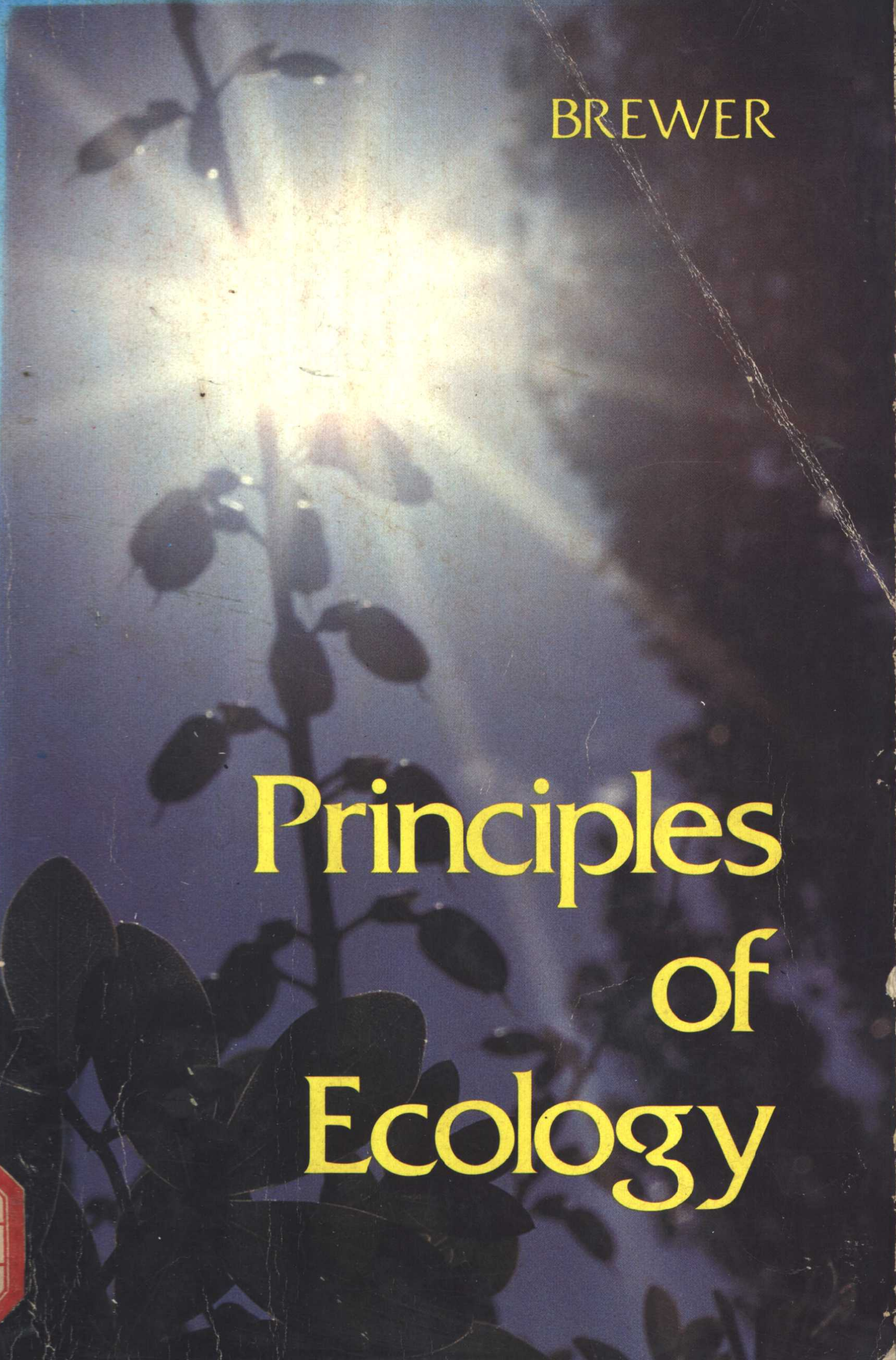

BREWER

Principles of Ecology

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PREFACE

There are many good ecology textbooks but most of them are aimed at the upper undergraduate or graduate student. This is an undergraduate text designed for a sophomore–junior level course in general ecology. It assumes no knowledge beyond that usually attained by the time freshman biology is completed.

