TERRESTRIAL PLANT ECOLOGY

Michael G. Barbour

Jack H. Burk

Wanna D. Pitts

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Michael G. Barbour
University of California, Davis

Jack H. Burk
California State University, Fullerton

Wanna D. Pitts
San Jose State University

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PREFACE

Our purpose in writing this book has been to condense the literature pertaining to the ecology of wild plants into a digestible survey for the undergraduate student. Most readers will be in a one quarter or one semester course at the upper division level and will have had previous courses in basic biology, botany, and possibly in general ecology or environmental science.

This is not a detailed, thorough, unbiased reference work, nor does it take us to a new level of understanding. Rather, it is a basic synthesis which we hope will be a useful starting point for instructors and students. The present science of plant ecology is so broad as to encourage specialization and to narrow one's perspective of the entire field. We believe it is essential to maintain a broad outlook, and to examine the important aspects of all the specialized branches of plant ecology, if we are to grasp the essentials of the interactions between plants and their environment.

This book is divided into four parts. The first part (Chapters 1 and 2) introduces the broad aspects of plant ecology and gives an historical overview of the development of the science. Part II (Chapters 3–6) discusses autecology, the responses of populations to their environment, and Part III (Chapters 7–12) focuses on synecology, that is, community attributes. Part IV (Chapters 13–19) describes the role of five environmental factors (light, temperature, fire, soil, and water) at both the autecological and the synecological levels. The concluding chapter, Chapter 19, describes the major vegetation types of North America, attempting to show how the many factors and responses covered individually in earlier sections interact to produce the vegetation of this continent. Except for this last chapter, which has its own list of references, the references cited are listed in one section at the end of the book. We hope these references offer a good starting point for the reader who wishes to go further with some topic of interest. Most chapters conclude with a relatively detailed summary.

We believe that the study of plant ecology may provide lessons that take us beyond the conventional, narrow limits of "science." It is possible that our social and psychological evolution has been influenced by vegetation. Natural settings have generated negative feelings in western (Judeo-Christian) societies, as well described by Roderick Nash:*

*Nash, R. 1973. *Wilderness and the American Mind.* Yale University Press.

. . . appreciation of the wilderness must be seen as recent, revolutionary, and incomplete. . . . Ambivalence, a blend of attraction and repulsion, is still the most accurate way to characterize the present feeling toward wilderness. . . . Wilderness has risen far on the scale of man's priorities. But the depth and intensity of previous antipathy suggests that it still has a long way to go.

The poet-anthropologist Loren Eisely reminds us how important our development in natural, wild vegetation will continue to be to us despite these negative feelings. "Man was born and took shape among earth's leafy shadows," and now he is to embark upon a new and difficult journey:*

> At the climactic moment of his journey into space he has met himself at the doorway of the stars. And the looming shadow before him has pointed backward into the tangled gloom of a forest from which it has been his purpose to escape. Man has crossed, in his history, two worlds. He must now enter another and forgotten one, but with the knowledge gained on the pathway to the moon. He must learn that, whatever his powers as a magician, he lies under the spell of a greater and a green enchantment which, try as he will, he can never avoid, however far he travels. The spell has been laid on him since the beginning of time—the spell of the natural world from which he sprang.

Many persons, some anonymous, have read all or part of the manuscript, providing valuable insights and corrections and helping maintain the intended focus of the book. We thank these reviewers, who include: Jerry M. Baskin, Gary L. Cunningham, Andrew M. Greller, H. Thomas Harvey, Gordon L. Huntington, Subodh K. Jain, Robert P. McIntosh, Jack Major, Bruce M. Pavlik, Robert W. Pearcy, Otto T. Solbrig, Robin Smith, James P. Syvertsen, Irwin A. Ungar, John L. Vankat, and Lynn D. Whittig. Final decisions concerning approach, presentation, and content were our own and we take full responsibility for any oversights or inaccuracies contained herein.

Several other individuals have contributed long hours in manuscript preparation and have tolerated and understood the sometimes intolerant authors. Special thanks go to Heather Stout, who worked many long hours organizing the Literature Cited, securing permissions, and preparing the index. We also thank Patricia Burk, Maggie Hummer, Jerry Pitts, and the many ecology students who "tried out" sections of this book as a text in courses during the past two years. We thank you for your help and patience.

