

Vegetation dynamics: patterns in time and space

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Abstract

This paper introduces the collection of contributions in this special volume on temporal and spatial patterns of vegetation dynamics. First, it is pointed out that the dynamics of any piece of vegetation, large or small, is always dependent on the degree of isolation of that piece towards its environment. Then ten types of island situation are treated ranging from very much to very little isolated: remote species-rich oceanic islands, remote species-poor islands, young big islands near a continent, small off-shore islands, emerging islands, isolated hills, landscape islands, isolated patches of vegetation, and gaps in stands of vegetation.

Also, eight forms of vegetation dynamics are treated, ranging from short-term to long-term changes and involving larger and larger units: individuals, patches, communities, landscapes and vegetation regions. The forms of dynamics are fluctuation, gap dynamics, patch dynamics, cyclic succession, regeneration succession, secondary succession, primary succession, and secular succession. Each form of dynamics may occur under varying degrees of isolation.

The general conclusion is that processes and patterns of vegetation dynamics cannot be generalized in any simple manner. The 20 papers collected in this volume, divergent as they are, express the complexity of vegetation dynamics.

Introduction

This volume is a selection of contributions presented at two symposia during the 14th International Botanical Congress in Berlin, under the titles 'Vegetation dynamics' and 'Vegetation dynamics under isolation'. These contributions cover the major part of this field of ecology, though without forming any coherent and comprehensive collection. On the other hand, there is some attraction in the variation in approach, type of object, phytogeographical region, discipline represented and scale in time and space of the various contributions. They may be considered an indication of the state of the art in vegetation dynamics.

If there is any continuous thread to put through this collection of contributions it would be the dependence of dynamical phenomena on scale, both in time and in space, and both within the system under study and in its wider surroundings. Ideally, dynamics of island ecosystems should be seen as more extreme cases of what can be considered the standard situation: dynamics in isolation. Every patch of vegetation develops to some extent in isolation from its surroundings: a gap in a forest, a forest patch in a cultural landscape, a low-lying bog or a lake in an otherwise dry forest landscape, etc. In addition, the size of the patch and the size of the surrounding included in the study will vary. A similar variety exists regarding the time scale: changes in vegetation are

always preceded by other changes, either in the environment or in existing vegetation, or in both. The scale of the latter may range from short term to long term and likewise the speed and duration of the vegetation response will vary.

This introduction aims at elucidating some aspects of scale variation, while reviewing some recent literature not covered by the various contributions. It will be restricted to terrestrial situations. There is an equally interesting island situation in the occurrence of lakes, notably in boreal countries, where regional 'archipelagos' of small lakes occur with in some cases much larger lakes as 'continents'. For vegetation dynamics we may take as previous landmarks two symposia organized in the summer of 1985 by the Working Group on Theoretical Vegetation Science in Uppsala, on Theory and models in vegetation science (Prentice & van der Maarel 1987), and the British Ecological Society in Southampton on Colonization, succession and stability (Gray *et al.* 1987) respectively. No such landmarks could be used regarding island biogeography.

First the various types of isolation will be discussed as a general framework for the major issue in this volume: vegetation dynamics.

Pluriformity of isolation

Starting from modern island biogeography, which is mainly built on experiences with a few animal groups (MacArthur & Wilson 1967; Gorman 1979), notably mobile animals, we find that the size of an island and its distance to a larger body of land are the most essential features. This is related to the following requirements and restrictions the average mobile animal has: a fairly large minimum viable population size, restriction to sexual reproduction, a limited reproduction and a relatively short life span. If we simplify island theory to the expected or required equilibrium between immigration and extinction, the first process is related to island isolation and the second to island size.

Plants are different and vegetation, communities of interacting plants, is still more different. Plants are less mobile on average, although some groups have large distance dispersal. Many plants are long-

lived, but many others are short-lived. More importantly, plants are much more diverse regarding mobility and life span and it is almost impossible to generalize. Anyway, island size and isolation are apparently less important for plants. (Maybe the focus on size and distance is found with the animal ecologist rather than with the animals themselves).

