# REVIEW

# Mechanisms of vegetation succession: a review of concepts and perspectives

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# INTRODUCTION

Vegetation succession has been the subject of many papers and several reviews. Nevertheless, there is much confusion in the field of terminology. The concept of vegetation succession has been gradually abandoned in favour of the more general term vegetation change (Burrows 1990). Phenomenological terms have been created to suggest knowledge of mechanisms, and these are labelled with terms such as 'models' (Connell & Slatyer 1977; Burrows 1990), 'scenarios' (Peet 1992), or 'classes' (Zobel & Masing 1987; Glenn-Lewin & Van der Maarel 1992). Pickett *et al.* (1987) distinguished

between pathways, causes and mechanisms of vegetation succession, and made an attempt to relate these to Connell & Slatyer's models. When distinguishing between autogenic and allogenic mechanisms, following Tansley (1935), the use of these terms is confusing if they are applied at different levels of organization (vegetation, ecosystem). In addition, we can only guess in which way recent mechanistic terms, such as soil-driven dynamics and transient dynamics (Tilman 1988), fit to these notions. Plant competition has for long been recognized as an important mechanism of vegetation succession. The move, during the last decennium, from a phenomenological approach towards a mechanistic approach in the research on plant competition (reviewed by Grace & Tilman 1990), has also positively influenced the view on mechanisms of vegetation change (Tilman 1988; Berendse & Elberse 1990). The emphasis on competition, however, might result in an underestimation of other mechanisms of vegetation change.

Overall, we felt challenged to review several concepts with regard to vegetation succession, focusing in particular on an evaluation of the perspectives they provide to enlarge our understanding of the mechanisms of vegetation succession. Only such knowledge enables the formulation of useful hypotheses and predictions. For this purpose, we first review concepts concerning vegetation and succession, and then attempt to create some order in the use of terms, thus providing a framework for further conceptual and experimental work. We will not repeat earlier reviews, but rather use their conclusions for the present purpose.

#### CONCEPTS

#### Vegetation

In successional terms, a plant community changes if there is a change in species composition, at least as long as we characterize the community on the basis of its floristic composition. In the present paper, dealing with mechanisms of succession, we do not worry about the distinction between stages of succession (from one phytocoenon to another) and phases of succession (from one phytocoenosis to another, within a phytocoenon). Here we focus on what the notion of 'species' implies when labelling vegetation change with the term 'species replacement'.

According to Tallis (1991), plant communities are particular assemblages of species, which in the history of global plant cover have come together opportunistically and have then been re-ordered as climate conditions continued to change (cf. also Whittaker 1975). The two aspects, individuality and order, were also recognized by Gleason (1926, 1939). In his 1926 paper he emphasized one side of the coin: 'Are we not justified in coming to the general conclusion, far removed from the prevailing opinion, that an association is not an organism, scarcely even a vegetation unit, but merely a coincidence?'. However, after having emphasized this coincidental aspect of plant communities, Gleason (1939) also acknowledged that 'a plant association is an aggregate of plant species forming an ecological unit with a definite successional status and of uniform physiognomy, recognizable by its floristic composition'.

In the majority of textbooks, vegetation is considered to be composed of *populations* of plant species, rather than being composed of plant *individuals*. The population approach has created a number of problems. For example, a species may disappear from a community while the population does not become extinct, either because the

boundaries of a phytocoenosis do not coincide with the boundaries of all of the component populations, or because the population survives as a dormant seed bank. Moreover, using the term population may suggest that population quality can be involved in vegetation science, in addition to quantitative aspects, which is not the case. Such problems can be avoided if a community is thought to be composed of visible individuals of overlapping populations. Only Westhoff (1951) and Müller-Dombois & Ellenberg (1974) recognized the community as being an association of individual plants.

Dominant species of a plant community are the main determinants of ecosystem characteristics such as productivity, stability and succession (Grime 1979 and 1987), while the aspect of species-richness is much more related to the subordinate species (Grubb 1977; Grubb et al. 1982; Grime 1987). Brown (1992) has shown that generalizations about life-history strategies of plant species in relation to successional age of the habitat may have been oversimplified. This draws our attention to considering vegetation not only as composed of individual plants, but also as a functional component of an ecosystem (Odum 1971). O'Neill et al. (1986) proposed to recognize a dual hierarchy, represented by a 'population-community approach' (dealing with life histories and evolution) and a 'process-functional approach' (dealing with cycling of energy and nutrients). They suggested that 'it is quite feasible and even reasonable to maintain an individualistic (Gleasonian) concept of the community and a holistic concept of ecosystem function'. The latter aspect has been neglected in several studies dealing with succession (e.g. White 1985; Falińska 1991; Myster & Pickett 1992) or with disturbance (e.g. Pickett et al. 1989; Van Andel et al. 1991). Westhoff's (1979) definition of vegetation acknowledges both aspects: 'A system of largely spontaneously growing plant populations [in his 1951 paper he wrote plant individuals, which we prefer] growing in coherence with their sites and forming part of the ecosystem together with their site factors and all other forms of life occurring in these sites'. In between, we are still far from getting to the bottom of insight into 'emergent properties' of communities, which result from interactions between organisms (see below).

