The Ecology of Plants

THIRD EDITION

GUREVITCH • SCHEINER • FOX

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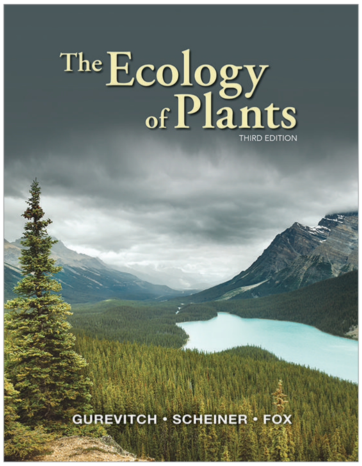

"Shades of Green"
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About the Cover

Peyto Lake and surrounding slopes in Banff National Park, Alberta, Canada (image reversed). The trees in the foreground are *Picea engelmannii* (Engelmann spruce); the high elevation forests in the photo also include *Abies lasiocarpa* (subalpine fir), and likely *Pinus contorta* (Lodgepole pine) and *Pinus albicaulis* (whitebark pine), interspersed with alpine meadows. Treeline is clearly visible, as is a sliver of a glacier. The surreal color of the lake is due to pulverized silt or "rock flour" ground by glaciers, and washed into the lake.

Back Cover

Top left: *Epilobium angustifolium* (fireweed, Onagraceae)

Top center: *Peonia suffruticosa* (Chinese tree peony, Paeoniaceae)

Top right: *Chondrosum gracile* or *Bouteloua gracilis* (blue grama, Poaceae)

Center left: *Crinum americanum* (swamp lily, Amaryllidaceae)

Center: *Banksia paludosa* (marsh or swamp banksia, Proteaceae)

Bottom left: *Gazania lichtensteinii* (yellow calendula or geelgousblom, Asteraceae)

Bottom center: *Leucospermum reflexum* (rocket pincushion, or perdekopspeldekussing, Proteaceae)

Frontispiece

Spatial pattern in spring wildflowers at Namaqua National Park, South Africa. Photo courtesy of Gordon Fox.

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From the Authors:
This book is dedicated to Andrew Sinauer,
who planted the seed and nurtured it into being.

JG
In memory of my parents, Esther and Louis Gurevitch,
and my teachers and students, for educating me.

SMS
To my mentors, Mike Wade, Jim Teeri, and Conrad Istock,
whose fingerprints are all over this book.

GAF
To Kathy, who has been with me for the whole journey.

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Preface

This book grew out of an informal chat at a conference. A long time ago (1994) in what seems like a galaxy far away, at the joint meeting of the Society for the Study of Evolution and American Society of Naturalists at the University of Georgia, one of us (GAF) was browsing the books on display by Sinauer Associates. Andy Sinauer struck up a conversation that at some point included the question "Who might be a good person to write a textbook on plant ecology?" GAF's immediate answer was something like, "I don't know," while he thought, "Please, not me!" Later that same day, in another of the casual chats that occur at academic conferences, GAF happened to mention this conversation to SMS, who expressed a similar feeling. A while later, as the two walked along, they returned to the topic, and one of them said something like "Well, we could do it if we involved someone else; how about JG?" Eventually the three of us went to Andy and told him that maybe we were interested after all. Andy encouraged us, but he also made clear what we'd have to do: write him a proposal convincing him that we knew what we were doing, and then actually go and write the book. We looked at one another with a bit of dismay and trepidation (well-founded, as it turned out).

Eventually we created the first edition. Along the way, some colleagues told us we were insane to undertake the project (too much time and effort, too little in the way of professional or financial reward, they cautioned). Many other colleagues and friends encouraged us. Our goal was to provide a comprehensive, readable textbook for an upper-level course in plant ecology, emphasizing a conceptual approach to the subject and an evolutionary focus. Evolutionary biology is essential to how we as scientists think about ecology, and we incorporated an evolutionary perspective throughout the book, as well as including a short introduction to the subject. We think we did that again and brought everything up to date, fixed some errors, added color illustrations, and published our second edition in 2006. The book brought us into contact with many students, instructors, and scientists we would not have had the opportunity to engage with otherwise, and we are grateful for that. Eventually it became apparent that we really were way overdue for bringing the book up to date, so 14 years later we are pleased to present a third edition.

Books don't write (or revise) themselves, and this book is certainly a collaborative effort. The order of authors' names must necessarily be printed in a linear fashion, and in most cases this implies the order of their contributions. In the case of this book, a circle would be more appropriate. The three authors of this book all contributed in multiple overlapping ways to the book; our contributions were different, but not greater or lesser. This book could not have been written by any one or two of us, and it very strongly reflects all our contributions and differing perspectives. It also offers a taste of our various senses of humor, and we hope that it provides at least a few chuckles to students and instructors wading through this sometimes intense and rather dense compilation of information and ideas.

We have been delighted with the response to the second edition of this book and have received many positive and useful comments from both students using the book and professors who have adopted it for their courses. The third edition is different in a number of respects. Most notably, 14 years have elapsed since the previous edition, and much has been learned in plant ecology as well as in ecology more broadly. We have endeavored to include new developments and new ideas, as well as new evaluations of older work. We hope that this edition will be useful in helping young ecologists make their way through the enormous literature of plant ecology and that we are effective in sharing our continued excitement about the discipline and our love for the natural world. We have added many new illustrations and photos and have updated and redrawn many others. In addition to including work published since the second edition, we have also reorganized and consolidated material and have developed certain sections to include a fuller treatment; for example, the material on how to think about and quantify diversity has been updated and consolidated into a single chapter; the explanations of Earth's climate and climate change have been integrated, sharpened, corrected, and we hope made clearer. Other, less central material has been deleted or shortened.

We assume that students using this book will have had an introductory course in biology, but they may or may not have had advanced biology courses and perhaps have not taken a course in general ecology. Recognizing that plant ecology may be the only ecology course a student will take, we have broadly covered the field of ecology, from individual plants through populations and communities, to large scale patterns and global issues. Thus, we strive to be comprehensive, albeit from a uniquely plant perspective. While topics are introduced at a basic level, there is sufficient depth, coverage, and leads to further references and information on the topics for more advanced students as well.

Plant ecology touches and builds on many subject areas that may not be covered in a typical introductory biology course. Therefore, we include background information that might be considered beyond the subject of plant ecology in its strictest sense. For example, we introduce aspects of plant anatomy and physiology, integrating the information on these subjects when we address herbivory and ecosystem ecology. We include common names, family affinities, and photos or drawings to make species more familiar to students. We discuss soils and belowground interactions, paleoecology, evolution, climate, and nutrient cycling in greater depth than might ordinarily be expected in an ecology text, and we address global climate change from the perspective of both the roles and responses of plants and those of people. Every college textbook is a reflection not only of the subject but of what the authors think is important and interesting, and this one is unabashedly so.

Ecology can be taught in many different sequences: it is conceptually a "hypertext" subject rather than a strictly linear one in which one topic clearly builds on the other and leads to the next one. For example, one can begin with ecophysiology of individuals and proceed to the global ecosystem; but the reverse order is equally valid. While we present the topics in a fairly conventional order starting from individuals and moving to global ecology, we recognize that other orders are equally logical and that different instructors cover the topics in a different order. In the classic film *The Wizard of Oz*, Dorothy reaches a crossroad and wonders aloud which way to go. The Scarecrow (who is still mounted on a post) points one way and says, "That way is a very nice way." Then he adds, pointing in the opposite direction, "It's pleasant down that way too." And so it is in ecology, including plant ecology. To facilitate those different approaches, we provide abundant cross-references for topics introduced or covered in other chapters. This book should be usable, therefore, in courses that begin with biomes, for instance, rather than with the ecology of individual plants.

Science has a language of its own. Acquiring that language can sometimes be daunting. Throughout the book we have placed words that may be unfamiliar in bold, and we have defined them in the text and in the Glossary. Scientific terminology may be tedious to learn, but it performs a necessary function: providing a concise and precise vocabulary that facilitates clarity and communication. In some cases, though, these definitions are presented not because we approve of the proliferation of jargon in ecology, but because these terms are commonly used, and students need to be familiar with them to understand the scientific literature.

Throughout the book we have provided an entry to the scientific literature through the use of examples and key references, incorporating key classic references as well as new literature and papers we think should be well known into the text itself. This edition has a longer bibliography than the previous editions, not only because more has been published, but because we believe strongly that science comes from work published in the scientific literature, and familiarity with this foundation is essential for students. Because of the large number of references, they have been collected into a searchable PDF available online at oup.com/he/gurevitch3e. An appreciation of both classic and contemporary work also helps convey some of the sense of plant ecology as a vibrant, dynamic, and exciting field of study.

Rather than presenting scientific information as a static collection of "facts," we attempt to portray the history and ongoing process of scientific study and discovery. By doing so, we hope to convey some of the excitement and turmoil that that process often involves, while showing how scientists learn how nature works. We extensively rewrote Chapter 1 to provide a stronger (and more modern) introduction to the philosophy of science, the theoretical underpinnings of the field, and the history of plant ecology—topics we think are essential parts of the education of ecologists. Because science is a human endeavor, we show the face of science by including photos of some of the important scientists (both classical and contemporary) whose work we discuss.

With the same goal, we include the first names of scientists whose work we discuss. While this is an unconventional format, we feel that it not only makes science more human, but also reveals the wonderful diversity of those doing important work in plant ecology. It adds something, somehow, in reading about the highly cited work of Waloff and Richards (1977), to learn that the first author was Nadia Waloff and to find out that she was a "formidable chain-smoking Russian entomologist" at Silwood Park of the Imperial College of London in the mid-twentieth century (Michael Crawley, unpublished); and to see, beyond the many Davids and Johns and Jameses, names that include Camille, Katherine, Valerie, Lynn, and Suzanne, and also Vigdis, Xianzhong, Mohamed, Akio, Ignacio, Govindan, Avi, Nerre Awana, and Staffan.

Acknowledgments

Plant ecology is also a global endeavor. As authors and scientists, the three of us have learned a great deal and benefited enormously from interaction with our colleagues and friends in many other countries. Our travels and sojourns internationally have been invaluable in expanding our understanding and knowledge about plant ecology and the natural world, and in providing the opportunity to take many of the photographs in this book. JG and GAF in particular owe their thanks to the Stellenbosch Institute for Advanced Studies for hosting us for an invaluable visit in 2014. We are delighted to know that students from many different countries have learned from the previous editions of this book. We hope that this edition will reach many more people in more places in the future.

For the third edition, we received comments, reviews, and corrections from Laura Aldrich-Wolfe, Peter Alpert, Mario Bretfeld, Cynthia Chang, Rebecca Cook, Jeffrey D. Corbin, Robert D. Cox, Michael Fleming, Zachariah K. Fowler, Suzanne Koptur, Daniel Laughlin, Diane Marshall, David McKenzie, Kerrie Sendall, Jeffrey Stone, Sarah M. Swope, Amy Trowbridge, Alexandra Wright, and several anonymous reviewers; we are much indebted to all of them, as well as to our colleagues and students who have offered comments and suggestions and pointed out errors on previous editions and along the way as we worked on this one. JG thanks Alan Robock, who helped clarify many issues and who answered many pesky questions about climate for this book and from whom she learned a great deal about the complex subject of climate science. Graham Chapman and his colleagues contributed at least one joke. Any errors, flaws, and oversights that remain are of course ours.

Textbooks are much more than just the words they contain; a well-produced textbook also includes illustrations that are attractive and instructive, has a useful index, and is laid out and assembled in a way that makes it appealing, readable, and accessible. Sinauer Associates and its new parent company, Oxford University Press, have long records of publishing scientific texts with these qualities, while at the same time managing to make the books accessible by keeping prices considerably lower than other publishers. We are delighted to continue our association with SA and OUP. But books aren't produced by a faceless company pressing buttons; special thanks are due to the skilled professionals who have worked so hard to make it happen. Jason Noe was our Aquisitions Editor, and a key player on our team for this book. We are especially grateful to Kathaleen Emerson, the supervising editor who provided a quiet and skillful hand to steering the project to completion; to Chandra Linnell, our skillful, patient, and driven production editor; and Lou Doucette, our copyeditor, who sometimes knew what we meant (or what we should have meant) even better than we did and who asked rather penetrating questions when she wasn't sure (because we hadn't made it clear). Jan Troutt's scientific illustrations and art grace this edition of the textbook and enhance both the science and the esthetics; it has been a delight to work with her. Mark Siddall's keen eye was invaluable in obtaining and choosing many of the photographs for the book, as well as overseeing the many issues about the photography used to illustrate the science and provide context for the words. Many friends, colleagues, and strangers generously shared their photographs for publication, sharing their passion for the organisms and landscapes they photographed. Michele Beckta meticulously oversaw the crucial job of obtaining permissions for figures and illustrations. Grant Hackett composed the very professional and useful index. The book was designed by project leader Meg Britton Clark, who along with Michele Ruschhaupt created the stunning page layouts. The cover was designed by Donna DiCarlo, and Joan Gemme provided exceptional support and overall project management. And we must mention that the final production of the book was carried out in the course of a global pandemic that had all of us working from home. Thank you all!

We began with a question from Andy Sinauer, and we want to thank Andy not only for his patience and wise advice about the first two editions of this book, but also for his larger contribution to our field. By publishing high-quality books in ecology and evolution for decades and by his encouragement and support for their authors (including the three of us), Andy provided an enormously valuable contribution for the sciences of ecology and evolutionary biology. We wish him well in his retirement.

Our spouses, children, and colleagues tolerated us while we were writing and revising this book rather than doing all of the things we were supposed to be doing or that they wished we were doing. We appreciate their forbearance. To all the students who use this book, we hope that you enjoy the book and learn a lot from it, and that some of you will go on to make scientific contributions of your own.

JESSICA GUREVITCH

SAMUEL M. SCHEINER

GORDON A. FOX

April, 2020

Go to oup.com/he/gurevitch3e to access the following resources for *The Ecology of Plants* 3e:

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Textbook Figures and Tables – provided in both JPEG and PowerPoint formats.

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Literature Cited – now online as a PDF for reference.

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1

The Science of Plant Ecology

The biological science of **ecology** is the study of the relationships between living organisms and their environments, the interactions of organisms with one another, and the patterns and causes of the abundance and distribution of organisms in nature. In this book, we consider ecology from the perspective of terrestrial plants. Plant ecology is both a subset of the discipline of ecology and a mirror for the entire field. In *The Ecology of Plants*, we cover some of the same topics that you might find in a general ecology textbook, while concentrating on the interactions between plants and their environments over a range of scales. We also include subjects that are unique to plants, such as photosynthesis and the ecology of plant-soil interactions, and others that have unique aspects in the case of plants, such as the acquisition of resources and mates. While we focus largely on terrestrial plants, we include freshwater and wetland plants in some discussions. Our emphasis is on the seed plants, particularly eudicots and monocots because they constitute much of the diversity in terrestrial environments, but we also discuss gymnosperms, which are dominant plants in some environments.

Above: The HMS *Beagle* sailed from England December 27, 1831, on a 5-year mission to chart the oceans and collect biological information from around the world.

1.1 Ecology Is a Science

Ecologists study the function of organisms in nature and the systems they are part of. Applied ecologists and conservation biologists are particularly concerned with the use of ecological principles to solve environmental problems, while fundamental ecology is concerned with basic knowledge of ecological principles, processes, and patterns. Sometimes the distinction between fundamental and applied ecology becomes blurred, as when the solution to a particular applied problem reveals underlying understanding about ecological systems. In both fundamental and applied ecology, the rules and protocols of science must be rigorously followed.

Ecology is *not* environmental advocacy or political activism, although ecologists are sometimes environmental activists in their personal lives, and environmental activists may rely on ecological research. Ecology is not about one's feelings about nature, although ecologists may have strong feelings about what they study. Ecological systems are complex, with a great many parts, each of which contributes to the whole in different ways. But ecology is indeed a science, and it works like other scientific disciplines.

Here it is important for us to call your attention to a major point. Much of the content of this chapter concerns the nature of science and the scientific method. Many students, at this point, may yawn and conclude that they do not need to pay much attention because they already know about the scientific method, and some students may feel that such discussions are dull and pointless. You might be surprised to know that the scientific method and the nature of science itself have always been the subjects of heated intellectual debate. In recent years it has even led to political controversy and a great deal of confusion among the general public about what is and what is not science and what value science has. The nature of science and the scientific method is the essence of how scientists add to and confirm scientific knowledge, and doing science, as well as learning science, requires a nuanced and thoughtful approach.

How do we know whether something is true? Science is one way of knowing about the world—not the only way, but a spectacularly successful one. In contrast to some of the other ways of knowing that are part of our lives, the legitimacy of science is not based on authority, or opinion, or democratic principles, but on the weight of credible, repeatable evidence.

Why is this characteristic of science so important? Consider the contrast between a scientific approach to an environmental issue—say, the consequences of fragmentation for the persistence of tropical rainforests—and an aesthetic approach. Addressing this issue from a scientific perspective might involve asking questions about how changes in the relative amount of forest edge will affect the physiology of some of the tree species, how these physiological changes translate into effects on population growth, and how dispersal between remaining fragments will affect these populations as a whole. By contrast, an aesthetic approach—often seen in popular literature on conservation—might emphasize the beauty of the intact forest. There is nothing wrong with this approach—indeed, many ecologists speak quite freely about such aesthetic values. But these values are not science; it is not meaningful to debate whether intact forests or fragmented forests are more beautiful, because there is no evidence that one could bring to bear that would settle the issue.

