MODERN ECOLOGY: BASIC AND APPLIED ASPECTS

Edited by
G. ESSER
and
D. OVERDIECK

ELSEVIER

MODERN ECOLOGY

Basic and Applied Aspects

This page intentionally left blank

MODERN ECOLOGY

Basic and Applied Aspects

Edited by

G. Esser
International Institute for Applied Systems Analysis (IIASA),
Schlossplatz 1, A-2361 Laxenburg, Austria

and

D. Overdieck
Institut für Ökologie der Technischen Universität,
Köningin-Luise-Strasse 22, D-1000 Berlin 33, Germany

Elsevier
Amsterdam – London – New York – Tokyo 1991

ELSEVIER SCIENCE PUBLISHERS B.V.
Molenwerf 1
P.O. Box 211, 1000 AE Amsterdam, The Netherlands

Distributors for the United States and Canada:

ELSEVIER SCIENCE PUBLISHING COMPANY INC.
655, Avenue of the Americas
New York, NY 10010, U.S.A.

ISBN 0-444-89183-8

This book is printed on acid-free paper.

Printed in The Netherlands

Preface

This book is dedicated by the editors and authors to the university teacher and outstanding researcher in ecology, **Helmut Lieth**, on the occasion of his 65th birthday and retirement.

Helmut Heinrich Friedrich Lieth was born in 1925 and grew up in Rhenania, Western Germany. He started his ecologically oriented education in the field of agriculture, receiving his apprenticeship at the agricultural school in Unterbrösch (Bergischer Landkreis), and completing his school education there in 1947. From 1947 to 1949 he studied philosophy and natural sciences at the "Philosophical and Theological College" in Bamberg (Bavaria), followed by two years of undergraduate studies at the Botany Department of the University of Cologne.

He continued graduate studies at the same university where he obtained his Ph.D. in 1953. The title of his thesis was "Untersuchungen über die Bodenstruktur und andere vom Tritt abhängender Faktoren in den Rasengesellschaften des Rheinisch-Bergischen Kreises" (Investigations into the effects of footstep frequency on the soil structure and other factors in the turf communities of Rheinisch–Bergisch county).

Early in his university career he served as a scientific assistant in the Botany Departments of the University of Cologne and the Agricultural University of Stuttgart–Hohenheim. In 1960, he was granted the title of lecturer (Privatdozent) by the University of Stuttgart–Hohenheim and was also appointed lecturer of ecology at the Technical University of Stuttgart.

During those years Helmut Lieth broadened not only his scientific interests but also his very practical personal activities enthusiatically to a global scale, starting from 1960 to 1961 with a National Research Fellowship at the Botany Department of the Université de Montréal, Canada. Back in Germany, he was appointed a senior lecturer (Diätendozent) at the Agricultural University of Stuttgart–Hohenheim in 1964, and soon became assistant professor (Außerplanmäßiger Professor) at the same institution. During those years he served as guest lecturer at the Universidad Central de Venezuela, and the Universidad del Tolima at Ibaque, Colombia. After a stay in Hawaii during 1967, he found his second home at the University of North Carolina, Chapel Hill (U.S.A.), where he stayed until 1977.

In the U.S.A., he initiated numerous studies in general ecology, concentrating on plant ecology and vegetation science, always taking into account the interactions and relationships between organisms on the ecosystem level, and looking for formulae and mathematical models in order to find general ecological rules which allow us to quantify the organismic response on varying environmental parameters. Among the authors of this book are several former students of Helmut Lieth from that period of very fruitful work.

As a guest researcher (1973-1974) at the Jülich Nuclear Research Center (Kernforschungsanlage Jülich, today Forschungszentrum Jülich), Federal Republic of Germany, he maintained his connections to the European scientific community. After teaching at the University of Bochum (F.R. Germany) as a guest lecturer in 1977, he was appointed the first professor of ecology at the newly founded University of Osnabrück in Northwest Germany. There, he was not only the first professor of ecology, but one of the first scientists in any branch of biology. He is a pioneer to whom the University of Osnabrück owes a new building for the Department of Biology. His vigorous efforts also led to the planning and foundation of a new Botanical Garden at Osnabrück, which is developing into a unique attraction both for scientists and for visitors searching for recreation.

Simultaneously, he carried out a great number of research projects at his home university, some of which will be continued beyond his retirement. At times, these projects have employed up to 30 students and junior scientists.

During his last years before retirement he also started a new program of study, Applied Systems Research (Angewandte Systemforschung), in the Mathematics Department of the University of Osnabrück in 1989.

In spite of all his duties in Chapel Hill and Osnabrück, he maintained a considerable number of international activities, serving as a guest professor at the Waseda University, Tokyo, and as a participant in scientific research projects in countries all over the world, including Iceland, Canada, Venezuela, Colombia, Brazil, Hawaii, India, Japan, USSR, U.S.A., Mozambique, and the United Arab Emirates. Many of the activities pertained to tropical ecology and phenology. During the last years of his university career Helmut Lieth gave much energy to a "greenification" project with salt tolerant plants, which was started in Abu Dhabi (United Arab Emirates) in 1980, and which after an interruption has been taken up again on a larger scale in 1989.

Helmut Lieth's international engagement earned for him the Biometeorology Research Foundation Award in 1982; the silver medal for his work in Agrometeorology during the 3rd Indian Agrometeorological Congress in Cochin in 1987; and the award for outstanding achievement of the International Society of Biometeorology during its 11th International Congress at Purdue University (U.S.A.) in 1988.