#### Succession

Until now we have been using the terms 'vegetation succession' and 'vegetation change' in a rather arbitrary way. Actually, the latter term would include fluctuations. According to Burrows (1990), there is so much confusion in the use of the term succession that it seems best to abandon 'succession' in favour of the non-committal 'vegetation change'. Though such an escape may seem useful when reviewing mechanisms of succession, it does not sufficiently acknowledge the historical value of the concept of succession. Tansley (1935) stated that this concept involves not merely change, but the recognition of a sequence of phases subject to ascertainable laws. Even if succession is 'a continuous process of change in vegetation which can be separated into a series of phases' (Tansley 1935), there is no need at all to abandon the concept of succession. The important part is the notion of 'a series' of phases or stages. When considering mechanisms of succession as mechanisms of vegetation change, it is quite useful to differentiate between fluctuation in species composition (or abundance) and a successional sere. Miles (1979), having defined vegetation dynamics in general as 'changes which markedly alter the appearance of a patch of vegetation such that it can be considered to have changed into a different type', added that fluctuations are reversible changes, whereas successions are directional changes away from an initial state. Similarly, Finegan (1984) defined succession as 'the directional change with time of the species composition and vegetation physiognomy of a single site where climate remains effectively constant'. This implies that succession is not only the change from pioneer stage to climax, but should have *some* direction. We do not consider the notions of progressive, regressive or degressive succession as contributing to our knowledge of mechanisms (cf. Bakker 1989). The only problem left is how to detect a change in vegetation type. Here it suffices to refer to Huisman *et al.* (1993), who presented a hierarchical set of models to distinguish between trends and fluctuations, and to Prach *et al.*'s (1993) proposal to calculate the rate of succession as the turnover rate of species from one year to another, thus avoiding the dilemma of 'stages' or 'phases' of succession. For a review of the history of the concept of vegetation succession, see McIntosh (1980), Miles (1987a) and Glenn-Lewin *et al.* (1992).

We start from Pickett *et al.*'s (1987) proposal to distinguish between pathways, causes, and mechanisms of vegetation change to describe, explain or predict aspects of succession: (i) *pathway* is the temporal pattern of vegetation change; (ii) *cause* is an agent, circumstance or action responsible for successional patterns; (iii) *mechanism* is an interaction that contributes to successional change. Consequently, a successional sere is a particular type of pathway, which might depend on particular sets of causes and/or mechanisms. Models are a conceptual construct to describe and explain successional pathways or predict the course of particular successions by combining various mechanisms, specifying the relationships between the mechanisms and the pathway as well as one another (cf. Fresco *et al.* 1987).

#### Kinds of succession: phenomenology

We adopt the notion of 'kinds of succession' from Müller-Dombois & Ellenberg (1974) to distinguish between different types of pathway. While studying the literature, we have been surprised by the amount of attention paid to phenomenological terminology, which implicitly suggests some information on mechanisms, but actually does not. The following may illustrate this statement.

Burrows (1990), in an attempt 'to encompass all kinds of vegetation change phenomena in all kinds of vegetation', distinguished five 'models' of vegetation change, partly on the basis of the initial condition (non-vegetated open areas vs. areas already fully covered by vegetation), for another part on the basis of causes and mechanisms (e.g. autogenic vs. allogenic influences). We do not take this proposal into consideration because we prefer to clearly separate kinds of succession vs. causes and mechanisms of succession. Glenn-Lewin & Van der Maarel (1992) proposed to distinguish seven 'classes' of vegetation dynamics, thus providing a framework based on an increasing scale of time and space: fluctuations, fine-scale gap dynamics, patch dynamics, cyclic succession, secondary succession, primary succession, and secular succession. Similarly, Zobel & Masing (1987) had proposed a 'spatio-temporal classification of several kinds of community and ecosystem dynamics', but these authors provided us with another set of jargon. Overall, as far as phenomenological terminology is concerned, we agree with McIntosh (1980) that it is an illusion to think that the search for regularity and simplicity, which is traditional in science, can be satisfied by replacing terms or introducing 'new-speak'.

The distinction of primary vs. secondary succession only marginally contributes to our understanding of mechanisms of succession. First of all, the difference between the two largely depends on an interpretation of what initially might have happened in the past. Secondly, mechanisms of succession depend much more on the initial abiotic

#### MECHANISMS OF SUCCESSION

conditions (e.g. climate, soil fertility) than on whether a succession is primary or secondary. The following examples may illustrate this view. Peet (1992), although recognizing that relatively small changes in environmental conditions can be critical factors driving long-term successional changes, considers *primary* succession as being principally driven by mechanisms involving environmental change (soil, climate change, etc.), whereas *secondary* succession would be driven primarily by mechanisms related to species interactions. Gleeson & Tilman (1990), however, recognized that secondary successions that begin on nutrient-impoverished soils may have more in common with primary successions than with secondary successions on rich soils. From this type of debate it is obviously confusing to relate mechanisms of succession to kinds of succession (such as primary and secondary seres). Therefore, we will stop discussing kinds of succession and start focusing on mechanisms at different hierarchical levels.