We could make a similar argument if we compared the scientific approach with moral, religious, or artistic approaches: the conclusions one might reach with nonscientific approaches do not depend on testing empirical evidence. This is not to say that only science is worthwhile; indeed, these other ways of interpreting the world play a large and critical role in our individual lives and in human societies. But they are fundamentally different from science.

Where does scientific knowledge come from?

Throughout this book, we examine how ecologists have come to their current knowledge and understanding of organisms and systems in nature. Ecology has both a strong and a rich theoretical basis and has developed from a foundation based on an enormous collective storehouse of information about nature.

Ecology, like all of science, is built on a tripod of pattern, process, and theory. **Patterns** consist of the relationships between elements or entities of the natural world. Processes are the causes of those patterns. **Theories** are the explanations of those causes. When ecologists carry out original scientific research, they seek to document patterns, understand processes, test and validate their understanding of those patterns and processes, and ultimately put together theories that explain what they have learned.

There is a distinction between the kind of research a scientist does and the kind of research done for a term paper, or by any member of the public trying to gather information about a topic using textbooks (such as this one), library books, or material posted on the internet. Although there are exceptions, the kind of research carried out by students or the general public is usually **secondary research**: gathering and summarizing facts that are already known. This kind of research is not only useful, but essential: every scientific study must begin by assessing what is already known. But the heart of what research scientists do is **primary research**: gathering information that no one has ever known before, confirming or refuting patterns and explanations from other scientific studies, or coming up with new, testable ideas about how nature works. These experiences of discovery are what make doing science so incredibly exciting and fun.

Scientists gain knowledge by using the **scientific method**. They carry out a series of steps, although not always in a fixed order (Figure 1.1). In ecology, these steps can be summarized as follows: observation, description, quantification, posing hypotheses, testing those hypotheses using experiments (in a broad sense of the word, as discussed below), and verification, rejection, or revision of the hypotheses, followed by retesting of the new or modified hypotheses. Throughout this process, ecologists gather various kinds of information, look for patterns or regularities in their data, and propose processes that might be responsible for those patterns. They often put together some kind of model to help in advancing their understanding. They construct theories, using assumptions, data, models, and the results of many tests of hypotheses, among other things. The building of comprehensive scientific theories proceeds simultaneously from multiple directions and involves numerous people, sometimes working in synchrony and sometimes at cross-purposes. Science in operation can be a messy and chaotic process, but out of this chaos comes our understanding of nature.

The construction of scientific theories is central to the scientific method. The word *theory* has a very different meaning in science than it does in common usage. A scientific theory is a broad, comprehensive explanation of a large body of information that, over time, must be supported and ultimately confirmed (or rejected) by the accumulation of a wide range of different kinds of evidence (Table 1.1). In popular usage, the word *theory* usually refers to a limited, specific conjecture or supposition, or even a guess or hunch. Equating the meaning of a scientific theory with "a guess" has caused no end of mischief in the popular press and in public debates on politically charged issues. A well-known example is the theory of evolution by natural selection: While sometimes portrayed as "just a theory" by creationists and advocates of "intelligent design," it is actually a comprehensive and rigorously tested explanation of an enormous amount of evidence from experiments and documentation of patterns in nature. In fact, it is one of the best-tested theories in biology.

When a theory is buttressed over many years by the accumulation of strong evidence, with new findings consistently supporting and amplifying the theory while producing no serious contradictory evidence, it becomes an accepted framework or pattern of scientific thought from which new speculation can spring. This is what occurred with Einstein's theory of relativity and Darwin's theory of evolution. Scientists use such overarching theories to organize their thinking and derive additional predictions about nature.

The ultimate goal is to produce a **unified theory**, consisting of a few, general propositions that characterize a wide domain of phenomena and from which can be derived an array of models. The best example in biology is the unification of Darwin's theory of natural selection with Mendel's theory of particulate inheritance. This unification—largely complete by the 1940s—allowed biologists to derive many specific models and testable predictions and to amass a large and coherent body of information and knowledge about the natural world, including many discoveries, both practical

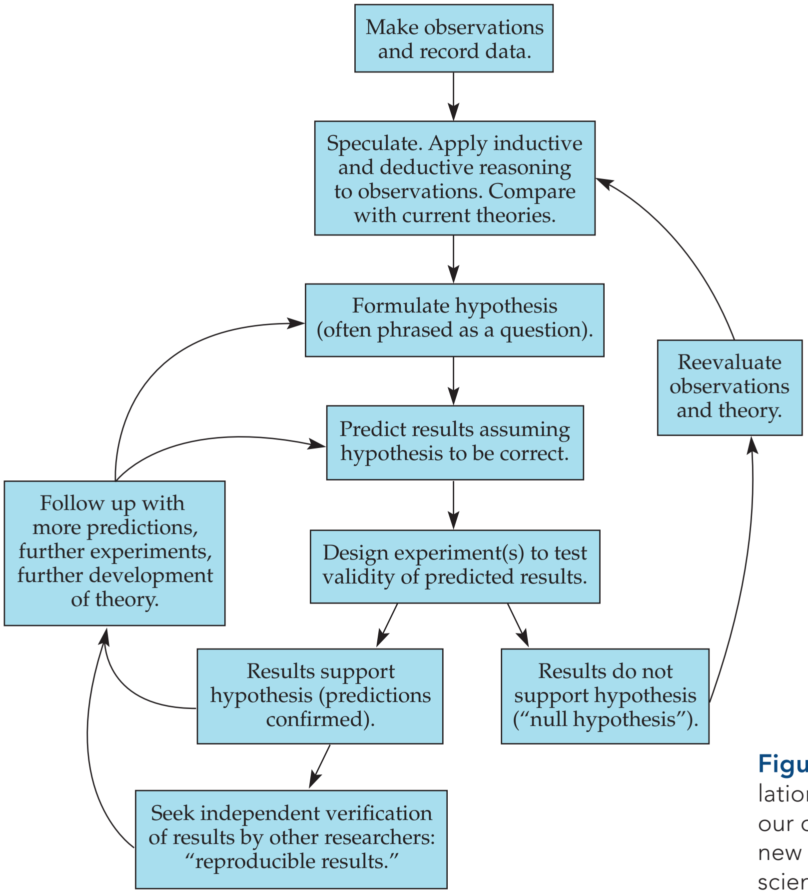


Figure 1.1 The scientific method. The cycle of speculation, hypothesis, and experimentation is a spiral, with our overall understanding of the world increasing as new questions constantly emerge from the answers scientists obtain.

TABLE 1.1 The components of a scientific theory

Component	Description
Assumptions	Conditions or structures needed to build a theory or model
Concepts	Labeled regularities in phenomena
Confirmed generalizations	Condensations and abstractions from a body of facts that have been tested
Definitions	Conventions and prescriptions necessary for a theory or model to work with clarity
Domain	The scope in space, time, and phenomena addressed by a theory or model
Facts	Confirmable records of phenomena
Framework	Nested causal or logical structure of a theory or model
Fundamental principle	A concept or confirmed generalization that is a component of a general theory
Hypotheses	Testable statements derived from or representing various components of the theory or model
Laws	Conditional statements of relationship or causation, or statements of process that hold within a universe of discourse
Model	Conceptual construct that represents or simplifies the natural world
Translation modes	Procedures and concepts needed to move from the abstractions of a theory to the specifics of model, application, or test

Source: After S. T. A. Pickett et al 1994. *Ecological Understanding.* Academic Press. San Diego, CA.

(of benefit to humanity) and fundamental (increasing understanding of living organisms).

A scientific **hypothesis** is a possible explanation for a particular observation or set of observations. A hypothesis is smaller in scope than a fully developed theory. Hypotheses must be testable by containing a prediction or statement that can be verified or rejected using scientific evidence. Experiments are the heart of science, and we discuss their design and use in more detail later in this chapter. A crucial characteristic of science is the need to revise or reject a hypothesis if the evidence does not support it. In science, hypotheses are not accepted based on belief. A scientist should not say, "I believe in human-caused climate change," but rather, "I am convinced by the accumulation of abundant evidence for human-caused climate change."

Some of the most important tools in the scientist's toolkit are models. A **model** is an abstraction and simplification that expresses structures or relationships. Models are a way in which the human mind attempts to understand complex structures, whether in science or in everyday life. Building a model airplane from a kit can tell you a lot about the basic form of an airplane; similarly, civil engineers often build small models of structures such as bridges or buildings (earlier, as physical models and now as three-dimensional images on a computer) before construction begins. You have no doubt seen models of DNA and of chemical reactions, and you may have heard about global climate models, which we discuss at length in Chapter 16.

Models can be abstract or tangible, made of words or plastic. They can be diagrams on paper, sets of equations, or complex computer programs. In science, models are used to define patterns, summarize processes, and generate hypotheses. One of the most valuable uses of models is to make predictions. Ecologists deal almost exclusively with abstract models that can range from a simple verbal argument to a set of mathematical equations. One reason their models so often rely on mathematics is that ecologists are often concerned with the numbers of things. (Is a species' population size so small that it is becoming endangered? How rapidly is an invasive species spreading? How many species can coexist in a community, and how does this number change as conditions change?) Mathematical models offer well-defined methods for addressing questions in both qualitative and quantitative terms, and they require that many assumptions be made explicit. Some ecological models are verbal, some rely entirely on complex computer simulations, and others use relational diagrams (graphs).

All models are necessarily based on simplifications and rest on sets of assumptions. Those simplifications and assumptions (both implicit and explicit) are critical to recognize, because they can alert you to the limitations of the model and because faulty assumptions and unjustified simplifications can sink even the most widely accepted or elegant model. It is often more clear what assumptions are being made in a mathematical or a simulation model than in other model types, but since models are just representations of more complex things, no model ever can state every assumption it requires—any more than a sentence can do so.

Scientific research involves objectivity, subjectivity, choice, and chance

When you read a typical scientific paper, it may at first seem obscure and difficult to penetrate. The format follows a rigid protocol, designed for efficiently conveying essential information to other scientists. Ideas are tightly packaged, with a clear logical line running from start to finish. It may seem as if the researchers knew exactly what they would find even before they began. We will let you in on an open secret: that is not how much of real science works. The results may not be what was anticipated at the start of the study. The justifications for the research presented in a paper's introduction may have been thought up or discovered long after the research project began, or even after the work was finished. Serendipitous discoveries, surprising natural occurrences, or other unplanned happenstance may modify the original course of a research project. However, this misdirection is now starting to change. Increasingly, the goals and protocols of a project are posted before it is initiated, especially in medical studies. If modifications are necessary, the reasons are made clear when the results are published. And those justifications that were previously added to the paper's introduction should more properly be placed in the discussion section at the end of the paper and considered as new hypotheses to be tested in subsequent studies.

Ideas in science, especially in ecology, come from a variety of sources. While everyone knows that science is held to the standards of being objective and rational, that is only half the story. In order to reach a genuinely new understanding, subjectivity and creativity must also come into play. What one chooses to study is a subjective decision. Do I pay attention to the entire forest or the individual trees? Which forest, and what am I asking about it? Given those choices, there is usually a range of possible places to look for answers—another subjective decision. Do I travel to the Arctic or Amazonia, or study urban forests close to home? Such choices depend on the questions one wishes to ask, but the system one chooses to study also shapes the questions. While determining the answers must be objective, choosing what questions to ask, and how to ask them, is largely subjective.

Many scientific endeavors are highly creative as well. Coming up with a good experiment, looking at a seemingly intractable problem from a new perspective, switching gears after a disastrous laboratory failure, and pulling a large number of disparate facts together to build a comprehensive theory are all highly creative activities. Tests and confirmation must be objective and rational to be science. Starting from the known and leaping across to the unknown requires creative, synthetic, and sometimes other-than-rational thought processes, as in the famous example of Kekule's dreamy vision of snakes swallowing their own tails leading to his discovery of ring structures in organic chemistry.

Many scientific discoveries start with casual observations, as with Newton's proverbial apple. Or an idea may arise as a what-if thought: What if the world works in a particular way? Or a previous experiment may have raised new questions. Sometimes we ask questions about what is not present, or what does not exist, rather than noticing what is present. What makes a scientist most successful is the ability to recognize the worth of these casual observations, what-if thoughts, and new questions. From these sources, an ecologist constructs hypotheses and designs rigorous, objective experiments to test them.

Observational studies detect and quantify patterns

If we didn't know what patterns exist, there would not be anything to try to explain. Since the earliest humans, observations of nature and attempts to recognize patterns of all sorts have been central to human survival. Early scientists recognized and documented patterns in nature, and this work continues to the present. The first part of finding patterns is to observe what exists and does not exist, and to attempt to generalize those observations. The next step is to quantify observations. Pattern detection and quantification included much of the work of gradient analyses and ordinations (see Chapter 15). Modern observational studies rely on analysis of remotely sensed images, large databases of plant traits and other variables (see Chapter 10), and spatial distribution data. The goal of such studies is documenting and quantifying patterns, rather than hypothesis testing, but the results are often critical to hypothesis generation and future tests.

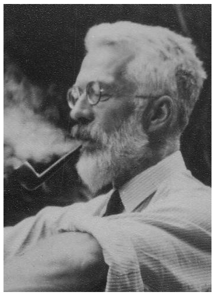
Experiments are central to research

A cornerstone of the scientific process is the **experiment**. We use the term *experiment* here in its broadest sense: a test of an idea. Ecological experiments can be classified into three broad types: manipulative, natural, and observational. **Manipulative experiments** are what most of us think of as experiments: a person alters a system in some way and looks for a pattern in the response. For example, an ecologist might be interested in the effects of nutrients on the growth of a particular plant species. One can grow plants under different nutrient treatments, replicating the plants exposed to the different treatments, measure such things as the height at flowering, and ask whether plants under one treatment are taller at flowering than under another. If the treatment groups differ, you have an answer!

This procedure sounds simple, but planning the experiment raises a number of questions. A central question is whether you can perform the experiment while making sure that the only things that vary are the parameter(s) of interest, such as the amounts of nutrients received by the plants. Classical scientific experiments—first laid out by Francis Bacon in the seventeenth century—vary only a single factor, and you may have learned that this is how experiments are properly done. Can you do this for a plant growth experiment? You might conduct the experiment in a growth chamber or greenhouse. You might try to rigorously control all of the sources of variation in your experiment, but experiments on living things invariably incorporate heterogeneity. Even controlled-environment growth chambers turn out to have environmental variation (e.g., some spots are warmer or cooler than others). You might unintentionally water plants at the rear less than others, because they are harder to reach. You might choose to use seeds that are highly inbred and do not vary genetically. But attempts to control variation have their own problems—the results may not be replicable if a greenhouse experiment is conducted at a different season, when the sun is at a different angle and daylight is longer. Even more problematic, they may not be replicable by other researchers, whose seeds and growth chambers differ. There may be no way to easily generalize your results.

Perhaps worse is this problem: plants grown in pots in artificial environments differ in a number of important respects from those grown in soil outside, so your results might not really be realistic. In sum, this sort of experiment can be useful, but it is also fraught with difficulties. It is easy to fool yourself into thinking that you have controlled all variation except in the factor that you are studying, and even if you have reduced that variation greatly, your results might not be generalizable beyond the conditions of the experiment. What to do?

Garden experiments are more realistic ecologically, with some factors controlled but many uncontrolled, and field experiments in nature may be the most realistic but with only the tested factors controlled and many other factors varying in an uncontrolled fashion. In a field experiment in a natural community, an ecologist might control one or a few factors—reducing herbivory and adding water, for instance, but factors such as soil, competing plants, and pathogens are uncontrolled and varying. One major approach to such experiments is, instead of attempting to control all variation, to randomize the variation due to factors other than the experimental ones among replicates, and base conclusions on the use of statistical inference. For a nutrient experiment in the field, you would need to take into account the fact that the soil probably varies in space, and you might need to think carefully about how to administer treatments so that plants with the same treatment receive the same doses of nutrients at the same time. The major tool used to design and analyze this kind of experiment is randomization. For example, you might assign replicated treatments to different areas (often called *blocks* in statistics). When you later analyzed the data, you would use standard techniques that allow you to account for the possibility that one block is, perhaps, wetter than others. Randomized experiments were first developed by Ronald A. Fisher (one of the founders of both modern statistics and population genetics) in the early twentieth century, and they are a mainstay of ecology and evolutionary biology. Their results are more generalizable than experiments that attempt to rigorously control all variation, because heterogeneity in responses is taken into account in the design and in the analysis of the results, instead of your having to try to eliminate it. Randomized experiments typically require larger samples than those in which you attempt to rigidly control variation. Where along this continuum of control versus realism ecologists carry out their experiments depends on practical considerations and on their scientific goals.