The language has nearly always been kept as plain as I can write. Special ecological terms are defined where they first occur, either directly or by context, as are special physiological, chemical, and other scientific terms.

Material within the six chapters is arranged in a fairly large number of rather brief sections. One of the considerations in the placement of material into sections was to allow some of the more complex material to be omitted without losing the fundamentals of the subject. For example, there are two sections on the ecological niche, one a simple descriptive treatment and one which develops G. E. Hutchinson's hypervolume model.

Most of the text is not mathematical but in a few places sections introducing certain mathematical aspects of ecology have been included. These sections require some knowledge of algebra, and a little calculus would help for some of them. They present what I hope are thorough, step-by-step explanations that even poor mathematicians may follow. For some introductory ecology courses these mathematical sections may be unnecessary and may be omitted with no loss of continuity.

I have taken particular care with the figures and tables, which are used to clarify or supplement the text. In several cases they extend the text by giving a more detailed treatment of a particular topic. For courses in which such detail is unnecessary the instructor can readily designate any tables or figures he does not wish to assign. Because beginning students sometimes have trouble interpreting graphs and tables, I have tried to provide fully descriptive captions.

The bibliographies at the end of each chapter are selective. They were designed to permit further study of a subject by including some of the more recent reviews in article or book form, some of the classic papers on the subject, and some recent research papers.

To save space and to avoid the dampening effect that scholarly apparatus has on some students, I have not included scientific names or in-text citations of literature. These omissions will cause few problems for the intended audience. Most common names used are standard ones, which can be readily connected with the appropriate Latin names in standard taxonomic sources.

This is a book of ecology; its framework is the major principles of the science. I have tried to cover these at all levels, from the ecology of the individual—a neglected area in most current textbooks—to that of the ecosystem. Many applied or practical aspects of ecology are discussed in the text in connection with appropriate ecological principles, with the final chapter dealing with the role of ecology in human affairs. Clearly, the book gives no complete treatment of the topic of the environment and man, but I believe that the treatment it does give is valuable on two counts. First, most of the unifying principles of environmental science are ecological. The names of pesticides may change but the rules that organisms, populations, and ecosystems follow do not. Accordingly, a knowledge of the basic principles of ecology and physiology prepares one as well for understanding pollution or the population problem as do catalogs of food additives, herbicides, or contraceptive devices.

I do not, however, mean to make light of the latter kind of specific information on environmental matters. My second reason for believing that human environmental concerns should be included in a basic ecology text is this: I see entirely too few biology majors and minors who have any sound knowledge of environmental problems. Too often it is assumed that the student will have learned of these problems by reading the newspaper and will have made the connection with the appropriate ecological or biological principles on his own, and too often this has not happened. Biologists must be ready to take a part in the solving of environmental problems—they are too important to be left to social scientists and engineers.

I have learned much of what I know about ecology and environmental matters directly from other individuals. I am grateful, first, to my formal teachers of ecology: S. C. Kendeigh, W. L. Gersbacher, the late A. G. Vestal, and J. W. Voigt. I am grateful to colleagues from boyhood to the present: J. W. Hardy, K. D. Stewart, C. Heckrotte, W. B. Robertson, Jr., G. C. West, G. W. Cox, W. L. Gillespie, T. S. Robinson, W. J. Davis, W. L. Minckley, R. W. Olsen, C. G. Goodnight, R. W. Pippen, J. G. Engemann, A. M. Laessle, D. L. Regehr, and M. L. Kaufmann. I am grateful, also, to the students who, in class and out, have tried to educate me. There are too many to list but I should mention M. T. McCann, who read and commented on the whole book.

Western Michigan University has provided support over the years.

Finally, for many favors, I am grateful to my wife, Lucy Sharp Brewer, to whom this book is dedicated, of course.

RICHARD BREWER

CONTENTS

Chapter 1

ECOLOGY AS A SCIENCE

Ecology is a relatively new science. The word was first defined just over a hundred years ago by the German zoologist Ernst Haeckel. He based it on the Greek word *oikos* meaning home, and wrote: "By ecology we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to its inorganic and its organic environment." This is basically the same definition as the one used today—the study of the relationships of organisms to their environment and to one another.

