BIOLOGY OF PLANTS

SECOND EDITION

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PREFACE TO THE SECOND EDITION

Since the first edition of BIOLOGY OF PLANTS appeared in 1970, we have received from teachers and students many constructive comments on the book's strengths and shortcomings, and some sound advice on how it might be improved. Ray Evert, one of those who taught from BIOLOGY OF PLANTS and had excellent ideas for making it better, has now joined us as coauthor. The substantial improvements in this edition owe a great deal to his talents as a scholar and teacher.

Over the past six years there have been major advances in our understanding of virtually every discipline of plant biology. The second edition takes this recent information into account and attempts to provide a thoroughly up-to-date introduction to the world of plants and those organisms traditionally associated with them. In addition, we believe that this time we have provided a more balanced treatment of all the major disciplines of plant biology.

Although we have reorganized and largely rewritten the text, we have tried to retain the best features of the first edition. Again the interrelationships of evolution, diversity, and ecology are emphasized throughout, and the dual themes of evolution and ecology still pervade the book.

We recognize that there is no "best" way to present plant biology, either in lecture or in laboratory. The new sequence of topics adopted for this edition reflects, in part, the present organization of the course in general botany that one of the authors has given over the past sixteen years. We have tried to make each section of the book as independent as possible, so that topics do not have to be presented in lockstep with our preferred sequence.

The section on plant anatomy, now Section 5, has been rewritten entirely, emphasizing the continuity of the plant body. In this new edition the coverage of plant anatomy has been expanded from two to five profusely illustrated chapters. All but a few of the illustrations in this section were prepared especially for BIOLOGY OF PLANTS. Throughout the book the abundant drawings, photographs, and electron micrographs will not only help students to understand the narrative but should also provide valuable resources for laboratory work.

We have expanded the section on the diversity of living organisms, also strengthening its evolutionary theme and its focus on interrelationships. More common examples are used, particularly in the chapters on algae and fungi.

There is so much new material, so many clarified presentations, that we cannot list them all here. Throughout the many months of rewriting we were most concerned with helping students really to understand what goes on and with conveying the excitement of current research and past observation. We hope that our enthusiasm throughout the book and the greater attention given to the inherently more difficult topics will foster curiosity and understanding in our readers.

PETER H. RAVEN
RAY F. EVERT
HELENA CURTIS

January 1976

ACKNOWLEDGMENTS TO THE FIRST EDITION

This book could not have been written without the help, at every stage, of experts in various areas of botanical research and teaching. We wish to acknowledge especially the assistance of Winslow R. Briggs of Harvard University, who helped in particular with the chapters dealing with plant physiology, and who also reviewed, criticized, and made valuable suggestions concerning other parts of the manuscript. Peter M. Ray of Stanford University was the principal reviewer of Chapter 25 on water movement in plants, and R. Paul Levine and Daniel I. Arnon were advisors for the chapters on photosynthesis.

Others who reviewed various parts of the manuscript and to whom we wish to express our thanks are: Constantine J. Alexopoulos, University of Texas; Lewis E. Anderson, Duke University; Daniel I. Axelrod, University of California, Davis; Harlan P. Banks, Cornell University; Charles E. Barr, State University of New York, Brockport; R. G. S. Bidwell, Case Western Reserve University; David W. Bierhorst, University of Massachusetts; W. Dwight Billings, Duke University; Olov Björkman, Carnegie Institution, Stanford; Walter F. Bodmer, Stanford University; Harold C. Bold, University of Texas; Allan M. Campbell, Stanford University; Elizabeth G. Cutter, University of California, Davis; Andrew J. Darlington, Imperial Cancer Research Fund, London; Theodore Delevoryas, Yale University; E. Lloyd Dunn, Stanford University; Paul R. Ehrlich, Stanford University; Ursula Goodenough, Harvard University; R. H. Hill, Cambridge University; Richard W. Holm, Stanford University; Albert W. Johnson, San Diego State College; George Johnson, Stanford University; Clifford B. Knight, East Carolina College; Bastiaan J. D. Meeuse, University of Washington, Seattle; Harold A. Mooney, Stanford University; Robert Ornduff, University of California, Berkeley; Johannes Van Overbeek, Texas A & M University; Marcus M. Rhoades, Indiana University; Frank B. Salisbury, Utah State University; W. B. Schofield, University of British Columbia; G. Ledyard Stebbins, University of California, Davis; William C. Steere, Director, New York Botanical Garden; Richard A. White, Duke University; Richard H. Wilson, University of Texas.

One of the authors would like to express his appreciation to his wife, Tamra Engelhorn Raven, for her assistance and encouragement.

By introducing young people not only to what is known about botany and ecology but particularly to the many unsolved problems in these fields, we hope to enlist new talents and new enthusiasms in working toward the solutions on which all of our futures depend.

April 1970

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ACKNOWLEDGMENTS TO THE SECOND EDITION

Special thanks and acknowledgment are due to Susan E. Eichhorn, of the University of Wisconsin, Madison, who supervised much of the organization and typing of the manuscript, as well as most of the preparation of illustrations for the second edition. Special recognition and thanks are also due Ellen M. Dudley for her many superb drawings and Damian S. Neuberger, University of Wisconsin, Madison, for his outstanding photographic work.

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INTRODUCTION

When a particle of light strikes a molecule of chlorophyll, an electron is jolted out of the molecule and raised to a higher energy level. Within a fraction of a second, it returns to its previous energy state. All life on this planet is dependent upon the energy momentarily gained by the electron. The process by which some of the energy given up by the electron in returning to its original energy level is converted into chemical energy—energy in a form usable by living systems—is known as photosynthesis. Photosynthesis is the vital link between the physical and the biological world, or, as Nobel laureate Albert Szent-Györgyi said, more poetically: "What drives life is a little electric current, kept up by the sunshine."