Another difference between plants and many animal groups so far included in island biogeography is that plants form communities on relatively small areas, which even on small islands only occupy a small part of the island.

This all may not make too much difference for a typology of islands, but it certainly does so for the ecological significance of each type. In the following tentative survey of 10 types of island situation the presumed essential features: 1) distance to larger similar areas, 2) size, and 3) local community size, vary much and therewith also conditions for succession and maintenance of communities. The general conclusion will be that simple island theory based only on immigration and extinction will not be of great significance.

Types of island situation

1. *Old species-rich islands.* These can be remote oceanic islands, such as the Hawaii and New Zealand islands, or continent-near so-called continental islands such as the Canary Islands. Their common characteristic is the long period of isolation, usually since the Tertiary. Most of the old islands have a high percentage of endemic species, so-called palaeo-endemics (See examples in Bramwell 1979). For such islands the usual immigration - extinction considerations are hardly relevant. Maintenance of community and species diversity is largely a matter of within-island regeneration processes. As far as there is immigration, it concerns alien species, both animals and plants which have usually been brought in by man. They often spread almost unlimitedly with dramatic effects on the native flora (and fauna). Examples are found in Bramwell (1979) and Holzner *et al.* (1983).

Most of the aggressive introduced plant species belong to the category of neophytes, species which ar-

rived on one or more places outside their original distribution area since the time of Columbus (e.g., Sukopp 1962, 1969; see also Kornas 1968, and in Holzner *et al.* 1983, who speaks of kenophytes). In so far the original, pre-Columbian plant communities on old islands are preserved, their community composition and dynamics are largely subject to the same forces as operating on continents.

2. *Remote species-poor islands.* Such islands may be relatively young or/and very remote. They have few endemic species, and usually not many species at all. Many of them may exhibit relatively broad ecological amplitudes, broader than in other parts of their distribution area. Examples are presented for the subantarctic island Marion by Gremmen (1981). The poverty of tree species on the Galapagos islands (see Hamann 1981) is another example. The cyclic succession in the open *Scalesia* woods on these islands described by Lawesson (1988, this volume), where only one species is involved, may even be related to species poverty in the canopy and this would be similar in the classical *Calluna* cycle (Gimingham 1988, this volume, and references therein)!

If such remote islands occur in archipelagos the smaller islands within them may to some extent act as real islands towards any bigger islands acting as the local continent. Itow (1988, this volume) shows how island forest communities (of this and other types) are less saturated with species than comparable forests on continents.

3. *Young big islands near a continent.* The British isles are an example here. The flora of such an island is poorer than nearby continental areas of the same size, because there are few (neo-) endemics to compensate for the number of species which never reached the island.

4. *Small off-shore islands.* They are usually of a different substrate as compared with the mainland, e.g. sandy barrier islands or coral keys. In at least some documented cases such as the Dutch Wadden islands the flora is richer than expected, simply because the habitat diversity is greater than on the nearby continent and because some of the island habitat types have a high alpha diversity (van der

Maarel 1982; Mennema & Weeda 1983). Because the main substrate (sand) deviates from that on the nearby continent (clay) there is only a partial floristic exchange with the nearby continent. This effect of habitat diversity has also been described for the Galapagos islands (van der Werff 1983). Because of their small size they are exposed to wind and salt spray and succession may be hampered, i.e. the forest stage may be missing.

A special case of off-shore islands is found in the Aegean, where in part very small islets occur with a summer-dry rocky environment. They may have special species combinations with poor colonization, but apparently also low extinction rates (Höner & Greuter 1988, this volume).