Ecology has gone from a word that few people knew a decade ago to one that is widely misused today (Fig. 1–1). A popular entertainer has been quoted as saying that he was traveling around the country preaching ecology. (If this statement does not sound a little odd, try substituting the name of some other science, say anatomy, for ecology.) Environmental concern is probably what is being preached; it is not ecology but is an activity to which ecology has a great deal to contribute. The phrase "environmental science" covers all the sciences—including ecology, geology, and climatology—that deal with the environment. A good term for these and all the other fields that have an interest in the use of the environment might be "environmental studies"; a list of these would run from economics to religion and back again.

Although ecology had a name by 1869, there was at that time no "body of knowledge" because almost no one was engaged in the kind of research that yielded ecological information. More and more such studies were begun in the later years of the nineteenth century, but it was not until about 1900 that certain biologists began to think of themselves as ecologists and the kind of work they were doing as ecology.

Although Germany, Denmark, France and other countries had scientists who contributed to the early development of the field of ecology, a good share of the early work at the beginning of this century was done in the United States. We can imagine an early ecologist setting out with

"How can a guy as old as you be a professor of ecology
when it didn't even exist six or seven years ago?"

Figure 1–1. Few ecologists would agree that Montgomery Ward's is anybody's ecology headquarters, but few will object to the public's casual use of the term as long as it indicates a knowledge of the earth's environmental problems and support for efforts to solve them. The cartoon (from *Audubon, 79*(3):121, 1977) illustrates a common misconception.

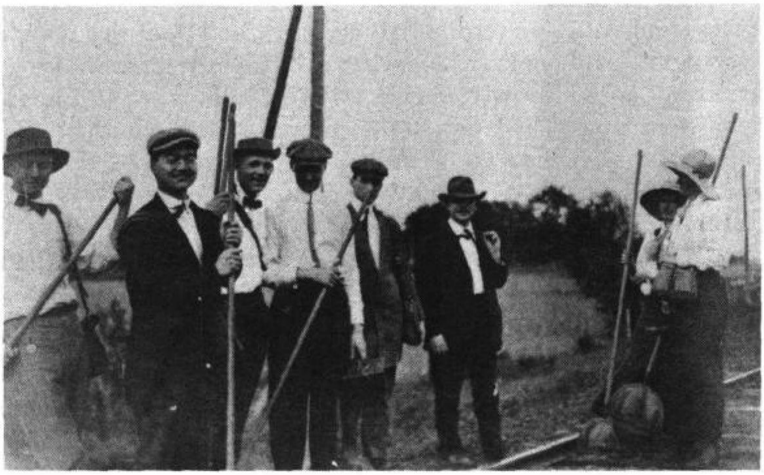

Figure 1–2. A field trip 20 May 1913 led by the pioneer ecologist C. C. Adams from the University of Illinois (Western Michigan Univ. Archives).

a class from the University of Illinois or Chicago or Nebraska (Fig. 1–2). The instructor and the students wear dark suits, ties, and hats after the fashion of the period. They travel by electric railroad to the station nearest their study area, and then walk. The study area may be a beech-maple forest, the beaches and dunes of Lake Michigan, or a bog. They conduct their studies, eat the sandwiches their landladies have fixed for them, and at the end of the day walk back to the station for the trip home. If some of the students are planning to become ecologists, they might be needled a bit by their classmates. What difference does it make what plants grow on sand dunes? What can a study of the animals that live on the bottom of the Illinois River tell us? Why waste time studying ecology when you can work on a good solid topic like the embryology of the sea urchin or go to medical school?

Times change. If we were to visit the bog studied by that class of 60 or 70 years ago we would travel by expressway rather than by interurban, and we might find, not lady's slipper orchids and cranberries, but a garbage dump or a housing development built on one. The beach would be different, too; there might be beer cans instead of sea rockets, and there would be other changes, some visible, some not. There would be large numbers of people, tanned and pale, slim and fat, packed onto the beach at a density greater than in the apartment houses they live in. Some chemical changes in the lake water and the organisms in it might not be visible; we cannot see the DDT in the fat of the fishes or the increased phosphate content of the water directly.