Only a few types of organisms—the green plants, the algae, and some bacteria—possess a type of chlorophyll that can, when embedded in the membranes of a living cell, carry out this energy conversion. However, once the energy is trapped in chemical form, it becomes available as an energy source to all other organisms, including man. Thus we are totally dependent upon photosynthesis, a process which our laboratories are just beginning to understand and to which green plants are so exquisitely adapted.

THE EVOLUTION OF PLANT LIFE

Like all other living organisms, plants have a long evolutionary history. The planet earth itself is some 4.7 billion years old, an accretion of dust and gases swirling in orbit around the star that is our sun. The earliest known fossils are about 3.2 billion years old and consist of small, relatively simple cells.

As events are reconstructed, these first cells were formed by a series of chance events. The raw materials—carbon, oxygen, hydrogen, and nitrogen—were present in the gases of the early atmosphere. (These four elements make up 98 percent of the tissue of all living things today.)

I-1
A cluster of cells of the freshwater green alga Cosmarium botrytis. *Algae are photosynthetic organisms that are either single-celled or have relatively simple multicellular structures (compared with plants) and are adapted to life in water. They are the subject of Chapter 12.*

Through the thin atmosphere, the rays of the sun beat down on the harsh, bare surface of the young earth, bombarding it with light, heat, and ultraviolet radiation. Water vapor cooled in the upper atmosphere, fell on the crust of the earth as rain, and steamed up again, driven by the sun's heat. Violent rainstorms, accompanied by lightning, released electrical energy. Radioactive substances in the earth's crust emitted their energy, and molten rock and boiling water erupted from beneath the earth's surface. The energy in this vast crucible broke apart the simple gases of the atmosphere and reformed them into more complicated molecules.

According to present hypotheses, the compounds that were formed in the atmosphere tended to be washed out by the driving rains and to collect in the oceans, which grew larger as the earth cooled. As a consequence, the ocean became an increasingly rich mixture of organic molecules. Some organic molecules have a tendency to aggregate in groups; in the primitive ocean, these groups probably took the form of droplets, similar to the droplets formed by oil in water. Such droplets of organic molecules appear to have been the forerunners of primitive cells, the first forms of life.

These organic molecules also served, according to present theories, as the source of energy for the earliest forms of life. The primitive cells or cell-like structures were able to use these compounds, which were abundant in the "primordial soup," to satisfy their energy requirements.

Such cells are known as *heterotrophs*, a category of organisms that today includes all living things classified as animals or fungi and many of the one-celled organisms, the bacteria and the protists. *Hetero* comes from the Greek word meaning "other," and *troph* comes from *trophos*, "one that feeds." A heterotrophic organism is one that is dependent upon others—that is, upon an outside source of organic molecules—for its energy.

As the primitive heterotrophs increased in number, they began to use up the complex molecules on which their existence depended—and which had taken millions of years to accumulate. Organic molecules in free solution (not inside a cell) became more and more scarce. Competition began. Under the pressure of this competition, cells that could make efficient use of the limited energy sources now available were more likely to survive than cells that could not. In the course of time, by the long, slow process of weeding out the less fit, cells evolved that were able to make their own energy-rich molecules out of simple nonorganic materials. Such organisms are called *autotrophs*, "self-feeders." Without the evolution of autotrophs, life on earth would soon have come to an end.

The most successful of the autotrophs were those that evolved a system for making direct use of the sun's energy—the process of photosynthesis.

The earliest photosynthetic organisms, although simple in comparison to modern plants, were much more complex than the primitive heterotrophs. To capture and use the sun's energy required first, a complex pigment system that could catch and hold the energy of a ray of light and, linked to this system, a way of fixing the energy in an organic molecule.

Thus the flow of energy in the biosphere came to assume its modern form: radiant energy channeled through photosynthetic autotrophs to all other forms of life.

Photosynthesis and The Coming of Oxygen

As photosynthetic organisms increased in number, they changed the face of the planet. This biological revolution came about because one of the most efficient strategies of photosynthesis—the one employed by nearly all living autotrophs—involves splitting the water molecule (H_2O) and releasing its oxygen. Thus, as a consequence of photosynthesis, the amount of oxygen gas (O_2) in the atmosphere increased. This had two important consequences. First, some of the oxygen molecules in the outer layer of atmosphere were converted to ozone (O_3) molecules. When there is a sufficient quantity of ozone molecules in the atmosphere, they filter the ultraviolet rays, highly destructive to living organisms, from the sunlight that reaches the earth. By about 450 million years ago, organisms, protected by the ozone layer, could survive in the surface layers of water and on the land.

Second, the increase in free oxygen opened the way to a much more efficient utilization of the energy-rich molecules formed by photosynthesis. As we shall see in Chapter 5, respiration* yields far more energy than can be extracted by any anaerobic (oxygenless) process. Until the atmosphere became aerobic, the only cells that evolved were *prokaryotic*—simple cells that lacked nuclear envelopes and that did not have their genetic material organized into complex chromosomes. Today, the surviving prokaryotes are the bacteria and the blue-green algae. According to the fossil record, the increase of relatively abundant free oxygen was accompanied by the first appearance of *eukaryotic* cells—cells with complex chromosomes, nuclear envelopes, and membrane-bounded organelles. All living systems are composed of eukaryotic cells, except for the bacteria, the blue-green algae, and the viruses (which actually are in a "twilight zone" somewhere between the living and the nonliving world).

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* It should be noted that respiration has two meanings in biology. One is the breathing in of oxygen and breathing out of carbon dioxide; this is also the ordinary, nontechnical meaning of the word. The second meaning of respiration is the oxidation of food molecules by cells—that is, the breaking down of energy-rich, carbon-containing molecules and their use by the cell as an energy source. This process, sometimes qualified as cellular respiration, is what we are concerned with here.

