in bold. See also Van der Maarel (1991)

	1978–1979	1980–1982	1983–1985	1986–1987	1989–1991	1992–1993	1994–1995
Dynamics	19	**26**	17	19	14	**30**	23
Synecology	11	11	**21**	**20**	12	17	9
Numerical methods, models	**30**	**21**	10	12	11	4	8
Systematics, regional studies	10	8	6	2	6	2	9
Structure, pattern, life form	6	6	3	7	**17**	3	3
Diversity studies	10	7	5	5	4	3	5
Interaction studies, niche	—	1	2	4	5	10	8
Seed bank, dispersal	—	—	—	—	3	6	5
Ecosystem ecology	5	3	2	3	2	8	5
Geography	1	1	9	2	2	2	3
Palaeoecology	2	1	1	6	2	1	2
Landscape ecology	—	—	1	1	1	—	1
Mapping, remote sensing	1	3	—	1	1	3	8
Autecology	1	2	6	1	2	3	5
Population ecology	2	1	5	5	7	1	1
Management	4	5	6	6	8	3	3
Vegetation science general	2	4	5	6	4	3	3

vegetation. However, an exhaustive review is both impossible and unnecessary. It is impossible within the few pages available because of the vast literature published, and it is unnecessary because there are several review papers and textbooks available. To start with the year 1979 itself, two important papers appeared (White 1979; Huston 1979), and a symposium on advances in vegetation science was held in Nijmegen (Van der Maarel 1980a,b). Further publications consulted for this paper include Pickett & White (1985), Pickett *et al.* (1987), Gray *et al.* (1987), Burrows (1990), Van Andel *et al.* (1993), Glenn-Lewin *et al.* (1992) and Agnew *et al.* (1993).

In 1979 a similar special meeting was held (Werger 1979), where I contributed with a review-like paper on numerical methods in vegetation science. Since this important aspect of vegetation science was not covered at this jubilee meeting, some developments of this branch have been included here, mainly so far as they apply to vegetation dynamics. Since I am involved in one particular branch of vegetation dynamics, i.e. gap dynamics, extra attention will be paid to recent work in Uppsala, perhaps at the expense of other new developments.

As follows from Table 1, some significant changes in focus of attention for different branches of vegetation science have occurred since 1990. The statistics are based on a sample from the journal *Vegetatio* covering the period 1978–87 and one from the *Journal of Vegetation Science* (*JVS*) 1989–95. These journals have covered a great deal of the developments in vegetation science since 1979. Each column in the table covers *c.* 100 papers. Since the editorial policy of *JVS* has been largely the same as that of *Vegetatio* in the years before 1989, the samples should be comparable. Although there are some irregularities—which can be explained by the appearance of special issues—several trends can be distinguished:

- Interest in the development of numerical methods (including pattern analysis and spatial modelling) has decreased.
- Interest in diversity issues was relatively high before 'biodiversity' became a hot issue (Van der Maarel 1996b).
- Interest in vegetation dynamics has increased, including dynamic modelling.
- Some new branches have emerged, notably interaction and niche studies as well as seed bank and dispersal studies; these are all related to dynamics.

This implies that a personal bias is evident in this contribution towards the above-mentioned journals in the selection of research papers. Also, a clear bias towards examples from Dutch and Swedish research must be admitted.

DEVELOPMENTS IN NUMERICAL VEGETATION ANALYSIS

Numerical vegetation analysis is a very useful tool in summarizing the complex relations between species, and between species and their environment as these change during succession. Its importance, which had become clear by the end of the 1970s, has only increased during the 1980s and 1990s.

Generally, multivariate methods are being stabilized, although continuously discussed. Also, people have discovered that some diversity in methods is acceptable as long as the results of each application are carefully interpreted and compared with other results. Refinements and improvements of methods for multivariate analysis have been published. Several textbooks have appeared since 1979. In the present context it suffices to refer to Jongman *et al.* (1987)—a new edition of this book (Jongman *et al.* 1995) is called a 'corrected version'; it hardly contains any new references. This book is particularly useful for the various ordination and constrained (floristic–environmental) ordination techniques contained in the CANOCO package and for the equally popular divisive clustering technique TWINSPAN. Some applications and new developments will be discussed in the next section.

Ordination

The most important extension developed is Canonical Correspondence Analysis (Ter Braak 1986), a 'restricted' form of CA, in which environmental variables are included in the analysis so that the site scores are restricted to be a linear combination of the environmental variables. This simply means that the main ordination axes are determined by one or more associated species which (co-)occur only locally in the dataset, and which vary in correlation with the variation in environmental variable(s). Obviously, CCA can also be used in the analysis of vegetation dynamics, by introducing the variable 'time', i.e. number of years since the beginning of a time series. One example is the study of vegetation development along the Baltic seashore near Uppsala by Cramer & Hytteborn (1987). The coastline is subject to a considerable post-glacial isostatic land uplift, *c.* 5 mm/yr; 135 1-m^2 permanent plots in four transects across the shoreline were analysed in 1978 and 1984. In the detrended variant of the CCA, DCCA, applied to one transect, the main axis of variation is elevation, with the plots relatively (but not perfectly) arranged from low to high, characterized by facultative halophytes such as *Aster tripolium* and *Triglochin maritima* at the low side of the transect and woodland herbs such as *Mercurialis perennis* and *Anemone nemorosa* at the high side. Axis 2 represents the variation over time, with the floristic distance between the first and

the second analysis increasing with elevation and with the low-lying plots generally moving to the right rather than downwards, meaning that the slight elevation all plots were subjected to causes the strongest floristic changes in the low-lying plots. The joint interpretation of these axes is of course primary succession, with irregularities in the graph interpreted as the results of fluctuations.

By means of this type of 'dynamics ordination' we can also elucidate the phenomenon that the composition and development of any plot is very much dependent on the composition of neighbouring plots. This is a special form of a phenomenon known as spatial autocorrelation (see below).

As to further improvements of CA, Økland & Eilertsen (1994) elaborated a technique suggested by Borcard et al. (1992) to increase the explanatory power of a CCA of a large dataset, with many external variables included, by so-called variation partitioning. The principle is that the external variables are divided into two groups (one group, for instance, including temporal and large-scale spatial variables, the other group environmental variables). CCA is run with one variable at a time in a group while maintaining the variables which contribute significantly to the total variation. Then partial CCA was employed whereby the significant variables in one group were included as covariables and those in the other group as constraining variables.

Critical comments on CA include inaccuracies and loss of solution stability by detrending (e.g. Knox 1989). Recently, Tausch et al. (1995) discovered instabilities in the results of some CANOCO programs (with repercussions for TWINSPAN), related to the sequence in which the samples and species are entered.

Perhaps other ordination techniques may take over the role of CA, which would be certainly interesting if they could be made 'canonical'. Candidates are (1) Non-metric Multidimensional Scaling, which was applied successfully in vegetation studies (e.g. Oksanen 1983) and explained and promoted particularly by Minchin (1987a,b), and (2) Fuzzy Set Ordination (Roberts 1986).

Classification

Ever since TWINSPAN was introduced (Hill 1979), this program has often been applied. The success of this program was determined by its general availability, its objectivity, its speed and the resulting dichotomous hierarchy, which is appealing to many vegetation scientists. Nevertheless, there are some problems with the program. Its objectivity is not as pronounced as it seems because the program has many options, and the recommended default options are not always realistic. Moreover, the dichotomy is rigid and indicator species appear in clusters and subclusters throughout the hierarchy. The older agglomerative cluster techniques have also been further developed (e.g. Van Tongeren 1986; Wildi 1989), including stopping rules for an optimal cluster solution (e.g. Popma et al. 1983; Noest & Van der Maarel 1989). Interestingly, the agglomerative methods have remained more popular than TWINSPAN in vegetation classification and vegetation dynamics.

An example of the use of cluster analysis in the description of succession is the study by Van Noordwijk-Puijk et al. (1979) of the vegetation development on a desalinating tidal flat in Lake Veere, southwestern Netherlands, which arose after the closing of one of the estuaries in the area. Vegetation analyses in permanent plots from 1963–73 were subjected to agglomerative cluster analysis; for each year the allocation of single analyses to clusters was determined and a transition scheme drawn. The cluster structure was arranged in a sequence from rapid to slow desalinization. In this way one acquires

a comprehensive picture of the amounts of constancy and change and the diversification of the plant community structure.