#### Causes, mechanisms and functions

At which level of community organization do we have to search for mechanisms? According to Tilman (1989), phenomenology and mechanism are not absolute entities but idealized ends of a spectrum: 'It is likely that, along the spectrum from phenomenological to mechanistic theory, there will be a point that is optimal for explaining any given ecological pattern. (...) The optimal point will be found only through the usual trial-and-error process of science.' In his view, theory allows us to formulate testable predictions derived from comparative observations, and manipulative experiments can determine whether correlations are based on causal relationships. Tilman (1989) treated conceptual problems related to the interpretation of experiments, many of which have occurred 'because ecologists have used short-term experiments to address long-term questions'.

Long-term observations are a conditio sine qua non to distinguish between successions and fluctuations (e.g. Westhoff 1969, 1987; Pickett 1982; Van Tooren et al. 1983; Beeftink 1987; Bakker 1989; Andresen et al. 1990; Turner 1990; Huisman et al. 1993). Only on the basis of knowledge of the exact sequence of species in a successional sere and of the relevant ecosystem processes, can we attempt to experimentally unravel mechanisms of species replacement (e.g. Olff et al. 1990; Olff & Bakker 1991; De Leeuw 1992). In the actual field situation, mechanisms of succession can be tested if we can find sites which definitely represent phases or stages of succession, i.e. chronosequences. In this context we need to be aware that spatial zonation frequently does not represent a chronosequence (see e.g. Roozen & Westhoff 1985; De Leeuw et al. 1993).

As far as autogenic succession is concerned, we may refer to 'relay floristics' and 'initial floristics and pre-emption' (Egler 1954; Wilson *et al.* 1992), 'obligate succession' and 'competitive hierarchy' (Horn 1976), 'life histories' and 'vital attributes' of species (Drury & Nisbet 1973; Pickett 1976; Noble & Slatyer 1980). With regard to allogenic factors, attention has been paid to biotic and abiotic aspects. So-called 'third party effects' (Grubb 1986; Glenn-Lewin & Van der Maarel 1992) represent the influences of biota other than higher plants on vegetation succession. Changes in abiotic factors, e.g. changes in salinity, nutrient supply, quantity and composition of groundwater, may also allogenically induce succession. Tansley (1935) stated: 'In 1926 I proposed to distinguish between autogenic and allogenic succession. (...) I think now that I should have gone farther than this and applied my suggested new terms in the first place to the factors rather than to the successions. It is the fact, I think, that autogenic and allogenic factors are present in all successions'. This classical view has not been sufficiently recognized until recently. Pickett *et al.* (1987) once again emphasized that the three mechanisms proposed by Connell & Slatyer (1977), i.e. the mainly autogenic 'models' of facilitation, tolerance and inhibition, are not alternative hypotheses about entire seres and that attempting to test them in that way is not likely to be productive. For the same reason, Peet (1992) suggested the models of Connell & Slatyer (1977) to be called 'scenarios' rather than mechanisms. Indeed, the relative importance of each of the scenarios may change in the course of a successional sere (cf. Walker & Chapin 1987; Farrell 1991). An additional problem is that observational studies are unlikely to distinguish between the different models of succession (Crawley 1986). Connell *et al.* (1987) suggested that the proposed mechanisms represent the extremes of a continuum of effects of earlier on later species; the strength and directions of the interactions could vary within a successional sequence. In our view, the main confusion results from not distinguishing between causes and mechanisms.

The specific interaction that is termed a mechanism depends on the level of organization a study addresses (O'Neill et al. 1986; Allen 1987). Indeed, according to Pickett et al. (1987), a mechanism on one level of organization can be considered an effect on another level. This implies that the use of the terms 'autogenic succession' and 'allogenic succession' is useful only if the system of study is clearly delimited. From a phytocentric point of view, it seems useful to identify autogenic processes as 'mechanisms of succession' and allogenic influences as 'causes of succession'. However, mechanisms and causes interact (see e.g. Hobbie 1992), and a mechanism can be considered 'an efficient cause' (Pickett et al. 1987). Therefore, this view can be held only as long as autogenic and allogenic influences can be clearly distinguished. Plant individuals being the actors of mechanisms of vegetation change, the ecosystem is the action field in which they have to fulfil functions. In other words, mechanisms of vegetation succession being the field of interest, these can be discovered by a reductionistic approach, but should also be evaluated in a wider context (cf. Tansley 1935; Odum 1983; O'Neill et al. 1986), i.e. a vegetation in the context of its functioning in the ecosystem, and an ecosystem in the context of its functioning in the landscape. For analogy, we quote from Frank & Slatkin (1992), who re-interpreted Fisher's fundamental theorem of natural selection: 'Fisher realized that the average fitness of a group is a useful quantity only in the wider context of other groups and the environment: a species in the context of competitors, diseases and food availability; a genotype in the context of a particular mix of competing genotypes within the population; or an allele in the context of the frequency of competing alleles at a locus'.

## **CLARIFICATION OF THE FRAMEWORK**

After having reviewed several concepts and the associated terminology, we feel the need to propose a reduction of the jargon along with a clarification. In the present review, we will start from the phytocentric point of view on vegetation succession in order to link up with current views, but will finish with considering ecosystem succession. As far as mechanisms and causes at different hierarchical levels are concerned, we take the following position.

(a) Interactions between plants, i.e. autogenic processes, will be termed vegetation mechanisms of succession.