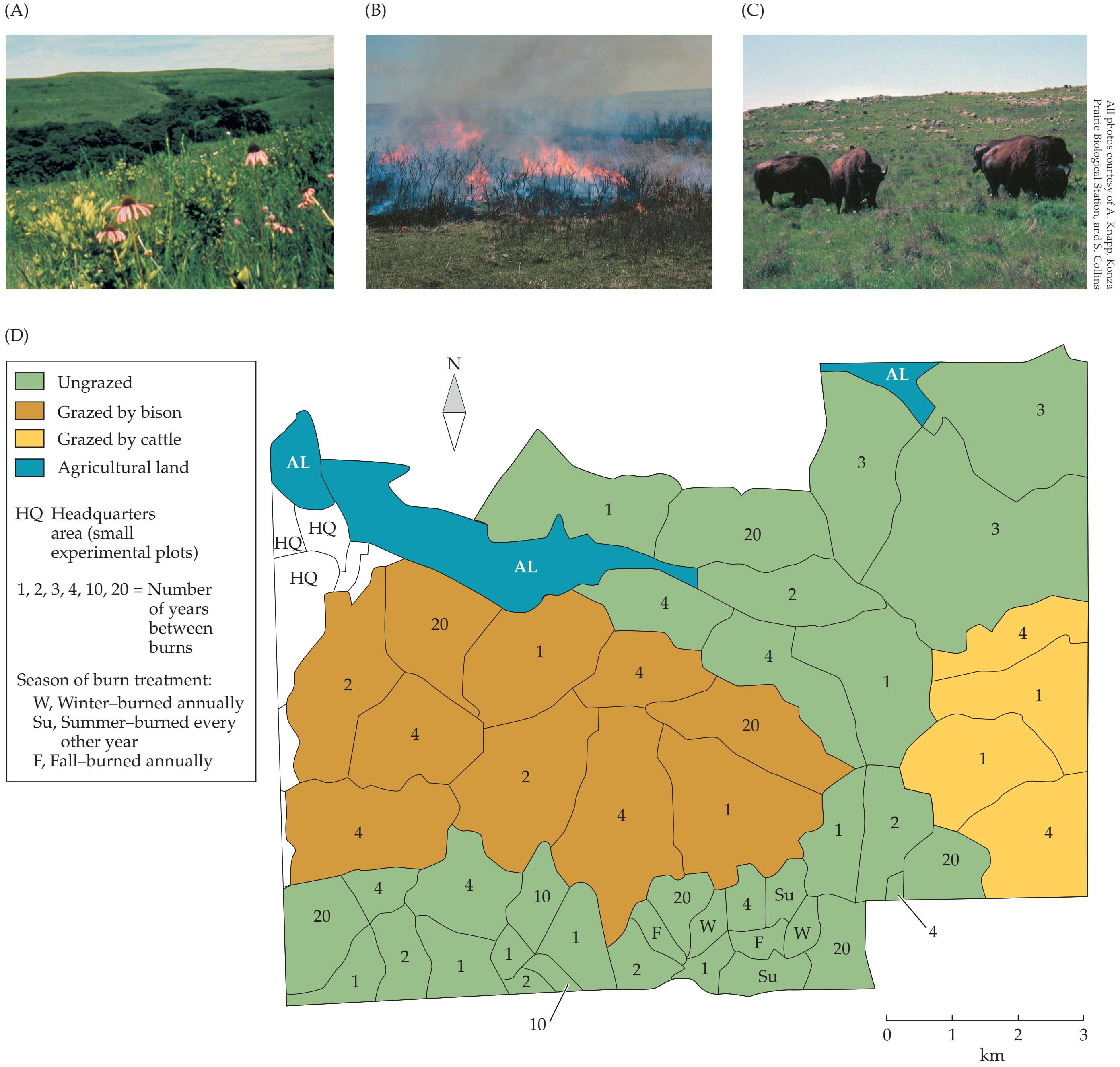


Courtesy of the University of Adelaide, Rare Books and Manuscripts

Ronald A. Fisher

These kinds of experiments (controlled environment, garden experiments, and experiments in natural communities) are called manipulative experiments, and they are powerful tools for two major reasons. First, the scientist can control which aspects of the natural world will be altered. Second, the experiment can separate factors that typically occur together so they can be tested individually. But there are also difficulties with manipulations. One problem is that sometimes they cause artifacts—outcomes that are side effects of the manipulation itself, rather than being responses to the experimental treatment being tested. For example, an ecologist interested in comparing seed production in self-pollinated versus open-pollinated flowers might place netting over some flowers to exclude pollinators. Seeds from those treated flowers would all be self-pollinated, but the flowers would also have experienced reductions in air flow and light, and this could conceivably affect seed production. A thoughtful experimenter might put netting on the "control" flowers but leave the netting open to pollinators as a way to get around this artifact, but it is often impossible in a biological system to really change only one thing at a time. Good experiments avoid or reduce artifacts, or they include ways to take them into account when the results are evaluated. As you read about experiments, consider what artifacts might be present that might explain some of the results.

There are also scales on which we cannot do experiments. Ecology is often concerned with learning about patterns and processes that occur across large extents of space and time—for example, finding why there are differences in the numbers of species on different continents, or predicting the responses of populations to climate change over the next two centuries. We cannot do manipulative experiments at these great extents of time and space, and in many cases, no true replicates (of continents, for example) could exist. Ecologists are increasingly making use of long-term and large-scale manipulative experiments (Figure 1.2; see Box 5B and Box 12D). Even so, there are often limits to the range of possible treatments. Prescribed fire must often be limited to particular seasons, for example, which may or may



All photos courtesy of A. Knapp, Konza Prairie Biological Station, and S. Collins

Figure 1.2 Large-scale manipulative experiments are being carried out at the Konza Prairie Research Natural Area in Kansas (A). Controlled burns (B) are done at various intervals to investigate the effects of fire and fire frequency on prairie communities. In addition, areas grazed by bison (C) are studied and compared with ungrazed areas and with plots subjected to cattle grazing. The experimental patches (D), which are watershed units, vary in size from approximately 3 to 200 ha. In this map, each patch is designated by a code indicating the burn treatment. Patches with the same code are replicates. All burns occur in spring, except for the seasonal burn treatments. (After A. K. Knapp et al. 1998. *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie.* Oxford University Press: New York.)

not be the seasons in which fire occurred naturally in the past. A more subtle problem of scale can occur when different parts of the system respond to the manipulation differently. For example, an ecologist might want to ask how much plant mortality is caused by drought in a desert plant and might design an experiment in which some plots get water added but others do not. Unfortunately, creating small patches of growing vegetation during a drought might well attract large numbers of herbivores, leading to more mortality among the watered plants. Because only experimental plots, and not the entire region, would receive more water, the treatment expected to reduce mortality might well increase it by attracting another source. Screening might exclude the herbivores, but it would also shade the plants and reduce wind on them, causing other responses.

Some types of experiments would be unethical to carry out. For example, we would not cause the extinction of a species just to study the effects of such an event. In such cases, ecologists must rely on two other types of studies. These are natural and observational studies, which may be thought of as different kinds of experiments.

A **natural experiment** is a “manipulation” caused by some natural occurrence. For example, a wildfire may occur in an area. Volcanic eruptions, hurricanes, and accidental introductions of pathogens are all examples of natural experiments whose effects ecologists have studied. Natural and manipulative experiments represent a trade-off between realism and precision, similar to the trade-off between laboratory and field experiments. Just as with a manipulative experiment, the ecologist compares the altered system either with the same system before the change or with a similar, unchanged system.

The major limitation of natural experiments is that there is never just a single difference before and after a change or between systems being compared. For example, if we are comparing sites burned in a wildfire with others that were not, the unburned sites might have been wetter, might have had different vegetation before the fire, or might be different in area. Natural experiments are essentially unreplicated. Therefore, it can be difficult to determine the true causes of any changes we might measure.

The best natural experiments are ones that repeat themselves in space or time. If we find similar changes each time, then we gain confidence about the causes of those changes. Another approach is to combine natural experiments with manipulative experiments. For example, the patches subjected to experimentally manipulated grazing and fire treatments at Konza Prairie (see Figure 1.2) are being compared with patches elsewhere, some of which are also experiencing grazing and fire but are not subjected to experimental manipulation.

Observational experiments consist of the systematic tests of hypotheses attempting to explain natural variation. Such observations are experiments if an ecologist starts with one or more hypotheses (predictions) to test. For example, one could measure patterns of species diversity across a continent to test hypotheses about the relationship between the number of plant species and productivity (see Chapter 19). A major limitation of this type of experiment is the potential for multiple factors to vary together. For example, if the number of herbivores is observed to increase as the number and productivity of plant species increases, the ecologist cannot be sure whether the increase in herbivores is a result of increased plant numbers and productivity, or whether the increased productivity is a result of increased herbivory.

As with natural experiments, observational experiments repeated in space or time add confidence to our conclusions (Figure 1.3). Other sciences, notably geology, climate science, and astronomy, rely strongly on observational experiments because of the spatial or temporal scales of their studies, or because direct manipulation is impossible. One way around this limitation is to run an “experiment” using a complex computer model. Variables in the model can be manipulated, and then the output from the model can be compared with empirical observations.

Ecological knowledge comes from combining information gained from many different sources and many different kinds of experiments. The ecologist’s use of this complex variety of information makes ecology a challenging and exciting science.

In ecology, “controls” are what you are using for baseline comparisons

All experiments involve comparisons. For example, an ecologist might compare how much leaf tissue is removed by insects when plants are raised in an environment with either enhanced CO_2 or ambient CO_2. Without the comparison, it would be difficult or impossible to interpret the cause(s) for the amount of herbivory in the enhanced CO_2 environment. Explanations of the scientific method often state that all experiments require a “control” treatment. A classic example is the typical medical experiment: some patients are given a pill that contains a drug, and others are given a placebo, a pill without the active ingredient, to control for psychologically caused effects of taking a pill, which can be substantial. This is an example of a null control treatment, one completely missing the studied factor. Null treatments can be useful but are not needed or even meaningful in all settings. In an experiment studying the effect of moisture availability on plant growth, it would not usually be meaningful to include a “no water” treatment as a control if all of the plants would simply die from no water. Instead, “control” treatments should be comparisons chosen to account for some possible cause, for example, comparing a treatment that just receives natural rainfall with one that includes additional watering.

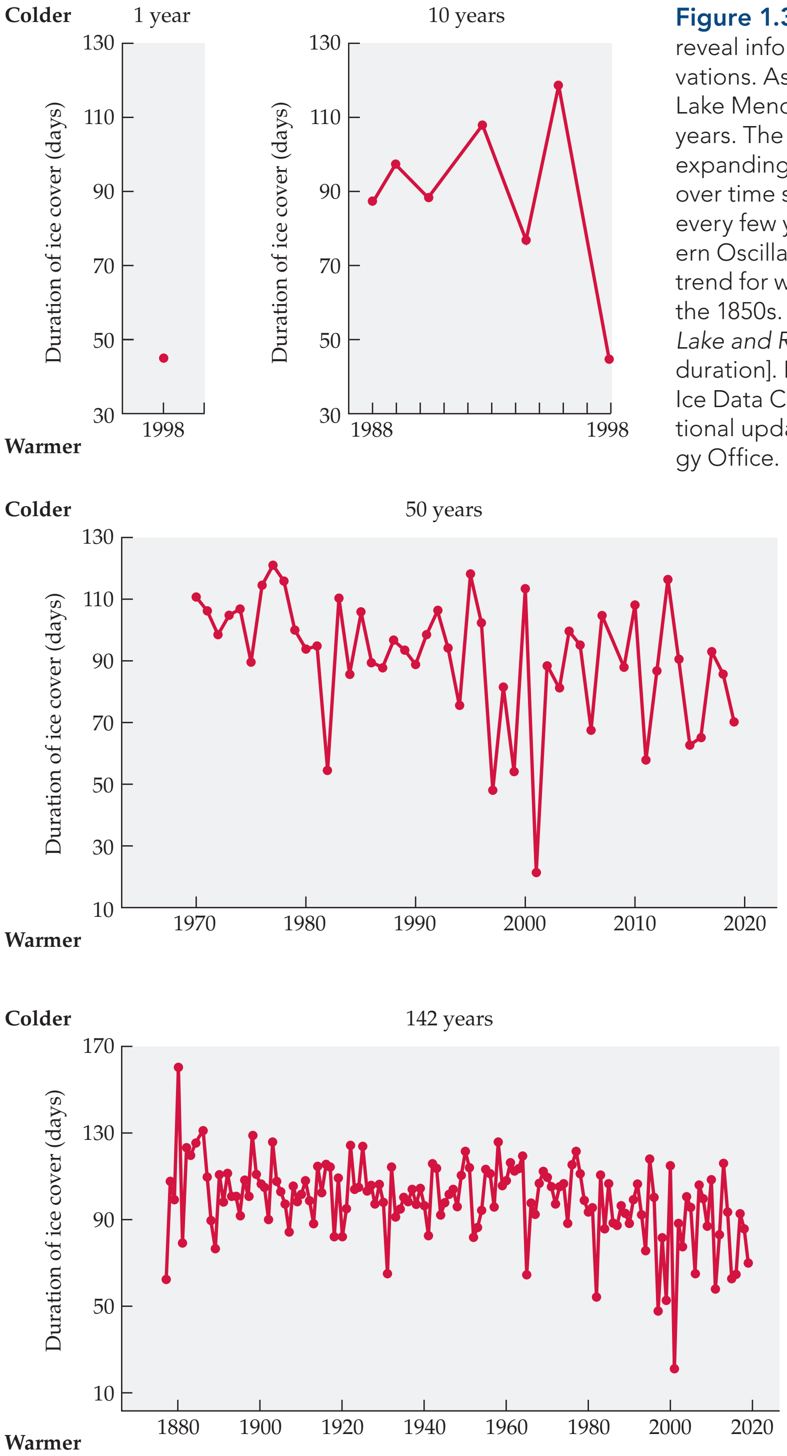


Figure 1.3 Repeated observations over space or time can reveal information that is not apparent from one or a few observations. As an example, records of the duration of ice cover on Lake Mendota, Wisconsin, have been kept for more than 158 years. The information for a single year is fairly meaningless, but expanding the context with increasing numbers of observations over time shows that there is a cycle of warmer winters recurring every few years (now known to be the result of the El Niño Southern Oscillation; see Chapter 16); and overall, there is a strong trend for winters in Wisconsin to be warmer now than they were in the 1850s. (Data from B. Benson et al. 2000, updated 2013. *Global Lake and River Ice Phenology Database*, Version 1. [Lake Mendota duration]. Boulder, Colorado U.S.A. NSIDC: National Snow and Ice Data Center. Doi: https://doi.org/10.7265/N5W66HP8); Additional updated data from E. Hopkins. 2020. Wisconsin Climatology Office. http://www.aos.wisc.edu/~sco/lakes/mendota-dur.gif.)

All treatments in a well-designed experiment should be chosen to make useful comparisons, and not for any other reason. Similarly, in randomized experiments, what one randomizes actually matters. We randomize to reduce possible biases—for example, we randomly assign individual plants to different treatments, to reduce the chance that plants receiving one treatment differ in some other way than just the treatment. Strict randomization can reduce all sorts of unintended biases, for example, to unconsciously choose the largest plants first for one particular treatment, or to put all of the plants for a particular treatment in a spot that happens to have the most moisture. Randomization, in other words, is a technique that should make our comparisons more meaningful. To then account for those randomized effects, we need statistics.

Statistical analysis of data is an essential tool in ecology and in science more generally. Ecologists use statistics for at least three reasons. First, we use statistics to describe data and search for patterns. In the case of prescribed fire, for example, an ecologist might find that in burned plots the average density of newly germinating individuals of *Pinus ponderosa* (Ponderosa pine, Pinaceae) was more than three times the density in unburned plots, but also that the variation in densities among plots was much greater for those that had burned. Averages and measures of variation are basic statistical descriptions of data. They might allow the ecologist to make statements about the relationship between fire and pine regeneration. Making such statements would involve the second reason ecologists use statistics: to assess hypotheses. In this case, ecologists might hypothesize that germination in this species depends heavily on fire. The third reason ecologists use statistics is to estimate quantities. For example, how much more germination occurs in burned sites, and how much does it vary? We often need these numbers either to evaluate the importance of particular processes, or to use in models (say, models of population growth or forest cover; see Chapter 8). While ecological statistics is much too large a subject to treat in this book (see Shipley 2000; Scheiner and Gurevitch 2001; Gotelli and Ellison 2004; Lindsey 2004; Fox et al. 2015), notice that almost every figure or table about real data includes statistics—for example, estimates of means, standard errors, and confidence intervals. As you read this book, consider what these quantities tell you.

How do we test theories?

The testing of scientific theories, especially ecological ones, is a more subtle, nuanced, and complicated endeavor than nonscientists or even students of science often realize. The popular image of the scientific method portrays it as a process of falsifying hypotheses. This approach was codified by the Austrian-born philosopher of science Karl Popper (1959). In this framework, we are taught that we can never prove a scientific hypothesis or theory. Rather, we propose a hypothesis and test it; the outcome of the test either falsifies or fails to falsify the hypothesis. While hypothesis testing and falsification is an important part of theory testing, it is not the whole story, for two reasons.