More complicated transitions diagrams were constructed for the long-term succession of a dune area, based partly on cluster analysis and partly on the interpretation of air photographs and vegetation maps. As Van Dorp *et al.* (1985) and Van der Maarel *et al.* (1985) have shown, the succession follows multiple pathways. Moreover, the transition frequencies vary from year to year, while new types arise. As Van Dorp *et al.* remarked, these latter characteristics make it difficult to apply Markov models to predict the further development of the vegetation. This will be discussed below.

Pattern analysis

As to pattern analysis, two approaches are usually distinguished, one based on presence/absence or quantitative data for species in series of small quadrats, the other based on distances between individuals or clumps. Regarding the first approach the textbook by Kershaw & Looney (1985) is a useful reference, and also because this book deals with dynamic plant ecology. The essence of this approach is to calculate statistics (usually variance) of the occurrence of species in quadrat strings of increasing length and detect deviations from random distributions at different scales. Newer variants have been published, e.g. one based on fractal geometry (Palmer 1988) and one based on multi-scale ordination (Ver Hoef & Glenn-Lewin 1989). See, for example, Ver Hoef *et al.* (1993) and Dale & Zbigniewicz (1995). Apparently we have not reached the final stage in the development of this approach.

The essence of the other 'distance-based' approach is to determine distances, and treat these in different statistical ways. Haase (1995) presented an account of this group of methods. Basically, one counts numbers of neighbours to individual target plants or clumps within circles of increasing radius. This approach is obvious if, indeed, data on individual species are available, as is the case with *i.a.* forest trees (e.g. Newbery *et al.* 1986) and desert plants (e.g. Prentice & Werger 1985). Although Ford & Renshaw (1984) used different scales and intensities of pattern in a spatial complex to interpret the processes behind, very little work on real changes has been published. Zhang & Skarpe (1995) found in a study on pattern in the semi-arid steppe plant *Artemisia halodendron* that over a few years the aggregates of shoots of this species increased in size for the small shoots but decreased for the large shoots, which was related to grazing intensity.

The ecological significance of pattern analysis and its appreciation as an important tool will depend on further applications of pattern analysis in time series of permanent transects or repeated measurements.

Diversity

Regarding the measurement of diversity little has happened. Most people still use the well-known Shannon-Weaver, Simpson and equitability indices (see Magurran 1988 for a survey), and often parallel to each other, even if it has been clear since Hill (1973) that these indices are very much related to each other. Moreover, the Shannon-Weaver and Simpson indices, although meant as diversity indices, are mixed indices, taking into account both the total number of species in the collection under study and the evenness amongst the proportions the different species are represented with. Van der Maarel (1996b) demonstrated with a simple example that they in fact measure evenness rather than species number. Clearly, alternative approaches are necessary such as those of

Van der Maarel (1988), who distinguished between species density and dominance; Magurran (1988) proposed the parallel use of two indices for species number and dominance. Species density should be measured as species number per unit area or by means of the species–area relation, either according to the species–log area 'logarithmic series' model linked to Williams (1964) or the log species–log area 'canonical lognormal' model linked to Preston (1962). Dominance can easily be estimated as the proportion of the most dominant species, that is the Berger-Parker index—which, incidentally was also introduced as a diversity index. See further, *i.a.*, May (1975), Magurran (1988) and Buys (1994). Tóthmérész (1995) discussed the concept of diversity ordering through families of diversity measures with a varying scale parameter, such as Hill's (1973) family. This approach is especially useful when comparing diversity levels during succession.

Dynamic modelling

This approach is new and still in full development. Basically, dynamic models predict the future state of a stand of vegetation or landscape element on the basis of the history of the stand. 'History' can be described simply as the *present state*, meaning the present species composition, resource levels, amount of disturbance and influx of diaspores (Van Hulst 1992). History should of course also include the recent past, which we may have described through permanent plot studies or repeated mapping (see above). Finally, long-term changes, as revealed by palaeoecological studies, should be taken into account. Van Hulst (1992) distinguished two types of models. One type he called *phenomenological*, and we may call the other type *mechanistic*.

Well-known phenomenological models are the so-called Markov models, which were introduced into vegetation dynamics in the 1970s (Horn 1975; Van Hulst 1979; Usher 1981; Hobbs 1983; see Usher 1992 for a review). Such models deal with the prediction of changes on the basis of a matrix of transition probabilities. The presumption is that the present state of a stand of vegetation is largely dependent on the previous state of that stand. However, in the dune example as well as in other examples the state is also dependent on the state of neighbouring stands. Another problem is that completely new types arise. Still, Markov models can be useful to formalize hypotheses on the development of a succession in relation to the mechanisms supposed to be in operation (Van Andel *et al.* 1993).

Mechanistic models are based on the growth characteristics of, and interactions between, the plant species of a plant community. They were developed to predict the regeneration in forest gaps (Botkin *et al.* 1972). This model, with the acronym JABOWA (after the three authors), was succeeded by many others, including FORET by H.H. Shugart (Shugart & West 1977) and FORSKA by I.C. Prentice (Leemans & Prentice 1987; Leemans 1989). Shugart (1992) has reviewed many of these 'individual-based' models. As a Dutch example of this type of modelling the extension to heathland dynamics by Van Tongeren & Prentice (1986) may be mentioned. The model includes general (species-independent) parameters, such as plot dimension and number of species included, and eight species parameters for the dwarf shrubs *Calluna vulgaris*, *Erica tetralix* and *Empetrum nigrum*, including rate of establishment, a growth constant, maximum patch diameter and maximum height. The model refers to post-fire succession and has a spatial component in that it is based on the yearly analysis of 1-m² subplots in a 12 m × 20 m plot. In this particular case *Empetrum* would take over.

Table 2. Relation between temporal and spatial scales of vegetation dynamics (after Van der Maarel 1988)

	Individual	Patch	Population	Community	Landscape	Region
Fluctuation	x	x	x			
Gap dynamics	x	x	x			
Patch dynamics	x	x	x			
Cyclic succession		x	x	x		
Regeneration succession		x	x	x		
Secondary succession		x	x	x	x	
Primary succession			x	x	x	
Secular succession				x	x	x

Clearly, the effectiveness of such simulation models in predicting succession is related to the accuracy with which the model parameters have been determined. This is in its turn dependent on the progress made in population ecology and ecophysiology of the species involved.

TYPES OF VEGETATION DYNAMICS

Most examples of the application of multivariate methods to vegetation dynamics mentioned above are long-term studies of primary successions, i.e. successions on virginal substrate. This is no surprise, since primary succession received much attention during the 1980s. In earlier periods the emphasis was on secondary succession, especially in the United States, and much of succession theory was in fact based on studies of secondary succession (e.g. Odum 1969; Horn 1981), and moreover using so-called chronosequences rather than permanent plots. The multiple pathway character of succession exemplified above is one obvious warning against the use of such chronosequences.

Nowadays, we have many long series of analyses of both vegetation and soil characteristics available, which enable us to start approaching succession through processes and mechanisms (Agnew *et al.* 1993). Olff (1992), having worked along the same lines, will elaborate on this theme on this issue.

The study of gap dynamics is another major development in vegetation dynamics during the 1980s. This is, basically, the dynamics within a largely stable community. The present contribution will give some extra attention to this type.

More generally, eight forms of vegetation dynamics can be distinguished: Fluctuation, Gap dynamics, Patch dynamics, Cyclic succession, Regeneration succession, Secondary succession, Primary succession and Secular succession (Table 2). Most of these terms are well-known but through the presentation on this level of differentiation and in this sequence, the suggestion arises that the different forms of vegetation dynamics can be arranged according to the intensity and spatial extent of an event—usually a disturbance—triggering the dynamics. Under reference to Van der Maarel (1988) and Glenn-Lewin & Van der Maarel (1992) only a few remarks may suffice to point to some clarifications and links.

Internal community dynamics

The first five types can be considered internal dynamics.

Fluctuation is non-directional quantitative change in the components of vegetation resulting from population responses to short-term stochastic environmental variation.

Gap dynamics results from the death of individual plants or local populations. Gaps may be as large as 100 m^2 in a forest and as small as 1 cm^2 in a short grassland, but are always small relative to the areal extent of the community.

Patch dynamics results from the disappearance of local populations creating gaps which are 10–100 times larger than in the previous case. Patch dynamics is the modern follow-up of 'pattern and process in the plant community' (Watt 1947, 1964; Van der Maarel 1996a).

Cyclic succession is patch dynamics with the patches having sufficient floristic differentiation to approach them phytosociologically (e.g. Stoutjesdijk 1959; Stoutjesdijk & Barkman 1992; Gimingham 1978, 1988).