- (b) Effects of biota other than higher plants within a community will be treated under the heading 'biogenic *causes* of vegetation succession'.
- (c) If autogenic mechanisms and allogenic causes are no longer distinguishable and it is particularly the interaction between these two that governs succession, we leave the phytocentric view and start discussing 'ecosystem mechanisms of succession'.

## VEGETATION MECHANISMS OF SUCCESSION

Interactions between plants, such as facilitation, competition and other emergent properties of a plant community, can occur only after the plants have become established. Therefore, we first treat mechanisms of colonization and regeneration, and only thereafter mechanisms of species interactions. In broad outline, we follow the framework proposed by Pickett *et al.* (1987).

#### Seed bank

Plant species can become established only if viable species are present, either in the seed bank or as a result of immigration from neighbouring populations (Hodgson & Grime 1990). These processes had already been mentioned by Clements (1916), who termed them 'migration', and 'ecesis', site availability ('nudation') being a first condition. Buried viable seed banks are part of the vegetation. They have received scientific attention mainly in the context of conservation and restoration of plant communities, as they are important predictors of potential plant responses to change in land use or management (e.g. Peart 1989a; Jiménez & Armesto 1992).

Seed banks of species have been classified as 'persistent' or 'transient' according to whether or not their germinable seeds were detected throughout the year (Thompson & Grime 1979). However, this classification of seed banks provides too little information about the longevity, because estimates of the latter are useful in so far as they can be related to the frequency of habitat disturbances (e.g. Voesenek & Blom 1992). Therefore, a more adequate seed bank classification has been proposed (Bakker 1989; Thompson et al. 1993; cf. also Poschlod 1991). These authors distinguished three types: (i) transient seeds that persist in the soil for 1 year or less; (ii) short-term persistent seeds that remain viable in the soil for a period of 1 to 5 years; (iii) long-term persistent seeds that remain viable in the soil for at least 5 years. Preliminary studies indicate that the majority of characteristic species in chalk grasslands (Willems 1983; Poschlod 1991), litter fens (Vyvey 1986; Pfadenhauer & Maas 1987; but see Van der Valk 1992), dry grasslands (Van Dijk & Sykora 1982), and moist grasslands (Bakker 1989) have no long-term persistent seed bank. This means that the process of re-establishment of species in disturbed ecosystems depends on the immigration of propagules, rather than on the seed bank. Fragmentation of nature reserves in the landscape increasingly poses problems of lack of seed availability of rare species if we do not introduce them (Gartner et al. 1983; McDonald 1993). Constraints in spatial dispersal of plant propagules as related to the rate of succession is an urgent research topic.

## Establishment

Once plants have become established and set fruits, microsite availability rather than seed availability may become limiting for the regeneration from seeds (e.g. Peart 1989c; Hester *et al.* 1991). In many ecosystems, a permanent existence of 'regeneration niches' (Grubb 1977) is a condition to maintain species richness, as has been shown for chalk

grasslands (Grubb et al. 1982; Schenkeveld & Verkaar 1984; Rusch 1993), for flood-plains (Voesenek & Blom 1992) and for salt-marshes (Hutchings & Russell 1989; Bakker & De Vries 1992). The concept of regeneration niche is much wider than seems to be indicated by the term 'safe site' (Harper 1977), as this niche includes all resource requirements during the entire process of regeneration, from dissemination to establishment.

Here, we do not feel the need to go into detail as far as germination physiology is concerned, because we agree with Angevine & Chabot (1979) that, for ecological purposes, species-specific germination physiologies can be arranged into 'germination syndromes' (cf. Rozijn & Van Andel 1985; Van der Valk 1992). The important aspect is that the germination physiologies are thought to be evolved in such a way that the emerged seedlings have a chance to survive (Voesenek et al. 1992). Therefore, the seedling stage is considered the most vulnerable part of the early photosynthetically active life of a plant. Olff et al. (1994) report the results from several studies on the germination characteristics of species in a secondary grassland succession: having been used for agricultural purposes, these grasslands had been cut for hay for different periods of time over a 25-years period. Early successional species, on relatively rich soils, germinated quickly to a high percentage, suggesting that these were capable of escaping competition for light by germinating in autumn. Later successional species, on less productive soils, germinated less and at slower rates, and they responded more clearly to stratification and alternating temperatures, thus suggesting a delay of germination until next spring.

Seeds of many pioneer species require a light stimulus and/or alternating temperatures to perceive the conditions for seedling survival (e.g. Grime & Jarvis 1975; Silvertown 1980; Van Baalen 1982; Van Tooren & Pons 1988; Pons 1991; Voesenek *et al.* 1992; Bouwmeester *et al.* 1993). Fenner (1987) discussed the properties of seeds as related to vegetation succession. In secondary successions on bare soils, in general, seeds of pioneer species (mainly annual and perennial ruderals) are smaller sized than the seeds of later successional species (such as shrubs and trees), but the relationship between seed size and colonizing ability is not straightforward among different species (Fenner 1978; Peart 1989b). Rather this seems to be the case within species along successional gradients, for example in *Solidago* species (Werner 1979) and in *Rhinanthus angustifolius* (Ernst *et al.* 1987). On the basis of this phenomenon, Werner (1979) proposed the 'colonization-competition hypothesis of succession'. In a primary succession on poor soil, Gleeson & Tilman (1990) similarly detected a decreasing reproductive allocation, suggesting a trade-off between colonization ability and competitive ability (for nitrogen in this case).

