Methods in Plant Ecology

EDITED BY
P. D. MOORE & S. B. CHAPMAN

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Preface

The last century has seen the gestation, birth and rapid evolution of the discipline of ecology. The very word has moved from obscurity into limelight, perhaps even into cliché, in the development of the English language over the past few decades. Concern for the environment and the recognition that man is not merely a factor influencing his surroundings, but also suffers the consequences of environmental mismanagement, has led to changing attitudes on the part of scientists and society. Ecology is no longer merely quantitative natural history, it is becoming an increasingly rigorous discipline as more specific (and more general) questions are being asked of it by concerned members of society.

The demands made upon ecologists as a consequence of problems ranging from pesticide misuse to acid rain, from nuclear winter projections to carbon dioxide accumulation, have placed the ecologist in an increasingly difficult dilemma. He now has the technical capacity to construct elegant analogue models of ecological systems, but often he lacks the raw data to feed into them. Some 10 years ago, when the first edition of this book was being prepared, the situation was quite different. Practical field and laboratory methods in ecology were developing rapidly, influenced by such concerted international efforts as the International Biological Programme, but the limitation on ecological advance lay in the area of data logging and analysis. The rapid development of computer science and, in particular, the current universal availability of quite sophisticated microcomputers, has broken this particular log jam and has left us in a position where more extensive and more accurate field and laboratory data are the major requirements for further advancement of the science. It is an awareness of this need which has stimulated the preparation of a second edition of this book.

Inevitably, the development of new ideas and methods during the past 10 years has not been evenly distributed over the entire field of plant ecology. Certain areas, such as production ecology and chemical analysis of ecological materials, had seen a rapid development in the 1970s under the patronage of IBP. In certain subjects, such as soil study, the chapters contained in the first edition have profoundly influenced more recent work. The subsequent developments in these areas have been significant, but perhaps not as dramatic and spectacular as, say, that of vegetation analysis, which has benefited specifically from the computer revolution, so its coverage is consequently expanded here. The new, numerical power in the hands of the ecologists has also led us to introduce a chapter on data handling, for so much of one's experimental design in field and laboratory depends upon an early appreciation of the analytical processes available and the careful choice of the most appropriate methods for specific problems.

One area of ecology which has emerged and flourished over the past 10 years is the study of plant populations. It has clearly become necessary to include in this book a section relating to the practical aspects of such study.

Another development area is that of physiological ecology. There has been a very healthy and productive movement of ideas across the barrier which once existed between laboratory-based plant physiology and field-based plant ecology, which has resulted in benefits to both subjects. Perhaps it is no longer even possible to regard them as separate. The consequence, as far as this book is concerned, is an expansion of the space devoted to this area of ecology; it now occupies two chapters (covering, respectively, nutrient and water relations) rather than the former one.

Another barrier which is becoming increasingly blurred is that between plant and animal ecology. A new section illustrating the opportunities presented in this twilight zone covers faecal analysis and exclosure studies as an aid to observing the consequences of plant/animal interactions. Perhaps, in future editions, we shall see further expansion of this theme into such areas as the chemistry and significance of secondary plant products, and pollination biology.

The study of environmental history has developed along two new paths. First, it has become a more integrated discipline, using evidence from a wide range of biological and chemical sources and, second, it has moved beyond the stage of regional vegetation and climatic reconstruction to one of local historical development of sites, studied by means of small sedimentary basins and soils. This aspect, it is felt, makes the subject more valuable to general ecologists who are interested in local and geologically recent events in the field locations of their studies.

All of the authors have been under pressure to confine their contributions to the minimum of space in order to keep down costs and thus make this compendium available to a greater number of ecologists. In many of the areas covered there have been important, useful and easily available publications produced recently which it would be wasteful to reprint or paraphrase here. So, wherever such methodological accounts are readily available, authors have been encouraged to refer to them rather than reproduce them. This book remains, however, a practical manual rather than a reference list, and important methods will be found here, discussed in detail and containing hints, warnings, advice and encouragement to those who would otherwise become lost in the current morass of published material.