Regeneration succession (see, *i.a.*, Veblen 1992) is the recovery of an entire plant community from a major disturbance, which can occur through natural agents such as fire, storm or a massive insect attack, or by human agents such as burning or clear-cutting.

Succession

The following three types of dynamics include several community types forming a successional series.

Secondary succession is the development of a plant community upon abandoning a human-influenced (semi-natural or agricultural) situation. In a way it is a form of regeneration on a larger temporal and spatial scale. Studies of this type of succession dominated the 1970s and 1980s.

Primary successions occur on newly exposed substrates, the best known examples being dune sand (e.g. Van Dorp *et al.* 1985), mud flats (e.g. Roozen & Westhoff 1985), volcanic deposits (e.g. Bjarnason 1991) and rocky, sandy or silty substrates emerging through isostatic land upheaval (e.g. Cramer & Hytteborn 1987), or artificially created by lowering the water table (e.g. Van Noordwijk-Puyk *et al.* 1979; Rydin & Borgegård 1988; Borgegård 1990a,b). Nowadays, this type of succession can be described more adequately because of the long-term studies of permanent plots which replace the earlier chronosequences and which are so effectively summarized by means of multivariate analysis (as summarized above).

Compared with relatively fast secondary successions, where soil and diaspores are available, primary succession proceeds slowly because (1) most of the diaspores have to reach the new substrate from large distances, and (2) the substrate is deficient of phosphate and/or nitrogen. Phosphate can be built up by microorganisms in mycorrhiza with the higher plants (Ernst *et al.* 1984). Nitrogen is usually a limiting factor, and the role of nitrogen-fixing organisms is limited (Van der Putten 1989), although species dominating in early phases of the succession with symbiotic nitrogen fixation, such as *Hippophae rhamnoides*, may add substantially to the nitrogen pool (Akkermans 1971; Oremus 1982). Vitousek & Walker (1987), Tilman (1988) and Olff (1992) are among those who have summarized nutrient relations during succession.

Recently it has become clear that the succession into later stages is connected to the decline of earlier stages. Dutch work on dune succession (Van der Putten 1989;

Van der Putten *et al.* 1993; De Rooij-Van der Goes *et al.* 1995; De Rooij-Van der Goes 1996) has indicated that harmful soil organisms, notably nematodes and soil fungi, may cause such decline. A related phenomenon is the die-back of several tree species in primary successions, but this is now ascribed mainly to climatic perturbations affecting even-aged cohorts of trees (Mueller-Dombois 1986, 1992; Akashi & Mueller-Dombois 1995).

Secular succession concerns the long-term changes in vegetation in relation to long-term and large-scale changes in the environment, particularly climate. Changes in community composition are the result of changes in the geographic distributions of individual species. Thompson (1981, 1983) and Walker *et al.* (1981) studied a chrono-sequence in coastal dunes in Queensland covering more than 120 000 years, thus including both Holocene and Pleistocene dune zones. The succession proceeds first from open foredune communities via shrubland to tall *Eucalyptus* forest, but on the Pleistocene dunes heath-like sclerophyllous shrubs dominate, which are adapted to extremely low levels of phosphorus remaining after leaching. Walker *et al.* (1981) use the term 'retrogressive succession' for this further development.

Another example of secular succession was described on the volcano Mauna Loa, Hawaii by Kitayama *et al.* (1995), covering 9000 years. In this case ash depositions, which increase the availability of nitrogen, cause an irregular course of the succession, which has not yet reached a climax state.

A third example concerns the long-term changes in the primary forest Fiby near Uppsala, for a long time considered as a primaeval forest with small-scale dynamics and community-level regeneration (Sernander 1936; Liu & Hytteborn 1991). Palaeoeco-logical studies (Bradshaw & Hannon 1992; Bradshaw 1993) have made clear how this forest has been subjected both to 'secular' changes, notably the immigration of *Picea abies*, and to grazing for at least 2000 years with long-term fluctuations in grazing intensity.

Restoration succession

A relatively new and deviating type of succession is the succession from degraded vegetation towards a more natural state by means of management measures (Bakker 1989). Such measures include cessation of fertilization, sod cutting (e.g. Jungerius *et al.* 1995), hay making (Bakker *et al.* 1980; Bakker 1985, 1989), and return to the original phreatic water table (e.g. Van Diggelen *et al.* 1991; Grootjans *et al.* 1995). Such 'restoration' usually concerns wetland vegetation. Restoration succession is in many ways a special type of secondary succession.

GAP AND PATCH DYNAMICS

Disturbance

Gaps arise through some form of disturbance (Pickett & White 1985; Van Andel *et al.* 1987; Van der Maarel 1993a), disturbance being defined here on the basis of the definition by Van Andel & Van den Bergh (1987): 'Disturbance of vegetation is a change in the environmental conditions which interferes with the current functioning of the vegetation'. Note that 'interference' may attain at least two different forms: (1) the destruction of photosynthetic tissue—emphasized by Grime (1979), and (2) the release of resources—emphasized by White & Pickett (1985), Tilman (1985) and others. Each

Table 3. Dimensions of disturbance

Extent	Gap	Patch	Community	Landscape
Frequency	Often	Regular	Irregular	Erratic
Intensity	Partial above-ground	Local above-ground	Total above-ground	Above and below-ground

Examples:
Landscape level: erratic intense extensive disturbance: catastrophe; e.g. volcanic eruption.
Community level: irregular medium-size medium-intense disturbance; e.g. fire.
Patch level: regular low-intense local disturbance; e.g. hoof tramp in a grassland; windthrow in a forest.
Gap level: constant superficial microsite disturbance; e.g. death of an individual.

disturbance can be described as to its kind, extent, intensity and frequency (Van Andel & Van den Bergh 1987; Glenn-Lewin & Van der Maarel 1992; Van der Maarel 1993a). These four dimensions of disturbance will always operate in some sort of combination (Table 3).

Species mobility
One of the most important forms of community dynamics is gap dynamics, the continuous response to frequent, small-scale, light disturbances. One important form of disturbance is the death of individual plants, or parts of plants. The arising open space is called gap, hence gap dynamics. Gaps may vary in size from less than 1 cm^2 in short grassland (e.g. Roxburgh *et al.* 1993) to more than 100 m^2 in a forest. Most gaps are rapidly recolonized by plants, either from the same species or from a few species present before the local disturbance, or/and other species. The continuous appearance and disappearance ('local immigration and extinction' in—less appropriate— biogeographical terms) causes species mobility and species turnover. The creation and colonization of gaps has been known since the early work of R. Sernander, A.S. Watt and others (Van der Maarel 1996a) and has become especially important in community dynamics since the work on heathlands by Gimingham (e.g. 1978, 1988) and the review paper on the regeneration niche by Grubb (1977).

The relation between pattern and process on a fine scale can be elaborated if we have data available on the occurrence of plant species in permanent plots of a very small size over a series of years. Such data are hardly available and they have not yet been used for purposes of species mobility (Van der Maarel & Sykes 1993). Some data will now be presented on 40 small plots of 10 cm × 10 cm situated in two rows of 20 plots alongside the long sides of a 2·5 m × 1 m plot in a species-rich *Veronica spicata–Avenula pratensis* association in an alvar limestone grassland on Öland, Sweden. This plot is a control plot included in a series of plots subjected to various fertilization schemes. The experiment started in 1985 and here results from yearly observations on the 100-cm^2 plots from 1986 to 1994 will be used (see Van der Maarel & Sykes 1993). The number of species per m^2 in this community is high, although not extremely high, 30–35, but on the smaller plot sizes record numbers of more than 20 per 100 cm^2 and up to 13 per 10 cm^2 have been observed.

Species mobility can be expressed as species accumulation on small plots within the community, i.e. the total number of species which appeared newly in any small plot after the starting year of a period of observation (Van der Maarel & Sykes 1993). Table 4

Table 4. Numbers of species in the first half of the 40 100-cm^2 plots in plot Gettlinge A-1 from 1986–95. In addition to the mean values, the highest and lowest values recorded in each year are presented. Also, overall mean values and cumulative species numbers are given. From Van der Maarel (1996)

	Mean	Highest	Lowest
1986	15	23	12
1987	14	19	10
1988	16	20	11
1989	16	19	11
1990	12	18	8
1991	15	20	9
1992	9	14	6
1993	10	15	7
1994	11	15	6
1995	13	17	8
Mean	13	16	11
Cum. no.	26	31	21

shows the rapid species accumulation on the 100-cm^2 plots. Where the average number of species per 100 cm^2 is 13, the cumulative number after 9 years is 26. On average, about three species disappear yearly from each small plot, and three species (re-)appear, of which one to two species are new for the small plot.