From 1979 to 1984 he was the elected president of the International Society of Biometeorology, from 1985 to 1988 the president of the International Society of Tropical Ecology, and in 1989 the vice-president of the "Gesellschaft für Ökologie". Since 1986 he has served as treasurer of the International Society of Ecology (INTECOL).

More than a hundred scientific publications prove that Helmut Lieth's work covered a wide range of ecological topics. Especially well known are "Die Stoffproduktion der Pflanzendecke" (1962), "Produktivitätskarte der Erde" (1964), "Klimadiagramm–Weltatlas" (1967-1969) which he developed together with Heinrich Walter, "Modeling the Primary Productivity of the World" (1972), "Primary Productivity of the Biosphere" (1974), and "Patterns of Primary Productivity" (1978). He is editor–in–chief of the book series "Tasks for Vegetation Science" (1979), the "Handbook of Vegetation Science" (1980), the "International Journal of Biometeorology" (1987) and "Vegetatio" (1989). He has been on the editorial board of several other scientific journals, including "Radiation and Environmental Biophysics" and "Journal of Biogeography".

The authors and the editors wish that Helmut Lieth should continue to contribute to ecological research for still many years.

We wish to thank all who contributed to the production of this book, which was typeset in the project–group of the first editor at the University Osnabrück using LaTeX.

We cordially thank Dipl. Biol. Margot Brosch for her organization of the work and for typesetting major parts of the book. Our thanks are also due to Dipl. Biols. Martina Lohmann, Barbara Meyer, and Alfred Stille for typesetting, Andreas Schürmann for reproducing the graphs, and Teresa Enders for English language editing.

Martina Jöstl–Segalla and Carolyn Fuhrmann helped to make final corrections, typesetting of tables, and Cynthia Ramirez assisted the first editor at IIASA.

We would like to give special thanks to all who have finacially supported the work, namely the University Osnabrück and the Biology/Chemistry Department, the Universitätsgesellschaft Osnabrück e.V., the Institute for Ecology of the Technical University of Berlin (West), and the Zentralverband des Deutschen Steinkohlenbergbaus.

Last, but not least, we wish to thank Elsevier Science Publishers for their kindness in having accepted a manuscript, although sizeable, contains a comprehensive amount of information we feel will help understand how Ecology might be organized in the next decade.

May 15, 1991

Gerd Esser
Laxenburg (Austria)

Dieter Overdieck
Berlin (Germany)

Editorial advisors

This page intentionally left blank

List of contributors

BETHKE–BEILFUSS, D.
Fachbereich Biologie/Chemie
der Universität
Barbarastrasse 11
D–4500 Osnabrück
Germany

BEYER, L.
Institut für Pflanzenernährung
und Bodenkunde
der Universität
Olshausenstrasse 40
D–2300 Kiel
Germany

BILBAO, B.
Centro de Ecologia
Instituto Venezolano
de Investigaciones Cientificas
Apartado 21827
Caracas 1020–A
Venezuela

BLUME, H.–P.
Institut für Pflanzenernährung
und Bodenkunde
der Universität
Olshausenstrasse 40
D–2300 Kiel
Germany

BOGENRIEDER, A.
Biologisches Institut II
der Universität
Schänzlestrasse 1
D–7800 Freiburg/Br.
Germany

DE BOK, C.
Department of Plant Ecology
and Evolutionary Biology
Utrecht University
Lange Nieuwstraat 106
NL–3512 PN Utrecht
The Netherlands

BOX, E. O.
Department of Geography
University of Georgia
Room 204, GGS Building
Athens, Georgia 30602
U.S.A.

BREYMEYER, A. I.
Institute of Geography
and Spatial Organisation
Polish Academy of Sciences
Krakowskie Przedmieście 30
PL–00 927 Warszawa
Poland

CABRERA CANO, E.
Smithsonian Environmental
Research Center
P.O. Box 28
Edgewater, MD 21037-0028
U.S.A.

CERNUSCA, A.
Institut für Botanik
der Universität
Sternwartestrasse 15
A-6020 Innsbruck
Austria

CHEN, T.
Abteilung Pflanzenökologie
FB Biologie/Chemie
der Universität
Achterstrasse 2
D-2800 Bremen 33
Germany

DIERSCHKE, H.
Lehrstuhl für Geobotanik
Systematisch-Geobotanisches
Institut
der Universität
Untere Karspüle 2
D-3400 Göttingen
Germany

EBER, W.
Fachbereich Biologie
der Universität
Ammerländer Heerstrasse 114-118
Postfach 2503
D-2900 Oldenburg
Germany

ENGELS, M.
Systematisch-Geobotanisches
Institut
der Universität
Untere Karspüle 2
D-3400 Göttingen
Germany

ERNST, W.
Department of Ecology
and Ecotoxicology
Faculty of Biology
Vrije Universiteit
De Boelelaan 1087
NL-1081 HV Amsterdam
The Netherlands

ESSER, G.
International Institute for
Applied Systems Analysis (IIASA)
Schlossplatz 1
A-2361 Laxenburg
Austria

FANGMEIER, A.
Institut für Pflanzenökologie
Heinrich-Buff-Ring 38
D-6300 Giessen
Germany

FORSTREUTER, M.
Institut für Ökologie
der Technischen Universität
Königin-Luise-Strasse 22
D-1000 Berlin 33
Germany

FRIEDRICH, F.
Fachbereich 11
Technische Fachhochschule
Königin-Luise-Strasse 22
D-1000 Berlin 33
Germany

FUNKE, W.
Abteilung Ökologie und
Morphologie der Tiere
Universität Ulm
Oberer Eselsberg M 25
Postfach 4066
D-7900 Ulm
Germany