#### **Facilitation**

It is well known that plants of different species can exhibit a beneficial, one-way or two-way, effect. This may be exemplified by the aeration of anoxic soils by aerenchymatous plants (Joenje 1978; Schat 1984; Laan *et al.* 1989; Schat & Van Beckhoven 1991), positive interactions between different *Vaccinium* species (Maillette 1988), the phenomenon of hydraulic lift in semi-arid areas (Caldwell *et al.* 1991), the transport of water and nutrients through interspecific mycorrhizal networks (Grime *et al.* 1987; Robinson 1991), and benefits from N-fixing plants, either as hosts for hemi-parasites (De Hullu 1985) or after their death (Akkermans 1971). We quote from Gigon (1990): 'Experiments in dry grasslands in Switzerland show that adult plants can have positive microclimatic and edaphic effects on the germination and establishment of other plant species. Other experiments and a literature survey show that positive interactions exist between adult individuals of many plant species. In most cases the beneficial effects are not direct but via other organisms'. Johnson *et al.* (1991) showed that the species composition of VAM fungal communities changed during secondary succession of abandoned fields to forest. The diversity of the VAM fungal community was positively related with soil C and N, thus indicating a concomitant inter-relationship between soil properties, plant productivity and VAM density.

Within the scope of the present paper on succession, we should distinguish between interactions which result in coexistence and those leading to succession. Facilitation (sensu Connell & Slatyer 1977) is confined to the latter aspect. This term is related to 'reaction' (Clements 1916), 'relay floristics' (Egler 1954) and 'obligate succession' (Horn 1976). Only if one plant species directly facilitates the establishment of successional plant species, is the term facilitation adequate. The most clear example of facilitation we know does not concern plants, but fungi, viz. the succession of fungal species on dead wood (Shigo 1975). As far as higher plants are concerned, Miles (1987a) and Glenn-Lewin & Van der Maarel (1992) mentioned only a few examples, from which we cite the study of Bradshaw et al. (1982) on the effects of the N-fixing legume shrub Ulex europaeus on succession. Similarly, Grove et al. (1980) showed an increase in the rate of N-fixation by the cycad Macrozamia riedlei after a fire in an Australian open forest, which may facilitate secondary succession. The majority of examples of facilitation are related to primary successions on initially poor soils (see Major 1974), e.g. in Glacier Bay (Crocker & Major 1955; Lawrence et al. 1967), in dune areas (Olson 1958; Gerlach et al. 1989; Westhoff & Van Oosten 1991; Olff et al. 1993), and in reclaimed polder areas (Joenje 1978).

Many of the facilitating processes of plants exhibit their beneficial effects not as a result of a plant-to-plant interaction (direct facilitation), but in an indirect way, via plant-induced soil changes and soil formation (Miles 1987b; Hobbie 1992), thus resulting in 'soil-driven dynamics' (sensu Tilman 1988). The latter might be called indirect facilitation (see Farrell 1991), analogous to the distinction between direct and indirect competition. In practice, however, direct and indirect facilitation can hardly be distinguished. Therefore, we prefer to consider facilitation as an ecosystem process and will discuss this under the heading 'ecosystem mechanisms of succession', at the same time leaving the term 'facilitation' in favour of ecosystem terms such as feedback mechanisms.

#### **Competition**

Competition for resources has for long been recognized as an important mechanism of succession (Clements 1916; Horn 1976; Connell & Slatyer 1977; Grime 1979; Pickett *et al.* 1987; Tilman 1990). None of these authors claim competition to be the only mechanism, but they differ in their view of the nature, intensity and the relative importance of competition in contrasting plant communities (cf. Welden & Slauson 1986). Grace (1990, 1991) discussed the views of Grime and Tilman by considering questions such as: (i) whether or not 'stress-tolerators' (Grime 1979) do compete for nutrients (Tilman 1987), and (ii) whether 'maximum resource capture' (Grime 1987) or 'minimum resource requirement' (Tilman 1985) is the main plant property in determining the outcome of succession. The question to be discussed here is whether we should have knowledge of the mechanism of competition to understand its role as a mechanism

of vegetation succession. In other words: Is it insufficient to treat competition as a phenomenon in this context? In view of the hierarchical levels, we can avoid the question of which plant properties determine the competitive ability of species when discussing competition as a mechanism of vegetation succession. On the other hand, if we want to quantify the intensity of competition and its relative importance in vegetation succession, the mechanisms of plant competition should be known. The most important advantage of Tilman's (1988) mechanistic approach is that it relates *species* responses (dynamics, growth, allocation) to an *ecosystem* parameter ( $R^*$ : the level to which its population in equilibrium can reduce limiting soil resources). In other words, this concept provides an interface between the population–community and the process–functional approaches, as advocated by O'Neill *et al.* (1986). Examples of experimental follow-up research on successional grasses can be found in Tilman & Wedin (1991) and Wedin & Tilman (1993), to which we only refer here.