5. *Emerging islands.* They occur along coasts subjected to land upheaval. The classical example is the Baltic skerry with many archipelagos and thousands of often very small islands, small even for plants. Here the processes of colonization are more pronounced than elsewhere (Vartiainen 1988, this volume). Another type of emerging island is the volcanic island, with the species-poor Surtsey near Iceland as an example, and the species-rich Krakatau (recently described regarding its succession to forest by Tagawa *et al.* 1985). Raus (1988, this volume) describes how immigration on young volcanic islands in the Aegean compensates for species losses either due to extinction or destruction.

6. *Islands in lakes.* These are usually small and of the same substrate as the land surrounding the lake. They will obey the laws of immigration and extinction, as was demonstrated by Nilsson & Nilsson (1978) for islands in a South-Swedish lake. Such islands are particular in the sense that the 'continent' is usually at a short distance and moreover it is everywhere around, which implies relatively high immigration rates. In another case, Lake Hjälmaren, the lake islands were created 100 yr ago by artificial lowering of the lake level and censored from the beginning. Rydin & Borggård (1988a) showed how Preston's parameter z of the canonical distribution as measured from the species-area relation, was near to the theoretical 'equilibrium' value of 0.26 already six years after colonization and succession had start-

ed and apparently it has no significance in relation to successional status.

Another special island situation was created in some of the estuaries in the SW Netherlands after closing them and lowering the water table. No island biogeographical studies have been published on this situation, but on the other hand extensive succession studies, which will be discussed later.

7. *Isolated hills.* Such hills or small mountains, also known under the German name of Inselberge have a substrate which is different from that of the surrounding lowland. Two well-known groups in Czechoslovakia I have seen are the limestone hills of Pavlov in southern Moravia (Pavlovske kopce) with a very species-rich steppe vegetation varying from hill to hill (Podpera 1928, see also Domin 1928), and the series of ultrabasic volcano hills near Louny, central Bohemia (Česke středohoří), again with a species-rich steppe vegetation (Slavikova *et al.* 1983). Although their flora and vegetation have been well described (as belonging mainly to the Festucetalia valesiacae, see Kolbek 1975) no island-biogeographical studies of such hill systems are known to me.

8. *Landscape islands.* They are the result of changes in the original vegetation of an area. Usually we are dealing with forest islands in a matrix of agricultural and seminatural landscape. Their study (see e.g. Burgess & Sharpe 1981) is becoming the domain of the emerging science of landscape ecology (Forman & Godron 1981, 1986; Risser 1987). One recent thorough study of Polish woodland islands (Dzwonko & Loster 1988) showed that their species numbers were not only a function of area and degree and time of isolation, but also of habitat diversity and successional status.

Landscape islands have also become subject of discussions in nature conservation. In particular the existence of corridors (both actual and, rather more often, potential) between islands (Forman 1982) has been considered important (e.g. Colaris 1983), although still little evidence is available to support this view.

A special case is formed by so-called remnant trees in forest clearings which during the period of

agricultural use (fields or meadows) act as shelter for men and animals, but also as sources of forest regeneration if agriculture is abandoned again. Guevara (1986, Guevara *et al.* 1986) distinguished four features with a positive effect on the establishment of woody species from the surrounding forest: 1). Physical and chemical conditions under the canopy of the remnant tree, promoting or inhibiting germination of immigrant diaspores; 2). Size of the tree (sometimes tree group); 3). Distance to the mature forest; and 4). Nature of the remnant tree, particularly its function as a food source for birds, transporting bird-dispersed species (which may make up over 80% of the total).

9. *Isolated patches of vegetation.* In many cases vegetation stands are to some extent isolated from their surroundings, such as in mosaic patterns in bogs and dunes, where hummocks and hollows, and dune tops and dune slacks may isolate each other. A case which is being investigated from the isolation point-of-view concerns dispersed gravelly deposits on the limestone plateau of southern Öland, where stands of the *Veronica spicata-Avenula pratensis* association (Rosén 1982; Krahulec *et al.* 1986) occur in different degrees of isolation from each other (van der Maarel 1988). Although the distances between patches of the same community type may be as short as a few m, clear discontinuities in the distribution of many plant species occur.