GRACE, J.
Institute of Ecology
and Resource Management
University of Edinburgh
Darwin Building
Kings Buildings, Mayfield Road
Edinburgh EH9 3JU
United Kingdom

HALL, D. O.
Division of Biosphere Sciences
King's College London
University of London
Campden Hill Road
London W8 7AH
United Kingdom

HELLMUTH, U.
Systematisch-Geobotanisches
Institut
der Universität
Untere Karspüle 2
D-3400 Göttingen
Germany

HURKA, H.
Fachbereich Biologie/Chemie
der Universität
Barbarastrasse 11
D-4500 Osnabrück
Germany

JAKUCS, P.
Ecological Institute
L. Kossuth University
H-4010 Debrecen
Hungary

JANZEN, D.
Pflanzensoziologie und Ökologie
der Universität GHS
Postfach 103764
D-4300 Essen 1
Germany

JOCHIMSEN, M.
Pflanzensoziologie und Ökologie
der Universität GHS
Postfach 103764
D-4300 Essen 1
Germany

KAPPEN, L.
Lehrstuhl für Ökophysiologie
Botanisches Institut
der Universität
Olshausenstrasse 40
D-2300 Kiel 1
Germany

KLOETZLI, F.
Geobotanisches Institut
ETH
Zürichbergstrasse 38
CH-8044 Zürich
Switzerland

KÖHLER, W.
Biometrie und Populationsgenetik
der Universität
Ludwigstrasse 27
D-6300 Giessen
Germany

KREEB, K. H.
Abteilung Pflanzenökologie
FB Biologie/Chemie
der Universität
Achterstrasse 2
D-2800 Bremen 33
Germany

KUTSCH, W. L.
Botanisches Institut
der Universität
Olshausenstrasse 40
D-2300 Kiel 1
Germany

KUTTLER, W.
FB 9 – Institut für Ökologie
Abt. Landschaftsökologie
Universität–GHS
Postfach 103764
D–4300 Essen 1
Germany

LANDOLT, E.
Geobotanisches Institut
ETH
Zürichbergstrasse 38
CH–8044 Zürich
Switzerland

LARSON, D. W.
Department of Botany
University of Guelph
Guelph
Ontario
Canada N1G 2W1

LESER, H.
Forschungsgruppe Physiogeographie
und Landschaftsökologie
Geographisches Institut
der Universität
Klingelbergstrasse 16
CH–4056 Basel
Switzerland

MARKERT, B.
AG Angewandte Systemwiss.
der Universität
Artilleriestrasse 34
D–4500 Osnabrück
Germany

MEDINA, E.
Centro de Ecologia
Instituto Venezolano
de Investigaciones Cientificas
Apartado 21827
Caracas 1020–A
Venezuela

MEENTEMEYER, V.
Department of Geography
University of Georgia
Room 204, GGS Building
Athens, Georgia 30602
U.S.A.

NAU, W.
Biometrie und Populationsgenetik
der Universität
Ludwigstrasse 27
D–6300 Giessen
Germany

NEUFFER, B.
Fachbereich Biologie/Chemie
der Universität
Barbarastrasse 11
D–4500 Osnabrück
Germany

NUMATA, M.
Laboratory of Ecology
Faculty of Science
Chiba University
74–13 Bentencho
Chiba 260
Japan

ORANJE, B.
Department of Plant Ecology
and Evolutionary Biology
Utrecht University
Lange Nieuwstraat 106
NL–3512 PN Utrecht
The Netherlands

OVERDIECK, D.
Institut für Ökologie
der Technischen Universität
Königin–Luise–Strasse 22
D–1000 Berlin 33
Germany

PONTAILLER, J.-Y.
Laboratoire d'écologie végétale
URA CNRS N° 121
Bâtiment 362, Université Paris Sud
91405 Orsay cedex
France

READER, R. J.
Department of Botany
University of Guelph
Guelph
Ontario
Canada N1G 2W1

RODD, H.
Forschungsgruppe Physiogeographie
und Landschaftsökologie
Geographisches Institut
der Universität
Klingelbergstrasse 16
CH-4056 Basel
Switzerland

ROTH-HOLZAPFEL, M.
Abteilung Ökologie und
Morphologie der Tiere
Universität Ulm
Oberer Eselsberg M 25
Postfach 4066
D-7900 Ulm
Germany

RUTHERFORD, M. C.
National Botanical Institute
c/o University of Cape Town
Cape Town
South Africa

RUTHSATZ, B.
Fachbereich III, Geobotanik
der Universität
Postfach 3825
D-5500 Trier
Germany

RYSZKOWSKI, L.
Department of Agrobiology
and Forestry
Polish Academy of Sciences
Świerczewskiego 19
60-809 Poznań
Poland

SAUGIER, B.
Laboratoire d'écologie végétale
URA CNRS N° 121
Bâtiment 362, Université Paris Sud
91405 Orsay cedex
France

SCHLESER, G. H.
Abteilung Biophysikalische Chemie
Institut für Chemie
Forschungszentrum Jülich GmbH
Postfach 1913
D-5170 Jülich
Germany

SCHMIDT, W.
Lehrstuhl für Geobotanik
Systematisch-Geobotanisches
Institut
der Universität
Untere Karspüle 2
D-3400 Göttingen
Germany

SCURLOCK, J. M. O.
Division of Biosphere Sciences
King's College London
University of London
Campden Hill Road
London W8 7AH
United Kingdom

STEUBING, L.
Institut für Pflanzenökologie
Heinrich-Buff-Ring 38
D-6300 Giessen
Germany

TAPPEINER, U.
Institut für Botanik
der Universität
Sternwartestrasse 15
A-6020 Innsbruck
Austria

TAYLOR, K. C.
Department of Botany
University of Guelph
Guelph
Ontario
Canada N1G 2W1

WERGER, M. J. A.
Department of Plant Ecology
and Evolutionary Biology
Utrecht University
Lange Nieuwstraat 106
NL-3512 PN Utrecht
The Netherlands

WESTHEIDE, W.
Fachbereich Biologie/Chemie
der Universität
Barbarastrasse 11
D-4500 Osnabrück
Germany

WHIGHAM, D. F.
Smithsonian Environmental
Research Center
P.O. Box 28
Edgewater, MD 21037-0028
U.S.A.