Berendse & Elberse (1990) have shown that the replacement of *Erica tetralix* by *Molinia caerulea* results from an increase in competitive ability of the latter species as a result of eutrophication of the habitat, and that this replacement is irreversible due to a positive feedback of *Molinia caerulea* on the nutrient cycling in the ecosystem. Similarly, Bobbink *et al.* (1988) showed *Brachypodium pinnatum* to become predominant in chalk grasslands as a result of an increase in N-supply. It is worth mentioning that Huisman (1993) shows that the model of competition for nutrients as proposed by Berendse & Aerts (1984, 1987), which is based on the concept of 'relative nutrient requirement', is a particular case of Tilman's (1982, 1988) more general model. In between, we should be aware that competition for light is much more complex than is competition for nutrients (Huisman & Weissing 1993).

'Inhibition' (sensu Connell & Slatyer 1977), meaning the prevention of plant establishment by existing plants, can be considered a particular aspect of competitive ability (cf. Peart 1989b). Wilson & Agnew (1992) treated 'positive-feedback switches in plant communities', which indicate all processes in which a community modifies the environment, making it more suitable for itself. In a way, this represents inhibition, at least the opposite of facilitation (or negative feedback switches). However, there is no gain in distinguishing between inhibition and competitive dominance. For example, stands of *Pteridium aquilinum* may inhibit further succession, due to competition for light and nutrients in addition to allelopathic competition. But a change in competitive abilities of species may result in successional change, be it cyclic (Watt 1947, 1955) or not (Marrs & Hicks 1986; Gimingham 1988). The term inhibition seems useful only in the context of a climax stage of succession.

## **BIOGENIC CAUSES OF VEGETATION SUCCESSION**

## Herbivory

Vertebrate herbivores. According to Oksanen (1990), the impact of herbivores on the vegetation depends on the productivity of the soil-plant system. At low primary productivity (due to limiting nutrients or low temperatures), vegetation is not attractive to herbivores. At intermediate levels of primary productivity the consumption pressure is assumed to be close to the carrying capacity, so that the standing crop is kept at a low level. In such a situation the herbivore is 'prisoner of its food supply' (Drent & Prins 1987). Probably, at still higher levels of primary productivity the herbivore densities are

no longer regulated by the vegetation, but rather by predators and parasites, so that the vegetation can develop into woodland.

This general picture indicates that the vegetation is relatively stable as long as either abiotic stress factors or biotic factors inhibit or at least retard further succession. This has been shown for a variety of ecosystems, e.g. salt-marshes grazed by waterfowl (Joenje 1985; Olff 1992) and cattle (Bakker 1985, 1989; Andresen *et al.* 1990), dune grasslands grazed by rabbits (Watt 1957; Zeevalking & Fresco 1977), coastal tundras grazed by lemmings (Batzli *et al.* 1980), and savannas grazed and browsed by large herbivores (see McNaughton & Georgiadis 1986; Prins 1989; Prins & Van der Jeugd 1993). As soon as the density of herbivores becomes reduced by some external factor, below the level of the carrying capacity, the rate of vegetation succession increases. Bakker *et al.* (1983) showed that moderate sheep grazing intensity resulted in patches of grassland being intensively grazed and kept intact, while other patches were avoided by the sheep, thus enabling succession. On calcareous former arable land, intended for restoration of species-rich grasslands, sheep grazing could result in modifications (deflections in a way) of the direction of succession, depending on the intensity of grazing (Gibson & Brown 1992).

Verkaar (1988) concluded from a review of the literature that the majority of studies indicate adverse effects of defoliation, while only a few examples of increased fitness as a result of defoliation have convincing evidence. In the latter case, a higher photosynthetic rate and a higher leaf area ratio may account for a temporal increase in relative growth rate following defoliation. He did not consider the consequences for light competition among species. Hik & Jefferies (1990) showed that the 'optimization of grazing intensity' by lesser snow geese on swards dominated by *Puccinellia phryganodes* and *Carex subspathacea*, was related to the speeding-up of nutrient recycling via faeces, which was responsible for the phenology of plant regrowth and its food quality. However, on a longer time-scale grazing and grubbing by the geese may result in destruction of the habitat (Kerbes et al. 1990; Hik et al. 1992).

Insect herbivores. In Calluna vulgaris heathland, high densities of the heather beetle Lochmaea suturalis may result in subordinate perennial grasses irreversibly replacing Calluna vulgaris (Berdowski 1987). A similar phenomenon was observed in prairie grasslands, after an attack of the dominant Solidago canadensis by chrysomelid beetles, Trirhabda spp. (McBrien et al. 1983), but in this case a fluctuation or even a cyclic succession was induced. In grasslands, most of the primary production is underground, and the rhizosphere supports a distinctive and complex microfloral/microfaunal community (see Stanton 1988, for a review). Insecticides have been applied to detect the impact of insect herbivores on individual plants and on vegetation succession (Brown 1990; Brown & Gange 1991, 1992). These authors showed that chewing larvae of mainly Coleoptera and Diptera feed on roots of early successional plants on bare sandy and acidic soil. Elimination of these soil herbivores during a period of 3 years first resulted in a relative increase of the cover of annual forbs, thereafter in a relative increase of perennial grasses and forbs. The latter effect was enhanced by above-ground Hemiptera herbivory, due to their preferential sap-feeding on annual forbs. In later successional phases, Cicadellidae feed on dominant grasses, which resulted in an increase of species richness. In conclusion, foliar-feeding insects caused a slowing of the rate of succession to a grass-dominated sward, and thus resemble the well-documented effect of vertebrate herbivores, whereas root-feeding insects effected an increase in the rate of succession.