Times change, and the science of ecology is no longer something of interest only to ecologists or a subject to be studied only for its intellectual fascination (although that still exists). Many of the major problems the world faces—pollution, overpopulation, the wise use of resources—are at heart ecological problems. Ecologists will help to find solutions to these problems, but so will everyone else. A knowledge of environmental science is necessary to all persons so that they may live, conduct their business, and vote in such a way so as to make solutions possible.

In the following chapters we will examine the science of ecology at three levels. The ecology of the *individual organism* will be considered first. The second level deals with the ecology of groups of individuals, or *populations*. Populations of several kinds of organisms, several species, live together in *communities*, the third level. At this same level we may consider the community along with its physical setting or habitat as a single, interacting unit, the ***ecosystem.*** A pond is a familiar ecosystem, with the plants and animals and bacteria forming the community, and the water, the dissolved salts and gases, and the mud of the bottom being elements of the rest of the system. We can recognize communities and ecosystems of various scales, from the stomach of a cow, with its interesting populations of microorganisms, on up to the earth itself, the largest ecosystem with which we are familiar.*

One of the great lessons of ecology is the interrelatedness of nature, so there is some justification for thinking of the ecosystem as the fundamental unit of study. There is a story that a few years ago DDT was used in Borneo to kill mosquitoes around houses, which it did. However, small lizards called geckos who lived in the houses and fed on insects began to die from their DDT-rich diet. Weakened geckos fell easy prey to house cats who also began to die. As the cat population dropped rats began to infest the houses, and in this area rats were dangerous as potential plague carriers. Borneo began to import cats.

I do not know whether this story is strictly true; I have not seen it documented. Whether or not it is true it expresses clearly the spirit of the profound truth that the parts of an ecosystem are all interconnected so that when we touch one part of the system, we eventually and in some way touch the rest.

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The field of ecology is fortunate in having a great many excellent textbooks. Because books in the following list have valuable information and ideas on a wide variety of topics, they are brought together here

*The entire global environment supporting life from the depths of the oceans and as far down in the soil as organisms occur up to the highest part of the atmosphere occupied by organisms is termed the ***biosphere.***

rather than being mentioned repeatedly in the bibliographies of later chapters.

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Chapter 2

ECOLOGY OF INDIVIDUAL ORGANISMS

TOLERANCE RANGE

We refer to the surroundings of an organism as its ***environment*** or ***habitat.*** The basic subdivision is between *terrestrial,* or land, habitats and *aquatic,* or watery, habitats. A trout is an aquatic organism, living in cool streams, while a trout lily is terrestrial, living in moist forests. Aquatic habitats are often subdivided into *marine,* or ocean, habitats, and *fresh-water* habitats which are lakes, ponds, streams, and springs whose waters have low salt concentrations. Much finer subdivisions can be made—habitats may be subdivided into subhabitats and eventually *microhabitats,* such as a south-facing slope, a tree hole, or the spaces between the sand grains along a beach.

Specific features of the habitat may be studied. For the trout we can measure such factors as water temperature and the amount of oxygen dissolved in the water. For the trout lily we can measure the amount of light reaching it on the forest floor and the concentration of calcium in the soil. If we are able to determine the whole range over which the species is able to live, for one of these factors, we then will know the ***range of tolerance*** of that species for that factor. A goldfish, for example, might be able to live in waters in which the temperature ranges from 2 to 34°C (about 36 to 93°F), but it will die of heat or cold at temperatures above or below this range.

Field observations give us some idea of the range of tolerance of a species, but the field work must be checked by experimentation. One of the reasons for this is that organisms interact with other organisms. The habitat features we have mentioned so far have all been *abiotic factors,* or factors of the physical environment. The organism also exists in a world

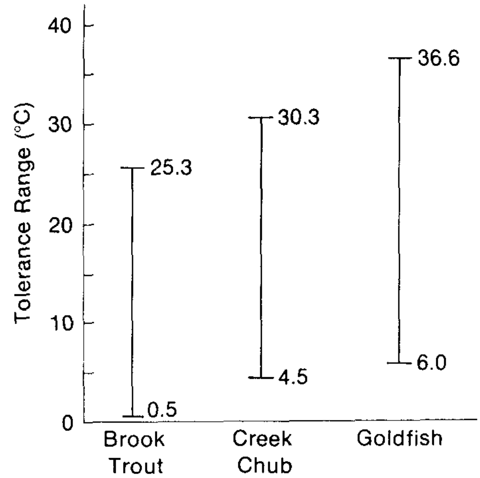

Figure 2–1 Different species have different ranges of tolerance. The goldfish is able to live in warmer waters than the brook trout but does not tolerate cold temperatures as well as the brook trout. (From J. R. Brett, "Some principles in the thermal requirements of fishes," *Quarterly Review of Biology, 31*:75, 1956.)