M.G.B., J.H.B., W.D.P.

*Eisely, L. 1970. *The Invisible Pyramid.* Scribners.

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PART I

BACKGROUND AND BASIC CONCEPTS

The origins of informal plant ecology go back hundreds of years to plant geographers, taxonomists, and naturalists who were people of energy and insight, such as Humboldt, De Candolle, and Darwin. In contrast, the science of ecology has had a very brief, intensive history which began less than a century ago. In that brief period, certain energetic men and women have had such a profound effect on the developing science that many current research projects and viewpoints are simply extensions of their work.

In this part, we will examine some of that history and some of those personalities, and we will present a common language to use in our study of plant ecology. There are many approaches to plant ecology, but each one attempts to answer the same basic question: how do plants cope with their environment? Some of the approaches we will discuss are paleoecology, phytosociology, community dynamics, systems ecology, and autecology.

CHAPTER 1

INTRODUCTION

Plant ecologists try to discover an underlying order to vegetation. They do this at finer and finer levels for the same reasons that biologists, chemists, and physicists pursue their worlds to the level of DNA, hydrogen bonds, and subatomic particles: there seems to be a human need to know the complete story, to explain the past, to predict the future What threads link plants to each other and to their environment? How flexible are these threads, and how intermeshed? How do plants "solve" the problems of dispersal, germination in a suitable site, competition, and the acquisition of energy and nutrients? How can they withstand unfavorable periods of fire, flood, or storm?

What can plants tell us by their presence, vigor, or abundance about the past, present, and future course of their habitat? Can plants be used as a scientific tool to analyze the intricacies of the environment or to test hypotheses about evolution?

What can plants tell us about our management hopes for the land? Once a forest is cut, what will replace it, how long will the process take, and how can we most efficiently manipulate this process? Once domestic livestock graze at a given density for a given time, what will the vegetation look like and how many animals will it then be able to support? Once topsoil is removed by strip mining in semiarid regions, what plants should be introduced to stabilize the remodeled landscape? Once brushfields have been sprayed, burned, and replanted as grasslands, what will happen to watershed quality, soil nutrient levels, and the rate of siltation behind nearby dams? What is the residence time of herbicides in soils and are there side effects on nontargeted organisms? How many backpackers can use an alpine trail without altering adjacent vegetation? If fire or flood is a natural catastrophe which must recur with a certain frequency to maintain particular vegetation types, how can we incorporate such regular disasters into state and federal park management plans?

All of these questions, and more, are being investigated by plant ecologists. Some researchers are more interested in generating basic information that has to do with the description of vegetation or the biology of component species. Others are more interested in applying that basic information to management problems. Applied plant ecologists may be called range managers, foresters, or agronomists, but they are all plant ecologists and they all share the same pleasure in discovering the subtle ways in which plants are adapted to their environment. Their objective is very close to a formal definition of **ecology**: the study of organisms in relation to their natural environment.

ECOLOGY, ENVIRONMENT, AND VEGETATION

The word ecology was coined little more than 100 years ago by the German zoologist Ernst Haeckel. He spelled the word "oekologie," but ecologists soon dropped the first o, to the annoyance and confusion of some purists. The word comes from the Greek roots *oikos*, home, and *logos*, the study of. Thus, oekologie translates loosely as: the study of organisms in their home, their environment.

Environment* is the summation of all **biotic** (living) and **abiotic** (nonliving) factors which surround and potentially influence an organism. Examples of biotic factors include competition, mutualism, allelopathy, and other interactions between organisms, which are described in Chapters 5 and 6. Abiotic factors include all chemical and physical aspects of the environment which influence a plant's growth and distribution.

The environment can be divided into two parts: the macroenvironment and the microenvironment. The **macroenvironment** is the prevailing, regional environment and the **microenvironment** is the environment close enough to an object to be influenced by it (Figure 1-1). The microenvironment may be quite different from the macroenvironment. For example, the microenvironment beneath a forest canopy is different from the macroenvironment above it in such traits as humidity, wind speed, and light intensity; the microenvironment beneath a rock in desert soil may be cooler and moister than other parts of the macroenvironment; the microenvironment just 1 mm above a leaf surface may differ in wind speed, humidity, and temperature from the macroenvironment 10 mm away. Each organ or part of a plant is exposed to a different microenvironment, as shown in Figure 1-2. Obviously, the microenvironment is what a plant responds to, and so the microenvironment will be emphasized in this book.