10. *Gaps in stands of vegetation.* The least conspicuous form of isolation is found in gaps. Each gap is an island, but with a minimal degree of isolation due to the possibility of colonizing this island by seeds from the seedbank and by vegetative growth from the immediate surroundings.

Aspects of ecological isolation

From this survey it will become clear that there are so many types of islands that generalization is very difficult indeed. Further the concept of ecological isolation emerges from the survey. At least four different aspects of ecological isolation are recognized, as is summarized in Fig. 1. In addition to the

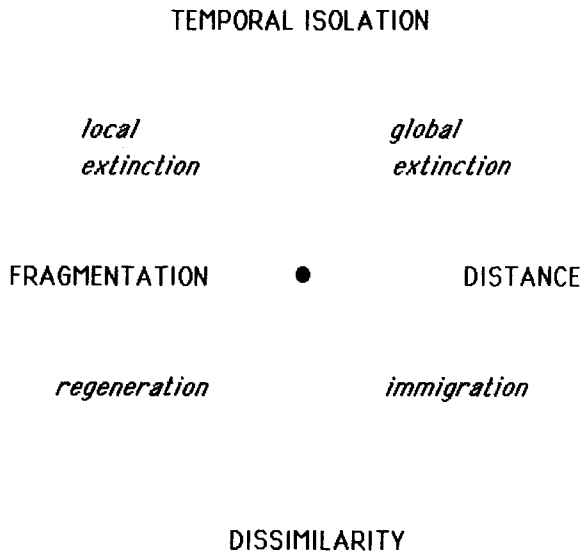


Fig. 1. Four dimensions of ecological isolation and four key processes in vegetation dynamics characterizing them. The position of each key process in between two dimensions suggests a particular significance for the pair of dimensions referred to.

traditional aspects of geographical distance and fragmentation (i.e. small island size) we add temporal isolation and environmental dissimilarity, i.e. between the island and the continent to be compared. The equilibrium status of an island will be dependent on all four aspects.

To each of the four aspects a key process can be linked. The four keywords denote the four major processes operating on any island biota. By putting a keyword to an island aspect it is suggested that the pertaining process is of relatively high significance there. The immigration of species is crucial in relation to geographical distance, extinction is especially important in relation to fragmentation. In fact the term extinction as used in island biogeography is misleading; we better call it local extinction! Global extinction, as different from local extinction is a process of particular significance to old islands, meaning that temporal isolation, usually connected with level of endemism, is related to the vulnerability of the island for disturbance by introduced alien organisms, leading to the general and definitive extinction of species. The fourth process is that of internal regulation which is decisive for the maintenance of biotic diversity in ecologically isolated islands and island situations.

Pluriformity of vegetation dynamics

There are many different ways along which vegetation may change. Although we know this (if not from own studies then from reviews like those by Whittaker & Levin 1977; McIntosh 1980 and Miles 1987) and although we have since long formalized some knowledge in an array of concepts on dynamics, we use to forget it every time we try to find unifying concepts, general mechanisms, etc. (Recent examples are Denslow 1980; Finegan 1984; Shugart 1984; Rosenzweig 1987 and Walker & Chapin 1987.)

Many of such general or generalizing approaches have been introduced or formalized in a more specific context, explicitly or not. To mention just one example: Connell & Slatyer's (1977) three main models (also called mechanisms) of succession, although presented in a more general framework, refer in fact, largely to what I will treat below as 'regeneration succession' following disturbance such as fire (cf McIntosh 1980). The companion system of vital attributes by Noble & Slatyer (1980) even explicitly refers to plant communities subject to recurrent disturbance. And yet, both systems are used for many types of vegetation dynamics. Pickett *et al.* (1987) provide further examples of what they call misapplication of the Connell and Slatyer's models and the originators themselves explain once more that their models were never designed to model any aspect of succession (Connell *et al.* 1987).