(a)

(b)

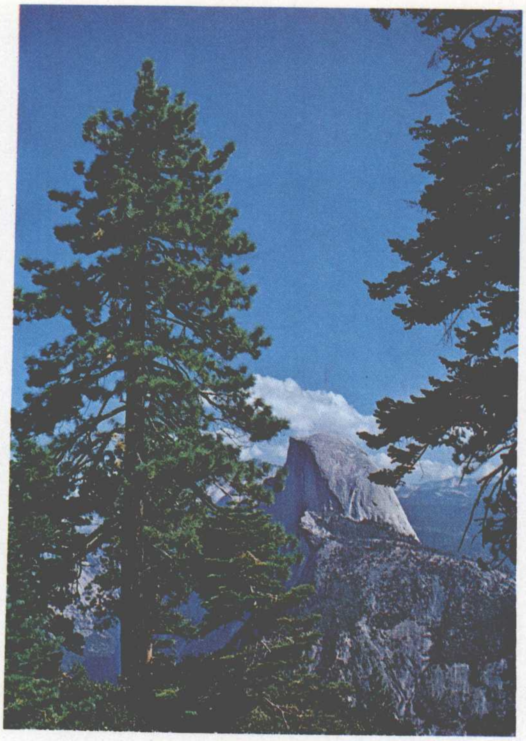
I–2
A modern heterotroph and a photosynthetic autotroph. (a) *A fungus,* Pholiota squarrosoides, *growing on an old cottonwood log in southeastern Alaska.* Pholiota, *which, like other fungi, absorbs its food in an organic form—often from other organisms—is heterotrophic. Fungi are the subject of Chapter 11.* (b) *Dutchman's breeches* (Dicentra cucullaria), *one of the first plants to flower in spring in the deciduous woods of eastern North America. Like most vascular plants, Dutchman's breeches is rooted in the soil; photosynthesis takes place chiefly in the deeply divided leaves of this autotrophic organism. The flowers are produced in well-lighted conditions before the leaves appear on the surrounding trees. The underground portions of the plant live for many years and spread to produce new plants vegetatively under the thick cover of decaying leaves and other organic material on the forest floor.*

The Sea and The Shore

Early in evolutionary history, the principal photosynthetic organisms were microscopic cells floating on the surface of the sunlit waters. Energy abounded as did carbon, hydrogen, and oxygen, but as the cellular colonies multiplied, they quickly depleted the mineral resources of the open ocean. (It is this shortage of essential minerals that is the limiting factor in any modern plans to harvest the seas.) As a consequence, life began to drift toward the shores, where the waters were rich in nitrates and minerals carried down from the mountains by rivers and streams and scraped from the coasts by the ceaseless waves.

The rocky coast presented a much more complicated environment than the open sea and, in response to these evolutionary pressures, living organisms became more complex in structure and more diversified. Some 650 million years ago organisms evolved in which many cells, connected by strands of protoplasm, were linked together to form an integrated, multicellular body. In these primitive organisms we see the beginnings of the modern plants and animals.

On the turbulent shore, those photosynthetic organisms that were multicellular were better able to maintain their position against the action of the waves, and, in meeting the challenge of the rocky coast, new forms developed. Typically, these organisms evolved relatively



I–3
Pinus ponderosa *in Yosemite, California, is an example of a vascular plant.*

strong walls for support and specialized structures to anchor their bodies to the rocky surfaces. As these multicellular organisms increased in size, they were confronted with the problem of how to supply food to the dimly lit portions of their bodies where photosynthesis was not taking place. As a consequence of these new pressures, specialized food-conducting tissues evolved that, extending down the center of their bodies, connected the photosynthesizing parts with the lower, nonphotosynthesizing structures.

The Transition to Land

The body of the familiar plant can best be understood in terms of its long history and, in particular, in terms of the evolutionary pressures involved in the transition to land. The requirements of a photosynthetic organism are relatively simple: light, water, carbon dioxide for photosynthesis, oxygen for respiration, and a few minerals. On the land, light is abundant, as are oxygen and carbon dioxide, both of which circulate more freely than in the water, and the soil is generally rich in minerals. The critical factor is water. Land animals, generally speaking, are mobile and able to seek out water just as they seek out food. Fungi, though immobile, remain largely below the surface of the soil or within whatever damp organic material they feed upon. Plants utilize an alternative evolutionary strategy. Roots anchor the plant in the ground and collect the water required for maintenance of the plant body and for photosynthesis. A continuous stream of water moves into the root hairs, up through the roots and stems, and then out through the leaves. All of the above-ground portions of the plant that are ultimately concerned with photosynthesis are covered with a waxy *cuticle* that retards water loss. However, the cuticle also prevents the necessary exchange of gases between the plant and the surrounding air. The solution to this dilemma is found in specialized openings called *stomata* (singular, stoma), which open and close in response to environmental and physiological signals, thus helping the plant maintain a balance between its water losses and its oxygen and carbon dioxide requirements.

In younger plants and those with a seasonal life span (annuals) the stem is also a photosynthetic organ. In longer-lived plants (perennials), the stem may become thickened and woody and covered with cork, which also retards water loss. In both cases, the stem serves both to support the chief photosynthetic organs, holding them to the light, and to house the plant's intricate and efficient vascular system. The vascular system has two major components: the *xylem,* through which water passes upward through the plant body, and the *phloem* (pronounced flow-em), through which food manufactured in the leaves and other photosynthetic parts of the plant is transported throughout the plant body. It is this efficient conducting system that has given the main group of modern plants, the vascular plants, their name.