Species mobility can also be expressed as species turnover on small subplots in the community plot under study (e.g. Huber 1994; Pärtel & Zobel 1995), or in the form of species replacement diagrams (Thorhalsdóttir 1990; Herben et al. 1993b).

The spatial aspect of this mobility can be shown in simple distribution maps of species, as shown in Fig. 1. Five main types of species behaviour are distinguished (Van der Maarel 1996a): *constant* species, being present in most of the small plots in most of the years involved; *local* species, present in only a few plots and usually in the same plots; *occasional* species, present in only a few plots, but in different plots from year to year; *pulsating* species, varying strongly in frequency from year to year; and *circulating* species, present with medium frequencies in most years, but occupying new plots all the time.

Table 5 shows how these mobility types are linked to the life forms to which we usually assign our species. Both expected and unexpected links appear. No less than 20 species are highly mobile and they are found in all life form types included. On the other hand, the local species are restricted to one type, the chamaephytes, and similarly all constant species are longer-lived hemicryptophytes.

In order to better understand the processes behind species mobility, it is highly recommended to extend the turnover studies with the description of the demography of individual species, particularly of the type Grubb (1990) emphasized. This is at the same time a welcome addition to the studies of generative regeneration, including seed bank analysis, which have already been started (see below). Herben et al. (1993b) described different forms of spatial extension of species in a study of the fine-scale spatial dynamics in a montane grassland.

Arenaria serpyllifolia   'occasional' $F_{mean} = 1.4$

		F	F_{cum}
1986	....	0	0
1987	.........±±.....±±................................	4	4
1988	....	0	4
1989	....	0	4
1990	.......±...+..........±±....±.	5	9
1991	..±.....................±.	2	11
1992	....	0	11
1993	......±.	1	12
1994	...............±.	1	13

Veronica spicata   'local' $F_{mean} = 6.8$

		F	F_{cum}
1986	.........+.+....................+.....	3	3
1987	......±+.+..............±..±+±......	7	7
1988	......++.+..............+..+++......	7	7
1989	......++.+..............+..+++......	7	7
1990	......++.+....................++......	5	7
1991	......+.±+............±...+±.+++......	9	9
1992	......+.................+++±......	5	10
1993	...±.±.+.+±............+..++++......	10	13
1994	.....±.++..+............+..+++........	8	14

Trifolium striatum   'pulsating' $F_{mean} = 6.1$

		F	F_{cum}
1986	.........+.+.....+.+++.+.......+.+.....	9	9
1987	........................±.................	1	10
1988	......±.+..............................	2	11
1989	....	0	11
1990	..±±±±±+±..+±.±.±.±+++±+±+±±±	21	25
1991	....	0	24
1992	....	0	24
1993	±.+.+++++..++±±±+...++++++++.....+±........	22	29
1994	....	0	29

Anthyllis vulneraria   'circulating' $F_{mean} = 20.0$

		F	F_{cum}
1986	+++.++.+++.........++++...+..+..+.+.++++.+	21	21
1987	+++±.+±++.±±......+.+.±±..±...+±+.++++.+	23	29
1988	++++++++++.++.±...++++±++...+..++++±+++.+	29	32
1989	++++++++++.+.+.....++++......±++++++.+.+	25	33
1990	.++++++++.++±...±++++.++.......++...+..+	22	35
1991	++++++++++.++++..+++++++++±.+±...++++++±+	33	38
1992	+.....+....+..........++.+.+.......+.....	8	38
1993	..+.......+........++....+.+........	6	38
1994	.+++++++.+++++..++++..++...++.++..+...+.	24	38

Fig. 1. Examples of occasional, local, pulsating and circulating species occurring in plot G1, Gettlinge alvar, Öland. + =appearance; .=(above-ground) absence; ± =new appearance. From Van der Maarel (1996a).

The carousel model

The conclusion of the study of this species-rich alvar limestone grassland was presented in the form of a phenomenological 'carousel' model suggesting that most species would move freely around in the community, some of them with a short, others with a long turn-around time. Work in progress (E. Van der Maarel & M.T. Sykes, submitted) will quantify individual and community-average species mobility by comparing the observed species accumulation in subplots according to three theoretical mobility models: (1) 'maximum mobility': species are allocated into new subplots until all subplots are occupied; (2) 'random mobility' where species (with the observed frequencies for the respective years) are distributed at random over the subplots; (3) 'minimal mobility', where species are not allowed to occupy new subplots unless the frequency would exceed

Table 5. Frequency of occurrence of the five mobility types in relation to life form structure (see Van der Maarel 1988). T=therophyte; Hb=short-lived hemicryptophyte; Hl=longer-lived hemicryptophyte; C=chamaephyte. From Van der Maarel (1996a)

	C	Hl	Hb	T	Tot
Occasional species	5	4	4	2	15
Pulsating species		1	2	4	7
Circulating species	2	3	5	3	13
Local species	3				3
Constant species		5			5
Total	10	13	11	9	43
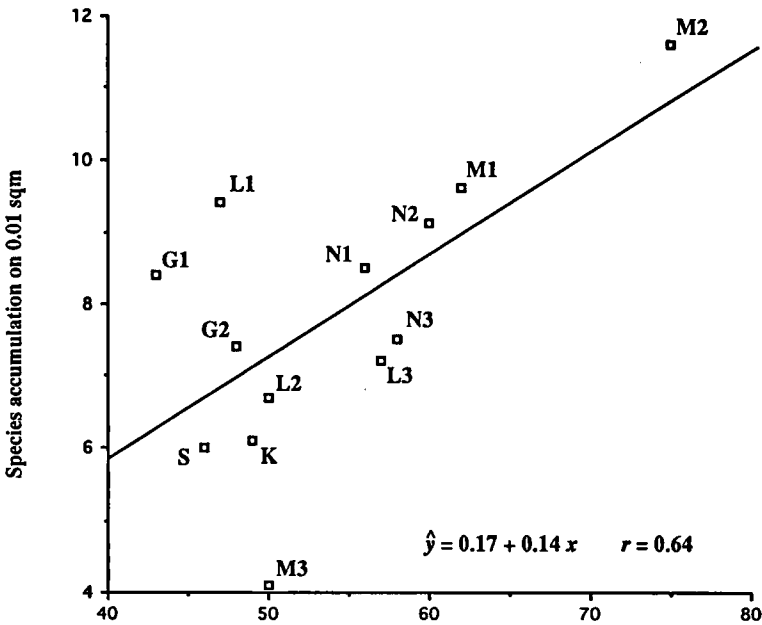
Fig. 2. Cumulative increase in species number on 0·01-m² subplots as a function of the cumulative species number on the 2·5 m² plot in grasslands on Öland: G=Gettlinge, S=Skarpa Alby, K=Kleva; in Limburg, the Netherlands: L; and in the USA: N=North Carolina, M=Mississippi. From Sykes *et al.* (1994).

the total of subplots visited so far. Preliminary results show that species such as *Helianthemum oelandicum* and *Cerastium semidecandrum*, mentioned by Van der Maarel & Sykes (1993: Fig. 2) as examples of species with a stable pattern and a high mobility, respectively, have accumulation values near to the minimum and random model, respectively. Indeed, many species appear to move at random or nearly so. This is a new way of confirming the old Gleasonian concept of the individuality of species (Gleason 1926). However, this remark is not meant to suggest any lack of community structure. Studies such as that by Thorhalsdóttir (1990) point to horizontal structure in grassland and Roxburgh *et al.* (1993) found consistent height relations, i.e. a vertical structure of the plant species occurring in a lawn.

Comments on the carousel model received include the supposition that the alvar grassland might be a particular type of community; this is true: it has a long history of human influence (Rosén 1982), it has been continuously grazed for probably more than 2000 years, is low in stature, subject to local disturbances by grazers and, most importantly, subject to the recurrent drought in the growing season (Rosén 1982, 1985; Huber 1994). These droughts (see Table 3) tend to be the driving force for species change in the community, creating gaps for new species to occupy (Grime 1990). Among these species there are relatively many annuals, biennials and short-lived perennials. However, a comparative study (Sykes *et al.* 1994) of 0·01-m^2 and 0·25-m^2 subplots in a no longer grazed alvar grassland, Dutch chalk grassland (Willems *et al.* 1993) and North American moist, tall grass-sedge savanna grasslands (Walker & Peet 1983), the latter having no annuals at all, showed similar high small-scale turnover and accumulation figures for these apparently less extreme grasslands (Fig. 2).