WICKLAND, D. E.
Ecosystem Dynamics and
Biogeochemical Processes Branch
Earth Science and
Application Division
NASA
600 Independence Ave., S. W.
Washington, D. C. 20546
U.S.A.

WILMANNS, O.
Biologisches Institut II
der Universität
Schänzlestrasse 1
D-7800 Freiburg/Br.
Germany

Contents

VIII Urban and landscape ecology 805

This page intentionally left blank

Part I

Morphology, stand structure, and competition

This page intentionally left blank

Chapter 1

Morphology in modern ecological research

W. EBER

1.1 Introduction

Both morphology and anatomy of plants belong to the basic subdisciplines of botany with a long tradition. Their subject is the structure of plants on the level of organs (external structure) as well as on the level of tissues (internal structure). Though botanists, especially morphologists (ESAU 1977, FOSTER and GIFFORD 1974, FAHN 1982), have always been aware of the intimate relation between structure and function, one scarcely finds examples of an appropriate treatment of both aspects on the same subject. Plant morphologists have nearly exclusively been concerned with the description and phylogenetic interpretation of form and structure, whereas plant ecology has mainly dealt with the analysis of environmental factors and the physiological response of plants.

During the past decades at least the external structure of plants has found increased interest in two special fields of ecology: on the one hand, in the study of vegetation pattern and on the other hand, in the analysis of plant populations. Nevertheless, the study of the internal structure is still a neglected field of ecological research, though improved histological techniques and the availability of image analysis devices have made anatomical studies more comfortable and attractive.

The contribution presented here is based on experiences in the study of primary production gained during our participation in the German IBP-Project and and subsequent studies in population ecology with increasing emphasis on plant architecture. The advantage or even necessity of a more intensive understanding of morphological aspects in modern plant ecology is emphasized.

1.2 Models of plant construction

The body of vascular plants can be regarded as constructed of only three principal plant organs: root, stem and leaf. The whole variety of plant form is due to a varied development or modification of size, form, proportions and arrangement of these organs. The special performance of each organ is determined by phylogenetical processes, its specific function or requirements of a specific environment. In addition to this classic phylogenetic model of the vascular plant, RITTERBUSCH (1977) has presented an "ecological model" which is based on the specific functions of each external structure such as storage, assimilation, absorption of water and mineral nutrients, elevation of leaves and flowers, regeneration (rejuvenalisation) of shoots and dispersion of propagules. Obviously this model has a greater ecological relevance and is of special advantage where resource allocation is investigated.

Another model has been developed by population biologists and is widely used in plant demographic studies. According to this model (HARPER 1977, WHITE 1979) the plant is regarded as a population of modular units which may remain attached to each other or may be separated in clonal growth. All parts derived from one zygote are termed genetic individual or genet. Genets may extend over a large area and may be fragmented into numerous parts of different size. Modules and phytons may be regarded as the fundamental modular units of construction into which the shoot system can be completely divided. The module in its original meaning (WHITE 1979, HALLE et al. 1978) is defined as the product of activity of one apical meristem terminated by either flowering or parenchymatization. Modules have proved to be especially valuable in the study of plant architecture and life history of clonal plants. Unfortunately, this term has also been used without any need in a more general sense synonymously with modular unit (HARPER and BELL 1979). Phytons are segments of the shoot consisting of a node with its leaf, axillary bud and internode. As the life history of individual phytons cannot be separated from that of the complete shoot, this unit has been used only in studies of plant construction. *Equisetum hyemale*, an evergreen horsetail, the shoots of which die internode by internode, is one of the rare examples where the internode or phyton is the appropriate unit for demographic studies (LEHMANN and EBER, in press). Axillary buds ("bud bank") and leaves, however, are of major importance in demographic studies (BAZZAZ and HARPER 1977, HUISKES and HARPER 1979, KOTANEN and JEFFERIES 1987, EBER and VEENHUIS, in press).

The ramet represents another type of modular unit, as it only includes parts of the shoot system and is more complex. HARPER (1977) defines the ramet as a shoot with its own root system which may follow an independent existence if severed from the parent system. According to this definition those subterranean parts which are not absolutely necessary for the independent existence of aerial shoots are not included. Ramets are regarded as the effective units of clonal growth that are readily counted in the field (HARPER 1977). In ecological research aerial shoots or ramets are predominantly used as "individual plant". As each ramet can represent a whole genet or be a physiologically dependent part of a genet fragment or an integrate genet, a precise characterization of the ramets in question is necessary. Where ramets occur aggregated, they may be supposed to belong to the same genet. The size of the area occupied by individual genets or genet fragments and the density of their ramets, which make up the sociability according to BRAUN-BLANQUET (1964), are often species characteristics within a certain range. Nevertheless, there are some species where no ramets can be recognized as they merely develop prostrate and often subterranean shoots. In species such as *Oxalis acetosella* the leaf is the only counting unit available (EBER 1982).