## Parasitism

In the Dutch estuaries, some 15 000 ha of evergreen submarine Zostera beds were cleared away around 1932. The pathogen Labyrinthula macrocystis is supposed to be responsible for this almost irreversible catastrophy, but this has never been proved (Den Hartog 1987). We agree with Harper (1990) that 'the crucial test of whether pests or pathogens influence the composition of plant communities has to be, not whether plants suffer or die from disease or pests, but whether the community develops differently if they are excluded'. The majority of studies concerning plant-pathogen interactions in natural communities focus on the two-species level (e.g. De Nooij & Van Damme 1988; Alexander 1990). If a plant community is dominated by only a few species, plantpathogen relations may affect both populations and the community as well. Zadoks (1987) mentioned a few studies which showed that pathogenic fungi, selectively parasitizing plant species in a community, may accelerate vegetation succession. For example, the willow rust Melampsora bigelowii killed many seedlings of the willows Salix pulchra and S. alexensis, pioneer species which formed nearly pure stands on gravel banks of the river Yukon in Alaska, once the ice had receded. This might have accelerated succession to birch and spruce. During the succession, the amount of rust declined, but various canker and heart rot fungi became dominant and killed the willows (Baxter & Wadsworth 1939), Nematodes of the genus Longidorus are capable of damaging stands of Hippophaë rhamnoides in coastal dune areas. They reduce the root system, including the N-fixing nodules, and the related mycorrhizal system, thus reducing the uptake of phosphate and other nutrients (Oremus & Otten 1981). This damage may result in acceleration of succession to, e.g. Sambucus nigra, Ligustrum vulgare and Rosa rubiginosa on calcareous soils, or to Empetrum nigrum on acidified soils. Endoparasitic nematodes appeared also responsible for reduced vitality of Ammophila arenaria in coastal dunes, thus favouring Festuca rubra ssp. arenaria (Van der Putten & Troelstra 1990; Van der Putten et al. 1993).

In contrast to research on plant-parasite interactions in the context of agriculture, (semi)natural ecosystems are unfortunately almost devoid of such a type of investigations.

#### Food webs

McNaughton (1992) has proposed that disturbance at one level in a trophic web can have effects far removed from the initial locus of disturbance. Because of the complexity of food webs, only a few case studies are to be referred to in the context of vegetation succession.

Prins & Van der Jeugd (1993) reconstructed savanna bush encroachment in East Africa as coinciding with events of rinderpest pandemic or anthrax epidemics among ungulates such as impala, which enabled the establishment of even-aged *Acacia tortilis* stands. So, after having treated the direct effects of parasites on plants in the former section, we should also be aware of the occurrence of indirect effects, via animals.

Farrell (1991) reported on a study of succession in an intertidal community on the central Oregon coast. Barnacles decreased limpet foraging activity and thereby increased algal abundance. Depending on the limpets, competition between two barnacle species could be symmetric or asymmetric, but it is not clear whether this has an effect on algal abundance.

Robertson (1991) studied mangrove forest ecosystems in tropical Australia. Insect herbivores consumed overall less than 5% of the canopy production, but the rates of

herbivory on individual tree species ranged from 0.3% (*Excoecaria agallocha*) to 35.0%(*Avicennia marina, Heritiera littoralis*) of the expanded leaf area, probably due to differences in chemical composition. Moreover, 20-80% of the propagules of eight of the common mangrove tree species were damaged by insects. In addition, sesarmid crabs are important post-dispersal predators on mangrove propagules and can influence the distribution patterns of species across the intertidal zone. These crabs (e.g. Sesarma messa) also contribute largely to the process of decomposition of mangrove leaves, thus playing a key role in the 'nursery ground function' of mangrove habitats.

References to these few case studies may serve to stress the need to recognize that the patterning and development of vegetation takes place in the context of complex interactions among community processes and ecosystem processes.

# ECOSYSTEM MECHANISMS OF SUCCESSION

For reasons of remaining in touch with existing literature, we have been distinguishing *autogenic mechanisms* and *allogenic causes* of vegetation succession. With regard to the latter, we confined ourselves to biogenic causes, because community components can clearly be distinguished. However, in the case of abiotic allogenic factors, it is no longer worthwhile to distinguish between allogenic causes and autogenic mechanisms at the level of the vegetation, because the continuous interaction (feedback mechanisms) between vegetation and soil renders the two types of process indistinguishable. This is generally the case in wetlands, where vegetation succession is involved in ecosystem succession to such an extent that it is advisable to make a choice for the 'ecosystem' as the entity of study.

The next few examples are meant to illustrate the interface between vegetation succession and ecosystem succession, with increasing emphasis on the latter.