Gap dynamics in changing communities

So far, the pattern and process approach to gap dynamics has referred to a stable community, i.e. a community which maintains its structure and floristic composition over a longer period of time, much longer than the patch-dynamic cycle(s). In the case of the alvar grassland on Öland this condition seems to be fulfilled. However, gap dynamics will also occur in communities subjected to some overall change, i.e. primary, secondary, regeneration or restoration succession. As a first example, two successional alvar communities studied by Pärtel & Zobel (1995) showed equally high species mobility as two related communities considered relatively stable.

The combination of small-scale turnover (Huber 1994; Pärtel & Zobel 1995) and accumulation figures should be further exploited for a better understanding of the species dynamics. Laborious but probably rewarding further studies concern the possibility of 'species group' mobility and of fixed sequences of disappearances and appearances of species in subplots.

Species pool

One interesting consequence of the carousel model is the continuous creation of suitable microsites for the immigration of species, either from outside the stand or from the local seed bank (Schmida & Ellner 1984). This led Sykes *et al.* (1994) to the analysis of species accumulation of small plots as a function of the species available in the stand. This analysis included the experimental plots in the alvar grasslands on Öland (Van der Maarel & Sykes 1993) as well as similarly analysed plots in Dutch chalk grassland (Willems *et al.* 1993) and North American moist, tall grass-sedge savanna grassland (Walker & Peet 1983), which were all included in a comparative experimental analysis of coexistence in species-rich grasslands (Peet *et al.* 1990). As Fig. 2 shows, there is a significant relation between the two parameters.

This relation could be considered as a first indication of the importance of the species pool, defined as a set of species around a target stand of vegetation from which the stand can be supplied, and discussed by Zobel (1992) and Eriksson (1993). Then, Pärtel *et al.* (1996) distinguished between the actual species pool, the set of species present in a plant community (including the transient diaspore bank) and the regional species pool, the set of species occurring in a region which is capable of coexisting in a target community. In this case the region was Estonia and the regional species pools of 14 Estonian plant
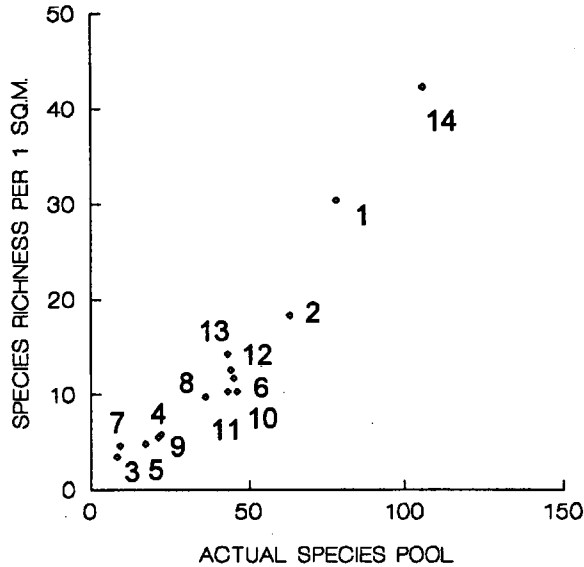
Fig. 3. Relation between actual species pool and mean species richness on $1\,m^2$ in 14 Estonian plant community types, ranging from dry pine forest (3) and raised bog (7) via nemoral mixed forest (11) to dry alvar heath (2) and species-rich alvar grassland (1, 14). From Pärtel *et al.* (1996).
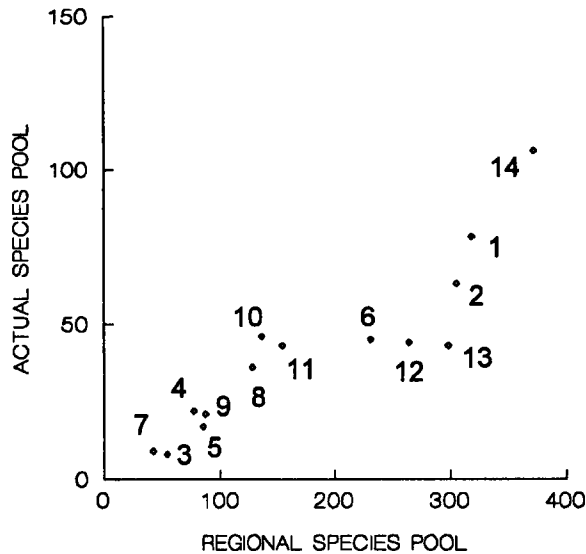

Fig. 4. Relation between regional and actual species pool in the same Estonian plant community types as in Fig. 3. From Pärtel *et al.* (1996).

communities, including grasslands, bogs, heathlands and forests, were determined on the basis of the ecological similarities between species according to their Ellenberg indicator values (Ellenberg *et al.* 1991). As Figs 3 and 4 show, the actual species richness on a small area, i.e. $1\,m^2$, is related to the size of the actual species pool of the community, and this pool is dependent on the size of the regional species pool.

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For many communities it remains to be investigated which role the local seed bank plays in the process of immigration. Much detailed information is available on the seed bank and the germination of limestone grassland species (e.g. Rusch 1993; Rusch & Van der Maarel 1992) and on germination conditions in a similar type of grassland (Ryser 1993). From these studies we know how often gaps arise in limestone grassland and how important regeneration by seedlings is. Not only all the annuals, making up 15–20% of the local species assemblage in the limestone grassland studied by Rusch, but also many perennials, up to 50%, regenerate frequently by seed (Rusch & Fernández-Palacios 1995).

IMPLICATIONS OF GAP AND PATCH DYNAMICS FOR VEGETATION TYPOLOGY AND ECOLOGY

It seems that the significance of internal vegetation dynamics is not limited to certain types of grassland. At least three consequences for vegetation typology arise, which may be of general interest and should be elaborated in vegetation science.

Syntaxonomy of patches
Patches distinguished within the community from a 'pattern and process' point of view are phytosociologically evaluated in different ways, depending on the level of complexity of the community under study. In grasslands and heathlands the various patches and phases are usually considered as intrinsic parts of an association; they do not receive a separate syntaxonomical status. In the case of bog regeneration complexes certain phases are distinguished as own associations, usually within the same higher syntaxon, notably the class *Oxycocco-Sphagnetea*, or within two classes, the former one and the *Scheuchzerietea*. In forests, however, early and late gap-colonizing phases are recognized as different associations assigned to different classes, e.g. the gap pioneer class *Epilobietea* and the gap shrubland alliance *Sambuco-Salicion capreae* in the class *Rhamno-Prunetea*, as regeneration stages in the forest, the mature phase of which is considered an association belonging to the forest class *Querco-Fagetea*. Ecologically, however, these syntaxa are patches within the same complex community. This is a conceptual problem that has not yet been solved in phytosociology.

Representative area
If, indeed, species turnover within a plant community is high, and species will move around in the carousel, several species characteristic of the community will be missed in any analysis of a smaller stand. Some of these species may even be character species. From the many formal descriptions of plant community types as syntaxa in the Braun-Blanquet system (see, e.g., Westhoff & Van der Maarel 1978) we know that character species need not occur frequently and/or with high cover-abundance. The consequence of the carousel model for vegetation typology is that the minimum area concept has to be revised (Van der Maarel 1993b). Since this concept has always been disputed and the method for determining it discussed repeatedly (e.g. Dietvorst *et al.* 1982), it may be good to abandon this concept. The two alternatives for a more realistic analysis would be: (1) the formal relevé should be made in a stand as large as possible; and (2) the relevé should be repeated over a series of years and a 'cumulative relevé' should be built up as a basis for the typology. As far as I could check—but statistics are

missing here—relevés used to be larger in the early days of phytosociology. Relevés of 100 m^2 in a grassland were usual, for example. Later, such large relevés were considered suspicious because they might refer to heterogeneous stands. Consequently, relevés were chosen smaller and smaller. With the advantage that the stand analysed will be homogeneous, but with the disadvantage the species list will be incomplete. Since it will normally be impractical to repeatedly return to a sample plot, it seems that we have to return to the classical approach and analyse stands as large as possible. Van der Maarel (1966) once coined the term 'maximum area', suggested to determine the largest homogeneous area on which a community type is represented, but this idea has never been taken up. Van der Maarel (1993b) suggested the 'representative area' rather than the minimum area.

Interestingly, J.J. Barkman (personal communication) distinguished between an analytical minimum area, i.e. the area necessary to obtain a representative description of the community, and the 'regeneration minimum area', i.e. (my words) the area a community needs to develop all regeneration patches included in the internal dynamics of the community. This concept could be reconsidered in the light of the foregoing.