As in the majority of perennial plants the subterranean component predominates, it is obvious that this component must not be neglected, though its investigation cannot be achieved without destructive sampling.

1.3 Diversity of individuals within populations

Plant populations do not consist of uniform members; on the contrary, the population structure is characterized by individuals which differ in age, size and developmental stage, and all these subdivisions respond to environmental factors in a specific way. Though both size and developmental stage are age dependent to a certain degree, close relations between these three parameters are rarely found under field conditions. In most species age cannot be determined at all or, as in trees or perennial herbs like *Limonium vulgare* (EBER 1987), only after destructive harvesting; nevertheless, it is of lesser ecological significance than size and developmental state. Without any doubt the investigation of each of them, of age and size classes as of developmental states has its own merits depending on the aim of the studies, and detailed population analysis can be regarded as a highly sensitive method to detect environmental changes. Population biologists have developed more or less detailed systems of ontogenetic states occuring during the life cycle of plants. PELTON (1953) distinguished the following stages which have been widely used by other authors: seed, seedling, juvenile, reproductive and senescent stage. Some authors (GATSUK et al. 1980, BALLEGAARD and WARNCKE 1985) have developed finer subdivisions of the juvenile (also termed vegetative or prereproductive) and senescent (postreproductive) stage. Enormous differences in size can even be found in mature stands of homogeneous age composition due to density dependent competition. This heterogeneity can be characterized by a scale of vitality classes ranging from dominant to suppressed individuals (RABOTNOV 1978). With increasing plant density the transition of the bell-shaped frequency curve of low–density stands to the L–shaped curve of high–density stands can be observed (KOYAMA and KIRA 1964). Due to density–dependent mortality a close relationship can be found between plant density and mean plant biomass (WHITE 1980).

The diversity within a population has to be taken into account where mean values for individual plants are calculated and is absolutely necessary in the study of population dynamics or succession since life cycle events such as birth and death rates are state and class specific. Populations of clonal plants may be rather homogeneous in size compared with the majority of annual plants and in extreme environments one ontogenetic state, the mature vegetative plant, may be represented nearly exclusively. This was the case in our first investigations on primary production of the herb layer of a forest (EBER 1971), where juvenile as well as flowering plants were rare during the period of intense studies. But in a subsequent year with high irradiation the proportion of flowering shoots increased from 5 up to 15 % (EBER 1986) and it is evident that the transition rates from one ontogenetic state to another have to be taken into account. On the contrary in populations of *Calla palustris* size differences are extreme and mean values are without any information, because there is a high annual recruitment of new members originating from branches of different size, brood shoots and seeds due to rapid fragmentation of the rhizome system (EBER 1983a). Furthermore, population structure changes from pioneer to mature stands and along environmental gradients (EBER, in preparation).

1.4 Application of morphological aspects in the study of primary production and related processes

Consideration of morphological aspects has proved to be of great advantage in many fields of ecology and has already been applied in most of them for some time. From our own experience, however, we think that especially in the study of primary production some progress will be possible by the application of methods based on a thorough morphological analysis of plant organization. These methods have been developed and tested by population biologists and may be adopted for the study of primary production as it is obvious that production biology and population biology are closely related fields of science. Both deal with the same process as is evident from their fundamental equations:

1. Production equation
   Net primary production = annual change in dry matter + losses to detritus + grazed material (LARCHER 1983)

2. Population equation
   $N_{t+1} = N_0 + \text{births} - \text{deaths}$ (HARPER 1977)

Immigrants and emigrants as well as import and export of biomass may be neglected for the majority of plants and ecosystems.

While production ecologists investigate changes in weight, population biologists focus on changes in number. But differences have diminished during the past decades, and in the study of resource allocation, for example, population biologists, too, are occupied with estimating biomass and production.

The most serious drawback in the study of primary production of vascular plants is that, in contrast to population biology, the majority of methods are indirect and mostly based on destructive harvesting. In the harvested quadrat method (NEWBOULD 1967) the vegetation is harvested at intervals from quadrats which are thought to be comparable, whereas in the individual plant method (NEWBOULD 1967) biomass contribution of each species is estimated separately as the product of individual plant weight and density data from countings on permanent plots. Reliability of the quadrat method depends very much on the homogeneity of the vegetation. The individual plant method, however, has no limitations of this kind. As it is more time-consuming and numerous individuals have to be sampled it is restricted to species-poor vegetation types and common species. In both methods primary production is usually calculated as the difference between maximum and minimum biomass. Two major sources of underestimation must be kept in mind. First, if species are not treated separately there may arise serious errors if the periods of their individual maxima differ significantly, and secondly, there may be considerable losses due to mortality between sampling dates, which are extremely high in species with a high turnover of shoots or leaves (MATTHEWS and WESTLAKE 1969). Many attempts have been made to develop adequate methods for the estimation of mortality (e.g. SMALLEY 1959, WIEGERT and EVANS 1964, MILNER and HUGHES 1968). These methods have been compared and modified by several authors (LOMNICKI et al. 1968, LINTHURST and REIMOLD 1978, WALLENTINUS 1973, GROENENDIJK 1984). One of those factors supposed to influence the results of any single method is the morphology of species (LOMNICKI et al. 1968), and this corresponds to the intentions of this paper.