Plant ecology is concerned not only with individual plants and plant species, but also with vegetation. **Vegetation** consists of all the

*Environment can be synonymous with habitat. A habitat is homogeneous; that is, it cannot be broken up into distinctly different subunits. Some (Whittaker et al. 1973) restrict habitat to mean the environment around an individual organism or species, and they use the term biotope to mean the environment around a community. We will not adopt this distinction, however.

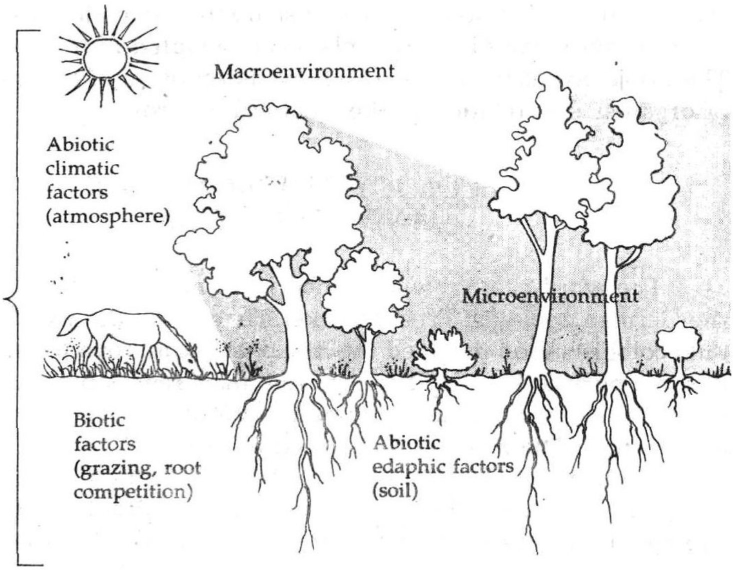

Figure 1–1. Components of the environment.

plant species in a region (the flora) and it is concerned with the pattern of how all those species are spatially or temporally distributed. If the region is large, its vegetation will consist of several prominent plant communities. Each vegetation type is characterized by the **life form*** of its dominant plants (the largest, most abundant, characteristic plants). Examples of life forms include annual herbs, broadleaf evergreen trees, drought-deciduous shrubs, plants with bulbs or rhizomes, needleleaf evergreen trees, perennial bunchgrass, and dwarf shrubs (Figure 1–3). Vegetation is also characterized by the architecture of its canopy layers, as shown in Figure 8–9. Different forest types have one, two, three, or four tree canopy layers.

Architecture and life form both contribute to the **physiognomy** (outer appearance) of vegetation, and each vegetation type has its own characteristic physiognomy. A vegetation type which extends over a

*Life form may include any or all of the following, depending on the context: (a) the size, life span, and woodiness of a taxon, for example, herb, annual, perennial, herbaceous perennial, woody perennial, shrub, tree, or vine; (b) the degree of independence of a taxon, for example green and rooted to the ground, parasitic, saprophytic, or epiphytic; (c) the morphology of a taxon, for example stem succulent, leaf succulent, rosette form, spinescent, or pubescent; (d) the leaf traits of a taxon, for example large, small, sclerophyllous, evergreen, winter-deciduous, drought-deciduous, needleleaf, or broadleaf; (e) the location of perennating buds, as defined by Raunkiaer (1934); and (f) **phenology**, the timing of life cycle events in relation to environmental cues.