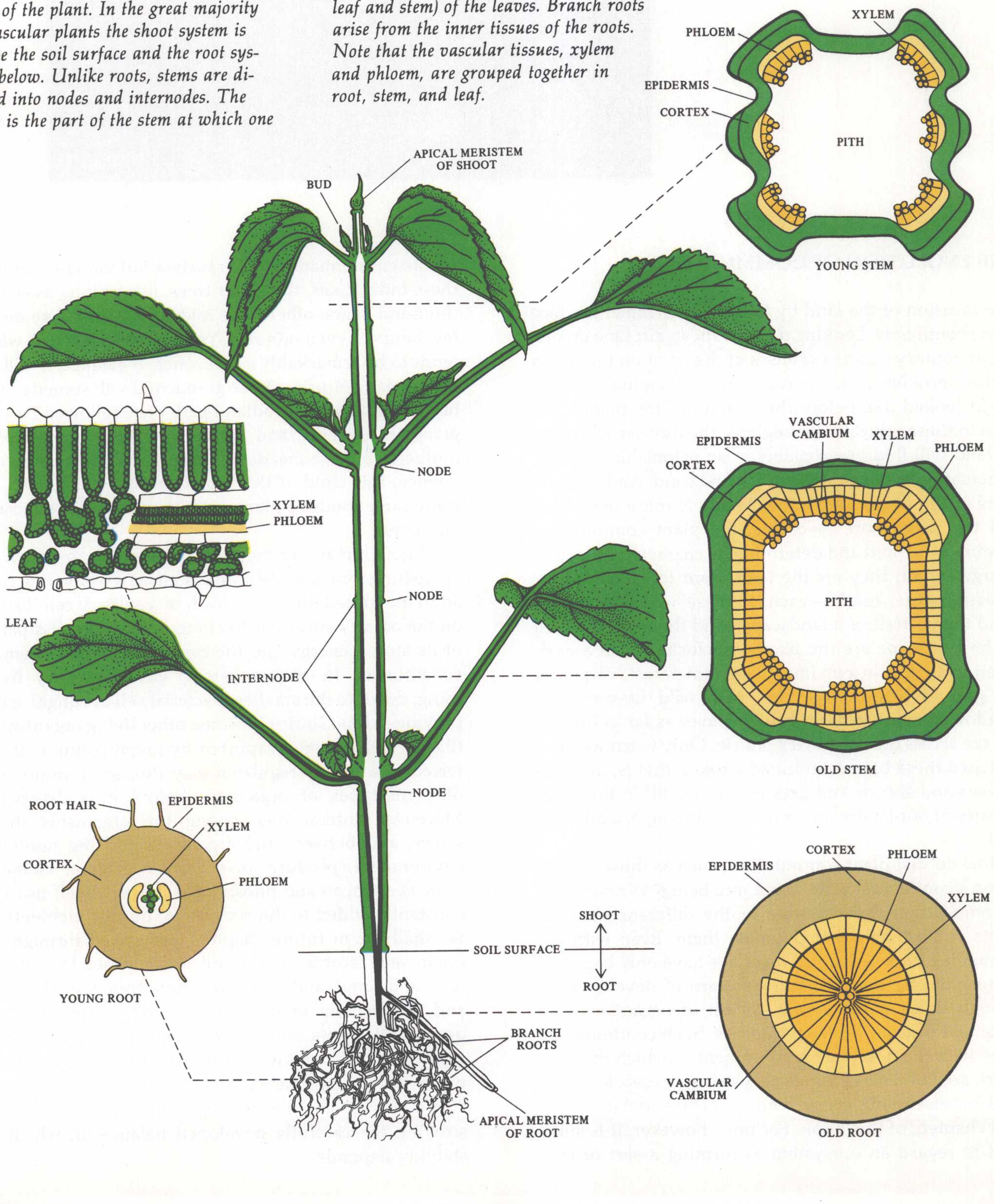
Perhaps also as a consequence of their immobility, vascular plants, unlike animals, continue to grow throughout their life spans. All plant growth originates in localized regions of perpetually embryonic tissues; these regions are called *meristems.* Meristems located at the tips of all roots and shoots are called *apical meristems.* These are involved with the extension of the plant body. Thus the roots move continually toward new sources of water, and the photosynthetic regions are continually expanded and extended toward the light. This type of growth that originates from apical meristems is known as *primary growth.*

The type of growth that results in the thickening of stems, branches, and roots is known as *secondary growth.* It originates in a second kind of meristematic tissue, the *vascular cambium.*

Thus, in sum, the vascular plant is characterized by a root system that serves to anchor the plant in the ground and to collect water and minerals from the soil; a stem or trunk that raises the photosynthetic parts of the plant body towards its energy source, the sun; the highly specialized photosynthetic organs, the leaves; all of which—root, stem, and leaves—are interconnected by a complicated and efficient system for the transport of food and water. All of these characteristics are adaptations to a photosynthetic existence on land.

I-4

Diagram of a Salvia plant, showing the principal organs and tissues of the modern vascular plant body. The organs—root, stem, and leaf—are composed of tissues, groups of cells with distinct structures and functions. Collectively, the roots make up the root system, and the stems and leaves together, the shoot system, of the plant. In the great majority of vascular plants the shoot system is above the soil surface and the root system below. Unlike roots, stems are divided into nodes and internodes. The node is the part of the stem at which one or more leaves are attached, and the internode is the part of the stem between two successive nodes. (In Salvia, two leaves are opposite each other at each node. Each pair is at right angles to the pair of leaves at the node above or below it.) Buds (embryonic shoots) commonly arise in the axils (upper angle between leaf and stem) of the leaves. Branch roots arise from the inner tissues of the roots. Note that the vascular tissues, xylem and phloem, are grouped together in root, stem, and leaf.



