Special Feature

Mechanisms and processes in vegetation dynamics: Introduction

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The study of vegetation change has provided one of the cornerstones of research throughout the history of vegetation science. During much of this time period, most studies focused on succession, defined as a more or less directional change in species composition at a site over time. The importance of succession as an ecological concept is reflected in the number of texts summarizing successional research (e.g. Clements 1916; Miles 1979; West, Shugart & Botkin 1981; Gray, Crawley & Edwards 1987; Burrows 1990; Glenn-Lewin, Peet & Veblen 1992). Recently, the focus of research has expanded beyond descriptive studies of successional patterns to a more mechanistically-oriented analysis of vegetation dynamics, a term referring to vegetation change without regard to directionality (e.g. Knapp 1974; Connell & Slatyer 1977; Miles, Schmidt & van der Maarel 1988; Pickett, Collins & Armesto 1987; Pickett & McDonnell 1989). This Special Feature on 'Patterns and mechanisms of vegetation dynamics' continues in this vain.

The papers in this volume were originally presented at the Symposium of the International Association for Vegetation Science held in Eger, Hungary, in 1991. This symposium was organized in four sessions, the second of which, 'Mechanisms directing and regulating community processes', may be seen as the 'core session' for this Special Feature. Indeed, this session is represented here with five lectures and poster contributions. However, we also included two lectures from session 3, 'Time and Space: Scale Dependence of Vegetation', and even seven from session 4: 'Vegetation dynamics in grasslands, Pioneer communities, and Forests. Generally, papers in the present volume were selected based on their direct application to the theme proper, especially papers that were attempting an experimental analysis of processes and mechanisms. Some good case studies of novel successional systems were also included.

Contributions to symposia are often heterogeneous; we have grouped the papers in this Special Features as those that deal more or less with vegetation dynamics at large, and those that focus on vegetation succession. Within each of these groups, the papers fall into two subcategories: analysis of patterns, and analysis of mechanisms.

Vegetation dynamics

Analysis of patterns

Patterns of vegetation change may occur at any spatial scale. From a hierarchical perspective, large-scale patterns are likely to change at slower rates than small-scale patterns. In the first paper in this series, *Collins, Glenn & Roberts*, echoing the comments of Shipley & Keddy (1987), suggest that the plant community continuum is a vague concept in need of refinement and analysis. *Collins et al.* propose an alternative, dynamic model for vegetation structure and dynamics, the hierarchical continuum concept, based on hierarchy theory and the core-satellite hypothesis (Hanski 1982). The model emphasizes the notion that abundance and distribution of species change over time, although rate of change may vary at different spatial scales. Data from North American tallgrass prairie show that species abundances in permanent plots were highly variable over time.

Support for the notion that species distributions change rapidly at small spatial scales is presented in four papers that describe, based on different methods and analyses, the highly dynamic and unpredictable nature of grassland vegetation. In the second paper, *Glenn & Collins* report that the number, size and composition of patches of vegetation in tallgrass prairie changed from year to year in the absence of disturbance. They found that experimental removal of a dominant bunchgrass increased species richness, but did not alter indices of patch structure.

Herben et al. use simple Markov models to predict vegetation change in small quadrats in mountain grassland in Bohemia. Actual changes differed markedly from predicted trajectories. In another paper, *Herben et al.* determined that species moved about spatially from year to year, and that the degree of spatial movement for many species was poorly related to life history strategy. Based on long-term studies in limestone grassland, *van der Maarel & Sykes* noted that the cumulative frequency of species among small quadrats in permanent plots increased strongly over time. Species were moving over time in such a way that within a few years most species could potentially have occurred in all the quadrats. Based on the similarity of species distributions, *van der Maarel & Sykes* question the validity of the niche concept, and they offer an alternative (descriptive) model, the carousel model to depict the small-scale dynamics of communities. It is interesting that this series of papers, based on several years of data in contiguous permanent plots from very different ecosystems, converged on the notion that the composition and structure of grassland vegetation is highly dynamic in space and time.

Analysis of mechanisms

A series of four papers deals more specifically with the causal mechanisms of vegetation dynamics. In the first paper, *Espigares & Peco* report that the germination behaviour of seeds of species in Mediterranean ecosystems can be arranged along a temperature gradient upon arrival of the first rains. Differences in germination response to moisture and temperature affect community structure from one year to the next by altering the competitive conditions that develop at the beginning of the growing season each autumn. *Ryser* assesses neighborhood effects on seedling establishment in grasslands. His results suggest that facilitation is necessary for the establishment of some species. Physical disturbance and pathogens were found to be more important for species recruitment than small gaps in the vegetation.