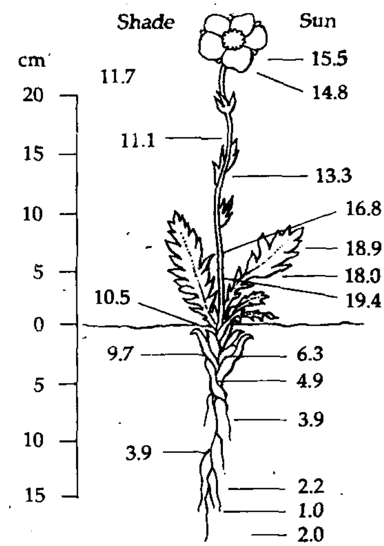

Figure 1–2. Temperature of the microenvironment (°C) near different parts of an alpine plant in sun and shade on a July day when the temperature of the macroenvironment was 11.7°C. (Redrawn from Tikhomirov 1963. Also cited in Larcher 1975.)

large region is called a **formation**. For example, a tropical rain forest is a formation dominated by broadleaf evergreen trees, and it is characteristic of thousands of square kilometers in humid tropical regions on several continents. Part of the formation classification scheme adopted by UNESCO (1973) appears in Table 1–1.

Formations may be subdivided into **associations**. An association is the collection of all plant **populations*** coexisting in a given habitat. It has the following attributes: (a) it has a relatively fixed floristic composition, (b) it exhibits a relatively uniform physiognomy, and (c) it occurs in a relatively consistent type of habitat. The same species tend to recur together wherever a particular habitat repeats itself. Associations are usually named by their dominant or most characteristic taxa; thus the red fir forest in California's Sierra Nevada, which occurs on well-drained, undisturbed sites between 1800 and 2400 m, is a red fir (*Abies magnifica*) association in a conifer forest formation.

Typically, several to many associations may belong to the same formation, all sharing a similar physiognomy, but each differing qualitatively or quantitatively in species composition. A fascinating ecological phenomenon is the similarity of vegetation types in similar macroenvironments scattered around the world. It is as though a particular

*A population is a group of individuals of the same species occupying a habitat small enough to permit interbreeding among all members of the group. Some populations do not interbreed, being self-pollinators or reproducing only asexually, but they exist in a habitat small enough to permit the *potential* exchange of genes. Very restricted species, endemic to a small area, may consist of only a single population, but most species include many populations. Consequently, the terms species and population are not usually synonymous.