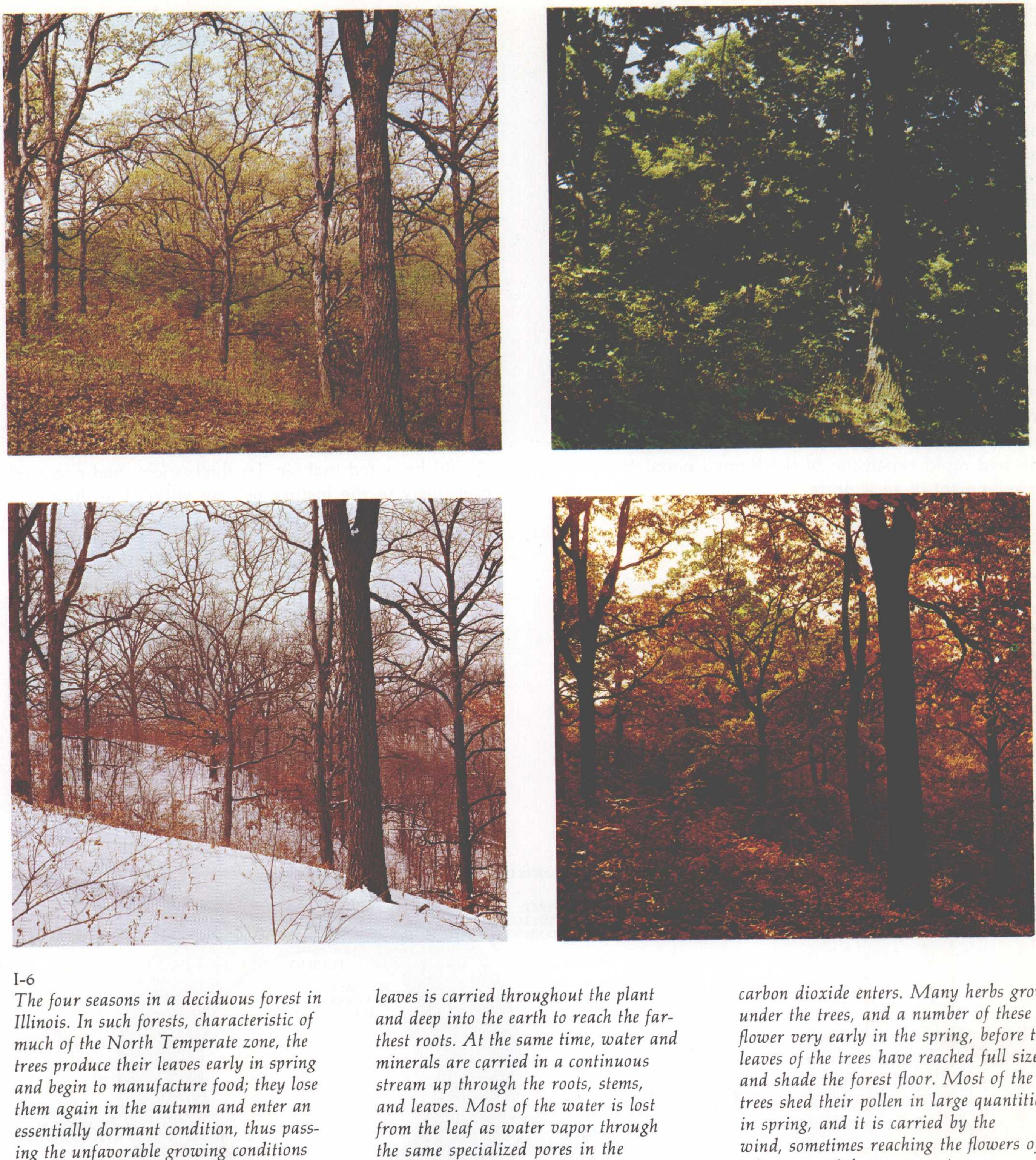
I–5
The prairies of the central United States are among the richest agricultural areas in the world, capable of retaining their productivity indefinitely if properly managed. This uncultivated prairie is dotted with wild flowers.

THE EVOLUTION OF COMMUNITIES

The invasion of the land by the plants changed the face of the continents. Looking down from an airplane on one of our country's great expanses of desert or on the peaks of the Sierra Nevada, one can begin to imagine what the world looked like before the coming of the plants. Yet even in these inhospitable regions, the traveler who goes by land will find green plants of an astonishing variety punctuating the expanses of rock and sand. And in those parts of the world where the climate is more temperate and the rains more favorable, the plant communities dominate the land and determine its character. In fact, to a large extent, they *are* the land. Rain forest, meadow, woods, prairie, tundra—each of these words brings to mind the portrait of a landscape. And the main features of the landscape are the plants—enclosing us in a dark green cathedral in our imaginary rain forest, carpeting the ground beneath our feet with wild flowers in a meadow, moving in great golden waves as far as the eye can see across our imaginary prairie. Only when we have sketched these biomes in broad strokes, that is, in terms of trees and shrubs and grasses, can we fill in the other features of our landscape—a deer, an antelope, a rabbit, a wolf.

How do vast plant communities, such as those we can see on a continental scale, come into being? We can trace to some extent the evolution of the different kinds of plants and animals that populate them. Even with accumulating knowledge, however, we have only begun to glimpse the far more complex pattern of development, through time, of the whole system of organisms that make up these various communities. Such communities, along with the nonliving environment of which they are a part, are known as ecological systems, or *ecosystems.* We shall be discussing ecosystems in greater detail in the final chapters of this book. For now, however, it is sufficient to regard an ecosystem as forming a sort of corporate entity, made up of transient individuals. Some of these individuals, the larger trees, live as long as several thousand years; others, the microorganisms, live only a few hours or even minutes. Yet the ecosystem as a whole tends to be remarkably stable; once in balance, it will not change for centuries. Your grandchild will someday perhaps walk along a woodland path once followed by your greatgrandparents, and where they saw a pine tree, a mulberry bush, a meadow mouse, wild blueberries, or a towhee, this child, if this woodland still exists, will see these same kinds of plants and animals and in the same numbers.

Although many of the organisms in an ecosystem are competing for resources, the system as a whole functions as an integrated unit. The death of a solitary cell floating on the ocean's surface is likely to involve the dissipation of its stored energy and the breakdown of its chemical constituents. In an ecosystem, virtually every living thing, down to the smallest bacterial cell or fungal spore, provides a food source for some other living organism. In this way, the energy captured by green plants is transferred in a highly regulated way through a number of different types of organisms before it is dissipated. Moreover, interactions among the organisms themselves, and between the organisms and the nonliving environment, produce an orderly cycling of elements such as nitrogen and phosphorus. Energy itself must be constantly added to the ecosystem, but the elements, as we shall see in future chapters, are cycled through the organisms, returned to the soil, decomposed by soil bacteria and fungi, and recycled. These transfers of energy and this cycling of elements involve complicated sequences of events, and in these sequences each group of organisms has its own particular and highly specific place. As a consequence, it is impossible to change a single element in an ecosystem without the risk of destroying the carefully developed balance on which its stability depends.