First, the falsification approach fails to recognize knowledge accumulation. In a strict Popperian framework, all theories are held to be potentially false. We never *prove* anything to be true; we merely *disprove* ideas that are false. This assumption goes against our own experience and the history of the accumulation of scientific understanding. Today we know that the Earth revolves around the sun, even though this was once just a hypothesis. We know that the universe is approximately 15 billion years old (give or take a few billion) and began with the Big Bang, even if we still do not know the details of that event. We know that life on Earth assumed its present shape through the process of evolution. We know that many diseases are caused by viral infections, not by “humours,” and that hereditary traits are conveyed by DNA (or in a few viruses, by RNA), not by blood. While we may acknowledge that all of this knowledge has not, in a strictly philosophical sense, been proved to be true but has only failed thus far to be falsified, we also recognize that some knowledge is so firmly established and supported by so many facts—by the accumulation of evidence—that the chance that we are wrong is infinitesimally small (Mayo 1996).

Second, and more important, is that the Popperian framework fails to account for a second type of question that we very commonly ask in ecology. Often the issue is not one of falsifying a hypothesis. Rather, we ask about the relative importance of different processes. When we examine the structure of a plant community, we do not ask, “Is it true or false that competition is occurring?” Instead, we ask, “How much, and in what ways, do the processes of competition and herbivory each contribute to shaping this community?” So, when we are building our theories about plant community structure, our activities are more akin to estimating the necessary quantities and assembling a complex model than to falsifying a set of propositions.

Falsification does play a role in science, but a more limited one than Popper envisaged. Theory construction is like assembling a jigsaw puzzle from a pile of pieces from more than one box. We can ask whether a particular piece belongs in this spot—yes or no—by erecting a hypothesis and falsifying it. We may even conclude that this particular piece does not belong in this puzzle. Less often are we attempting to completely throw away the piece, saying that it does not belong in any puzzle.

Controversy also plays an important part in ecology, as it does in all scientific fields. During the process of amassing evidence regarding the validity of a theory, different interpretations of experimental data, and different weights given to different pieces of evidence, will lead different scientists to differing opinions. These opinions may be passionately held and argued forcefully; discussion can sometimes become heated. As the evidence supporting a theory accumulates, some scientists will be willing to accept it sooner, while others will wait until the bulk of the evidence is greater (see Box 13A).

If the issue under debate has political or economic implications, nonscientists will also contribute to the debate and may be able to offer valuable insight, judgment, and perspective to the discussion. But when the evidence in favor of a scientific theory becomes overwhelming, and the vast majority of scientists knowledgeable in that field are convinced of its validity, then the matter becomes settled (unless startling new evidence or a new, broader theory forces a reevaluation). When a scientific consensus has been reached on a scientific theory, it is unreasonable to consider that theory to be just another guess or opinion and to hold that everyone’s opinion is equally valid. That may work for a democratic process, but it is not how science works. Opinions not supported by evidence are not the same as those supported by the weight of a great deal of evidence; giving them equal weight would be contrary to the way science works. The controversy over teaching creationism or “intelligent design” in science classes in American public schools is interesting in this light: Some have argued that since many Americans are persuaded by one of these viewpoints, they should be taught in science classes. Along with nearly all scientists, we argue instead that these ideas are not scientific ideas (because it is impossible to prove or disprove the existence and function of a deity, and no evidence can refute a faith) and that their only potential place in science classes is to illustrate the difference between science and religion.

The fact that scientists are the judges of science should not be interpreted as meaning that scientists should decide issues of public policy. For example, if scientists are in strong agreement about something—say, that if more than 50% of its remaining habitat is lost, then plant species X has a 90% chance of extinction within the next 20 years—that does not necessarily dictate any particular public policy. Policy decisions depend on how important people think it is to save species X and on what costs they are willing to pay to do so. While we personally hope this would never happen, we recognize that people who wanted (for whatever reason) to exterminate a plant species could use the scientific conclusions for their own ends, just as we could use those same scientific conclusions to promote conservation.

Ecologists also have a responsibility to carry out their research in an ethical manner. We have already mentioned one imaginary pertinent example: deliberately causing a species to go extinct to study the effects of that extinction. In that case, the ethical position is clear—unless, of course, we are considering the extinction of a deadly pathogen, such as the malaria parasite *Plasmodium falciparum.* Other situations are more complex, however, involving instances in which one must weigh the ethical values on either side of an issue. For example, how much of a protected area is it acceptable to disturb in order to study the processes that affect it? Is it acceptable to dig up some plants or cut down multiple trees? What if the study increases the chances that an endangered species might go extinct, even if only by a very small amount? A new field of ecological ethics is being developed that focuses on establishing ethical principles for ecological research and procedures for resolving ethical dilemmas (Minteer and Collins 2005).

We also have a responsibility to be ethical with respect to the science itself. Other scientists need to know how we gathered our data and how we analyzed it. In principle, the steps in every study should be understandable by any scientist, and therefore replicable. Many fields of science—including ecology—are experiencing what has been called a "replicability crisis" because single results are too often accepted without further replication. The movement toward "open science" emphasizes replicability, transparency, and other aspects of how we conduct science. We discuss several examples in this book in which ideas became widely accepted with remarkably little empirical support. Insofar as the scientific literature is not clear about what was done in a study, this cannot be resolved. These and other problems ecology faces in terms of academic transparency are summarized by Timothy Parker and his colleagues (2016).

Replication can be especially difficult in ecology. As Shinichi Nakagawa and Timothy Parker (2015) discuss, part of the problem is that different settings for studies are different. Can a study done in a tropical forest in Peru in 2015 be precisely replicated if we try to do so in a tropical forest in Brazil in 2020? Not always! But as Nakagawa and Parker point out, there are different sorts of replication. Replication of studies can be done to fairly account for measurement error, or it can be done to ask how general some results are. Many results can be expected to vary quantitatively if studies are done in different locations at different times, but if the results can be qualitatively replicated, they may have some generality. For example, the removal of herbivores in two different experiments might increase the total number of species in a plot, even if the exact numbers of species and their identities differ. While traditionally academic success at all levels has depended heavily on developing new results in new systems, the replicability crisis tells us that some of this is illusory: we need more replicative studies to actually assess our ideas.

Beyond being scrupulously honest in your experimental design, data collection, analysis, and writing, what can an individual scientist do? Deliberate dishonesty makes the replicability crisis worse, but it is only a very minor cause of the replicability problem. A number of things can help. Data were once regarded by many scientists as private property, to be guarded jealously. Today many journals and funding agencies require that the entire data set (not just the published portion) from a study be deposited in a freely available online archive, along with sufficient information (metadata) that a reader can interpret each column and row in the data file. Many journals and agencies also require that the computer code used to analyze the data be freely available online. Using these two measures, any scientist should be able to see how results were obtained and also reanalyze the data as desired. We strongly support these measures, and we urge future scientists to make their data and computer codes available even when not required to do so.

Another measure advocated by open science initiatives includes preregistration of studies and plans of data analysis. This is simplest to think about in the case of a drug study: if company A preregisters a study of what it hopes will be a promising new drug, and the study does not find that the drug is very helpful, the results cannot simply be hidden. Similarly, if you want to study the effect of prescribed fire on soil nitrogen, a preregistered study makes it clear what you plan to do and why. You might still change your plans, but then you would need to make clear that you did so, and why. Preregistration helps to reduce the problem of selectively publishing only studies that favor a desired outcome, sometimes called cherry picking. Cherry picking can also occur within a study: measuring 20 variables and then only publishing results about the one that you find interesting. But if data and computer code are public, including the parts of the data that we choose not to pursue, cherry picking becomes obvious. Highlighting unexpected findings is okay, but you need to treat those as new hypotheses to be further tested, rather than as a test of a hypothesis that was actually built only after seeing the data.

Open science presents both opportunities and challenges for ecology and for science as a whole. Not only can it help make our science more robust, it can foster interactions among scientists and between scientists and interested individuals outside of science. Learn more about it, and we hope that you too will embrace it.

Studies can lead to specific results but contribute to general understanding

Because ecologists work at such a variety of scales and on such a diversity of organisms and systems, the question arises about how far one can extend the conclusions of a particular study to other organisms or places. In the fields of chemistry and physics, the results of an experiment are considered to be absolutely true for all times and places: an atom of helium is made up of two protons and two neutrons, which in turn are made up of quarks, with no qualifications needed. This is the popular image of scientific theories.

Ecology is different. Do the results of a field experiment on competition between two plant species extend to other seasons or locations, or to other pairs of species within the same families or functional groups? Experiments involving helium deal with a universal entity, the helium atom. In contrast, in experiments on plant competition, the exact composition of the entities changes (e.g., the individual plants used each time are not genetically identical), and the surroundings change as well (e.g., the weather this year is different from last year). For this reason, extremely cautious scientists take the position that no conclusion can be extended beyond the particular conditions that existed when the experiment was conducted. These ecologists have argued that ecology is a collection of case studies. We do not agree. If this were so, ecology would not be a science, and there would be little value in doing any experiments, because anything they would tell us would be of such limited scope as to be virtually meaningless.

The truth is somewhere between the extremes of universal truth and a collection of disparate cases, creating a constant and dynamic tension in ecology. One approach to resolving this tension is to see how the outcome of a particular experiment fits into the workings of existing models, and whether it supports or rejects the predictions of those models. Another approach is to use methods for the quantitative synthesis of the results of independent experiments. These methods, known collectively as **meta-analysis** (see Box 10B), can be used to evaluate where the outcome of a particular experiment fits in with—or differs from—the results of other similar experiments conducted on different organisms at different places and times. This approach has been used to evaluate the broad body of experimental evidence for many important ecological questions (Gurevitch et al. 2001).

Science is ultimately consistent, but getting to consistency is a challenge

Science demands internal and external consistency. Ultimately, theories must be consistent with one another, and data must be consistent with theories, although contradictory data and theories can coexist for long periods of time before they are reconciled. Other ways of interpreting the world do not share this characteristic. Works of art can be self-contradictory. Systems of morality or religions may or may not include obvious contradictions, but none demand consistency with data, in any sense of the term.

It is important not to take this too far and conclude that only science is useful. Science is useful for addressing scientific questions (such as whether wildfires increase or decrease the species diversity of a forest), but not questions that cannot be addressed scientifically. Science cannot tell you how to behave, whether a novel is good, or what color clothing you should wear.

Making science internally and externally consistent is a constant effort. Theories—even successful ones—can contradict one another in places. Some experimental results seem to contradict theory at times. Well-designed studies can contradict one another. This is the stuff that allows our knowledge to continue to grow. The fact that we find contradictions simply means that we are still learning. Resolving those contradictions can be some of the most exciting areas of research.

1.2 Ecological Phenomena Are Heterogeneous in Many Ways

All electrons are the same. All ^{12}C atoms are the same. But we cannot make statements like this about ecological phenomena or processes. Individual plants within a clone are different from one another, and different salt marshes are certainly quite different from one another. Similarly, processes like herbivory or carbon cycling vary over time and space.

Most things ecologists study are heterogeneous, and we often need to account for that heterogeneity. A glaringly obvious example concerns weather: "average weather" is not actually what occurs anywhere, ever. If a study site experienced the average precipitation, there would be constant rainfall at a location—but of course, the site really experiences stormy periods and periods without much precipitation. Thinking about averages can be useful (it really is true, and meaningful, that on average, London is rainier than Tucson, Arizona) but for many purposes it is a mistake to think of averages as the only things that matter. Within a plant population, individuals experience different microhabitats, and (usually) they differ somewhat genetically; that heterogeneity can be important!

A great deal of recent interest in ecology has been generated by consideration of how ecological patterns and processes vary as a function of the scale at which they operate and are studied (see Figure 15.2). The same phenomenon can be seen very differently when studied within a small local area and across a landscape or region—that is, at different spatial extents. Likewise, one's perspective can change dramatically when studying an ecological process over a single growing season of a few months or over a period of decades or centuries (see Figure 1.3). Different kinds of things may be going on over different spatial extents, and expanding one's focus to more than one extent can be richly rewarding. In a study of a local community, for example, we might see that competitive interactions keep individual plants of a particular species at a distance from one another. At a larger extent, we might notice that the plants are grouped together across the landscape, because individuals that are too far apart from any others never become pollinated and fail to leave descendants or because the seeds have limited ability to disperse. At a regional scale, herbivory might be important in determining plant densities and occurrence, while at a continental extent, the plants may exist in several large but separated enclaves, determined by patterns of glaciation and species migration thousands of years in the past.

We often refer to these scale changes in terms of a hierarchy, and one can move up and down many different kinds of hierarchies in ecology. For instance, one can move from the level of molecules to tissues to organs to entire organisms. A different kind of hierarchy could expand from individual organisms to populations to communities to ecosystems and up to entire biomes; an alternative hierarchy might move from things that occur at the level of organisms to those that function at the level of habitats, landscapes, **watersheds**, regions, and so on up to global phenomena. These different kinds of levels are not necessarily congruent. One might, for instance, study the individual adaptations of plants over a range of different environments across an entire landscape or even a region, or consider how population interactions at local extents contribute to the global range limitations of a species. Likewise, one's interpretation of data collected over a short time period may be completely upended when the same data are examined for trends over longer periods of time.

One of the reasons scale is now recognized as being so central to ecology is that the world is a very heterogeneous place. Even over very small distances, conditions can change in ways that may be important to living organisms. Environmental conditions are a particular concern in plant ecology because plants cannot move—or, at least, mature terrestrial plants generally are firmly rooted in place, although their offspring may be dispersed some distance away. So, the environment immediately surrounding an individual plant is overwhelmingly important to its survival, growth, and reproduction.The **habitat** of a population or species is the kind of environment it generally inhabits, and it includes the set of **biotic** (living) and **abiotic** (nonliving) factors that influence it in the places one usually finds it. But the conditions in the immediate surroundings of an individual plant—its **microhabitat**—may differ considerably from the average conditions in the general habitat (see Figure 15.3). Factors operating to distinguish a microhabitat from others around it include the composition of the soil; the microclimate of the immediate area; the presence, size, and identity of neighboring plants; and other organisms in the immediate surroundings (e.g., grazers, pollinators, seed eaters or dispersers, and mutualistic or pathogenic fungi or bacteria).

Similarly, the environment varies from moment to moment. There are no specific ecological terms for the components of temporal heterogeneity, but time also exists at many extents, and that has major consequences for plants. Variations in conditions from day to night; from summer to winter; across periods of wet years, cold years, or snowy years; and at a longer extent as climate changes over thousands of years all have important influences on plants. Depending on the ecological process being studied and the organisms involved, it may be the small-scale, moment-to-moment variation that matters most (such as fluctuations in light levels in a small forest gap on a partially cloudy day), or it may be long-term average conditions (such as CO_2 concentration in the atmosphere), or it may be the interplay between processes occurring at different durations (such as CO_2 flux in a forest canopy over the course of a day or a season).

Groups of organisms, such as populations and species, sometimes average these microenvironmental influences over larger areas and over generations of organisms' lives. This averaging acts to counter the effects of heterogeneity, particularly over evolutionary time. At even larger scales, heterogeneity again becomes critical. As continents are carried apart on tectonic plates and climates are altered, organisms must respond to changing conditions by evolving or changing their distributions, or else become extinct. However, there are many situations in which the heterogeneity, and not the average, is what matters. A major theme in much current ecological research is understanding the interplay between heterogeneity (whether temporal or spatial) and long-term or large-scale averages.

1.3 Plant Ecology Has Developed through the Interaction of Observation, Measurement, Analysis, Technology, and Theory

Ecology is a synthetic subject. By that we do not mean that it is unnatural or artificial, but that it brings together a very wide range of other fields of science (Figure 1.4). Some of the fields that ecology encompasses or overlaps with include geology, geography, climatology, soil science, anthropology, sociology, evolutionary biology, genetics, statistics and other branches of mathematics, systematics, behavior, physiology, developmental biology, molecular biology, and biochemistry. We touch on many of these fields throughout this book, showing you how they fit into the toolkit of an ecologist and how familiarity with them affects the ways in which ecologists think about and study organisms in nature.

This is not the place to present a detailed and definitive history of plant ecology. Instead, we sketch some of its major milestones, with an admitted bias toward the English-speaking scientific community. Other historical details are scattered throughout the book as we discuss particular topics and subfields. While no single definitive history of plant ecology exists, several books and papers describe parts of its history (McIntosh 1985; Westman and Peet 1985; Nicholson 1990; Allen et al. 1993).

Plant ecology began with simple observations, because even in prehistoric times, people's health and survival depended on their abilities to understand many aspects of the ecology of plants. Ecology as a science began with the Greeks, most notably Aristotle, in the fourth and fifth centuries BCE. He and his students wrote about relationships among some plants and animals, but much of this knowledge was descriptive in nature.