Plant community carousel

Kaźmierczak *et al.* (1995) found that the variation in community types in kettle-holes in central Poland could hardly be related to the variation in environmental factors included in the study. They assumed a chance occurrence of species, which appear and disappear in these sites which are often subjected to processes of disturbance such as strong fluctuations in water level, including periods of water stress, and eutrophication pulses from intensive agriculture surrounding the kettle-holes. These depressions may provide a small number of broad habitat types, within each of which several species may form short-lived plant communities. Well-represented classes are *Bidentetea*, *Chenopodietea* and *Plantaginetea*, which consist of therophytes and short-lived perennials. There were also many communities from the *Phragmitetea* present; the dominant species are known as longer-lived perennials, but apparently they are short-lived in these kettle-holes. Repeated analysis of sample plots (which is ongoing in this particular case) is necessary to test the hypothesis of a 'carousel' of plant communities.

Community theory

Patch dynamics, in the wider sense developed from the original ideas of A.S. Watt, must be assumed to be a characteristic of each plant community. In terms of the debate on the nature of the plant community, still being referred to as the controversy between Gleason and Clements, the 'individualistic behaviour' of plant species applies very well to the small-scale dynamics and as such it is a reinforcement of the Gleasonian idea. However, this aspect of the plant community may be simply a response to the stochastic external fluctuations acting upon the community. At the same time, the growing knowledge about fine-scale competition and exclusion on the one hand and about mycorrhiza and dependent relations on the other hand, points to the Clementsian, or rather Wattian concept of the community as a working mechanism. Facilitation and inhibition aspects of species replacement should also be subjected to further experimental studies.

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REFERENCES

Agnew, A.D.Q., Collins, S.L. & Van der Maarel, E. (1993): Mechanisms and processes in vegetation dynamics. *J. Veg. Sci.* **4**: 145–278.

Akashi, Y. & Mueller-Dombois, D. (1995): A landscape perspective of the Hawaiian rain forest dieback. *J. Veg. Sci.* **6**: 449–464.

Akkermans, A.D.L. (1971): *Nitrogen Fixation and Nodulation of Alnus and Hippophae Under Natural Conditions.* Ph.D. thesis, University of Leiden.

Bakker, J.P. (1985): The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio* **62**: 391–398.

Bakker, J.P. (1989): *Nature Management by Grazing and Cutting.* Ph.D. thesis, University of Groningen. Also *Geobotany* **14**, Kluwer Academic Publishers, Dordrecht.

Bakker, J.P., Dekker, M. & De Vries, Y. (1980): The effect of different management practices on a grassland community and the resulting fate of seedlings. *Acta Bot. Neerl.* **29**: 469–492.

Bjarnason, Á. (1991): Vegetation on lava fields in the Hekla area, Iceland. *Acta Phytogeogr. Suec.* **77**: 1–110.

Borcard, D., Legendre, P. & Drapeau, P. (1992): Partialling out the spatial component of ecological variation. *Ecology* **73**: 1045–1055.

Borgegård, S.-O. (1990a): *Primary Succession in Man-made Environments.* Ph.D. thesis, Uppsala University.

Borgegård, S.-O. (1990b): Vegetation development in abandoned gravel pits: effects of surrounding vegetation, substrate and regionality. *J. Veg. Sci.* **1**: 675–682.

Botkin, D.B., Janak, J.F. & Wallis, J.R. (1972): Some ecological consequences of a computer model of forest growth. *J. Ecol.* **60**: 849–872.

Bradshaw, R.H.W. (1993): Tree species dynamics and disturbance in three Swedish boreal forest stands during the last two thousand years. *J. Veg. Sci.* **4**: 759–764.

Bradshaw, R.H.W. & Hannon, G.E. (1992): Climatic change, human influence and disturbance regime in the control of vegetation dynamics within Fiby Forest, Sweden. *J. Ecol.* **80**: 625–632.

Burrows, C.J. (1990): *Processes of Vegetation Change.* Unwin Hyman, London.

Buys, M.H., Maritz, J.S., Boucher, C. & Van Der Walt, J.J.A. (1994): A model for species–area relationships in plant communities. *J. Veg. Sci.* **5**: 63–66.

Cramer, W. & Hytteborn, H. (1987): The separation of fluctuation and long-term change in vegetation dynamics of a rising seashore. *Vegetatio* **69**: 157–167.

Dale, M.R.T. & Zbigniewicz, M.W. (1995): The evaluation of multi-species pattern. *J. Veg. Sci.* **6**: 391–398.

De Rooij-Van der Goes, P.C.E.M. (1996): *Soil-borne Plant Pathogens of Ammophila arenaria* in Coastal Foredunes. Ph.D. thesis, Agricultural University of Wageningen.

De Rooij-Van der Goes, P.C.E.M., Van der Putten, W.H. & Van Dijk, C. (1995): Analysis of nematodes and soil-borne funi from Ammophila Arenaria (Marram grass) in Dutch coastal foredunes by multivariate techniques. *Eur. J. Plant Pathol.* **101**: 149–162.

Dietvorst, P., Van der Maarel, E. & Van der Putten, H. (1982): A new approach to the minimum area of a plant community. *Vegetatio* **50**: 77–91.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1991): Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobot.* **18**: 1–248.

Eriksson, O. (1993): The species-pool hypothesis and plant community diversity. *Oikos* **68**: 371–374.

Ernst, W.H.O., Van Duin, W.E. & Oolbekking, G.T. (1984): Vesicular–arbuscular mycorrhiza in dune vegetation. *Acta Bot. Neerl.* **3**: 151–160.

Ford, E.D. & Renshaw, E. (1984): The interpretation of process from pattern using two-dimensional spectral analysis: modelling single species patterns in vegetation. *Vegetatio* **56**: 113–123.

Gimingham, C.H. (1978): *Calluna* and its associated species: some aspects of co-existence in communities. *Vegetatio* **36**: 179–186.

Gimingham, C.H. (1988): A reappraisal of cyclical processes in *Calluna* heath. *Vegetatio* **77**: 61–64.

Gleason, H. (1926): The individualistic concept of the plant association. *Bull. Torrey Bot. Club* **53**: 7–26.

Glenn-Lewin, D.C. & Van der Maarel, E. (1992): Patterns and processes of vegetation dynamics. In: Glenn-Lewis, D.C., Peet, R.K. & Veblen, T.T. (eds): *Plant Succession—Theory and Prediction*, pp. 11–59. Chapman & Hall, London.

Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds) (1992): *Plant Succession—Theory and Prediction*. Chapman & Hall, London.

Gray, A.J., Crawley, M.J. & Edwards, P.J. (eds) (1987): *Colonization, Succession and Stability*. Blackwell, Oxford.

Grime, J.P. (1979): *Plant Strategies and Vegetation Processes*. Wiley, Chichester.

Grime, J.P. (1990): Mechanisms promoting floristic diversity in calcareous grasslands. In: Hillier, S.H., Walton, D.W.H. & Wells, D.A. (eds): *Calcereous Grasslands: ecology and management*, pp. 51–56. Bluntisham Books, Bluntisham.

Grootjans, A.P., Lammerts E.J. & Van Beusekom, F. (1995): *Kalkrijke duinvalleien op de Waddeneilanden. Ecologie en regeneratiemogelijkheden*. KNNV, Utrecht.

Grubb, P.J. (1977): The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev. (Cambr.)* **52**: 107–145.

Grubb, P.J. (1990): Demographic studies on the perennials of chalk grasslands. In: Hillier, S.H., Walton, D.W.H. & Wells, D.A. (eds): *Calcereous Grasslands: ecology and management*, pp. 93–99. Bluntisham Books, Bluntisham.

Haase, P. (1995): Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. *J. Veg. Sci.* **6**: 575–582.

Herben, T., Krahulec, F., Hadincová, V. & Skálová, H. (1993a): Small-scale variability as a mechanism for large-scale stability in mountain grasslands. *J. Veg. Sci.* **4**: 163–170.

Herben, T., Krahulec, F., Hadincová, V. & Kovárová, M. (1993b): Small-scale spatial dynamics of plant species in a grassland community over six years. *J. Veg. Sci.* **4**: 171–178.

Hill, M.O. (1973): Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**: 427–432.

Hill, M.O. (1979): TWINSPAN—*A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes*. Ecology and Systematics, Cornell University, Ithaca, NY.

Hobbs, R.J. (1983): Markov models in the study of post-fire succession in heathland communities. *Vegetatio* **56**: 17–30.