The relationships between productivity and diversity were experimentally examined by *Willems, Peet & Bik*. They showed that productivity doubled following fertilization, yet species diversity was reduced by less than 50 %. Neither production nor growth form were sufficient to explain patterns of diversity in these limestone grasslands. Rather, diversity was most closely related to structural heterogeneity of the vegetation. *Montalvo et al.* examined causes of diversity in grasslands along an elevation gradient in Spain. They report that plant-herbivore interactions are important for the maintenance of species diversity. They describe grazing and disturbance through ploughing in grasslands as mechanisms for maintaining and reducing diversity, respectively, whereby grazing also acts as compensatory mechanism on diversity restoration after reduction through disturbance.

As a whole, these studies emphasize the high degree of temporal dynamics in grassland vegetation. It is interesting to note that the composition of grassland vegetation was heterogeneous in space and time in the absence of disturbance. In contrast to predictions from disturbance theory (e.g. Pickett & White 1985), disturbances such as grazing and fertilizer application alter grassland community structure, and may actually lead to a decrease in the natural rate of change in these systems.

Vegetation succession

Analysis of patterns

The majority of successional studies in this Special Issue address patterns and mechanisms of some form of secondary succession. The one exception in this Special Feature is the contribution by *del Moral & Wood*. Based on 10 yr of permanent plot data on Mount St. Helens, Washington, the authors conclude that a mechanistic interpretation of succession is not yet appropriate. Rather, patterns of primary succession appear to be a function of local environmental conditions, landscape configuration, dispersal distances, and chance.

Wilmanns describes patterns during succession in vineyards, in which different types or 'agroforms' of plant communities develop in response to different agricultural treatments. In Mediterranean France, the native *Quercus pubescens* has been replaced by *Q. ilex*. Studies of seed germination behavior by *Bacilieri et al.* suggest, however, that vegetation change will continue and that *Q. ilex* will be replaced by other species.

In a permanent plot study of succession on nutrient poor soils, *Schmidt & Brübach* found that the spatial distribution of the conspicuous plants showed remarkable changes over time. Such dynamics correspond to the rapid changes noted in undisturbed grassland, lending further credence to the notion that plant succession does not lead to the development of stable, deterministic species associations.

Analysis of mechanisms

Studies by both *Leuschner* and *Rode* focused on processes associated with succession from heathland to oak-beech forest. Leuschner found that transmission of photosynthetically active radiation decreased during succession. Soil-nutrient concentrations either stayed the same or increased during succession. Soil nutrient quality was tied directly to leaf nutrient quality. In a complimentary study, Rode focuses on leaf nutrient dynamics along the heathland to oak-beech sere. Nutrient content in the leaves was low, as it was in the soil, however, leaf nutrient content was higher in trees than in shrubs on similar soils. Rode concludes that leaf turnover rates increase during succession because of the higher nutrient quality of leaves of late successional trees.

In Mediterranean shrublands, *de Lillis & Federici* quantified gas exchange, photosynthesis, and water potential in early and late successional species. In all cases, net photosynthesis peaked in early spring when leaf nitrogen contents were highest, but light availability was lower than later in the growing season. Thus, nitrogen, not light, controls rate of photosynthesis in this system. Pioneer herbs showed higher rates of photosynthesis after cutting than late successional trees and shrubs. Net photosynthesis of herbs after fire was the same as in climax vegetation. Thus, carbon gain appears to be related to successional stage more so than life form, per se.

Finally, *Agnew, Wilson & Sykes* describe a particular mechanism in a regeneration succession, which they call vegetation switch, i.e. a positive feedback between vegetation and environment in the form of the creation of dead-log microsites by fallen trees which permit seedlings to develop.

Perspective

The papers in this special issue cover a broad range of ecosystems and temporal gradients. Although patterns of change in response to disturbance have frequently been reported (e.g. Pickett & White 1985), the high degree of small-scale spatial dynamics noted in many of these studies offer an interesting challenge to some long-held concepts in vegetation science. Scale increasingly becomes an issue when general models, such as the intermediate disturbance hypothesis (Connell 1978) or initial floristic composition (Egler 1954), are applied to studies of vegetation dynamics. The surprisingly rapid small-scale changes, both spatial and temporal, noted in many studies suggest that it is time to rethink the basic notions about vegetation-environment relationships, community stability, and niche relationships. Hierarchical models of local dynamics constrained by larger-scale processes, and the concept of nodal succession (Yarranton & Morrison 1974) may provide a useful insight into the processes and mechanisms of vegetation dynamics.

Finally, the various papers make clear that we have not reached the state where we can understand vegetation dynamics by describing mechanisms. In many cases we can at best describe and quantify processes, which later have to be understood by finding underlying mechanisms.

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