of *biotic factors*, consisting of its relationships with other organisms. These relationships are of several kinds: one organism may use another as food and at the same time serve as food for a third; two organisms may compete for food, for nesting sites, or for some other requirement. An organism may not be able to live in an area where physical factors are favorable for it due to some biotic factor. A common weed called sheep sorrel provides a good example. If we test the soil where these plants naturally grow, we almost always find that the soil is acid. If we plant its seeds and grow the plant in a greenhouse in soils of various acidity and alkalinity, we find that it grows best in neutral or slightly alkaline soils. Why is there this inconsistency? The answer seems to be that many plant species can grow in neutral soil and some of these can outcompete sheep sorrel under such conditions. Relatively few plants, however, can grow well in strongly acid soil. Thus, in nature, sheep sorrel is restricted by competition to one end of its tolerance range.

Tolerance ranges differ from one species to another. We would expect carp or goldfish, for example, to be able to tolerate warmer temperatures and lower oxygen concentrations than trout, and this is exactly what we find when we make the appropriate tests (Fig. 2–1). The fact that different species have different tolerance ranges is one basic reason why different habitats support different communities, and why communities vary geographically from warmer to cooler and from wetter to drier regions.

WHEN CONDITIONS CHANGE

Few habitats stay the same for very long. Some, such as the ocean depths, come very close, but for most habitats environmental factors change between day and night, between drought and a wet period, between summer and winter. When some important feature of the habitat changes, the organism changes in response. The change may be mainly *physiological.* As it warms up during the day, a plant and a bird both exposed to the sun will undergo physiological changes because of the heat. These changes often have the effect of keeping certain important aspects of the organism's internal environment constant despite the changing external environment. This tendency, which is an important physiological principle, is known as *homeostasis.* The bird may respond by lowering its rate of heat production and by arranging its feathers so as to lose heat rapidly, resulting in its body temperature remaining constant. If the sun keeps shining and the temperature keeps rising, an important difference between the plant and the bird or the trout lily and the trout may be seen. The plants are stationary, attached to one spot (*sessile*), whereas the animals can move about (*motile*). The bird or trout can move away from unfavorable conditions—the bird can go into the shade, the trout can swim to cooler water. These are *behavioral* changes which occur in addition to the purely physiological ones.The range of behavioral responses for a sessile organism is much smaller. Usually it can only remain in one place and tolerate the changed condition—or, if the change is too great, fail to tolerate it.

ACCLIMATION

There is one kind of physiological change shown by organisms that deserves special attention. The range of temperature tolerance of a fish (or an insect or a pine tree) may vary from season to season, depending on the temperature at which it has recently been living (Fig. 2–2). In

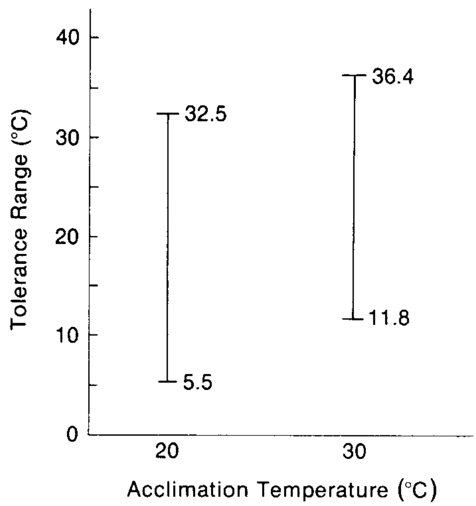

Figure 2–2. The tolerance range of organisms may be changed by acclimation. Kept at 20°C, the large-mouthed bass has an upper limit of temperature tolerance of just over 32°C. If the aquarium temperature is slowly raised to 30°C and kept there for a few days, the fish now acclimated to 30°C are able to tolerate temperatures of over 36°C. At the same time, however, they lose some of their ability to tolerate lower temperatures. (From Brett.)

midwinter, a fish may be able to live in the range from 0 to 24°C but in summer the same individual may have a tolerance range that extends all the way up to 33°C but down only to 15°C. Such adjustments in the ecological response to a changed environment are known as ***acclimation.*** Acclimation does not occur just in temperature tolerance; organisms may also acclimate to different oxygen levels in the air (if they go to higher altitudes, for example) and to other changed conditions.