Horn, H.S. (1975): Markovian properties of forest succession. In: Cody, M.L. & Diamond, J.M. (eds): *Ecology and Evolution of Communities*, pp. 196–211. Harvard University Press, Cambridge, MA.

Horn, H.S. (1981): Succession. In: May, R.M. (ed.): *Theoretical Ecology. Principles and applications*, pp. 187–204. Blackwell, Oxford.

Huber, R. (1994): Changes in plant species richness in a calcareous grassland following changes in environmental conditions. *Folia Geobot. Phytotax.* **29**: 469–482.

Huston, M.A. (1979): A general hypothesis of species diversity. *Am. Nat.* **130**: 169–198.

Hytteborn, H. & Packham, J.R. (1985): Left to nature: forest structure and regeneration in Fiby urskog, central Sweden. *Arboric. J.* **9**: 1–11.

Jongman, R.H.G., Ter Braak, C.J.F. & Van Tongeren, O.F.R. (1987): *Data Analysis in Community and Landscape Ecology*. Pudoc, Wageningen.

Jongman, R.H.G., Ter Braak, C.J.F. & Van Tongeren, O.F.R. (eds) (1995): *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.

Jungerius, P.D., Koehler, H., Kooijman, A.M., Mücher, H.J. & Graefe, U. (1995): Response of vegetation and soil ecosystem to mowing and sod removal in the coastal dunes 'Zwanenwater', the Netherlands. *J. Coast. Conserv.* **1**: 3–16.

Kaźmierczak, E., Van der Maarel, E. & Noest, V. (1995): Plant communities in central Poland: chance occurrence of species? *J. Veg. Sci.* **6**: 863–874.

Kershaw, K.A. & Looney, J.H. (1985): *Quantitative and Dynamic Plant Ecology, 3rd edn.* Edward Arnold, London.

Kitayama, K., Mueller-Dombius, D. & Vitousek, P.M. (1995): Primary succession of Hawaiian montane rain forest on a chronosequence of eight lava flows. *J. Veg. Sci.* **6**: 211–222.

Knox, R.G. (1989): Effects of detrending and rescaling on correspondence analysis: solution stability and accuracy. *Vegetatio* **83**: 129–136.

Leemans, R. (1989): *Description and Simulation of Stand Structure and Dynamics in Some Swedish Forests*. Ph.D. thesis, Uppsala University.

Leemans, R. & Prentice, I.C. (1987): Description and simulation of tree-layer composition and size distributions in a primaeval Picea–Pinus forest. *Vegetatio* **69**: 147–156.

Liu Qinghong & Hytteborn, H. (1991): Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *J. Veg. Sci.* **2**: 391–402.

Magurran, A. (1988): *Ecological Diversity and Its Measurement*. Chapman & Hall, London.

May, R.M. (1975): Patterns of species abundance and diversity. In: Cody, M.L. & Diamond, J.M. (eds): *Ecology and Evolution of Communities*,

pp. 81–120. Harvard University Press, Cambridge, MA.

Minchin, P.R. (1987a): An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**: 89–107.

Minchin, P.R. (1987b): Simulation of multidimensional community patterns: towards a comprehensive model. *Vegetatio* **71**: 145–156.

Mueller-Dombois, D. (1986): Perspectives for an etiology of stand-level dieback. *Annu. Rev. Ecol. Syst.* **17**: 221–243.

Mueller-Dombois, D. (1992): A natural dieback theory, cohort senescence as an alternative to decline disease theory. In: Manion, P.D. & Lachance, D. (eds): *Forest Decline Concepts*, pp. 26–37. APS Press, St Paul, MN.

Newbery, D.McC., Renshaw, E. & Brünig, E.F. (1986): Spatial pattern of trees in kerangas forest, Sarawak. *Vegetatio* **65**: 77–89.

Noest, V. & Van der Maarel, E. (1989): A new dissimilarity measure and a new optimality criterion in phytosociological classification. *Vegetatio* **83**: 157–165.

Odum, E.P. (1969): The strategy of ecosystem development. *Science* **164**: 262–270.

Økland, R.H. & Eilertsen, P. (1994): Canonical correspondence analysis with variation partitioning: some comments and an application. *J. Veg. Sci.* **5**: 117–126.

Oksanen, J. (1983): Ordination of boreal heath-like vegetation with principal component analysis, correspondence analysis and multidimensional scaling. *Vegetatio* **52**: 181–189.

Olff, H. (1992): *On the Mechanisms of Vegetation Succession*. Ph.D. thesis, University of Groningen.

Oremus, P.A.I. (1982): *Factors affecting growth and nodulation of* Hippophaë rhamnoides *ssp.* rhamnoides *in coastal sand dunes of the Netherlands*. Ph.D. thesis, University of Utrecht.

Palmer, M.W. (1988): Fractal geometry: a tool for describing spatial patterns of plant communities. *Vegetatio* **75**: 91–102.

Pärtel, M. & Zobel, M. (1995): Small-scale dynamics and species richness in successional alvar plant communities. *Ecography* **18**: 83–90.

Pärtel, M., Zobel, M., Zobel, K. & Van der Maarel, E. (1996): The species pool and its relation to species richness—evidence from Estonian plant communities. *Oikos* **75**: 111–117.

Peet, R.K., Van der Maarel, E., Rosén, E., Willems, J.H., Norquist, C. & Walker, J. (Joan) (1990): Mechanisms of coexistence in species-rich grasslands. *Bull. Ecol. Soc. Am.* **71**: 283.

Pickett, S.T.A. & White, P.S. (eds) (1985): *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, FL.

Pickett, S.T.A., Collins, S.L. & Armesto, J.J. (1987): Models, mechanisms and pathways of succession. *Bot. Rev.* **53**: 225–371.

Popma, J., Mucina, L., Van Tongeren, O. & Van der Maarel, E. (1983): On the determination of optimal levels in phytosociological classification. *Vegetatio* **52**: 65–76.

Prentice, I.C. & Werger, M.J.A. (1985): Clump spacing in a desert dwarf shrub community. *Vegetatio* **63**: 133–139.

Preston, F.W. (1962): The canonical distribution of commonness and rarity. *Ecology* **43**: 185–215, 410–432.

Roberts, D.W. (1986): Ordination on the basis of fuzzy set theory. *Vegetatio* **66**: 123–131.

Roozen, A.J.M. & Westhoff, V. (1985): A study on long-term salt marsh succession using permanent plots. *Vegetatio* **61**: 23–32.

Rosén, E. (1983): Vegetation development and sheep grazing in limestone grasslands of south Öland, Sweden. *Acta Phytogeogr. Suec.* **72**: 1–104.

Rosén, E. (1995): Periodic droughts and long-term dynamics of alvar grassland vegetation on Öland. *Folia Geobot. Phytotax.* **30**: 131–140.

Roxburgh, S.H., Watkins, A.J. & Wilson, J.B. (1993): Lawns have vertical stratification. *J. Veg. Sci.* **4**: 699–704.

Rusch, G. (1993): *The Role of Regeneration by Seed in the Dynamics of Limestone Grassland Communities*. Ph.D. thesis, Uppsala University.

Rusch, G. & Fernández-Palacios, J.M. (1995): The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. *J. Veg. Sci.* **6**: 417–426.

Rusch, G. & Van der Maarel, E. (1992): Species turnover and seedling recruitment in limestone grassland. *Oikos* **63**: 139–146.

Rydin, H. & Borgegård, S.-O. (1988): Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology* **69**: 916–927.

Ryser, P. (1993): Influences of neighbouring plants on seedling establishment in limestone grassland. *J. Veg. Sci.* **4**: 195–202.

Sernander, R. (1936): Granskär och Fiby urskog. *Acta Phytogeogr. Suec.* **8**: 1–232.

Shmida, A. & Ellner, S. (1984): Coexistence of plant species with similar niches. *Vegetatio* **58**: 29–55.

Shugart, H.H. (1992): Individual-based models of forest succession. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds): *Plant Succession—Theory and Prediction*, pp. 249–292. Chapman & Hall, London.

Shugart, H.H. & West, D.C. (1977): Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *J. Environ. Manage.* **5**: 161–170.

Stoutjesdijk, Ph. (1959): Heaths and Inland Dunes of the Veluwe. *Wentia* **2**: 1–96.

Stoutjesdijk, Ph. & Barkman, J.J. (1992): *Microclimate, Vegetation and Fauna.* Opulus Press, Uppsala.