The fundamental problem in this context is the heterogeneity of the samples. Considerable differences in age, activity and fate of the material make it impossible to get reliable results on increment and losses which are the basic factors of primary production. Therefore it is obvious that the accuracy of estimations and the extent of information increases with the degree of appropriate subdivisions. Until now the harvested material has predominantly been separated into above-ground and below-ground material which might be adequate for practical reasons to facilitate harvesting and to distinguish between autotrophic and heterotrophic parts. Unfortunately, many investigations are confined to the aerial parts alone which must be regarded as problematic considering the manifold translocation processes between subterranean and aerial organs. When the contributions of individual species are separated, quadrat samples often do not contain enough material to allow exact estimations of peak biomass of each species. Rare examples of a more detailed separation into shoots, leaves, rhizomes and roots are found. These conventional modes of subdivision are unspecific and do not provide subsamples suitable for the estimation of increments and losses. Therefore a more promising approach is suggested here which is based on the modular construction of plants and the life history of modular units. A characteristic feature of this approach is the combination of the non–destructive methods of population biology with the destructive harvesting of production biology. These ideas are not completely new; substantial elements can already be found in the studies of CALLAGHAN (1976), GRABHERR et al. (1978) and JACKSON et al. (1986).

1.5 The analysis of plant architecture

At the beginning of each investigation a careful investigation of the architecture of each individual species should be carried out as the basis for the design of an appropriate programme for the study of the production process.

The study of the organization of whole genets or genet fragments of herbaceous plants demands a procedure very similar to that one used in the study of primary production. The biomass is harvested as completely as possible, but in addition attention must be paid to keep the connecting rhizomes intact. The period between the end of the season and early spring, when the annual growth is finished and the tender annual organs as leaves and fine roots are no longer present, has proved to be the most suitable time. Ramets should be marked and their original position in the field be fixed in a scetch before excavation. In the laboratory plants have to be cleaned thoroughly and attached dead roots and leaves have to be removed.

After this procedure a great variety of characters become visible which were obtected before: scars of leaves, branches, inflorescences and roots, regular changes in length and width of internodes and a specific pattern of branching and flowering indicating rhythmic growth. Many species with a high proportion of subterranean organs have a highly jointed rhizome system the analysis of which yields information on

1. annual increments
2. age of the genet or number of generations still present
3. life span of individual organs or structures
4. birth rates and mortality of modular units
5. spatial pattern of modular units
6. resource allocation

In species with long–lived organs the history of genets or genet fragments can be reconstructed with some accuracy as demonstrated for entire genets of *Limonium*

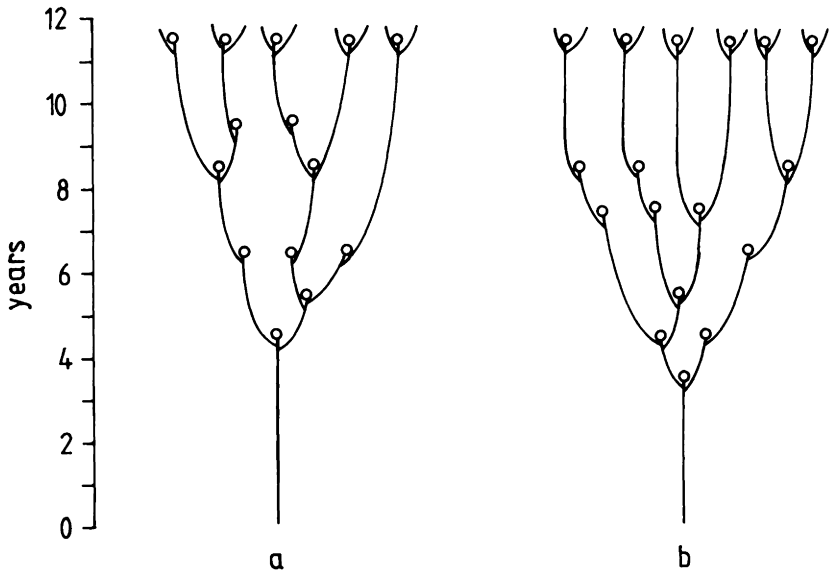

Figure 1.1: Schematic diagram of the rhizome organization of 12 years old individuals of *Limonium vulgare*. Circles indicate inflorescences or their remainders (from EBER and VEENHUIS, in print)

vulgare (Fig. 1.1) and a genet fragment of *Luzula luzuloides* (Fig. 1.2), which are subjects of detailed studies.

The principles of construction are species–specific and genetically fixed, but the specific form of the shoot system of each individual genet is subject to modifications by the influence of environmental factors. Size, birth rates, mortality of structures, number of inflorescences and flowers and the direction of growth are influenced by the climatic conditions of the season and soil environment.

In studies on primary production it is important to distinguish between the current year's increments and older parts which are subject to gradual destruction. If this separation has been carried out carefully, it should be possible to get reliable results on the subterranean biomass as well. Methods based on this principle have rarely been applied so far (IWAKI and MIDORIKAWA 1968, PERSSON 1975).

