Permanent quadrats: An interface for theory and practice

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Abstract

Certain neglected concepts for studying vegetation dynamics are reviewed, particularly the incorporating of temporal and spatial heterogeneity; examples are given. Few studies have been of sufficient length to allow partition of the various types of temporal fluctuation influencing vegetation composition. Studies of changes in spatial pattern with time are similarly few. The formation of patches of vegetation and their change with time (nucleation) may determine the entire spatio-temporal structure of the ecosystem, e.g. vegetation groves in arid zones. Simultaneous study of temporal and spatial heterogeneity is required. Future studies will necessitate higher standards of evidence than previously accepted. The practice of equating a few spatially separated sites having different periods of time since a specific disturbance should not be accepted in the absence of evidence that their potential vegetation dynamics has been similar during those periods.

Permanent quadrats with an appropriate experimental design are needed to overcome these problems. The requirements to be met by such a design are discussed, including the role of location, contiguity, perturbation or synthetic experimentation and demographic measurement.

Introduction

Vegetation dynamics may be defined as the change with time of a vector of some suitable measurements of plant species performance. The study of vegetation dynamics is, and has been for some years in a state of flux. Many workers have studied succession, i.e. unidirectional change in vegetation, rather than vegetation dynamics. Numerous reviews of succession have been written in the last decade (Miles, 1979). Some have attempted to present a new conceptual framework: Odum's (1969) statement of trends in ecosystem properties has perhaps been the most influential. Others (McCormick, 1968; Dury & Nisbet, 1973; Colinvaux, 1973; Connell & Slatyer, 1977) have criticized the traditional Clementsian concept of succession towards a single climatic climax. MacIntosh (1980) has, in an extensive scholarly review of the literature, taken these authors to task for attacking an outmoded concept which few recent workers took seriously.

Students of succession often make the convenient assumption that temporal and spatial variability can be regarded as random noise and ignored. To study any form of vegetation dynamics, we need to be able to partition variability into its components whether they are successional trends, climatic fluctuations, cyclic changes, the persistent effect of episodic events or random noise. If not, how can we be sure that succession rather than a climatic fluctuation is responsible for the changes we observe?

I shall examine some of the research problems of vegetation dynamics and present a case that pro-
gress is only likely if it is based on the use of permanent quadrats preferably with an imaginative experimental design.

There are three prerequisites for successful research: relevant concepts, suitable standards of evidence and appropriate research methods. There have been several reviews of methods (Slatyer, 1976, Austin, 1977; van der Maarel & Werger, 1978; MacIntosh, 1980; Noble & Slatyer, 1980), and I shall not review them there. It is necessary however to review the current concepts and standards of evidence used in the study of vegetation dynamics before discussing the appropriate use of permanent quadrats.

Relevant concepts

With the exception of Egler's (1954) ideas on 'initial floristic composition' and their extension by Connell & Slatyer (1977) (see also Noble & Slatyer, 1980; Noble in press), few positive suggestions for a new conceptual framework have been advanced (though see Odum, 1969).

Connell & Slatyer (1977) attempted to provide a more general framework for succession studies than the rigid Clementsian one. They recognized three possible types of vegetation sequences during succession.

1. Facilitation or 'relay floristics' (classical Clementsian model)
2. Tolerance
3. Inhibition.

Both (2) and (3) are forms of the 'initial floristic composition' idea of Egler (1954); (2) where species may tolerate each other's presence and composition is determined by the earliest arrivals and (3) where species established earlier may inhibit the establishment of other species arriving later. The ideas have been developed further by Noble & Slatyer (1980) who suggest that certain vital attributes of individual species may determine succession after disturbance by fire. The use of these vital attributes for analysis of fire-induced succession in Australian conditions seems to have considerable potential, but if all aspects of vegetation dynamics are considered then the list of possible vital attributes becomes infinite for all practical purposes.

Two major concepts are often ignored but must be considered in any study of vegetation dynamics:

1. the multitude of dynamic processes which may be operating, and
2. the degree of spatial heterogeneity which these processes will produce at any given moment.

Temporal heterogeneity

The variability through time of the vegetation composition of specific sites has not been well-studied. Individual species populations have been examined in a few cases (Tamm, 1948, 1956, 1972; Sarukhan & Harper, 1973; Harper & White, 1974; Williams, 1970; Williams & Roe, 1975). Such population dynamics studies as reviewed by Harper (1977) are concerned with the age-class cohorts of the population rather than total numbers. Not all species are amenable to this type of study, and so far results are not sufficient to differentiate different types of temporal effects on the survival of particular age-classes. The detailed study required and limited applicability to certain growth forms means that the full complement of species in a community are unlikely to be examined in this way.

Studies using only total population estimates have shown that temporal 'fluctuations' can be relatively long-lasting in herbaceous communities. Albertson & Tomanek (1965) have shown the marked fluctuations which can occur in a thirty-year period in different mixed prairie communities in Kansas (Fig. 1a). Watt (1957, 1960, 1962, 1971) has presented some of the most detailed observations recording different types of temporal behaviour. Some examples are shown in Figure 1b, c. Van den Bergh (1979) has recently drawn attention to the periodic population eruptions and declines that can be observed in some of the few long-term studies of temperate grassland (e.g. Fig. 1b, c). Williams (1969, 1970) has examined similar changes in Australian semi-arid grasslands (see also Austin et al., this symposium). However the problem of distinguishing long-term fluctuations from trends or long-term cyclic regeneration remains. The problem of having sufficient observations through time to partition the components is well seen in the figure (Fig. 1d) which shows variations in two species in one of the Park grass plots at Rothamsted for 125 yr. The period 1919 to 1948 contains many more observations than prior to 1919 and what may appear to be long-term trends in the earlier period...