We have aimed the book at a fairly broad spectrum of ecologists, from the specialist to the generalist, from the professional research worker to the undergraduate project student, from the field conservationist to the laboratory technician. It is hoped that specialists may find within the chapter dealing with their specific field some new ideas, information and guidance. It is also hoped that such specialists will look beyond their own field towards the problems encountered by others and how they have been tackled. In this way the greatest possible benefit will be gained from the book, and perhaps it may contribute to an even more rapid development of methods in plant ecology over the next decade.

Many people have contributed to the compilation of this volume and have helped authors with individual chapters. We extend to them all our thanks. Specific thanks must be given to Bob Campbell of Blackwell Scientific Publications Ltd, Oxford, for his boundless energy, enthusiasm and optimism, and also to Penny Baker for her laborious and careful preparation of the text for publication.

P.D. Moore
S.B. Chapman

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1 Production ecology and nutrient budgets

S.B. CHAPMAN

1 Introduction

An ecologist can find himself involved in the study of biological production and nutrient budgets for one of a number of reasons. He may wish to use the estimates of primary production for a comparison of sites within a particular type of ecosystem, or to use them as the basis for comparing very different types of ecosystem (Westlake, 1973). The study of primary production, nutrient budgets and energy flow are important in attempting to understand the function of natural communities, but it should be remembered that they represent only one particular approach to the problem and that other viewpoints in ecology may be just as important in helping to obtain a more complete analysis and understanding of ecosystems and ecological processes.

One particularly important feature of production ecology is the way that it provides a strong and unifying link between a number of different aspects of the subject. The distinctions between types of ecologists working in this field tend to break down, and an individual engaged in a production study may often wonder whether he is a botanist, a zoologist or even a pedologist.

This chapter is divided into three main sections; the first provides an introduction to some of the more important definitions and concepts that relate to production ecology, the second describes some of the methods that are available for the estimation of primary production and associated processes, and the third deals with methods that are relevant to the study of nutrient budgets.

2 The ecosystem

2.1 The ecosystem concept

In a paper presented in 1935, Sir Arthur Tansley dealt with a number of terminological and conceptual problems that beset ecologists of the time. He rejected such contemporary terms as 'complex organisms' and 'biotic community', and introduced the term ECOSYSTEM in the following terms:

> 'Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system.'

The ecosystem has since been defined by many authors as a functional unit that includes the biotic components (organisms including man) and the abiotic components (environmental physico-chemical) of a specified area (Fig. 1.1). While it is generally recognized that the ecosystem includes interrelationships between biotic and abiotic factors it is often forgotten that the definition includes 'a specified area'. Tansley stated, 'ecosystems are of the most various kinds and sizes. They form one category of the multitudinous