Sykes, M.T., Van der Maarel, E., Peet, R.K. & Willems, J.H. (1994): High species mobility in species-rich plant communities: an intercontinental comparison. *Folia Geobot. Phytotax.* **29**: 439–448.

Tausch, R.J., Charlet, D.A., Weixelman, D.A. & Zamudio, D.C. (1995): Patterns of ordination and classification instability resulting from changes in input data order. *J. Veg. Sci.* **6**: 897–902.

Ter Braak, C.J.F. (1986): Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167–1179.

Thompson, C.H. (1981): Podzol chronosequences in coastal dunes of Eastern Australia. *Nature (Lond.)* **291**: 59–61.

Thompson, C.H. (1983): Development and weathering of large parabolic dune systems along the subtropical coast of Eastern Australia. *Z. Geomorph. N.F.* **45**: 205–225.

Thorhalsdóttir, T.E. (1990): The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. *J. Ecol.* **78**: 884–908.

Tilman, D. (1985): The resource ratio hypothesis of succession. *Amer. Nat.* **125**: 827–852.

Tilman, D. (1988): *Plant Strategies and the Dynamics and Structure of Plant Communities.* Princeton University Press, Princeton, NJ.

Tóthmérész, B. (1995): Comparison of different methods for diversity ordering. *J. Veg. Sci.* **6**: 283–290.

Usher, M.B. (1981): Modelling ecological succession, with particular reference to Markovian models. *Vegetatio* **46**: 1–18.

Usher, M.B. (1992): Statistical models of succession. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds): *Plant Succession—Theory and Prediction,* pp. 215–248. Chapman & Hall, London.

Van Andel, J. & Van den Bergh, P.J. (1987): Disturbance of grasslands. Outline of the theme. In: Van Andel, J., Bakker, J.P. & Snaydon, R.W. (eds): *Disturbance in Grasslands. Causes, effects and processes,* pp. 3–13. Junk, Dordrecht.

Van Andel, J., Bakker, J.P. & Grootjans, A.P. (1993): Mechanisms of vegetation succession: a review of concepts and perspectives. *Acta Bot. Neerl.* **42**: 413–433.

Van Andel, J., Bakker, J.P. & Snaydon, R.W. (eds) (1987): *Disturbance in Grasslands. Causes, effects and processes.* Junk, Dordrecht.

Van der Maarel, E. (1966): *Over vegetatie-structuren,–relaties en–systemen in het bijzonder in de duingraslanden Van Voorne.* Ph.D. thesis, Utrecht University.

Van der Maarel, E. (ed.) (1980a): Classification and ordination. *Vegetatio* **42**: I–X, 1–188.

Van der Maarel, E. (ed.) (1980b): Succession. *Vegetatio* **43**: I–VIII, 1–151.

Van der Maarel, E. (1988): Species diversity in plant communities in relation to structure and dynamics. In: During, H.J., Werger, M.J.A. & Willems, H.J. (eds): *Diversity and Pattern in Plant Communities,* pp. 1–14. SPB Academic Publishing, The Hague.

Van der Maarel, E. (1991): What is vegetation science? *J. Veg. Sci.* **2**: 145–146.

Van der Maarel, E. (1993a): Some remarks on disturbance and its relations to diversity and stability. *J. Veg. Sci.* **4**: 733–736.

Van der Maarel, E. (1993b): Plant species turnover and minimum area in a limestone grassland. *Abstr. Bot.* **17**: 173–178.

Van der Maarel, E. (1996a): Pattern and process in the plant community: 50 years after A.S. Watt. *J. Veg. Sci.* **7**: 19–28.

Van der Maarel, E. (1996b): *Biodiversity: From Babel to Biosphere Management.* Opulus Press, Uppsala, Leiden.

Van der Maarel, E. & Sykes, M.T. (1993): Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *J. Veg. Sci.* **4**: 179–188.

Van der Maarel, E., Boot, R., Van Dorp, D. & Rijntjes, J. (1985): Vegetation succession on the dunes near Oostvoorne, The Netherlands: a comparison of the vegetation in 1959 and 1980. *Vegetatio* **58**: 137–187.

Van der Putten, W.H. (1989): *Establishment, Growth and Degeneration of* Ammophila arenaria *in Coastal Sand Dunes.* Ph.D. thesis, Agricultural University, Wageningen.

Van der Putten, W.H., Van Dijk, C. & Peters, B.A.M. (1993): Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* **362**: 53–56.

Van Diggelen, R., Grootjans, A.P., Kemmers, R.H., Kooijman, A.M., Succow, M., De Vries, N.P.J. & Van Wirdum, G. (1991): Hydro-ecological analysis of the fen system Lieper Posse, eastern Germany. *J. Veg. Sci.* **2**: 465–476.

Van Dorp, D., Boot, R. & Van der Maarel, E. (1985): Vegetation succession on the dunes near Oostvoorne, the Netherlands, since 1934, interpreted from air photographs and vegetation maps. *Vegetatio* **58**: 123–136.

Van Hulst, R. (1979): On the dynamics of vegetation: Markov chains as models of succession. *Vegetatio* **40**: 3–14.

Van Hulst, R. (1992): From population dynamics to community dynamics: modelling succession as a species replacement process. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds): *Plant Succession—Theory and Prediction*, pp. 188–214. Chapman & Hall, London.

Van Noordwijk-Puijk, K., Beeftink, W.G. & Hogeweg, P. (1979): Vegetation development on salt-marsh flats after disappearance of the tidal factor. *Vegetatio* 39: 1–13.

Van Tongeren, O. (1986): FLEXCLUS, an interactive program for classification and tabulation of ecological data. *Acta Bot. Neerl.* 35: 137–142.

Van Tongeren, O. & Prentice, I.C. (1986): A spatial simulation model for vegetation dynamics. *Vegetatio* 65: 163–173.

Veblen, T.T. (1992): Regeneration dynamics. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds): *Plant Succession—Theory and Prediction*, pp. 152–187. Chapman & Hall, London.

Ver Hoef, J.M. & Glenn-Lewin, D.C. (1989): Multi-scale ordination: a method for detecting pattern at different scales. *Vegetatio* 82: 59–67.

Ver Hoef, J.M., Cressie, N.A.C. & Glenn-Lewin, D.C. (1993): Spatial models for spatial statistics: some unification. *J. Veg. Sci.* 4: 441–452.

Vitousek, P.M. & Walker, L.R. (1987): Colonization, succession and resource availability: ecosystem-level interactions. in: Gray, A.J., Crawley, M.J. & Edwards, P.J. (eds): *Colonization, Succession and Stability*, pp. 207–223. Blackwell, Oxford.

Walker, J. (Joan) & Peet, R.K. (1983): Composition and species diversity of pine-wiregrass savanna of the Green Swamp, North Carolina. *Vegetatio* 55: 166–179.

Walker, J. (Joe), Thompson, C.H., Fergus, I.F. & Tunstall, B.R. (1981): Plant succession and soil development in coastal sand dunes of subtropical eastern Australia. In: West, D.C., Shugart, H.H. & Botkin, D.B. (eds): *Forest Succession. Concepts and applications*, pp. 107–131. Springer Verlag, New York.

Watt, A.S. (1947): Pattern and process in the plant community. *J. Ecol.* 35: 1–22.

Watt, A.S. (1964): The community and the individual. *J. Ecol.* 52 (Suppl.): 203–211.

Werger, M.J.A. (ed.) (1979): *The Study of Vegetation.* Junk, The Hague.

Westhoff, V. & Van der Maarel, E. (1978): The Braun-Blanquet approach. In: Whittaker, R.H. (ed.): *Classification of Plant Communities*, pp. 287–399. Junk, The Hague.

White, P. (1979): Pattern, process and natural disturbance in vegetation. *Bot. Rev.* 45: 229–299.

White, P. & Pickett, S.T.A. (1985): Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A. & White, P.S. (eds): *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 3–13. Academic Press, Orlando, FL.

Wildi, O. (1989): A new numerical solution to traditional phytosociological tabular classification. *Vegetatio* 81: 95–106.

Willems, J.H., Peet, R.K. & Bik, L. (1993): Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *J. Veg. Sci.* 4: 203–212.

Williams, C.B. (1964): *Patterns in the Balance of Nature and Related Problems in Quantitative Ecology.* Academic Press, London.

Zhang Wei & Skarpe, C. (1995): Small-scale species dynamics in semi-arid steppe vegetation in Inner Mongolia. *J. Veg. Sci.* 5: 583–592.

Zobel, M. (1992): Plant species coexistence: the role of historical, evolutionary and ecological factors. *Oikos* 65: 314–320.