The development of worldwide transportation was essential to the modern science of plant ecology. Begun as what was called natural history in the eighteenth and nineteenth centuries, ecological science was conducted at first by professional and amateur naturalists in Europe and North America and in their travels throughout the world. Once they could travel readily, it was possible to discern many of the patterns that are now well known to ecologists and to begin to consider how those patterns may have developed. The travels of the early nineteenth-century Prussian naturalist Alexander von Humboldt (see Figure 18.10)—at one time deservingly one of the world's most renowned scientists—led him to systematize information on the effects of altitude and air pressure on patterns of temperature and precipitation. Von Humboldt was also the first to codify our understanding of how coastal climates differ from those inland. From von Humboldt's research comes our current understanding of the major causes of climate in the world, as well as their connection with the major causes of patterns in vegetation. While earlier sailors had certainly noticed that the plants in, say, Brazil were different from those in England, von Humboldt was the first to generalize descriptions of these patterns, discovering and writing about what we now call biomes, as well as proposing how these patterns were related to variation in climate. A fine (and very readable) introduction to his life is the book by Andrea Wulf (2015).

Charles Darwin was another traveler whose work is one of the foundations of ecology. As the ship's naturalist on the British ship HMS *Beagle*, a vessel commissioned to provide geological information to the British navy, Darwin acquired the basis for his later work on the theory of evolution by natural selection. The story of his travels from 1831 to 1836 became a widely read book after its publication in 1839 (Figure 1.5). The patterns he described (in geology, but also patterns of the sorts of animals and plants in Brazil, Argentina, Chile, Ecuador,

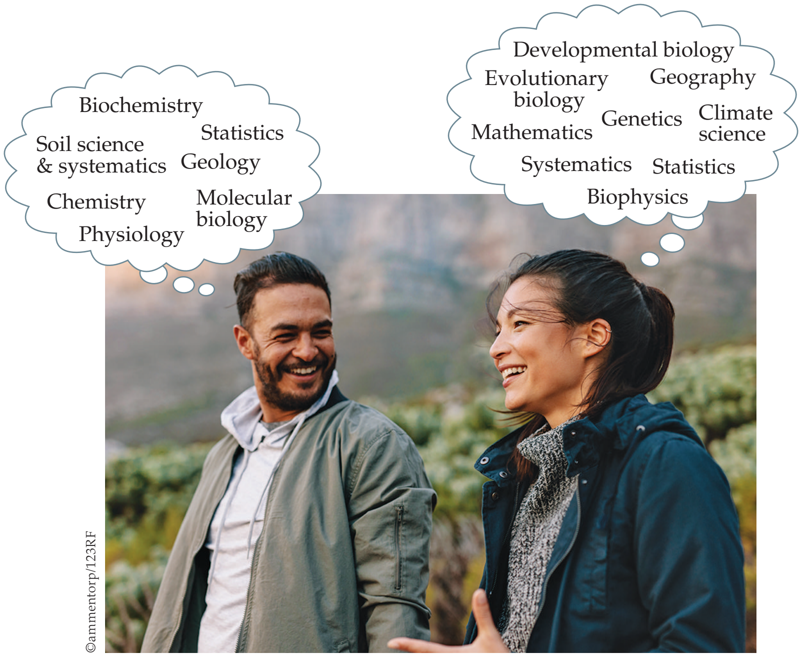


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Figure 1.4 Ecology requires information from many fields of science and mathematics. No ecologist is conversant with all of these, but all ecologists need to know something about some of these other disciplines. There are good reasons your ecology instructors expect you to have some background in other areas!

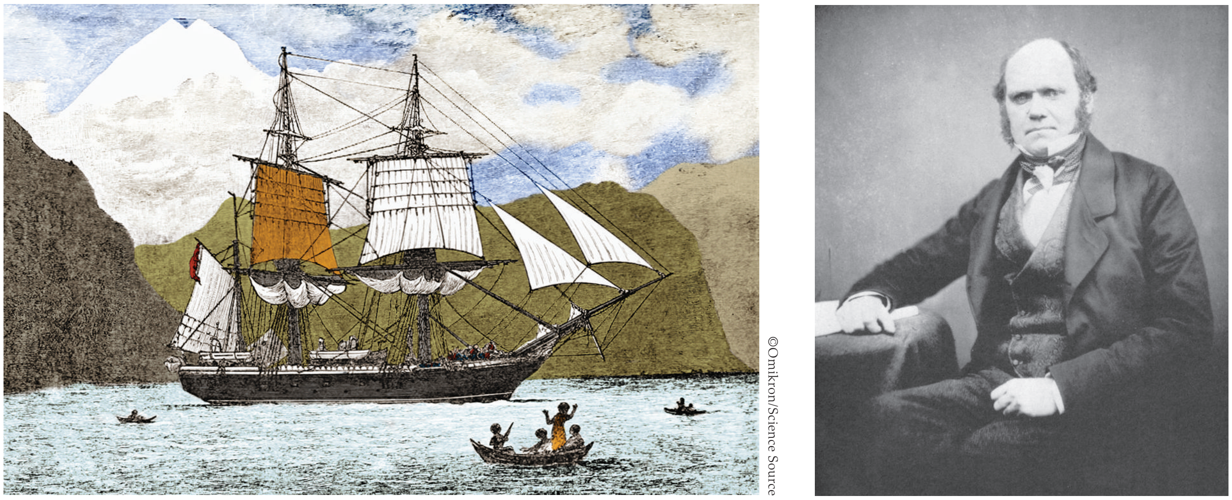

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Figure 1.5 The HMS *Beagle* sailed from England December 27, 1831, on a 5-year mission to chart the oceans and collect biological information from around the world. Charles Darwin sailed with the *Beagle* as ship's naturalist; he is pictured here at the age of 27, shortly after completing the voyage. Darwin collected vast numbers of plant and animal specimens and recorded copious scientific observations that were instrumental in the creation of his most famous work, *On the Origin of Species*.

Australia, and elsewhere and the fossil animals of Argentina) were new to the world and, in many cases, quite astonishing. Darwin later published a key theory explaining much of the world's biota in his work, *On the Origin of Species* (Darwin 1859). While this book is famous for its ideas and their continuing influence, it was not the only book that reflected and attempted to synthesize the new information that was available from the travels of European ships; indeed the period from the late eighteenth century through the nineteenth century saw many important discoveries and syntheses of the natural world, especially in biology and geology. The first map of mean monthly world temperatures was published in 1848. Two decades later, in 1866, the first world vegetation map was produced. Over the next several decades, a number of naturalists developed formal classifications of plant communities, noting the relationships between different types of communities (such as forests and grasslands) and the climate at different latitudes and altitudes.

What was different about what Darwin and von Humboldt contributed was that beyond their observations, they proposed theories to explain many of those observations, as well as verbal models that were applications of those theories to more particular problems. Like all science, ecology has depended not only on observation and on technology that permits new sorts of observation, but also on theory that makes sense of the observations and suggests new testable hypotheses and new ways to look at the world.

Ecology as a recognized discipline coalesced in the latter half of the nineteenth century. The German biologist Ernst Haeckel, a major voice in support of Darwin in central Europe and influential morphologist of marine animals, coined the term *oecology* in 1866. Among the first to write specifically about the topic of plant ecology was the Danish scientist J. Eugenius Warming, considered by many to be the founder of plant ecology as a distinct field. During the period from the 1870s to the end of the nineteenth century, Warming developed an evolutionary, adaptation-based perspective, and he created the concept of plant communities. During the same period, the German scientist Andreas Schimper created the first map of plant distributions, information that was critical to early progress in plant ecology. By the early twentieth century, the Ecological Society of America and the British Ecological Society had formed.

Developments in many other fields have made modern ecology possible. Understanding of weather and climate also depended on the development of travel and, more recently, on fast communication and data storage. Prior to the mid-1700s, no one had realized that weather moves in predictable ways across the globe—news traveled far more slowly than weather (McIlveen 1992). On October 21, 1743, Benjamin Franklin attempted to observe a lunar eclipse in Philadelphia but was prevented from seeing it by a storm. Later, he was surprised to learn that the eclipse had been visible in Boston and that the storm had arrived there the following day. By contacting people living between the two cities, he was able to reconstruct the movement of the storm. It was the development of communication technology, however, that really changed the sciences of meteorology and climatology. When the telegraph became available after 1844, it became possible to organize large numbers of people to observe and forecast the movement of storms. Modern weather data wasn't available, however, until well into the twentieth century. Accumulation and analysis of large quantities of data required the development of modern computers, which has also greatly affected ecology.

Two other fields deserve special mention: genetics and statistics. Many topics in ecology could not be addressed without genetic data and an understanding of the processes underlying changes in gene (and phenotype) frequencies. And no data would be interpretable without modern statistics, including graphs, which were invented in the late eighteenth century by William Playfair (1786), a Scottish engineer and economist. Both of these are areas that continue to develop and continue to permit new ecological insight. It is also now clear that much evolutionary change occurs more rapidly than was previously thought, so ecological and evolutionary dynamics can play out together, influencing each other. The older view was that the two types of processes happened on very different time scales and that ecology provided the "theatre" in which an evolutionary "play" was performed (Hutchinson 1965). Instead, the two sorts of processes are closely interlinked, and often one cannot be studied without considering the other.

Plant ecology is situated in the more general theoretical framework of ecology

There is a general theoretical framework of ecology, and plant ecology fits within it. Ecology concerns the spatial and temporal patterns of the distribution and abundance of organisms, including causes and consequences. By distribution and abundance, we mean that ecological studies focus on numbers of individuals (or related properties such as biomass or size) and on numbers of species and how those individuals and species vary across space and time. Although the examination of causes makes up the bulk of the science of ecology, consequences also are an important component. For example, climate change is driven in large part by the accumulation of CO_2 in the atmosphere, and that accumulation in turn is driven in part by how plants cycle CO_2 through the biosphere (see Chapter 2 and Chapter 16).

What are the basic principles of ecology? They are actually rather simple (Table 1.2). The complexity of ecology lies in thinking out what their consequences are, how they interact with one another, and when each of them is important (Scheiner and Willig 2011a):

1. Organisms are heterogeneously distributed. Large-scale heterogeneity is discussed in Chapter 15, Chapter 17, Chapter 18, and Chapter 19, while heterogeneity at the scales of individuals underlies much of Chapter 2, Chapter 3, and Chapter 4.
2. Plants interact with one another, as well as with animals, fungi, and other kinds of organisms. Some of these interactions cause heterogeneity in space or time, some are consequences of that heterogeneity, and some are both causes and consequences. Part I of this book is primarily concerned with abiotic interactions; Parts II and III are primarily concerned with biotic interactions.
3. Contingencies ("accidents of history") affect the distributions of organisms and their interactions. This idea has grown in importance in ecological theory over the past 50 years. A seed lands in once place but not another, and a particular species originates on a particular continent, setting the stage for later events. Contingencies play a particularly important role in Part II of this book.
4. Individual organisms vary in their characteristics. In turn, this variation creates variation in ecological patterns and processes. The individual oak trees in a forest vary in their photosynthetic rates for a number of reasons, and this affects many characteristics of the

TABLE 1.2 The general principles of the theory of ecology

1. Organisms are distributed heterogeneously in space and time.
2. Organisms interact with their abiotic and biotic environments.
3. The distributions of organisms and their interactions depend on contingencies.
4. Variation in the characteristics of organisms results in variation of ecological patterns and processes.
5. Environmental conditions as perceived by organisms are heterogeneous in space and time.
6. Resources as perceived by organisms are finite and heterogeneous in space and time.
7. Birth rates and death rates are a consequence of interactions with the abiotic and biotic environment.
8. The ecological properties of species are the result of evolution.

Source: S. Scheiner. 2010. *Q Rev Biol* 85: 293–318.

population and forest. Individual plants within a population vary in their chances of birth and death, and this affects population growth (see Chapter 8).

5. The environment varies in space and time. But most important, the variation is of a type to affect plants, animals, and other species. It is warmer in one spot than another; one location has sandier soil than another nearby. This variation is important for the processes in Part I, and plant growth is affected by this heterogeneity (see Chapter 6).
6. Resources are finite and their availability varies in both time and space and on many scales. Water is available to some plants (depending on their characteristics—see principle 4) at some times of year but not others. This resource heterogeneity is again important for the processes in Part I, and it strongly affects plant-plant interactions (see Chapter 10).
7. All living organisms were born at some point, and their death is inevitable. The rates at which births and deaths happen are results of how organisms interact with both the abiotic and biotic environment (see Chapter 6, Chapter 7, and Chapter 8).
8. Organisms, and therefore their ecological properties, are consequences of evolution. Evolution plays an important part in every chapter, and the processes are discussed in detail in Chapter 9.

We have deliberately retained the word *organisms* in this list because these principles apply to all organisms. But if you substitute the word *plants*, you will find a basic list of statements that provide much of the structure of plant ecology. This list is a bare sketch of the theoretical underpinnings of ecology; more are found throughout this book. You also can glean much more from the book edited by Samuel Scheiner and Michael Willig (2011b), which is both about ecology and its theory in general, and about particular theories within ecology. Ecology is a subject with rich theoretical underpinnings that are constantly being extended.

Ecology has a range of subdisciplines

Plant ecology as a discipline is made up of a number of different subdisciplines, some of which have quite distinct traditions and histories. Some early plant ecologists and botanists focused on whole communities, while others focused on single species and the properties of individuals. The older (now largely archaic) terms for these two subfields are **synecology** and **autecology**. Plant community ecologists, in particular, were active in the origins of ecology as a discipline in the last part of the nineteenth century and dominated plant ecology during the last two-thirds of the twentieth century. A more detailed discussion of the history of plant community ecology and some of the key figures in that history is given in Chapter 12.

Early studies in plant autecology were especially concerned with understanding unique plant adaptations to extreme environments, such as deserts, and a number of famous studies were concerned with plant performance in the field. Although some major insights were gained, technological limitations severely hampered the development of the field. As instrumentation and methodology became more sophisticated, plant physiologists began to carry out most of their research in controlled laboratory environments.

Considered then as part of autecology, as far back as the nineteenth century, individuals in many countries around the world were carrying out studies that today we would call plant physiological ecology or plant population ecology. Around the middle of the twentieth century, autecology began to divide into subfields that focused on single individuals and on populations. Studies of individuals were enhanced by further advances in technology that made it possible for physiological studies to come out of the greenhouse and into nature, creating the fields of plant physiological ecology and functional ecology. Plant population ecology as a recognizable subdiscipline had its origins in Great Britain in the 1960s, particularly with John Harper and his students. It then spread to North America in the 1970s.

For the most part, during the first three-quarters of the twentieth century, plant ecology developed independent of animal ecology. Animal community ecology has a long history parallel to that of plant community ecology (Mitman 1992). Substantial work in animal population ecology extends back to at least the 1920s (to the work of G. F. Gause, Raymond Pearl, Alfred James Lotka, and others). Plant population ecology drew on these ideas and theories as it was developing, as well as on other ideas that originated among plant ecologists. Eventually, new theories were needed as discoveries about the unique nature of plants made it obvious that they could no longer be shoehorned into many of the theories constructed for animals.

Conversely, physiological ecology advanced earlier and more rapidly among plant ecologists than it did among animal ecologists. Undoubtedly this was because the characteristics of plants are much easier to measure, and their environments easier to characterize, than those of animals (for most purposes, one does not have to catch plants!). On the other hand, in the 1980s, animal physiological ecology joined with evolutionary biology to create the field of evolutionary physiology (Feder et al. 1987), a move that plant biologists have not yet clearly made.

The gap between the fields of plant and animal ecology was bridged in the 1970s, although distinct subfields continue to this day. Two related developments were responsible. The first was the rise of studies of plant-animal interactions, especially pollination (see Chapter 6) and herbivory (see Chapter 11). The second was the burgeoning interest in the evolutionary aspects of ecology in the 1970s and 1980s, which transcended the traditional separation of the studies of plants and animals.

Recent changes in the field of plant ecology include the rise of landscape ecology and conservation ecology as recognized disciplines in the late 1980s. Landscape ecologists came to the discipline from various different directions, including fields as diverse as plant community ecology and remote sensing. Conservation ecologists likewise created their field from backgrounds in mathematical modeling and population, community, and ecosystem ecology. The 1990s saw the creation of the discipline of urban ecology, of which plant ecology is an important component, and the general recognition that nearly all parts of the globe have been affected by humans to at least some extent. At around the same time, the fields of biogeography and biogeochemistry emerged, building in part on areas of plant ecology and on new technological developments and interactions with remote sensing and climatology. Other fields within plant ecology have seen major shifts in emphasis. Plant community ecology has seen a large shift from questions about whole-community patterns and processes to a major focus on questions about interactions within and among species.

A major trend in contemporary ecology, including plant ecology, is toward larger, more integrated research projects that involve many collaborators and examine phenomena across large extents of space and time or across levels of organization. Except in the subdiscipline of ecosystem ecology, which was undertaking projects with large teams of scientists in the 1960s and 1970s, such multi-investigator studies were very rare in ecology until recently. Current ecological research, including that in plant ecology, is almost always the work of collaborations among scientists rather than the work of single individuals. These collaborative groups are often international, facilitated by the ubiquity of electronic communication. Contemporary studies in plant ecology range from molecular genetics up through ecosystems and social systems, and they are erasing many of the traditional boundaries among subdisciplines. Plant ecology is experiencing exciting times, and we hope you will sense and share that excitement in this book.