On the concept of succession

It may be useful to first define succession, the most central and most appealing form of dynamics. The definition by van der Maarel & Werger (1978), with the formal, phytosociological term phytocoena replaced by the more generally recognized one, plant communities, comes close to what many ecologists consider succession: 'the successive occurrence of plant communities at a given site'. (For similar definitions from other ecological approaches, see Rabotnov 1974 and Miles 1979.) A plant community in turn can be defined (largely after Westhoff & van der Maarel 1978) as a part of a vegetation consisting of interacting populations growing in a uniform en-

vironment and showing a floristic composition and structure that is relatively uniform and distinct from the surrounding vegetation. This includes the classical case of a succession from a pioneer community to a climax (or more neutrally: terminal) forest community via a series of developmental communities (be it without Clementsian and neo-Clementsian philosophy as now generally dismissed, e.g. by Miles 1979, 1987).

On the other hand, even if there usually is a clear continuum of transitional stages, this need not be approached with Gleasonian dogmatism, even if modern community ecologists who apparently ignore the modern vegetation-ecological literature would like us to do so (e.g. Crawley 1986). On the contrary, separate communities can be and indeed are recognized, both in modern European and American approaches (cf. Whittaker 1974; Westhoff & van der Maarel 1978).

There is a (confusing) terminology on such series of stages for which Westhoff & van der Maarel (1978) prefer the term climax complex. Although Braun-Blanquet phytosociologists are aware of the dynamical coherence within such a complex (examples in Braun-Blanquet 1964) they did not develop a systematic approach to describing them as units of their own on a higher hierarchical level until Tüxen (1973) introduced the concept of sigma-association and a standard procedure to describe and typify them. Ever since many such sigma-units have been described but usually as ad hoc local community complexes, which are landscape ecological units rather than dynamical entities.

On the basis of this definition pair of community and succession it is relatively easy to distinguish succession s.s. from other forms of vegetation dynamics, i.e. to discern it from dynamics of units below the level of the plant community as well as of community complexes.

This 'community approach' does not preclude the actual study of succession by means of population dynamics. Fekete *et al.* (1988, this volume) and Symonides (1988, this volume) give examples of population characteristics that can be measured and compared: different reproductive allocation and photosynthetic activity of annual versus perennial species in early successional grassland stages, and

self-pollination and seed polymorphism of annuals of disturbed environments respectively.

Major forms of vegetation dynamics

There are many ways of classifying dynamics, but few of the classifications presented are comprehensive and an attempt to integrate them all is still lacking. The most useful general classification is probably the one based on the variation in the time-scale, although there is the complication that the relevance of the time-scale is dependent on the average life-span of the prevailing plant species. Major's (1974) scheme of 'kinds of changes in vegetation', in part based on earlier literature, included also ontogenetic and evolutionary changes. Miles (1987) presented a similar scheme, which in a simpler form (e.g. Miles 1979) consists of fluctuation, regeneration and secondary and primary succession. The time-scale classification can easily be integrated with the 'hierarchy of successional causes' of Pickett *et al.* (1987).

Fluctuation. The first and lowest level of vegetation dynamics which we may deduce from these schemes is that of *fluctuation*. Changes in vegetation are considered on the level of the plant individual or shoot and may be either ontogenetical or due to external factors such as predation, competition etc. Pickett *et al.* (1987) give a fairly complete list of processes and include stochastic environmental stress, which equals Miles' (1987) climatic fluctuations as a cause of change. Generally, the changes are rapid in relation to the time interval with which the stress may occur. This is of course more obvious in grasslands and similar communities with species able to rapidly change their biomass production.

According to both American and European ecologists the most important expression of fluctuation is the (quantitative) change in the relative dominance of species. Any quantitative community composition may reappear in the course of time and there is no clear direction of change (evidence for and examples of fluctuation in, e.g., Braun-Blanquet 1964; Rabotnov 1974; Miles 1979). Obviously fluctuation may have a cycle long enough to make it difficult to distinguish it from longer term trends of change.