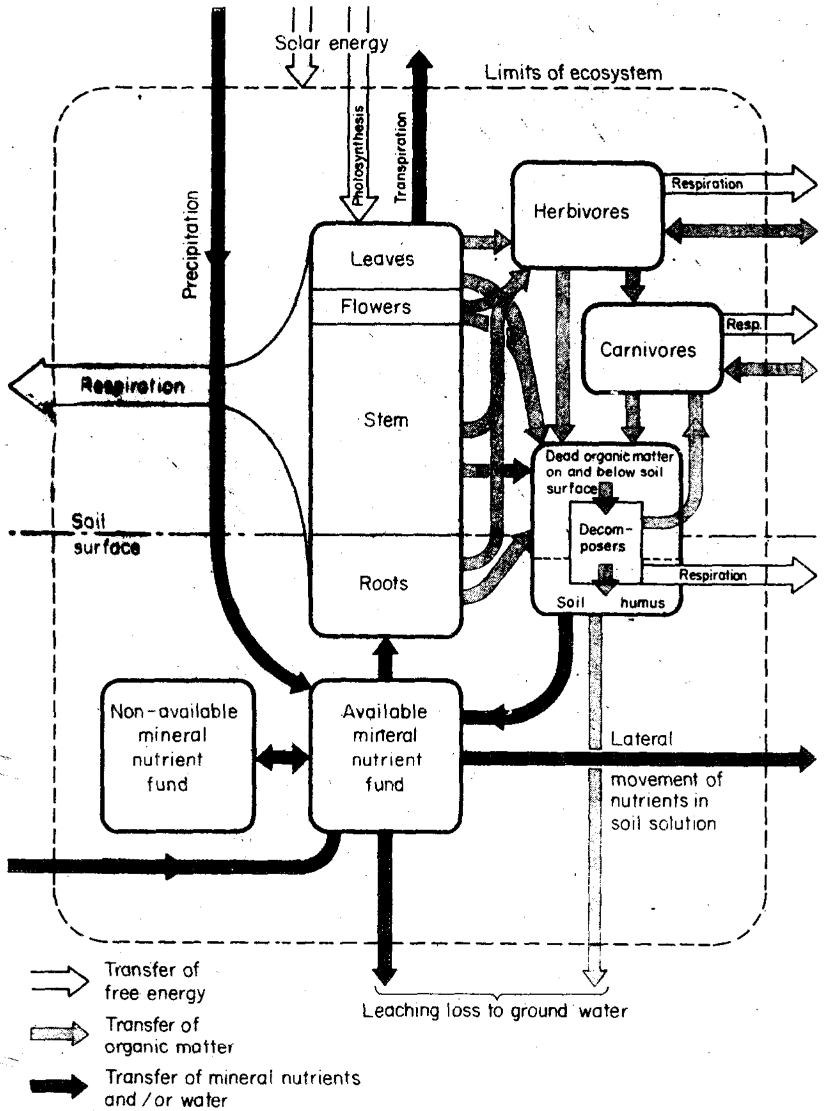


Figure 1.1 General representative diagram of an ecosystem.

physical systems of the universe, which range from the universe as a whole down to the atom'. Unfortunately, many people now use the term ecosystem in a general way without defining the limits of the system to which they refer. Whenever the term ecosystem is used in reference to an ecological study the physical and biological limits of the system should be made clear. It should be remembered that ecosystems are inter-related functional units and that any separation is an artificial division for the purposes of simplification and investigation. The historical development of the ecosystem concept has been described in detail by Major (1969).

2.2 Ecosystem modelling

In recent years most ecologists have become familiar with the terms 'ecosystem modelling' and 'systems analysis' even if they are not sure of their full meaning or implications. A model is no more than an abstraction that serves to describe or simulate all or part of some process or situation. Models can take a number of forms: mathematical models, word models, box models and flow diagrams. It is inevitable that modelling, the systems approach, and the ability of computers to handle large amounts of complex data, have a great deal to offer ecology in the future. It should be emphasized that systems analysis is not the only way of studying an ecosystem, but that a particularly important feature of the approach is the way in which it emphasizes the need to define and to quantify the basic components of the system.

A detailed account of systems analysis and modelling cannot be attempted here but Smith (1970), Jeffers (1972, 1978), Reichle *et al.* (1973), de Wit & Goudriaan (1974), Hall & Day (1977), Clark & Roswall (1981) and Smith (1982) are references that will be of interest to those requiring an introduction to the subject.

3 Production, decomposition and accumulation

3.1 Definitions, concepts and units

For the successful measurement of production, and the associated processes of decomposition and accumulation, it is necessary for a number of basic terms to be defined and for the relationships between them to be clearly understood.

3.1.1 Production

It would be most satisfactory if gross primary production was the fundamental estimate upon which other estimates of production could be based or against which comparisons could be made. If this were the case then a number of problems such as root production would possibly seem less intractable. Unfortunately, the measurement of gross production involves the use of sophisticated and expensive apparatus that does not lend itself readily to the degree of replication generally required in ecological studies, and reasonable proximity to a laboratory is often an important requirement of such techniques. A good case can be made that, as far as some components of the ecosystem are concerned, it is only net primary production that is important. In the case of some herbivores it may only be one particular fraction of the net primary production that is of interest. In a great deal of the ecological literature primary production is taken to be synonymous with net production. It is not intended to deal with methods for the estimation of gross primary production but workers requiring information upon this subject should refer to a specialized text such as that by Coombs & Hall (1982).

PRODUCTION is the weight or biomass of organic matter assimilated by an organism or community over a given period of time.