Science is a human endeavor

Science is a way of understanding; it is not a list of disembodied facts that somehow were handed to us anonymously. Of course you know this, but it is easy to lose sight of the fact that scientists are real people who do scientific research. Throughout this book we try to make it a bit easier to keep this in mind. We often refer to researchers by their full names. We have included photos of many scientists (living and dead) whose contributions to plant ecology are important. They vary quite a bit: they are women and men of many countries and nationalities, as well as different times. What they have (or had) in common is a fascination with the natural world, especially of plants, and a drive to understand it better. Some of you will become scientists as well; in any case, we hope that you will learn to appreciate the contributions these people have made.

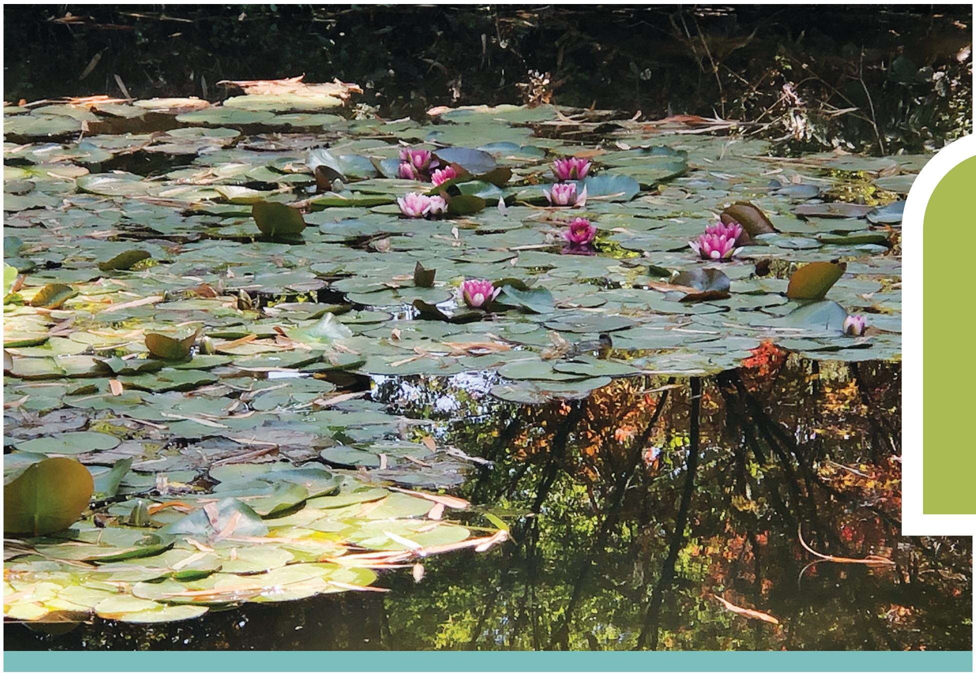
We began this chapter by saying that ecology is a science and that it is distinct from environmentalism. We stand by those statements, but we think it is important to add something: ecology is a *useful* science. Most people become ecologists because they are interested in the natural environment and want to help protect it. When we authors were graduate students, this was also true, but there has been a big change since those days: in academia few ecologists then worked on applied problems, like conservation, although ecologists employed within federal and state agencies and nongovernmental organizations certainly did. Most academics worked instead on what they considered fundamental science, in systems that they thought were undisturbed.

Today we recognize that no place on Earth is free of human influence and that we may often be able to advance the science of ecology by furthering its application. Despite the enormous environmental problems the world faces, there is a great deal of beauty that remains and is worth saving—at all scales, from continents and biomes down to individual plants and their organs. It is also quite wonderful to learn about. We have been studying it for many years and still find it gratifying and exciting to learn more. We hope you will too!

PART I

Individuals and Their Environments

Courtesy of J. Gurevitch



Courtesy of J. Gurevitch

2

Photosynthesis and Light

How does a plant detect and respond to the environment that surrounds it? Why can some plants survive extremes of temperature and drought while others cannot? What enables certain plants to thrive in the deep shade of the understory of a tropical rainforest, and others to succeed only in the sunniest habitats?

The **functional ecology** of plants is concerned with how the molecular biology, genomics, biochemistry, and physiology of individual plants determine their responses to their environments within the structural context of their anatomy and morphology. **Physiological ecology** is concerned specifically with the physiological mechanisms underlying whole-plant responses to the environment. Plant functional ecology is shaped by evolution, and it is fundamental for what happens at population, community, and higher ecological levels. Part I of this book begins with plant functional ecology and then continues with how plant function scales up to ecosystem processes.

Plants must acquire energy and materials for growth, maintenance, and reproduction. They must also limit their losses; for example, if a plant loses too much water, it will wilt and eventually die. Plants must also allocate resources in ways that maximize their chances of contributing offspring to the next generation while simultaneously maximizing their chances of surviving to reproduce. In this chapter and the next three, we examine how plants capture the energy of sunlight and incorporate carbon from the atmosphere in photosynthesis, their adaptations to the light environment, their water relations, and the mineral nutrients they get from the soil. These processes in turn can play out at the larger scope of ecosystem processes. We also will take a look at the structures in which some of these processes take place and some of the biochemistry involved. There is a tremendous amount of work currently on the genetic and hormonal control of photosynthesis that is beyond the scope of this book; interested readers should see reviews by Sujith Puthiyaveetil and John

Above: Water lilies in Yunnan, China.

Allen (2009), Paul Jarvis and Enrique Lopez-Juez (2013), and Norman Hüner and colleagues (2016).

While we focus first on processes occurring at the small scale of a cell, a leaf, or an individual plant, it is important not to lose sight of the forest: Plants have evolved and live in an ecological context. Photosynthesis is usually carried out in natural environments, not in a laboratory. The photosynthetic machinery, and the leaf in which it is housed, are both adapted by natural selection and adjust to the moment-to-moment and longer-term environment in which the individual plant is living. The temperature and the amount of available light, water, and nutrients in the environment determine when and how rapidly a leaf can photosynthesize and the rate at which the plant grows and is likely to survive.

The physical conditions that a plant experiences are determined not only by the physical features of the environment, but also by other living organisms in that habitat. The amount of light available for photosynthesis may be limited by other plants competing for that light. Pathogens and pollutants may reduce the plant's ability to photosynthesize. A plant's ability to capture carbon and energy may be diminished by herbivores eating its leaf tissue. Individual plant processes translate to how vegetation responds to and affects regional and global environments. A plant responds to its environment as an integrated unit, although in textbooks (like this one) we arbitrarily separate the plant's responses into categories for convenience, treating them in different chapters. We begin looking at plants' interactions with their environment by considering the process by which they acquire energy and carbon: photosynthesis.

2.1 Photosynthesis Is the Engine of Life on Earth

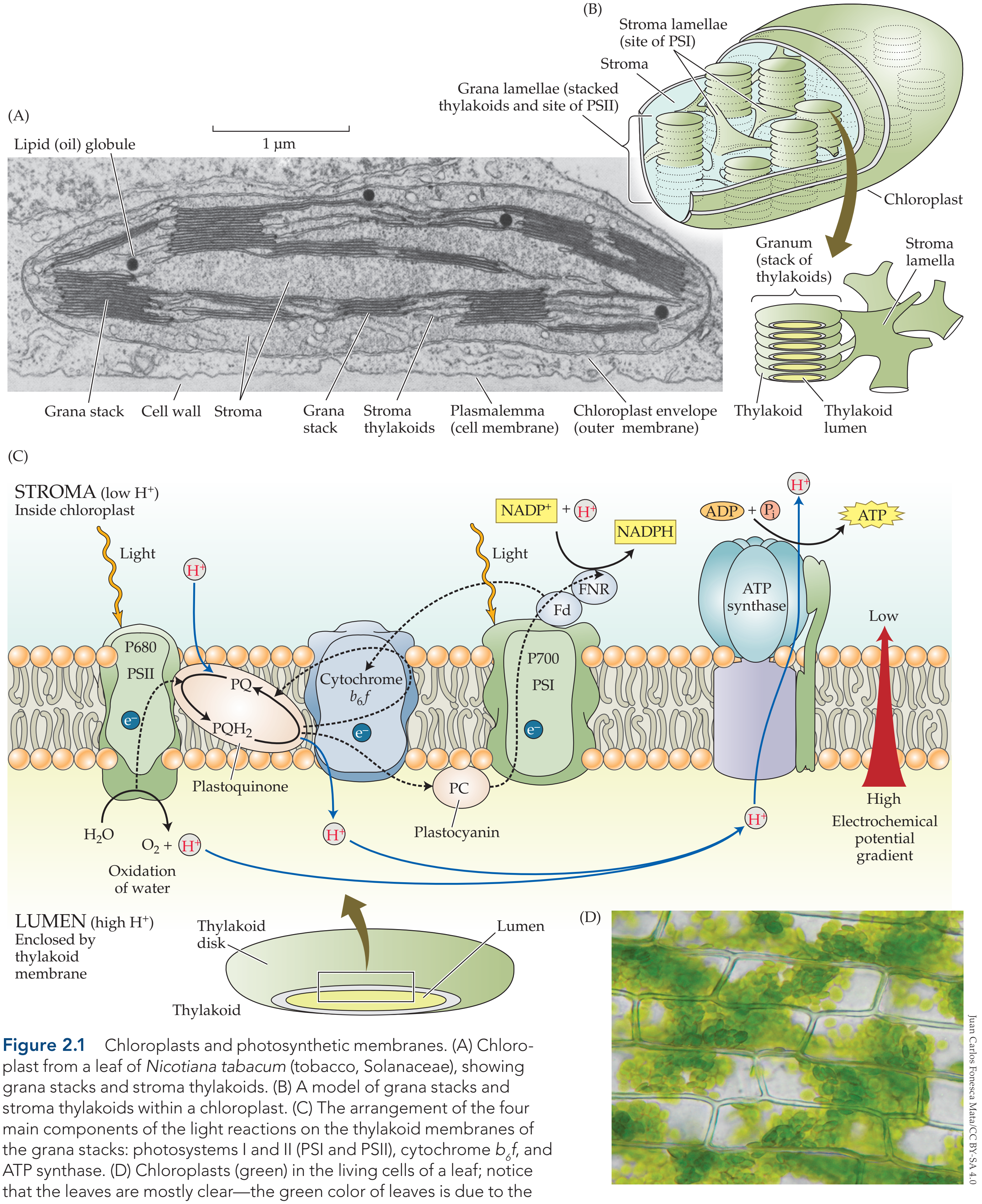
Photosynthesis is the set of biochemical processes by which plants acquire energy from sunlight and incorporate it with carbon from the atmosphere into organic compounds. Photosynthesis consists of two distinct parts that take place in different parts of the chloroplast. The first part, the **light reactions**, captures light energy from sunlight and temporarily stores it in high-energy chemical bonds. The second part is photosynthetic **carbon reduction** (called "fixation" in older literature), where that energy together with carbon from CO_2 is incorporated into organic compounds. The organic molecules formed in photosynthesis are used by the plant to create new tissues, regulate the plant's metabolic processes, supply energy to those metabolic processes and for many other processes such as reproduction and plant defense. The energy and carbon captured in photosynthesis are the foundation for almost all terrestrial and aquatic food webs, and this is where animals ultimately obtain their energy and the backbone of the molecules in their bodies.

The light reactions of photosynthesis occur on the membranes that make up **thylakoid disks** in the interior of the chloroplasts. The thylakoid disks are piled up in the form of **grana stacks** alternating with sheets of interconnecting membranes called **stroma lamellae** (also known as stroma thylakoids; Figure 2.1A,B). There might be anywhere from fewer than a dozen to about 100 grana stacks in a chloroplast. The successful capture of light energy depends on the precise spatial arrangement of these photochemical reactions on the membranes on which they occur (Figure 2.1C). The architecture of the thylakoid membranes is complex and very specific, and plant scientists have made great progress in understanding their structure and components. The machinery of light capture in photosynthesis takes place inside chloroplasts, which are commonly inside the cells of leaves (Figure 2.1D).

Light absorption in photosynthesis depends on pigments, which are organic molecules that absorb specific wavelengths of light energy. The pigment molecules responsible for the capture of light energy form two distinct molecular complexes in multicellular plants, **photosystem I** and **photosystem II** (Figure 2.1C and Figure 2.2). Unicellular eukaryotic algae, such as those in the Chlorophyta, and prokaryotic cyanobacteria also have photosystems I and II, while other photosynthetic bacteria have only photosystem I. Photosystem II is located mostly on the grana stacks, and photosystem I is mainly on the stroma lamellae.

Photosynthetic rates depend on the light wavelengths—called "light quality"—and not only on the total amount of light (Figure 2.3A,B). Most of the energy in sunlight is in the visible part of the spectrum (Figure 2.3C). Blue and red wavelengths are preferentially captured by the light reactions. Paradoxically, given our image of the beautiful green world, green wavelengths are particularly *ineffective* for photosynthesis. We see nature as green because green light is reflected by plants—"discarded" rather than used. The wavelengths of light that can be used in photosynthesis are termed **photosynthetically active radiation**, or **PAR**. The amount of usable light energy impinging on a leaf per unit time is called the **photosynthetic photon flux density** (**PPFD**).

Each photosystem consists of hundreds of pigment molecules, including several forms of chlorophyll plus accessory pigments, which form an "antenna" for capturing certain wavelengths of light. In terrestrial plants, the accessory pigments are primarily the orange- and yellow-colored carotenoids known as carotenes and xanthophylls. Each antenna has up to 400 molecules of accessory pigments. The accessory pigments can absorb wavelengths of light that chlorophyll molecules are poor at capturing (Figure 2.3D). They then transfer the energy from the wavelengths of light they captured



Juan Carlos Fonesca Mata/CC BY-SA 4.0

Figure 2.1 Chloroplasts and photosynthetic membranes. (A) Chloroplast from a leaf of *Nicotiana tabacum* (tobacco, Solanaceae), showing grana stacks and stroma thylakoids. (B) A model of grana stacks and stroma thylakoids within a chloroplast. (C) The arrangement of the four main components of the light reactions on the thylakoid membranes of the grana stacks: photosystems I and II (PSI and PSII), cytochrome b_6f, and ATP synthase. (D) Chloroplasts (green) in the living cells of a leaf; notice that the leaves are mostly clear—the green color of leaves is due to the reflection of green light by chlorophyll in the chloroplasts. (A from K. Esau. 1977. *Anatomy of Seed Plants*. John Wiley: New York, NY; B after L. Taiz et al. 2018 *Fundamentals of Plant Physiology*, 1st ed. Oxford University Press/Sinauer: Sunderland, MA; C from L. Taiz and E. Zeiger. 1998. *Plant Physiology*, 4th ed. Oxford University Press/Sinauer: Sunderland: MA.)

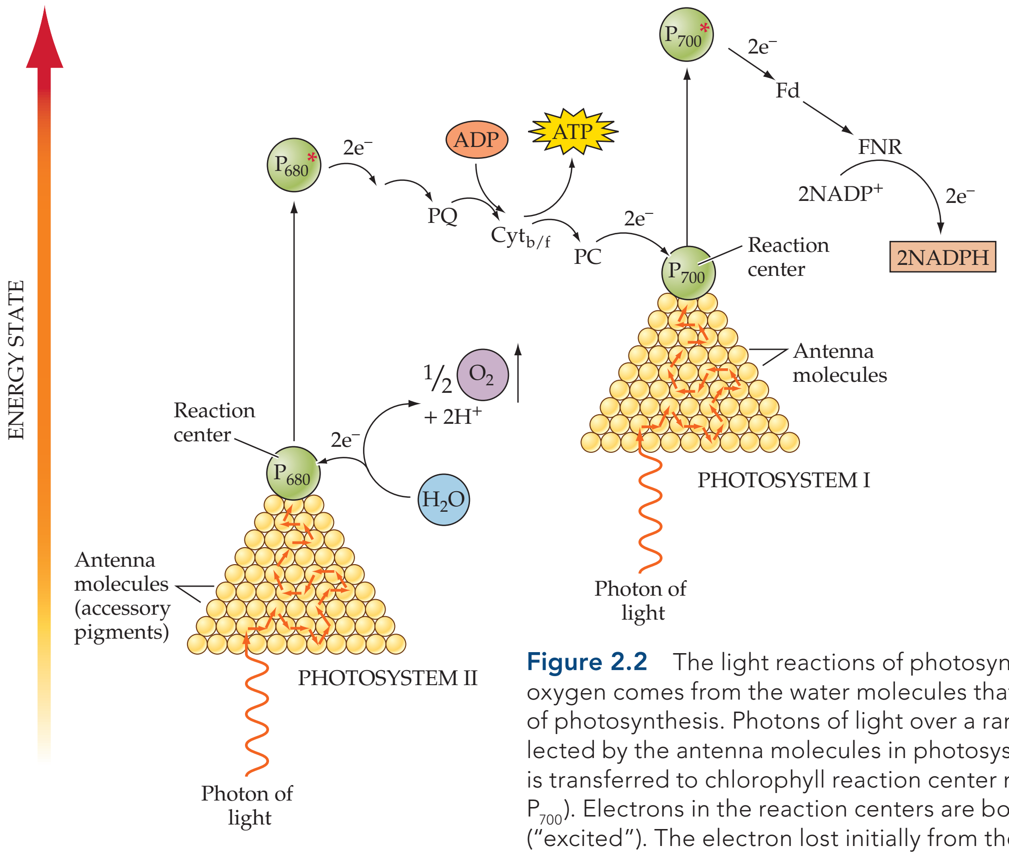


Figure 2.2 The light reactions of photosynthesis in plants. Atmospheric oxygen comes from the water molecules that are split in the light reactions of photosynthesis. Photons of light over a range of wavelengths are collected by the antenna molecules in photosystems I and II, and the energy is transferred to chlorophyll reaction center molecules (chlorophyll P_{680} and P_{700}). Electrons in the reaction centers are boosted to higher energy states ("excited"). The electron lost initially from the reaction center of photosystem II is replaced with an electron removed from a water molecule, which is split in the process. Oxygen ions from two split water molecules are joined to form an oxygen molecule, which is released to the atmosphere, plus hydrogen ions. The reactions in the two photosystems occur essentially simultaneously. (PQ, plastoquinone; $Cyt_{b/f}$, cytochrome b_6f; PC, plastocyanin; Fd, ferrodoxin; FNR, ferredoxin–NADP⁺ reductase.)

to chlorophyll molecules, using a process called resonance transfer. The accessory pigments can also protect leaves from sun damage by absorbing excess light energy when photosynthesis cannot keep up with the amount of light received. Beta-carotene and lycopene are some of the photosynthetic carotenoids that are also important nutrients for people. (Carotenoids are also found in other parts of plants; for instance, they are what make carrots, marigolds, some autumn leaves, and pumpkins orange or yellow.) Eukaryotic algae and photosynthetic bacteria also use other accessory pigments. For example, phycobilins are important photosynthetic pigments in red algae, enabling these eukaryotic organisms to absorb red, orange, yellow, and green wavelengths of light. Those red algae that photosynthesize deeper in the ocean than any other organisms have green-absorbing phycobilins that enable them to capture the wavelengths of light that penetrate deepest in water (to about 100 m).