The estimation of the aerial primary production can also be done by separate weight estimations of current year's and previous years' increments (Fig. 1.3) and the application of life–table and other demographic analyses to shoot and leaf birth and death. This has been shown to be feasible and to permit ecological interpretations at a more sophisticated level than is possible from classical growth analysis (BAZZAZ and HARPER 1977). At intervals the lengths of stems and leaves

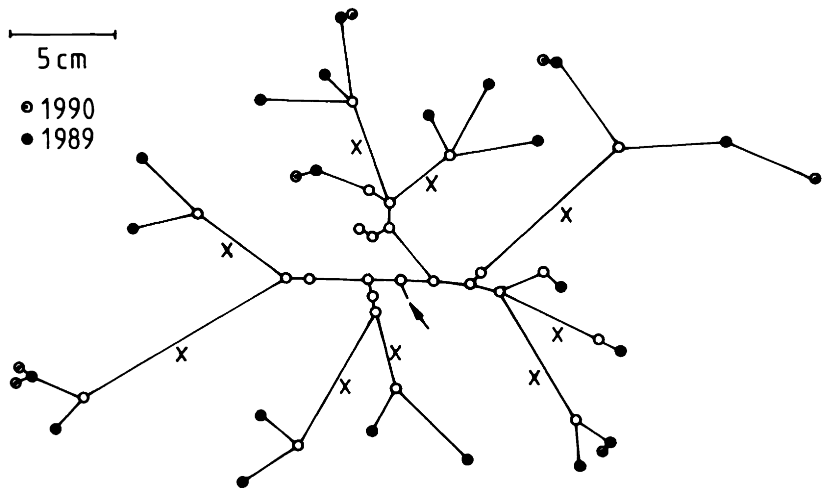

Figure 1.2: Schematic diagram of the rhizome system of a clone fragment of *Luzula luzuloides* with the growth of seven years. Circles indicate ramets, the arrow the oldest parts of the system. Note the enormous increments of the year 1988 (×).

and, if possible, leaf area are to be measured for each developmental state and leaf cohort (leaves of the same age) separately. For the conversion to weight units length: weight and area: weight regressions have to be established. Thus it is possible to estimate increments between sampling dates from weight differences of organs already present before and the difference between parts produced and lost within the sampling interval.

It is obvious that this method has some limitations as it is very time-consuming and some morphological provisions must be made. It is of special value in species with clonal growth, moderate mortality, density and sufficient size of modules and leaves. In our intended long-term studies on the population biology and primary production of salt marsh angiosperms and plant communities (EBER in preparation) it has already proved to be applicable to *Halimione portulacoides* (FISCHER and EBER in press), *Aster tripolium* (STRUTZ-FISCHER and EBER, in preparation), *Limonium vulgare* (EBER and VEENHUIS in press, EBER 1987), *Plantago maritima* and *Spartina anglica* (EBER, unpublished), but we suppose there will be some problems with *Puccinellia maritima* and *Festuca rubra*. Nevertheless, these restrictions in mind this method will be of advantage where a high accuracy of estimations is wanted, and as a variety of rough estimates is already available for many ecosystems and vegetation types, there seems to be no need of further ones. On the contrary, there is need of more precise information which allows broader ecological interpretations and applications for various purposes.

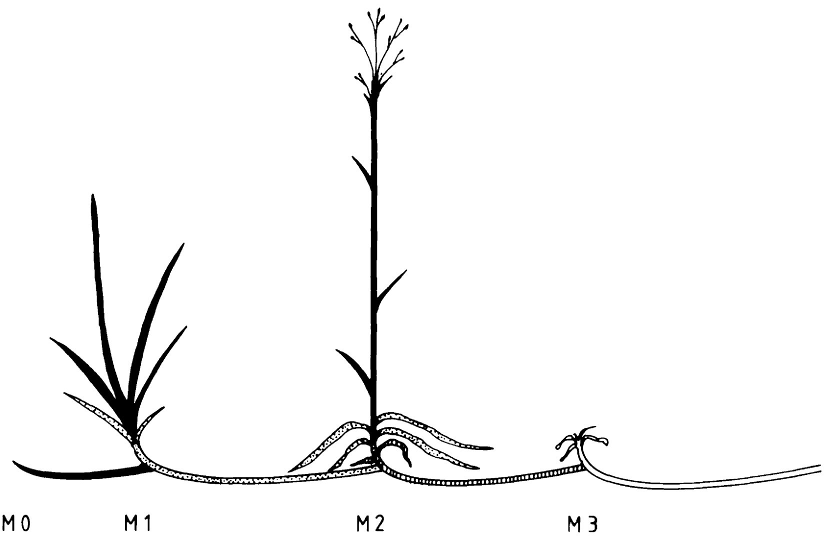

Figure 1.3: Schematic diagram of the module system of *Luzula luzuloides*. M0–M3 represent modules of subsequent years. Black = increment of the current year, dotted = increment of the previous year.

1.6 Resource allocation

The detailed compartmentation of plant material recommended above will be of special value in the study of resource allocation and, based on it, mineral cycling and energy flow. The analysis of resource allocation has found increasing interest among population biologists (e.g. HARPER and OGDEN 1970, OGDEN 1974, ANDEL and VERA 1977), and particularly reproductive allocation ("reproductive effort") has become one of the fundamental subjects of population biology and has been intensively discussed under the aspect of evolutionary strategies (GADGIL and SOLBRIG 1972). It is difficult to make a clear delimitation between reproductive and non-reproductive structures and results differ depending on whether seeds, fruits or entire inflorescences are regarded as sexual reproductive organs. Comparableness is only guaranteed if comparable structures are treated. As reproductive effort is usually expressed as percentage of net production, the accuracy of production estimates is a crucial point. The majority of investigations exclusively deal with dry matter allocation though, as stressed by HARPER and OGDEN (1970) and ABRAHAMSON and GADGIL (1973) a particular mineral nutrient may be likewise the limiting resource and important in the evolution of strategies. There are only few examples for a more comprehensive treatment of resource types (e.g. EBER 1983b, OHLSON and MALMER 1990, FITTER and SETTERS 1988, BENNER and