Moreover, there will always be fluctuations be superimposed on any directional change. Another aspect is that drastic fluctuational stress may easily change the course of longer-term successional changes (e.g. Austin & Williams 1988, this volume).

Multivariate methods have shown to be helpful in discriminating between fluctuation and trend (Austin *et al.* 1981; Cramer & Hytteborn 1987). Wildi (1988, this volume) contributes to this methodology by developing trend analysis further.

Gap dynamics. Ontogenetically determined as well as externally imposed death of plant individuals may imply qualitative changes in vegetation as opposed to the merely quantitative changes with fluctuation. As a consequence species have to regenerate in order to maintain themselves in the community, while at the same time new possibilities for such re-establishment are provided. This aspect of dynamics has become more and more important, especially since Grubb (1977) emphasized the crucial role of the regeneration niche in community dynamics.

Both in forest and grassland dynamics the term gap is used for any opening resulting from the disappearance of plants (or parts of larger plants) and the term *gap dynamics* as used in the forest literature (e.g. Shugart 1984; Pickett & White 1985; Leemans & Prentice 1987) may be chosen to indicate this second level of vegetation dynamics. Gap dynamics in grasslands is thought equally important but more difficult to study. Silvertown & Smith (1988, this volume) show how grassland gaps can be detected more objectively and how one can study their significance for recolonization.

Patch dynamics. A third level of dynamics concerns the disappearance of local populations or patches of one species, or more species together, where the changes continue over a longer period of time. This is roughly equivalent to pattern dynamics as involved in Watt's (1947) classical approach on pattern and process in short vegetation, and to the patch dynamics in forests (e.g., Pickett & White 1985). Such changes may be cyclic in the sense that a given patch structure may re-appear in the course of time. Hence the term replacement cycles used in Major's (1974) scheme. The time-span involved may (but need not)

be longer than in the case of gap dynamics, but the main (though gradual) difference is the size of the patch relative to the size of the community. As a label for this level *patch dynamics* may be suggested. A complicated example of patch dynamics in conjunction with fluctuation is found in the famous Białowieża forest studied by Faliński (1986, 1988, this volume).

Cyclic succession. The fourth level, only gradually differing from the third one concerns the cyclic replacement of the major part of a community. This is particularly the case when the disappearing population is the dominant one. Examples of simply structured forests are found in the early work of Watt (1925) and discussed by Knapp (1974). Miles (1979) presents a scheme of cyclic changes where different dominant species follow each other. Facts about the classical example, the *Calluna* heath are updated in this volume (Gimingham 1988, this volume). Although the various phases in the *Callunetum* cycle have not been formally described as plant community types (part of them are cryptogamic communities for which a formal system has hardly been developed) the structural and floristic differences between the phases are big enough to talk of a succession and hence the well-known term *cyclic succession* (e.g., Braun-Blanquet 1964; Knapp 1974) may be maintained.

Clearly, the transition between patch dynamics and cyclic succession is gradual, not only in the *Callunetum* case. A special complication, of course is the semi-natural character of the heath in most parts of its distribution area. If any of the management practices (sheep grazing, regular mowing, burning, taking sods) would stop, woodland would take over though not beyond the tree limit.

Cyclic succession may be linked to stand dieback, i.e. the massive death of a canopy dominant, either by endogenous processes or by insect attacks and now also air pollution. This phenomenon has recently been claimed to be more universal than hitherto assumed and moreover spreading as a result of direct and indirect effects of air and soil pollution (Mueller-Dombois 1986). Loehle (1988, this volume) extends the theory on dieback by including tree defences against certain attacks. We also have the

Scalasia example mentioned above (Lawesson 1988, this volume). Sherman & Warren (1988, this volume) summarize the factors causing mortality of two tree species in the Yosemite valley forest and show how man, by excluding fire from the area, plays a role in the interplay between *Pinus ponderosa* and *Calocedrus decurrens*, in this case leading to *Calocedrus* taking over dominance from *Pinus*.