I-6

The four seasons in a deciduous forest in Illinois. In such forests, characteristic of much of the North Temperate zone, the trees produce their leaves early in spring and begin to manufacture food; they lose them again in the autumn and enter an essentially dormant condition, thus passing the unfavorable growing conditions of winter. Food manufactured in the leaves is carried throughout the plant and deep into the earth to reach the farthest roots. At the same time, water and minerals are carried in a continuous stream up through the roots, stems, and leaves. Most of the water is lost from the leaf as water vapor through the same specialized pores in the leaves, the stomata, through which carbon dioxide enters. Many herbs grow under the trees, and a number of these flower very early in the spring, before the leaves of the trees have reached full size and shade the forest floor. Most of the trees shed their pollen in large quantities in spring, and it is carried by the wind, sometimes reaching the flowers of other trees of the same species.

PLANTS AND MAN

Man is a relative newcomer to the world of living things. If we were to measure the entire history of the earth on a 24-hour time scale, starting at midnight, cells would appear in the warm seas at about dawn and then we would pass through the day and the twilight. The first multicellular organisms would not be present until well after dark, and man's earliest appearance (about one million years ago) would be at less than ½ minute before the day's end. Yet man, more than any other animal—indeed almost as much as the plants that invaded the land—has changed the surface of the planet, shaping the biosphere according to his needs, his ambitions, or his follies.

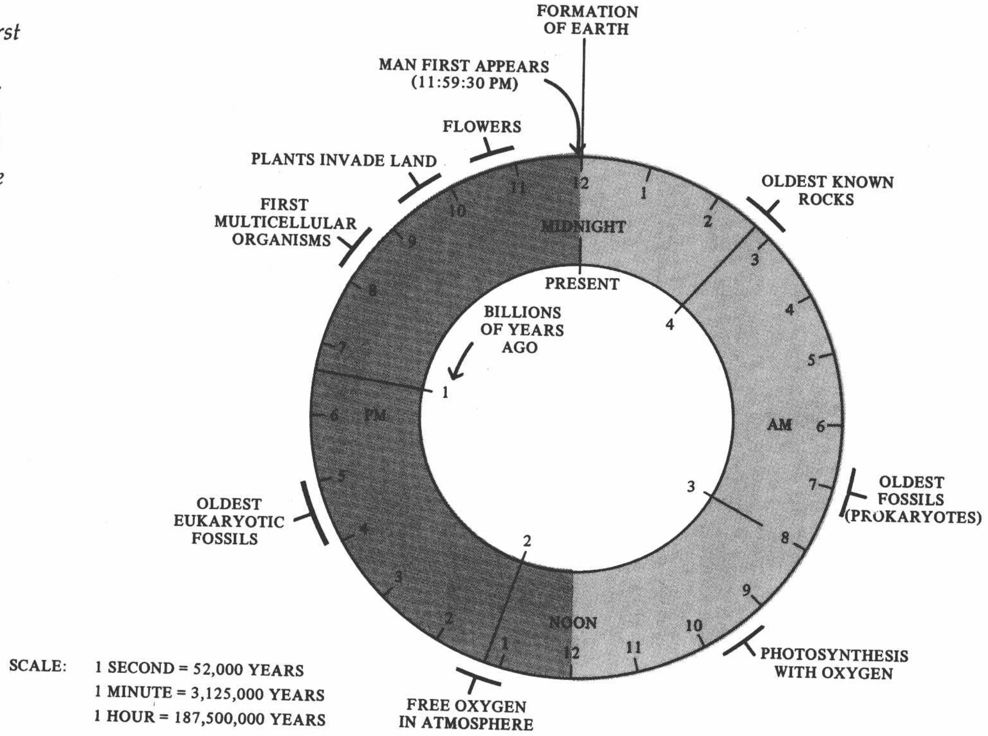
At the close of the Pleistocene epoch, some 10,000 years ago, man was already the most widely distributed land mammal. Humans, who then numbered about 5 million, were hunter-gatherers, living in small nomadic bands. The stage was set for the first major advance that allowed rapid expansion of the human population: the development of agriculture.

Origins of Agriculture

The reasons for the change to the agricultural way of life are not clear. One factor seems to have been changes in the climate. The most recent of the glaciations began to retreat about 18,000 years ago, withdrawing slowly for about 6000 years. As the glaciers retreated, the plains of northern Europe and of North America, once cold grasslands or steppes, gave way to forest. The great herbivores that roamed these steppes retreated northward and eventually vanished; the woolly mammoth was last seen in Siberia about 12,000 years ago. While some animals became extinct, men adapted, as they had during the entire period of violent climatic changes that have marked their evolutionary history. With the migratory animals gone, man shifted his attention to smaller game, such as deer, which tended to be resident in the same area throughout the year. Fishing became an important part of the economy at this time also; ponds and lakes were filling, and streams were rushing with waters from the melting glaciers. Hunters made canoes and paddles and seines and other fishing equipment. The hunting and gathering of small animals—instead of large migratory herbivores—undoubtedly resulted in a less nomadic existence for the hunters and formed a prelude to the agricultural revolution. (However it should be noted that similar fluctuations had occurred previously in the history of man without leading to a cultural revolution.)

The Transition

The earliest traces of agriculture are found in an area in the Near East generally known as the Fertile Crescent. Here were the raw materials required by an agricultural economy: cereals, which are grasses with seeds capable



I-7
The clockface of biological time. Life first appears relatively early in the earth's history, before 7:00 A.M. on a 24-hour scale. The first multicellular organisms do not appear until the twilight of that 24-hour day, and man himself is a late arrival—at about 20 seconds to midnight.

of being stored for long periods without serious deterioration, and herbivorous herd animals, which can be readily domesticated. The grasses in the Fertile Crescent were wild wheats and barley; they still grow wild in these foothills. The animals were wild sheep and goats.