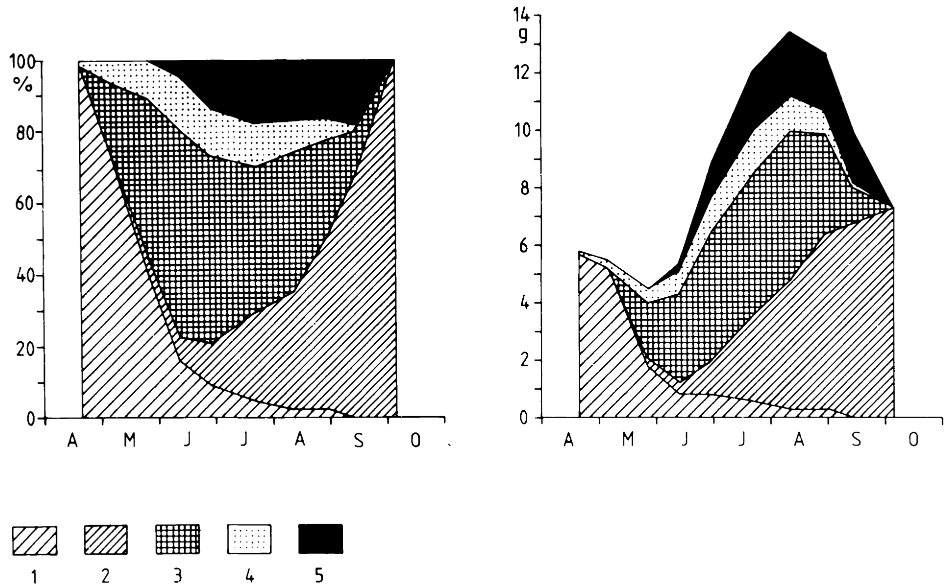

Figure 1.4: Dry matter allocation patterns in *Calla palustris*:
a) proportional representation (EBER 1983a, modified)
b) absolute values (EBER, in preparation).
1 rhizome of the previous year, 2 rhizome of the current year, 3 leaves, 4 roots, 5 inflorescences.

BAZZAZ 1988).

The annual course of the allocation process may be presented by allocation pattern diagrams. Proportionate representations (Fig. 1.4a), which are much easier to establish, serve best the purposes of population biology. Allocation pattern diagrams with absolute values (Fig. 1.4b), however, provide additional information on translocation processes and resource budgets, but are influenced by size differences within populations (OHLSON and MALMER 1990, EBER, in preparation). Allocation patterns can be estimated for each developmental state separately as well as for the whole population. The allocation to sexual reproduction and clonal growth have proved to be competitive activities. Individuals of *Geum reptans*, the flowers of which had been removed, developed longer stolons (BRZOSKA 1983) than the control, and in *Calla palustris* populations the production of extremely long rhizomes was accompanied by poorer flowering (EBER 1983a). As has been shown in field investigations (EBER 1983b) and experiments (HARPER and OGDEN 1970, OGDEN 1974, ANDEL and VERA 1977) resource allocation patterns are species–specific, but vary in a high degree with nutrient supply and according to the resource form (dry matter, energy, mineral nutrients) under consideration.

1.7 The growth form, clonal growth and lateral spread

Many herbaceous perennials are able to develop aerial or subterranean plagiotropic shoots (stolons or rhizomes) which serve lateral spread as well as the multiplication of ramets. The term "clonal growth" is now widely used instead of "vegetative reproduction", which has been rejected by HARPER (1977). According to his opinion reproduction should be confined to sexual reproduction only. Among species with clonal growth two categories can be distinguished according to the length of connections between individual ramets: one with modular units closely packed together and another one with widely–spaced modular units. Both categories can be found between species as well as within species, in the latter case as a plastic response to differences in the environment of the population. These different growth forms have been described as strategies by LOVETT DOUST (1981): the "guerilla" strategy of plants which infiltrate the surrounding vegetation with long stolons, and the "phalanx" strategy of plants which maximize their interspecific contacts. The interpretation of the function implied in these terms, which seem to have been coined by CLEGG (HUTCHINGS and SLADE 1988) is doubtful. In general the conservative "phalanx" type as a consequence of its low mobility must be able to exploit its area intensively and to withstand competitors, whereas the more opportunistic "guerilla" type with its ability of rapid and extensive stolon elongation is capable of colonizing adjacent areas.

The analogy between the pattern of growth of a stoloniferous or rhizomatous plant and the search path of a foraging animal has recently been emphasized, and, in consequence, the term "foraging" has been applied for plants to describe the activities of acquiring essential resources (SLADE and HUTCHINGS 1987b). It has been assumed that plants growing in a patchy environment branching probability should be higher in better patches and internode length should decrease with patch quality, but only the first assumption was consistently supported by a literature review (SUTHERLAND and STILLMAN 1988).

As both types may be developed within the same population, it is necessary to examine the conditions that favour the one or the other. The experiments of SLADE and HUTCHINGS et al. (1987, 1987a, 1987b) demonstrate that in *Glechoma hederacea* low light intensity and low soil nutrient availability produced extensive foraging, whereas a greater supply of nutrients resulted in a more intensive foraging and consolidation of site occupation. Changes in the water–table also influence growth form. In an experiment (EBER, unpublished) stolon elongation in *Ranunculus repens* increased rapidly when the water level was raised. As CALLAGHAN (1988) states in *Lycopodium annotinum*, the "guerilla" form may have been selected to avoid competition rather than invade and efficiently exploit nutrient–rich pockets where intense competition is likely to occur or develop. The mobility of *Potentilla anserina* has also been interpreted as a mechanism of escape from superior competitors (ERIKSON 1986). Effective vegetative spread is also an important