Regeneration succession. The next level of dynamics concerns the recovery from a total disturbance of a mature community, by natural agents such as storm, fire and insect attack, or human impact such as burning and clear-cutting. In the various recovery stages communities can easily be recognized and formally we better speak of regeneration succession than just regeneration. The difference with cyclic succession is gradual but clear: in the case of regeneration succession the duration of the mature stage is long on average in relation to the time needed for recovery, whereas in cyclic succession the mature stage is usually relatively short.

Secondary succession. This form of dynamics we will here define as succession towards a mature stage starting from a semi-natural or cultural situation. The starting point is usually a field, but may also be a grassland, whether grazed or mown. The original Clementsian concept takes the in situ developed soil organic matter as a criterion, as available after disturbance of any mature vegetation (see, e.g. Miles 1979; Vitousek & Walker 1987). Hence it includes our regeneration succession. Braun-Blanquet (e.g. 1964) takes previous anthropogenic disturbance as a criterion, which implies a division of regeneration + secondary succession into naturally versus man-induced.

Most of our knowledge of secondary succession stems from 'old-field successions'. And even much of our modern theory does, starting with Egler's (1954) classical paper on initial floristic composition as an important factor in old-field succession. The large number of studies of such secondary successions have learnt us that general conclusions are not easy to draw. The two contributions in this volume are no exception. Bornkamm (1988, this volume) concludes that all three mechanisms included in the

Connell & Slatyer approach: facilitation, tolerance and inhibition operate at the same time, on different species.

Most studies deal with fertile soils allowing a rapid return to relatively rich well-structured forest. Clearly, findings from such environments do not necessarily apply to succession on poor soils. Examples are known from the Netherlands where secondary succession on poor sandy soils does not proceed at all through phases with ruderals, tall grasses and shrubs (see e.g., Pickett 1982), but through open short grassland and open *Calluna* heath. Succession on abandoned dense grassland may not even start at all during a number of years, because species of further stages cannot enter the community, or only a slow shrub colonization takes place (e.g., Miles 1979; Schmidt 1988, this volume). Examples of either possibility from one limestone grassland type are found in Rosén (1982), while Rusch (1988) found how the closed canopy of an ungrazed grassland site in this type hinders the germination of most species.

In this connection it does not seem appropriate to compare succession on newly harrowed ground and that on abandoned permanent (be it young) grassland in a search for patterns and strategies during succession in general, as done by Brown & Southwood (1987). A more differentiated approach of secondary (+ regeneration) succession follows from the scheme of van der Maarel (1975) where post-cultural, post-agricultural, post-seminatural and post-natural developments are distinguished.

In the present-day landscape of many areas with an intensive land-use we find post-agricultural and post-seminatural successions in complex patterns, simultaneously with still ongoing anthropogenic degradation of remaining natural woody vegetation. Both Borhidi (1988, this volume) and Poli Marchese *et al.* (1988, this volume) show how on the islands of Cuba and Sicily respectively the natural vegetation has been predominantly forest and diversified in relation to environmental variation, how these forests have disappeared, and in which complex ways certain types can be regained or at least approached through secondary succession.

Primary succession. The next level of dynamics is succession on a virginal substrate, i.e. where no re-

mains of earlier vegetation development occur. Such virginal environments are usually poor in nitrogen, which implies that nitrogen-fixing organisms (often algae prior to phanerogams) are important in early stages, provided phosphorus is available (Vitousek & Walker 1987). Another general characteristic is the absence of diaspores and the relatively large distances to be covered by colonizing species. There are exceptions to both rules, however. Beaches with drift-lines may be locally rich and so are the sand flats in some of the enclosed estuaries in the Southwest Netherlands, well-described by Beeftink and colleagues (van Noordwijk-Puijk *et al.* 1979; Hogeweg *et al.* 1985). Also, diaspores could easily enter a nearby primary succession. Examples are the same sand flats and also new land in land upheaval areas (Cramer & Hytteborn 1987; Vartiainen 1988, this volume). Another special case of primary succession on generally fertile soil on artificially created islands in a Swedish lake is described by Rydin & Borgegård (1988b).