Acclimation is undoubtedly of great importance in allowing organisms to exist permanently in changeable environments. Without this ability many organisms would either die or be forced to migrate during unfavorable seasons. Of course, some organisms do show these two strategies. Many birds, which are probably the most highly mobile of organisms, move back and forth seasonally between a summer and a winter range. Such organisms as annual weeds and many insects die each winter but produce seeds or eggs that have a much lower temperature tolerance limit than the parent organism.

ECOTYPES

The fact that two individuals belong to the same species does not guarantee that they will respond identically to some ecological factor such as temperature or light. Nearly every elementary biology textbook has illustrations of geographical variation in the size or color of some animal: there are large specimens from cold regions and small ones from hot regions, dark-colored animals from wet regions and light-colored ones from dry areas. Ecological differences may be more difficult to illustrate than these but they also exist (actually body size and color probably have ecological importance).Two botanists at the University of Missouri conducted an interesting experiment to show ecological variations in different portions of the geographic range of a species. Seeds of a plant called white snakeroot were gathered from widely separated localities and planted in a greenhouse. After the plants had reached a certain size, they were exposed to light equivalent to the long day lengths conducive to flowering in this species. After 120 days the plants grown from North Dakota seeds had produced mature fruits, those from South Dakota seeds had just reached full flower, and those from Kansas had not yet produced flower buds. These differences corresponded very well to the growing season (the length of time between the last frost in the spring and the first in the fall), which is 129 days in North Dakota and 195 in Kansas. Those plants having the responses of the Kansas population would probably be unable to reproduce in the short growing season found in the northern part of the range of the species. Because the plants were all grown under similar conditions we may conclude that the differences seen are genetic, or hereditary. Evolution apparently has produced local populations which are well adapted to do two things in their particular locality: (1) to take advantage of as much time as is available for vegetative growth and food-making; but also (2) to flower and set seed before a killing frost occurs. The different populations of a species which show genetic differences that have ecological significance are known as *ecotypes.*

EXTREME CONDITIONS

The ability of many organisms to acclimate to temperature, the salt content of water, and various other factors is one complication that must be dealt with in going from the laboratory to the field—that is, in explaining the occurrence of organisms in nature on the basis of experimental findings. The existence of ecotypes is another complication. Another fact that must be remembered is that conditions need not be perpetually outside the tolerance limits of a species for the species to be absent.* In other words, you only have to kill a plant or animal once. Six days a week a stream may be well within the tolerance limits of a certain fish but if on Saturday night a factory releases a dose of toxic effluent, the fish will not be found living there. The occasional extreme condition may be more important than the average condition in determining whether or not an organism can exist permanently in a given area.

LIMITING FACTORS AND THE ENVIRONMENTAL COMPLEX

So far we have considered only the organism's response to a single factor of its environment, but the environment of every organism is composed of many factors. The law of limiting factors, stated by a plant physiologist named F. F. Blackman, will often help us to understand a particular case. Liebig's law of the minimum is an earlier, less general statement of the same idea. This law states that when some process depends on several different factors the speed of the process at a given time is limited by the "slowest" factor. The slowest or **limiting factor** may be either too little or too much of something. A process may be limited early in the morning by too little light and limited in the middle of the day by temperatures that are too high.

Good farmers and gardeners understand the law of limiting factors. They know that if their soil is deficient in calcium, adding phosphate will not make their crops grow any better; calcium is the limiting factor and only if calcium is added will growth improve. If enough calcium is added then some other factor will become limiting, perhaps some other mineral

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*This was pointed out by W. P. Taylor, one of the early students of wildlife management in the western U.S.