Although we do not know exactly when or where it first happened, the first deliberate planting of seeds can be seen as the logical end of a simple series of events. The wild cereals are weeds, ecologically speaking; that is, they grow readily on open or disturbed areas, patches of bare land where there are few other plants to compete with them. Also, early man, judging from his campsites, was not very tidy. It is easy to envision how seeds might be spilled or discarded with garbage on open land around man's habitations. And the presence of the archaeological remains of what are clearly permanent dwellings indicates that men were staying in one place long enough to recognize and reap their accidental harvest. From this it would have been an easy step to the deliberate saving of seeds and tending of crops.

Because men selected the seeds that they gathered and planted, they soon produced changes in the wild strains. In wild wheats, for instance, the stalk (rachis) on which the flower clusters grow and on which, eventually, the seeds develop, becomes brittle when the seeds mature and breaks off, scattering the seed. Among these wild plants, occasional mutants can be found in which the rachis is not brittle. It is these plants, at a disadvantage in the wild, that are more likely to be harvested by men and, as a consequence, more likely to be planted. Thus, just as men came to be dependent upon their crop plants, the plants they grew for food—such as cereals that could not seed themselves—came to be dependent upon man.

About 11,000 years ago, new cultures appeared around the Fertile Crescent. They were characterized by implements associated with the harvesting and processing of grains, such as flint sickle blades, grinding stones, or stone mortars and pestles.

By 8100 years ago, agricultural communities were established in eastern Europe; by 7000 years ago (about 5000 B.C.), agriculture had spread to the western Mediterranean and up the Danube into central Europe, and by 4000 B.C., to Britain. During this same period, agriculture originated separately in Central and South America, and perhaps slightly later in the Far East.

From the Old World sites, we have fossil imprints of cultivated wheat and barley, remains of domesticated goats, sheep, and cattle, and pottery vessels, stone bowls, and mortars. The farmers of the New World grew corn, pumpkins, squash, gourds, and cotton. The potato, the sweet potato, the peanut, and the tomato are also examples of New World crops. Today, of course, the vast majority of all the foods we eat is the result of deliberate cultivation.

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Primitive methods of wheat production in Lebanon.

The Consequences of the Agricultural Revolution

The change to agriculture had profound consequences. Populations were no longer nomadic. Thus, they could store food not only in silos and granaries, but in the form of domesticated animals. In addition to food stores, other possessions could be accumulated to an extent far beyond that previously possible. Even land could be owned and accumulated and passed on by inheritance. Thus, the world became divided into semipermanent groups of haves and have-nots, as it is today.

Because the efforts of a few could produce enough food for everyone, the communities became diversified. People became tradesmen, artisans, bankers, scholars, poets, all the rich mixture of which a modern community is composed. And these people could live much more densely than ever before. For hunting and food-gathering economies, 5 square kilometers, on the average, are required to provide enough for one family to eat.

One immediate and direct consequence of the agricultural revolution was an increase in populations. A striking characteristic of hunting groups is that they vigorously limit their numbers. A woman on the move cannot carry more than one infant along with her household baggage, minimal though that may be. When simple means of birth control—often just abstention—are not effective, she resorts to abortion or, more probably, infanticide. In addition, there is a high natural mortality, particularly among the very young, the very old, the ill, the disabled, and women at childbirth. As a result, populations dependent upon hunting tend to remain small.

Once families became sedentary, there was no longer the same urgent need to limit the number of births, and probably there was also a decrease in the mortality rates.

The Population Explosion

About 25,000 years ago there were perhaps 3 million people. By the close of the Pleistocene epoch, some 10,000 years ago, the human population probably numbered a little more than 5 million, spread over the entire world. By 4000 B.C., about 6000 years ago, the population had increased enormously, to more than 86 million, and by the time of Christ, it is estimated, there were 133 million people. In other words, the population increased more than 25 times between 10,000 and 2000 years ago.

By 1650, the world population had reached 500 million, many people living in urban centers, and the development of science, technology, and industrialization had begun, bringing about further profound changes in the life of man and his relationship to nature.

By 1976, there were more than 4 billion people on our planet (Table I-1). This is an almost incomprehensibly large figure; moreover, the rate of increase of this enormous population is also unprecedented. The birth rate in the United States has decreased drastically since 1972, and the population could stabilize during the next century. For the world as a whole, however, the population is growing at about 2.2 percent per year. This means that about 175 people are added to the world population every minute, about 250,000 each day, and 90 million every year. If this rate of increase is sustained, in place of the 4 billion people living in the year 1975, there will be 7 billion people on earth by the year 2000. Over a century, a 2.2 percent growth rate leads to an eightfold increase in population.

At the time of the World Food Conference held in Rome in November 1974, it was estimated that at least 460 million people were suffering from hunger and severe malnutrition, whereas another 1.5 billion were con-

Table I-1 *A demographic summary of peoples of the world. (Taken from Environmental Fund 1975)*

	1975					1958–1963	1965
AREA	POPULATION ESTIMATES (MILLIONS)	GROWTH RATE (%)	BIRTH RATE (PER 1000)	DEATH RATE (PER 1000)	POPULATION UNDER 15 (%)	GROWTH RATE (%)	BIRTH RATE (PER 1000)
Africa	420.1	2.8	47.0	21.0	44	2.3	46
Asia	2407.4	2.5	39.0	14.0	>40	1.8	38
Europe	474.2	0.8	15.4	10.4	26	0.9	19
Latin America	327.6	2.9	38.0	11.0	43	-	-
North America*	242.4	1.0	15.0	9.1	27	1.6	22
Oceania	20.9	2.1	23.0	9.7	33	2.1	27
World	4146.9	2.2	35.0	13.0	37	2.0	36

* Canada and the United States. At least half the growth shown derives from immigration.

sidered undernourished. The less developed countries of the world, with populations growing much more rapidly than the average, had an immediate need at that time for an additional 8 to 10 million metric tons of grain per year. Unless production is increased drastically, the United Nations has estimated that the annual deficit could reach 85 to 100 million metric tons of grain by 1985. The high cost of producing fertilizer due to the increasing world energy shortage is contributing severely to the problem. Consider the fact that the more than 5 million tractors in the United States alone require 30 billion liters (8 billion gallons) of fuel, the equivalent of the energy content in the food produced. As fossil fuels become more scarce and more expensive, the costs of food will continue to increase. For Americans, who spend on the average less than 20 percent of their personal income on food, this already occasions serious concern. For those in developing nations who may spend 80 to 90 percent of their income on food, it can be a death sentence.