A complicated example of primary/secondary succession has been described for a coastal dune area, the older part of which underwent a rapid secondary succession after being released from overgrazing. However, the multi-pathway succession from open communities via scrub to woodland could not be distinguished from a really primary succession having started simultaneously on dunes which rapidly developed in front of the older dunes (van der Maarel *et al.* 1985; van Dorp *et al.* 1985).

Another phenomenon, regularly discussed in a general way (e.g., Beard 1974; Dansereau 1974) and approached more quantitatively by van der Maarel *et al.* (1985) is that of retrogression or regression, the development during succession of a vegetation structure which is lower and/or less complicated than in some previous stage. Apart from local catastrophies such as fire or mechanical disturbance there are intrinsic mechanisms, mainly the death of a dominating shrub or tree population, e.g. of *Betula pendula*, with a life-span shorter than the time needed to reach the climax stage. This is, in fact, canopy dieback as discussed above, but without any indication of a cyclic succession involved. Piotrowska (1988, this volume) gives an example of regression of dune forest subject to dune abrasion and inblowing

sand.

Among the many dichotomies and trichotomies of succession (see e.g. Sjörs 1980) one is important especially for primary succession: the subdivision into autogenic, allogenic and biogenic succession, which goes back to Tansley (see Dansereau 1974). Biogenic succession is nothing else than regeneration (as well as secondary) succession. Autogenic succession is primary succession on a substrate that changes only under the impact of the developing vegetation (soil development). Allogenic succession is development on a substrate that is also changing through input of material from outside. The classical examples are salt marsh succession, where the colonizing first stages of vegetation capture clay and coastal dune succession where the same happens with inblowing sand. In both cases the substrate is changing. Instead of considering this a clear case of facilitation one could also view each subsequent community adapted to the new soil conditions a new terminal stage of a mini-succession.

Secular succession. This is the final level of succession, also called synchronology in phytosociology (Braun-Blanquet 1964). It concerns long-term changes in a landscape as a whole as a result of a long-term changes in the environment, usually climate. The apparent changes are in the distribution area of individual species and through palaeoecology much has become known on postglacial secular changes in forest vegetation, especially in the northern hemisphere (see e.g., Davis 1986 for a survey of papers in the vegetational context).

One fascinating aspect of secular succession is the gradual change in the composition and even the structure of the climax community as a result of changes in soil conditions (Beard 1974). Walker *et al.* (1981) describe a sequence of dune systems in Queensland with ages increasing to probably 400000 yr and considerable leaching of nutrients. The 'climax' community on the older dunes is an open low heathlike community and compared with the taller forest on younger dunes it is a phase of retrogression.

Table 1. Two-dimensional scheme to relate spatial and temporal scales of vegetation dynamics to each other. x: ongoing research; X represented in this volume.

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

Conclusion

The only conclusion to be drawn for this introduction is that there is a threefold variation complicating the discussion on vegetation dynamics: 1) in temporal scale of the dynamical phenomena, 2) in degree of isolation of the piece of vegetation undergoing dynamics, and 3) in level-of-integration on which vegetation is actually studied. Hence it is impossible to create general theories on vegetation dynamics and confusing to apply bits of theory developed in one part of this complex field to other parts. Table 1 lists the various levels of dynamics and of integration and indicates on which cross-roads research on vegetation dynamics takes place.

The present volume covers only a part of these activities, and before starting to learn from its contents one should realize its limitations!

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