PRIMARY PRODUCTION is the production of organic matter by photosynthesis and SECONDARY PRODUCTION the subsequent conversion of that organic matter by heterotrophic organisms. Primary production can be expressed in two ways:

(a) GROSS PRIMARY PRODUCTION, the total amount of organic matter produced (including that lost in respiration) over a given period of time.

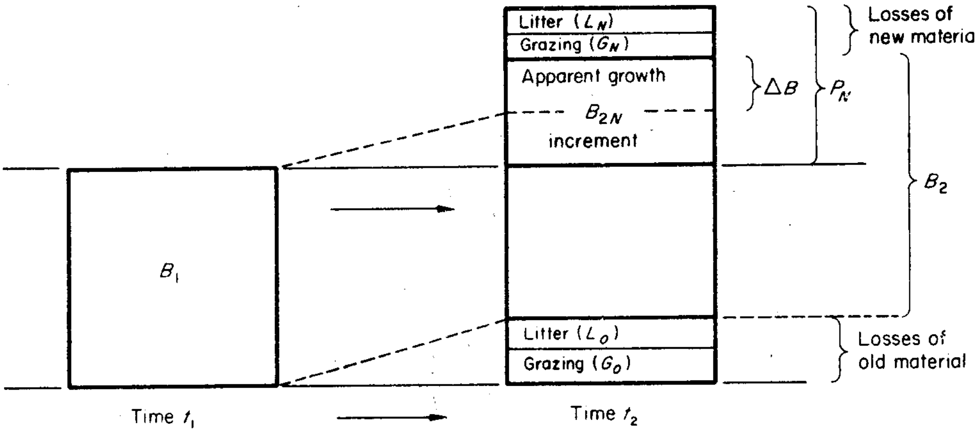
(b) NET PRIMARY PRODUCTION, the amount of organic matter incorporated by a plant or an area of vegetation (gross primary production minus the loss due to respiration) over a given period of time.

It is net primary production that is generally the concern of the plant ecologist and it is often further qualified by reference to some particular part of the plant or vegetation (aerial, root or seed production, etc.).

BIOMASS or STANDING CROP is the weight of organic matter per unit area present in some particular component of the ecosystem at a particular instant of time. Biomass is generally expressed in terms of dry weight and on occasion may be given in terms of ash free dry weight (see Section 4.4.1).

The relationship between biomass, time and production, has been given in a standard form in the handbooks produced for the International Biological Programme (Newbould, 1967; Miller & Hughes, 1968).

B_1 = Biomass of a plant community at time t_1.
B_2 = Biomass of a plant community at time $t_2 (= t_1 + \Delta t)$.
ΔB = Change in biomass during the period $t_1 - t_2$.
L = Plant losses by death and shedding during $t_1 - t_2$.
G = Plant losses by grazing etc. during $t_1 - t_2$.



$$P_N = B_{2N} + L_N + G_N$$

$$\text{or } P_N = \Delta B + (L_O + L_N) + (G_O + G_N) = \Delta B + L + G$$

Figure 1.2 The relationship between production, apparent growth increment and change in biomass (based on Newbould, 1967).

P_N = Net production by the community during $t_1 - t_2$.

In terms of these symbols:

$$P_N = \Delta B + L + G,$$

so that if ΔB, L and G can be estimated satisfactorily P_N can be calculated. The use of this relationship requires estimates of biomass to be made at least twice, and generally with at least a year between the determinations.

There is an alternative approach (Fig. 1.2; Newbould, 1967): if the components of production can be recognized at the end of the growing season it should be possible to obtain an estimate of production from a single visit to the site.

$$P_N = P_{\text{flowers}} + P_{\text{green}} + P_{\text{wood}} + P_{\text{roots}}$$

By the end of the growing season some of the current year's production may well have been lost by grazing, or by death and loss as litter, so that the apparent growth increment will be an underestimate of production.

The addition of the total grazing and litter losses to the apparent growth increment will result in overestimation of the net production as part of the losses will have been from previous years' production.

3.1.2 Decomposition

DECOMPOSITION is the process by which organic matter is physically broken down and converted to simpler chemical substances,