Although there are gains to be made in bringing additional land under cultivation, the most promising approach seems to lie in the development of existing crops grown on presently cultivated land, in terms not only of their yield, but also of their protein content. Agricultural technology, including methods of irrigation, can also be improved considerably. These are among the most vital areas of concern to the plant scientist. The effort to stimulate agriculture by the development of new crop plants—especially grains—has been called the Green Revolution.

Enormous progress is being made. The production of wheat in Mexico has quadrupled since 1950. Between 1968 and 1972, India and Pakistan doubled their wheat production. China, the most populous nation in the world, has become agriculturally self-sustaining, largely as the result of adopting these new strains. Techniques of breeding, fertilizing, and irrigation are being applied to rice and other crops in developing countries throughout the world. A new manmade hybrid, *Triticale,* one of the most promising products of this program, is described on page 162. Among the important areas of current research are the improvement of photosynthetic efficiency and the fixation of atmospheric nitrogen; both will be discussed in later chapters.

Despite its acknowledged success, this massive effort has come under criticism in recent years. One reason is the increasing cost of fertilizer; these new grains require intensive cultivation. Because the large landowners are able to afford the investment in fertilizer and farming equipment that the small-scale farmers cannot, these new agricultural developments are seen as accelerating the consolidation of farm lands into a few large holdings by the very wealthy. Bad weather—both droughts and floods—diminished yields in 1972, 1973, and 1974. Most serious of all, although food production is still outstrip-

(a)

(b)

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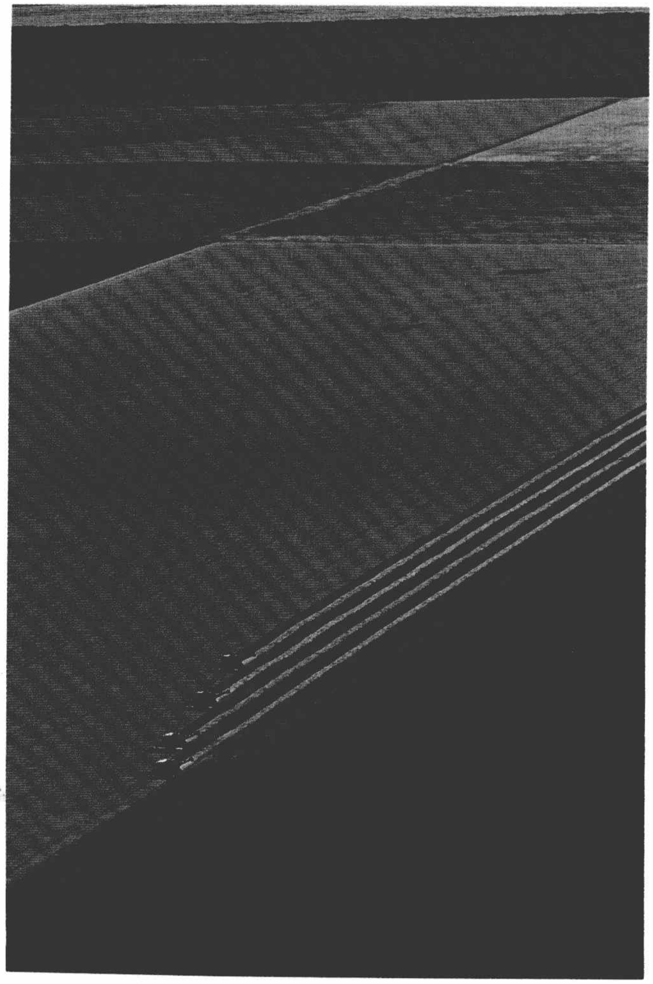
(a) *Norman Borlaug, who was awarded the Nobel Peace Prize in 1970. Borlaug is the leader of a research project sponsored by The Rockefeller Foundation under which new strains of wheat have been developed in Mexico. Widely planted, these new strains have changed the status of Mexico from that of a wheat importer when the program began in 1944 to that of an exporter by 1964.* (b) *Field workers weeding a rice plot at the International Rice Research Institute in the Philippines. The most recent strains are highly disease-resistant; however, they will grow only on irrigated land, which forms only about 30 percent of the cropland in Asia.*

ping population growth, the Green Revolution, at its most productive, will not be able to keep pace for long with the rapid growth of the world's population.

Finally, there is a more fundamental though more elusive reason for the dissatisfaction with the Green Revolution. When it was first introduced, it appeared to many to be an almost magical solution to problems so enormous and distressing that they had seemed insoluble. It is now clear, however, that poverty and famine and the unrest and violence they may bring will not be solved by a "technological fix." The Green Revolution must of course go forward. At the same time, we must recognize that the broader solutions are social, political, and ethical, involving not only the growth of food but its distribution, not only the limiting of populations but the raising of living standards of these populations to tolerable levels.

This introduction has ranged from the beginnings of life on this planet to the evolution of land plants and of plant communities to the development of agriculture and of modern society, with its most pressing current problem, the unprecedented growth of the human population. These broad topics are of interest to many people other than botanists. As we turn to Chapter 1, in which our attention narrows to a cell so small it cannot be seen by the unaided eye, it is well to keep in the back of our minds these broader concerns. A basic knowledge of plant biology is useful in its own right and essential in many fields of endeavor, but it is also increasingly relevant to some of society's most crucial problems and to the difficult decisions that will face us in choosing among the proposals for diminishing them. Thus this book is dedicated not only to the botanists of the future, whether teachers or researchers, but also to the informed citizens, scientists and laymen alike, in whose hands such decisions lie.



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Modern wheat production.