When a photon of light is captured by the complex of tightly packed antenna molecules on the **thylakoid membranes**, it is passed from one molecule to another by the process of resonance transfer, until it is finally trapped by the chlorophyll molecule at the reaction center. The chlorophyll molecule then becomes "excited"—the molecule is at a higher energy state, and its electrons jump to higher energy orbitals. The excited chlorophyll molecule at the reaction center then passes a light-excited, high-energy electron to an electron acceptor, which passes it to other electron acceptors (see Figure 2.2). The energy in this high-energy electron is ultimately captured in high-energy bonds in ATP and NADPH. The photochemical reactions occur incredibly quickly—the whole process is complete within picoseconds (trillionths, 10^{-12}, of a second).

These electrons ultimately come from water molecules, which are split when their electrons are donated to photosystem II. The oxygen that we breathe was released into the atmosphere from water molecules in the light reactions of photosynthesis that were split to replace the electrons in photosystem II. Oxygen from photosynthetic light reactions that occurred in photosynthetic bacteria was first released into the atmosphere beginning about 2 billion years ago.

The light reactions provide the energy for incorporating CO_2 into organic molecules. That energy is stored as high-energy bonds in ATP and NADPH. These molecules move from the thylakoid membranes into the stroma

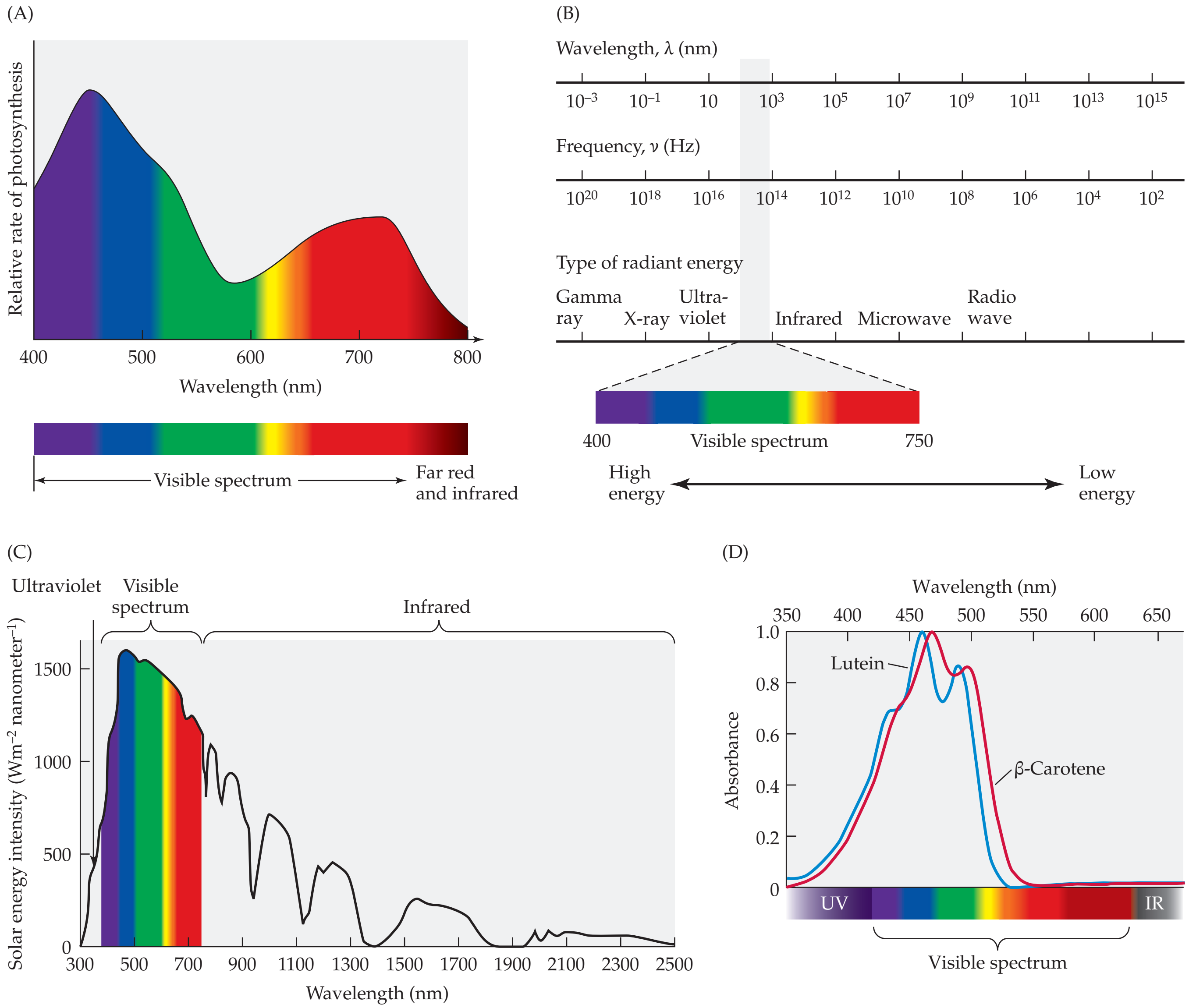
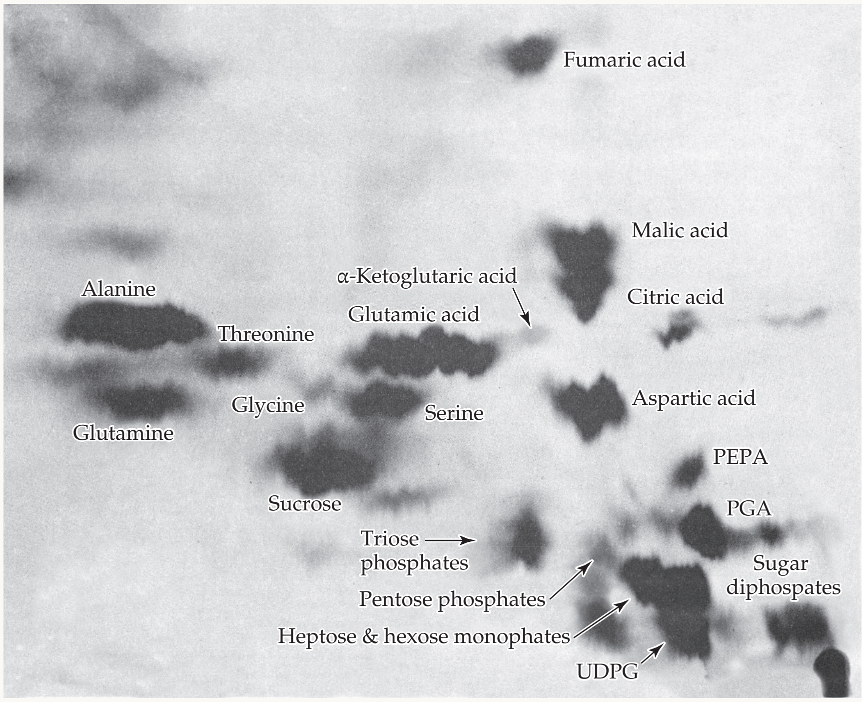


Figure 2.3 (A) All wavelengths aren't equal: the action spectrum identifies the wavelengths that are actually absorbed and used in photosynthesis. Green wavelengths are reflected and not used in photosynthesis. (B) Visible wavelengths are only a small part of the electromagnetic spectrum. (C) Most of the energy in sunlight reaching Earth's surface is in the visible part of the electromagnetic spectrum. (D) Absorption spectra for two of the most important accessory pigments, lutein and beta-carotene. (B after L. Taiz et al. 2018. *Fundamentals of Plant Physiology*, 1st ed. Oxford University Press/Sinauer: Sunderland, MA; C after ASTM G173-03. U.S. Department of Energy, Office of Energy Efficiency and Renewable Energy, National Renewable Energy Laboratory. https://www.nrel.gov/grid/solar-resource/spectra-am1.5.html; D after A. M. Collins et al. 2011. *PLOS ONE* 6: e24302. CC BY 4.0. https://doi.org/10.1371/journal.pone.0024302).

of the chloroplast, where they fuel carbon reduction. Carbon reduction occurs in the biochemical reactions of the **Calvin-Benson cycle** (Figure 2.4; Box 2A), in which CO_2 is taken up from the atmosphere and the carbon is incorporated into organic compounds, along with the energy captured in the light reactions. These reactions take place in the **stroma**, the watery matrix that fills the chloroplast. In C_3 plants (plants with the most common type of photosynthetic pathway, discussed later in this chapter), large amounts of the enzymes that catalyze the reactions of the Calvin-Benson cycle (sometimes called the Calvin cycle) are dissolved in the chloroplast stroma. The **quantum yield** (or quantum efficiency) of photosynthesis is the number of moles of CO_2 fixed per mole of photons absorbed; it depends on the wavelength of the light absorbed as well as other factors.

To sum up photosynthesis: the reduction of carbon is powered by the light reactions, and the light energy

BOX 2A The Discovery and Elucidation of Photosynthetic Carbon Reduction



Two minutes after exposure of cells of the green alga *Chlorella pyrenoidosa* (Chlorellaceae) to radioactive CO_2 ($^{14}CO_2$), many of the products of photosynthesis show up on this radioautograph. (From J. A. Bassham and M. Kirk. 1960. *Dynamics of the Photosynthesis of Carbon Compounds 1. Carboxylation reactions. UCLR-9033.* Lawrence Radiation Laboratory, University of California: Berkeley, CA.)

From L. Orr and Govindjee. 2013. *Photosynth Res* 115:179

Melvin Calvin and Andrew Benson

The Lawrence Berkeley Laboratory at the University of California, Berkeley, was a physics facility that was central to the development of the atomic bomb and radar during World War II, as well as fundamental research in physics. Because it had the ability to generate and work with radioactive isotopes, after the war the "rad lab" also became the site of research on photosynthesis using radioactivity to decipher the mechanisms by which inorganic carbon was reduced to become organic molecules. Chemists Sam Ruben and Martin Kamen were the first to synthesize radioactive ^{14}C in 1940; Sam Ruben was killed in 1943 at age 30 in a horrific lab accident while working on this project (Benson 2002b). Following World War II, Andrew Benson, as a young scientist working in the lab of Melvin Calvin, used radioactive ^{14}C to be able to trace the pathway of CO_2 incorporation into organic compounds by using $^{14}CO_2$ to see which compounds the radioactive ^{14}C was incorporated into. In these experiments, algal cells were exposed to light and air, then the air was flushed with pure N_2, and a solution of $^{14}CO_2$ dissolved in water (making labeled bicarbonate) was injected into a flask with the algal cells. After a short time, the cells were dropped into boiling alcohol to kill them, and paper chromatography was used to separate the compounds that had taken up the ^{14}C. The paper chromatogram was used to expose X-ray film, and the "spots" were subsequently analyzed to identify them (Bassham 2003). Benson discovered that RuBP and CO_2 were joined to create the first product of photosynthesis, 3PGA, catalyzed by the enzyme rubisco, in 1949 and 1950 (Benson 2002a; Bassham 2003; Govindjee and Krogmann 2004; Nonomura et al. 2016). He was subsequently dismissed by Calvin from his position at the lab, apparently for persuing this line of research when Calvin had a competing theory he was working on (Benson 2010; Sharkey and Weise 2015). At first there were several hotly competing theories for the mechanisms of photosynthesis, including one promoted by Calvin himself (later disproved), and it was unclear whether the light reactions and carbon reduction occurred together in a single set of reactions or as two distinct but intertwined parts of photosynthesis. James Bassham, starting as a graduate student in the lab, worked first with Benson and later with Calvin to more fully elucidate the pathway of photosynthetic carbon reduction. Calvin received a Nobel Prize for this work in 1961. Andrew Benson eventually obtained a position as a research professor at the University of California at San Diego, where he had a long and distinguished career.

C_4 photosynthesis was discovered and uncovered over a period of time, as the biochemistry, anatomy, and other features were slowly pieced

BOX 2A (*continued*)

together (recounted by Hatch 2002). Hugo Kortschak, a plant physiologist working in Hawaii on photosynthesis in sugarcane (*Saccharum officinarum*, Poaceae, a tropical grass) and also using labeled $^{14}CO_2$, was the first to recognize, in 1954, that there was a novel photosynthetic type operating in this species, but he did not publish his findings in a scientific journal until 1965. A young Russian scientist, Yuri Karpilov, also worked on the biochemistry of C_4 photosynthesis in the late 1950s but only published in Russian; that and his early death in a bicycle accident prevented wide recognition of his work. The pathway was finally fully worked out largely by two Australian plant biochemists, Marshall Hatch and Roger Slack, culminating in several major publications in the late 1960s and early 1970s and general recognition that an entirely new type of photosynthesis had been discovered, 20 years after the main mechanisms of C_3 photosynthesis were understood. Aspects of CAM were identified slowly over a long period starting in the 1800s, and even the name was developed over time by several different scientists (Black and Osmond 2003), but it began to be more definitively understood (and named CAM) by a Welsh scientist, Meirion Thomas, in 1946. Research on C_4 photosynthesis spurred a large group of researchers to plunge into research on CAM, and from the late 1960s through the entire 1970s the anatomy and biochemistry of CAM were finally worked out. While we can only introduce a few of the major names here, in fact many different scientists at different labs all over the world contributed to working to uncover the mechanisms by which plants use sunlight and CO_2 from the air to create the compounds that fuel essentially all ecosystems on Earth.