#### Dune valleys

Successional seres in primary dune valleys (Westhoff 1947; Grootjans et al. 1988, 1991; Westhoff & Van Oosten 1991) may exemplify the complex interaction between allogenic causes and autogenic mechanisms. The calciphilous association Junco baltici-Schoenetum nigricantis may develop from various pioneer communities, i.e. the Centaurio-Saginetum or, under more saline conditions, the Parnassio-Juncetum atricapilli. Further successional pathways depend mainly on the local hydrological regime, governing the rates of acidification, desalination, and sand blowing. These factors are mainly of allogenic origin, but they may be modified by autogenic build-up of organic matter (indirect facilitation). At the very beginning of these successional seres bare and blowing sand becomes stabilized by the formation of microbial mats (Pluis 1993), among which green algae and cyanobacteria play an important part by fixation of C and N (Stal 1985; Visscher 1992). This is the primary allogenic cause, either on beach plains (De Wit 1989) or in blown-out dunes (Van Dieren 1934; Pluis & De Winder 1990). After the early establishment of plants, the rate of decalcification and the hydrological regime are the main allogenic (and partly autogenic) determinants of how long the pioneer stage can persist (Grootjans et al. 1991). High pH values, a low input of nutrients, and an autogenically induced oxic environment around the plant roots (Ernst & Van der Ham 1988; Roelofs et al. 1984) retard the succession to higher productive communities. Both carbonates from mollusc shells, and secondary precipitation of calcite may act as

buffering agents in the root zone, thus preventing organic matter deposition and soil formation (F. P. Sival, personal communication).

## Moist grasslands

When intensively used agricultural grasslands in the Drentse A brook valley system were abandoned and cut for hay to restore the former semi-natural species-rich hayfields, the productivity of the plant-soil system decreased. The secondary succession on these peaty soils appeared to be largely governed by the response of the successional species to changes in limiting nutrients (Pegtel 1987; Olff 1992). The productivity of the entire vegetation was first limited by N and K, and later by P in addition. As a result, indicators of eutrophic conditions, such as *Holcus lanatus* and *Agrostis stolonifera*, were replaced by *Plantago lanceolata, Anthoxanthum odoratum* and *Rhinanthus angustifolius*, which in turn had to make room for a *Juncus acutiflorus* dominated community (Bakker 1989). Here, the competitive abilities of the successional species (an autogenic mechanism) depend on the nutrient status of the soil. With regard to the latter, allogenic and autogenic influences are indistinguishable, and thus demand an ecosystem approach of the plant-soil system.

#### Salt-marshes

Olff (1992) reconstructed 200 years of development of coastal bar island salt-marshes. Here, plant species replacement during succession was observed to be faster on the lower parts of the gradient, probably due to the higher rate of sedimentation of clay. The progress of nitrogen accumulation in the clay sediments from the sea (an allogenic cause) rather than the desalination appeared responsible for vegetation succession. In the course of succession short plant species were replaced by taller species, as a result of which the relative importance of light competition (an autogenic mechanism) was supposed to increase. Though in this case autogenic and allogenic influences could be distinguished in retrospect, the study of the geomorphological development of the ecosystem provided more evidence for the understanding of vegetation succession than had been derived from studying species responses and competitive abilities.

## Mire systems

Zobel (1988) reviewed bog succession in boreal mires. He clearly showed that his use of the term 'autogenic succession' or 'self-development of mires' regards ecosystem processes rather than vegetation succession in itself. He came to the conclusion that, in comparison with mineral land communities, bog succession is characterized by a more deterministic (though not unidirectional) development, where it is difficult to differentiate between external and internal factors. Though it may sometimes seem possible to determine autogenic processes, for example when searching for comparable sequences in peat formation over a wider area, it is also likely that we are dealing with allogenic processes, e.g. when the water table was rising faster than the peat could accumulate (Wheeler 1992) or when a bog has been drained and unusual sequences are encountered. Ilomets (1984) showed that in bog development allogenic and autogenic types of development may occur simultaneously. However, without knowledge of the hydrological conditions of a bog it is very difficult to distinguish between autogenically and allogenically induced *Sphagnum* growth. Small changes in the hydrological regime may result in acidification of the top layer (Van Wirdum 1991; Van Diggelen et al. 1991).

Bog succession actually is ecosystem development, so that the terms autogenic and allogenic become meaningless. During bog formation, structures arise which may drain or flood other parts of the mire. The hydrological functions these structures perform can be expressed in hydrological terms to explain the continuous growing of the bog. An ecologist can easily communicate with hydrologists and contribute to such research by identifying the hydrological feedback mechanisms with respect to water flow, based on structural characteristics of individual moss species or even carpets of moss species. Phytocentric discussions on autogenic or allogenic processes entangle such a type of research, because it should be simultaneously carried out on various spatial scales. As Zobel & Masing (1987) put it: 'In case of bogs the discussions about the nature of succession, e.g. is it a unidirectional autogenic process or a random complex of undirectional changes caused by a certain disturbance regime, which are frequently met in the literature, should be considered as artificial'.

In the above examples, it appeared useful to study vegetation succession in the context of ecosystem succession. In the present paper on mechanisms of vegetation succession, ecosystem succession could only receive additional attention, as this would require another review (see e.g. Gorham *et al.* 1979). But these examples are meant to emphasize that the study of ecosystem processes does enable at least as much understanding of vegetation succession as does the mechanistic approach. We quote from Odum (1983): 'In choosing the boundaries for an analysis of a system of interest, one may focus on the unit of interest by making all its influences outside forcing functions. However, this procedure is reductionistic and concentrates on details of a single unit and limits one's ability to understand the interplay of pathways to forcing functions. We sometimes say that one must model and simulate a system that is one size larger than the one of interest.'

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