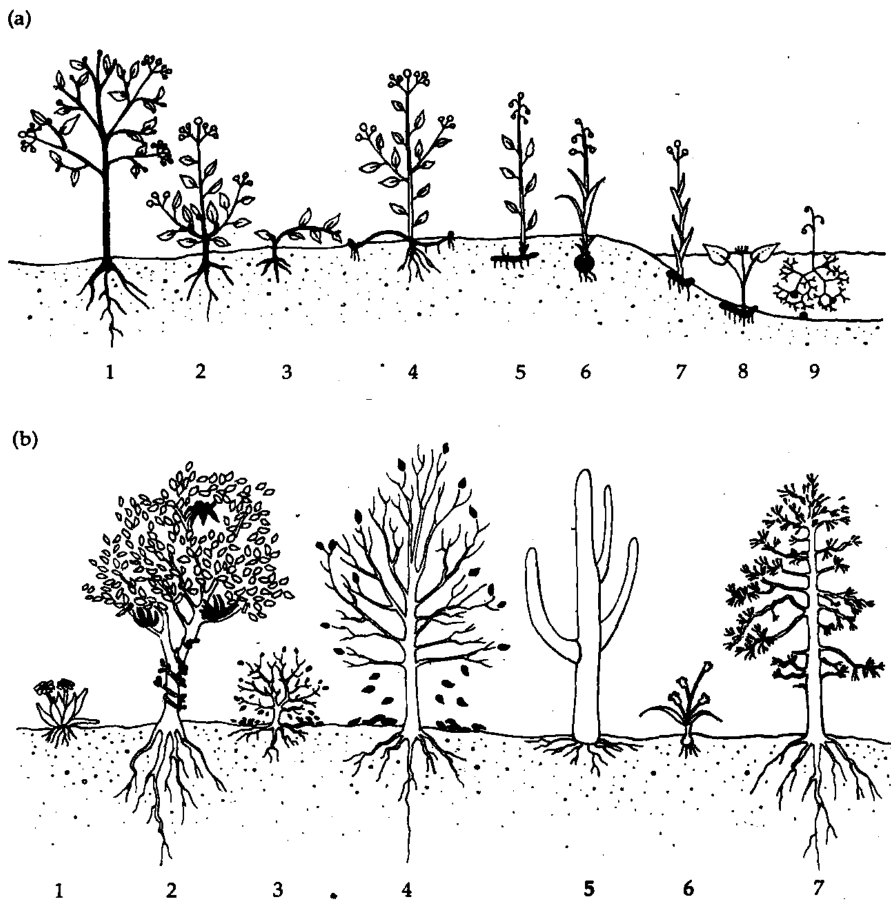

Figure 1–3. Examples of life forms (growth forms). (a) A scheme of classification by Raunkiaer (1934) based on the location of overwintering, perennating parts, such as buds, bulbs, or seeds, shown in dark, solid areas: (1) phanerophyte, (2–3) chamaephytes, (4) hemicryptophyte, (5–9) cryptophytes (also called geophytes). (b) Life forms based on other criteria, such as length of life, succulence, and leaf traits: (1) annual herb, (2) broadleaf evergreen tree with a liana (a woody vine) and an epiphyte (a plant which grows on another plant but uses it only for mechanical support, not as a source of nutrients), (3) drought-deciduous shrub, (4) broadleaf deciduous tree, (5) stem succulent, (6) bulbous herbaceous perennial, (7) needleleaf evergreen. ((a) redrawn from C. Raunkiaer. 1934. *The Life Forms of Plants and Statistical Plant Geography.* Courtesy of Clarendon Press, Oxford.)

physiognomy has been selected for in similar but isolated habitats. Evidently there has been convergent evolution among vegetation types (see Chapter 7).

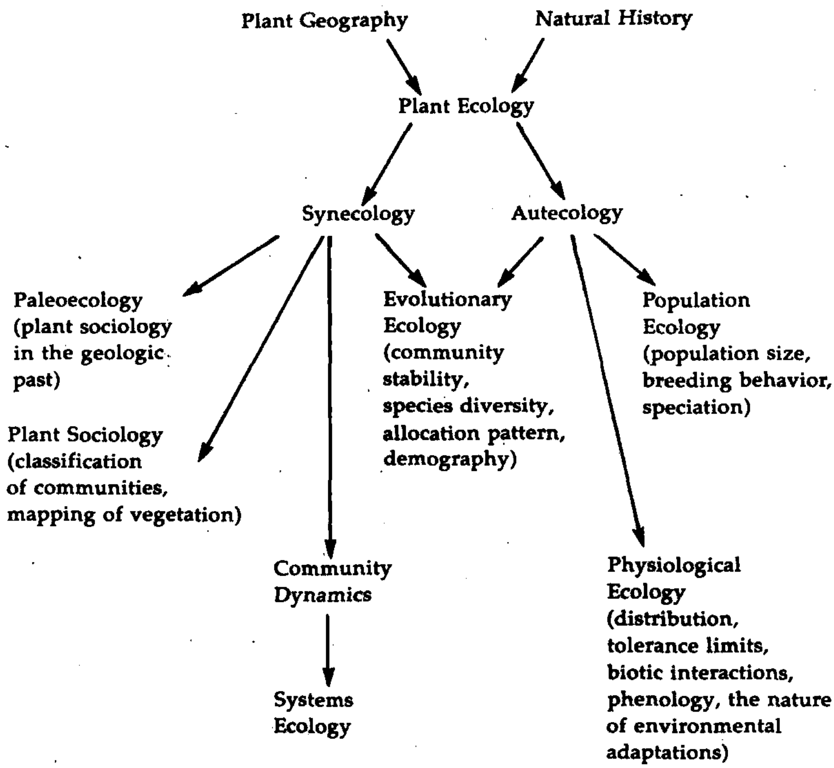

Figure 1–4. The relationship between and origins of specializations within the field of plant ecology.

SPECIALIZATIONS WITHIN PLANT ECOLOGY

Synecology

One large segment of plant ecology has followed directly from plant geography (Figure 1-4). This is **synecology**, and some of its many synonyms include community ecology, phytosociology, geobotany, vegetation science, and vegetation ecology.

One phase of synecology is **plant sociology**, the description and mapping of vegetation types and communities.* In the past 50 years there has been a proliferation of standard methods for sampling vegetation and treating and analyzing sampling data. With these standard methods valid conclusions can be drawn and vegetation from all

*Community (phytocoenose) is a general term which can be applied to any vegetation unit, from the regional to the very local.