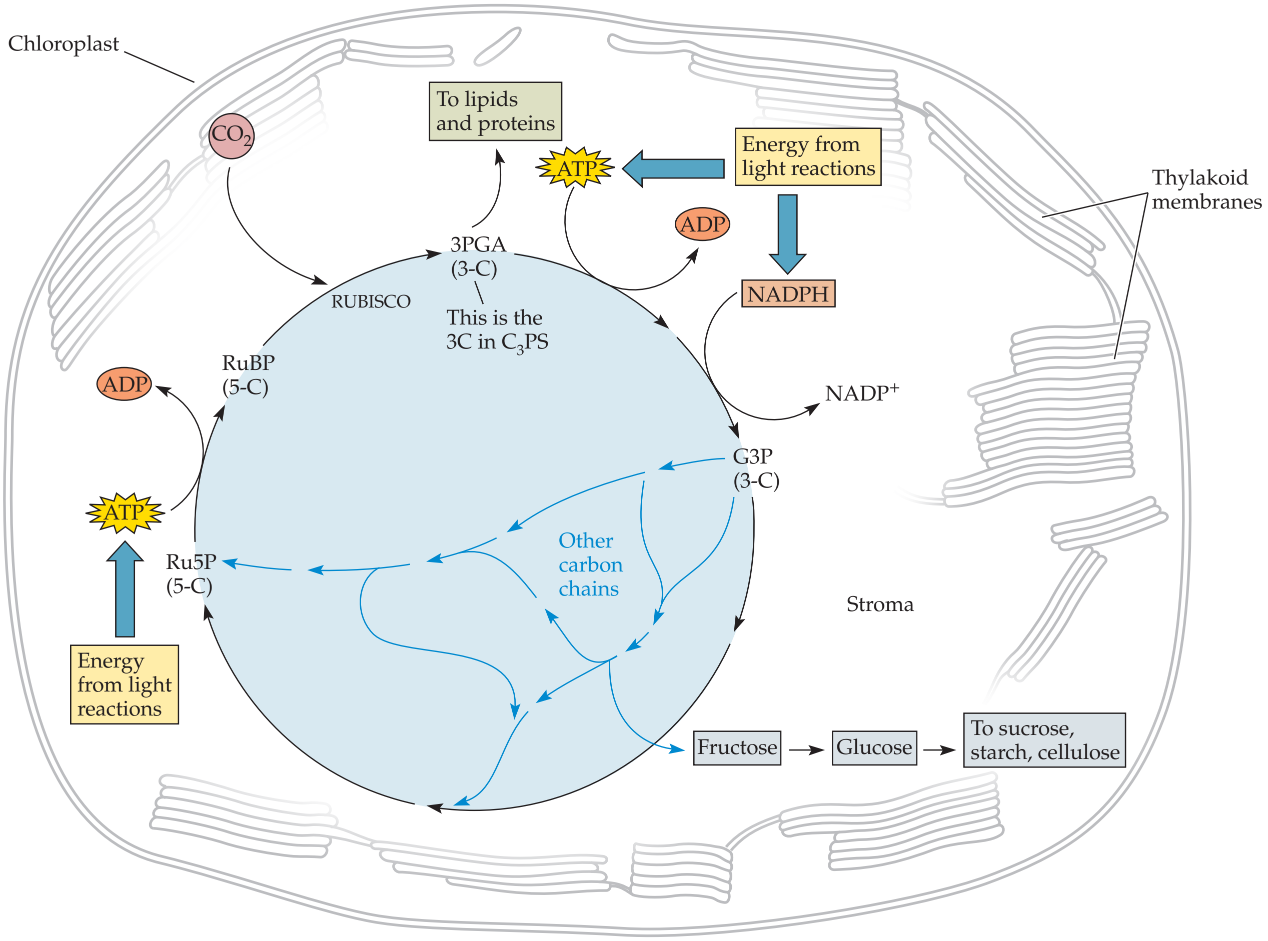


Figure 2.4 The Calvin-Benson cycle of carbon reduction in plants. CO_2 enters the stomata from the air surrounding the leaf. In a reaction catalyzed by the enzyme rubisco, CO_2 is joined with the five-carbon molecule RuBP to form two three-carbon molecules (3PGA). Eventually, simple sugars such as fructose and glucose are formed, to be ultimately transformed into many other organic (carbon-based) molecules.

captured in photosynthesis is ultimately stored in the chemical bonds of carbohydrates and other organic molecules.

2.2 Photosynthesis Is Affected by the Environment and by Plant Adaptations

The rate at which a leaf can capture light energy and fix carbon is determined by several factors. Plants, like other aerobic organisms, use oxygen and release CO_2 in the process of **cellular respiration**, by which organic compounds are broken down to release energy. **Gross photosynthesis**, or the total amount of carbon captured, is reduced by the plant's respiratory release of CO_2. Photosynthetic uptake of CO_2 by plants is far greater on average than respiratory losses, however, resulting in a net gain of carbon by plants.

The amount of light available limits photosynthesis

The most basic factor limiting photosynthesis is the total amount of light energy that reaches the thylakoid membranes. In darkness, cellular respiration results in a net loss of carbon and energy from the plant, as there is no photosynthetic capture of either light or carbon (for a partial exception, see the discussion of CAM photosynthesis below). As the light level increases, plants begin to take up CO_2. At the **light compensation point**, photosynthetic gains exactly match respiratory losses (in other words, net CO_2 exchange is zero) (Figure 2.5). Beyond that point, the more light that is available to be captured, the greater the photosynthetic rate, up to a maximum, at which the rate plateaus in most plants. Too much light can damage the tissues, and the accessory pigments and photorespiration (below) can be important in protecting the leaf from this destructive excess energy.

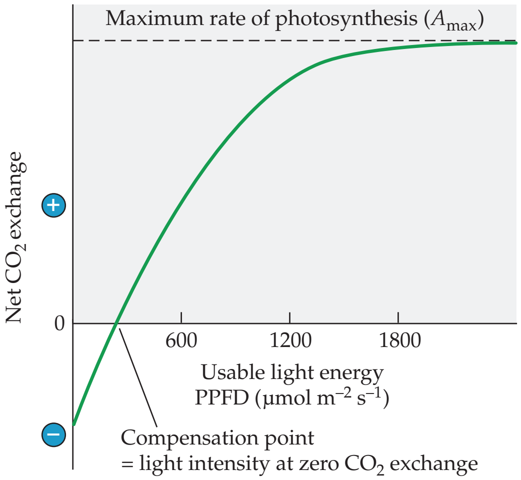


Figure 2.5 Net CO_2 exchange (per unit leaf area) for a typical C_3 leaf as a function of increasing light levels, showing the light compensation point and a plateau at a maximum rate of photosynthetic carbon assimilation, A_{max}. (After A. H. Fitter and R. K. M. Hay. 1981. *Environmental Physiology of Plants*, 3rd ed. Academic Press: London, U.K.)

The light compensation point can differ among plant species living in different regions or even within a single habitat or within individual plants, depending on the structure and biochemical constituents of the leaves and on the light environment and season. David Rothstein and Donald Zak (2001) contrasted the photosynthetic characteristics of three forest floor herb species within a northern hardwood deciduous forest. Light levels are high in the understory under trees in early spring before the trees produce their leaves, low in midsummer, and higher again in autumn as leaves start to fall. A **spring ephemeral** (active above ground only for a short time in spring), *Allium tricoccum* (wild leek, Liliaceae), had a constant light compensation point (Table 2.1) but was photosynthetically active only during a short period in spring when light levels were high. In

TABLE 2.1 Maximum photosynthetic rates (A_{max}), light compensation points (LCP), and rubisco levels for three forest understory herbs

	Spring			Summer		Autumn
Parameter	*Allium*	*Viola*	*Tiarella*	*Viola*	*Tiarella*	*Tiarella*
A_{max}	15.4 ± 0.9	12.1 ± 0.7	6.8 ± 0.7	5.6 ± 0.5	3.9 ± 0.5	5.4 ± 0.3
LCP	21.6 ± 1.4	8.4 ± 1.3	9.0 ± 1.0	4.1 ± 0.9	3.2 ± 0.5	6.5 ± 0.8
Rubisco	2.83 ± 0.21	1.84 ± 0.25	1.47 ± 0.12	0.93 ± 0.07	0.50 ± 0.17	0.78 ± 0.11

Source: D. E. Rothstein and D. R. Zak. 2001. *Func Ecol* 15: 722–731.

Note 1: Values are expressed on a per unit leaf area basis. A_{max} is given in μmol CO_2/m^2/s; LCP is given as the PPFD at which net CO_2 assimilation is zero, in μmol/m^2/s; and rubisco levels are in g/m^2. Values are means ± 1 standard error, with $n = 5$ plants per measurement.

Note 2: The duration during which each species had green leaves above ground was: *Allium tricoccum*, about 75 days; *Viola pubescens*, about 150 days; and *Tiarella cordifolia*, about 185 days.

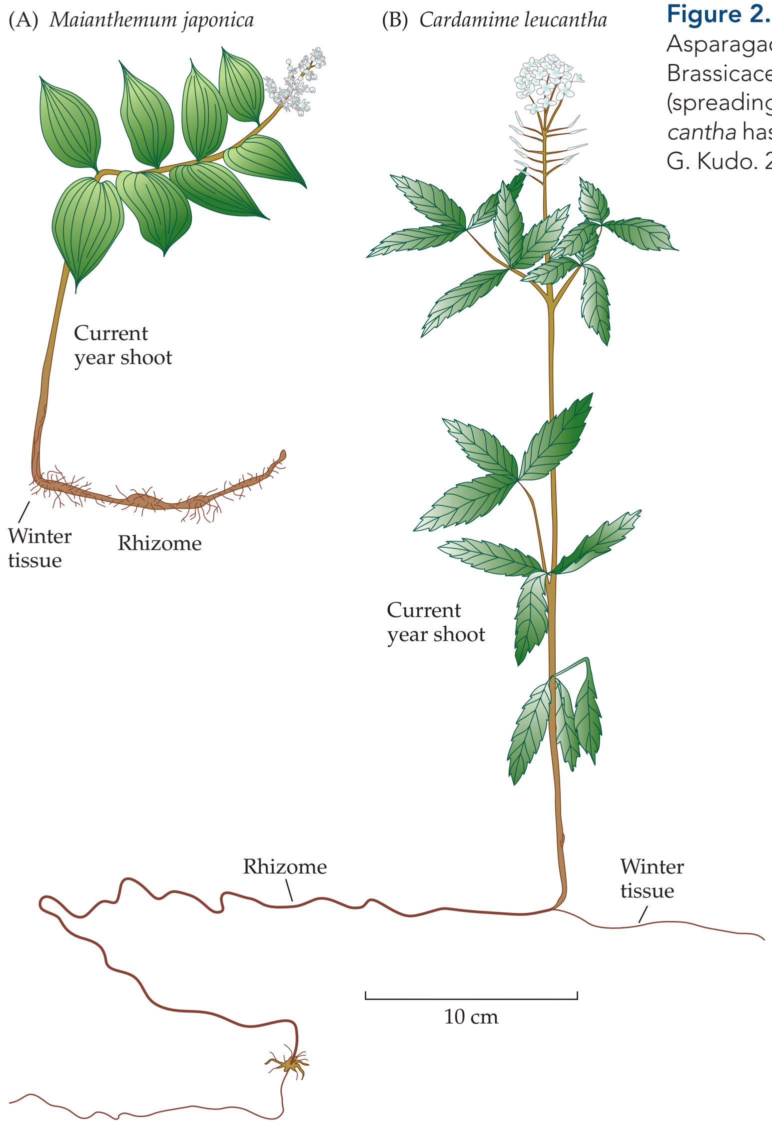


Figure 2.6 (A) *Maianthemem japonicum* (false Solomon's seal, Asparagaceae) and (B) *Cardamine leucantha* (Korean bittercress, Brassicaceae). *M. japonicum* has thick underground rhizomes (spreading underground stems) that store nutrients, while *C. leucantha* has little underground storage. (After T. Y. Ida and G. Kudo. 2009. *J Plant Res* 122: 171–181.)

contrast, a summer-green plant, *Viola pubescens* (downy yellow violet, Violaceae), shifted its light compensation point downward from spring to midsummer, while a semievergreen species, *Tiarella cordifolia* (foamflower, Saxifragaceae), also shifted its light compensation point downward over that period, but it shifted upward again in autumn. The spring ephemeral appears to be adapted to optimize its photosynthetic uptake in the high-light environment it experiences in spring, while the other two species are both better adapted for photosynthesis under shady conditions, at least in part due to their ability to shift the light compensation point.

Similar kinds of adaptations may occur in similar but geographically distant environments. Takashi Ida and Gaku Kudo (2009) studied photosynthetic rates and carbon allocation in two perennial herbaceous plants, *Cardamine leucantha* (bittercress, Brassicaceae) and *Maianthemum japonicum* (false Solomon's seal, Asparagaceae; called *Smilacina japonica* in the original publication), living in the understory of a deciduous forest in Hokkaido, northern Japan (Figure 2.6). In spring, light is high in the forest understory before the canopy trees leaf out, and both species had similar maximum photosynthetic rates. In summer, when the canopy trees were in full leaf, the maximum photosynthetic rates of both species were approximately half of their spring photosynthetic rates. However, in light gaps in the tree canopy in summer, the two species were very different, with *C. leucantha* having almost the same high rates as in spring, while *M. japonicum* had the same low photosynthetic rates in the canopy shade and in light gaps. This difference is linked to a difference in the turnover of leaves in the two species. *C. leucantha* has rapid leaf turnover, so new leaves with higher photosynthetic rates were continually being produced, while *M. japonicum* has limited leaf production in summer, and photosynthetic rates decreased as the leaves got older. Instead of investing in new leaves, *M. japonicum* allocates much of the carbon gained in photosynthesis to storage tissue in the rhizome, which is important for its longer-term survival.

The quantity of light reaching the thylakoid membranes of a chloroplast can be limited by a number of factors. The location of the chloroplast within the leaf can affect the light reaching the thylakoid membranes, as can the angle at which sunlight hits the leaf. In a typical C_3 leaf, photosynthesis takes place in the spongy and palisade parenchyma cells that make up the **mesophyll** (the photosynthetic tissue between the upper and lower epidermis of a leaf) (Figure 2.7). There are many chloroplasts in each photosynthetic cell. On a larger scale, self-shading by other leaves on the same plant, or shading by competitors, can also limit the amount of light available to be captured. We will examine some of these factors in more detail in other chapters.

Robin Chazdon (1985) studied the efficiency of light capture in two understory dwarf palms in the rainforests of Costa Rica, *Asterogyne martiana* and *Geonoma cuneata* (both in the Arecaceae). Both species have narrow, spirally arranged leaves that minimize self-shading.

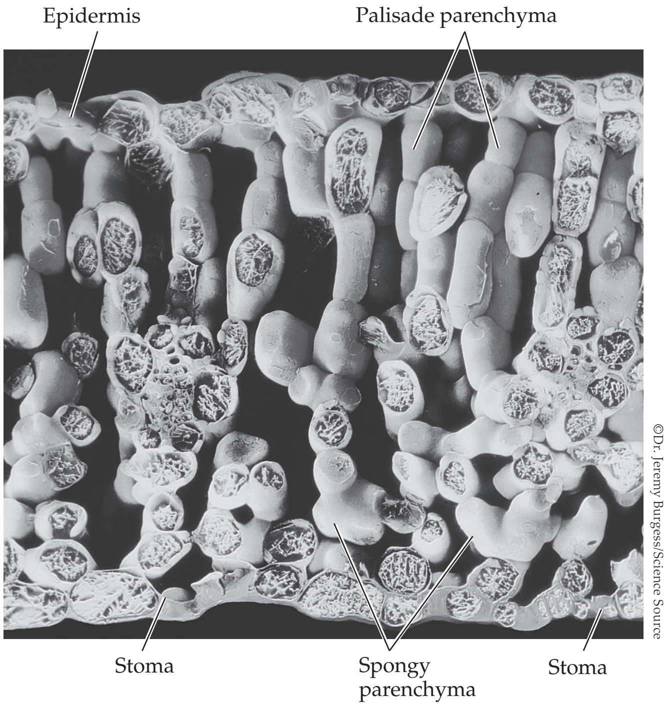


Figure 2.7 Scanning electron micrograph of a cross section of a leaf of *Brassica septiceps* (turnip, Brassicaceae), showing the palisade parenchyma and spongy parenchyma cells inside which most chloroplasts are found and in which most of the plant's photosynthesis takes place. Many of the cells in this micrograph have been broken open to expose their internal structure. The upper epidermis is visible, as are several stomata on the underside of the leaf, along with the substomatal cavities they open into on the inside of the leaf.

A. martiana was found in locations with somewhat higher light levels, and had a greater number of leaves and a greater total leaf area, than *G. cuneata*. As a result, *G. cuneata* had greater efficiency of light interception (the proportion of incident light intercepted by the plant canopy, which depends on leaf arrangement and display angle), but *A. martiana* had a greater total capacity to capture light (where the light interception capacity, or effective leaf area, is the product of total leaf area and light interception efficiency). Akio Takenaka and associates (2001) analyzed the effects of leaf display on light capture efficiency in another understory palm, *Licuala arbuscula* (Arecaceae), which grows in lowland rainforests in Southeast Asia. This species has compound, fan-shaped leaves with long petioles. The authors found that the angle at which the petioles are held changed as the number of leaves increased. As plants grew from juveniles with few leaves to mature plants with many leaves, this shift reduced self-shading to a minimal level and optimized light capture for individuals of very different forms and total leaf areas.

Leaves are not the only plant organs that can contain chloroplasts and carry out photosynthesis, although most photosynthesis most of the time in most terrestrial plants takes place in leaves. Bark, stems, the skin of ripe or unripe fruit, and the sepals covering flower buds that have not yet opened may be important for photosynthesis under some conditions and for providing energy for developing structures (Figure 2.8).

Differences in species' adaptations to different light levels was the focus of an experimental study in Hawaii Volcanos National Park by Jennifer Funk and Sierra McDaniel (2010), where invasive, non-native grasses had become dominant. Experimental shading was used to mimic a canopy understory and to investigate shading as a restoration technique for the native woody species. Seedlings of native woody shrubs and trees had lower rates of photosynthesis in both sun and shade compared with the grass seedlings. In full sun, the biomass of the invasive grasses was much higher than that of the woody species, but the grass biomass was reduced much more than that of the native woody plants in the shade. The invasive grasses also had greater reductions in survival in experimental shade than the native woody species did. The results suggested that creating shade might help with restoration of native species in these degraded Hawaiian landscapes.

The light environment also varies on a global scale. Day and night are close to being equally long at tropical latitudes, and this pattern is the same all year, while at polar latitudes it is continuously light at midsummer and continuously dark at midwinter (see Chapter 16). Maximum daily PPFD is greater in the tropics than in polar regions, and greater at high altitudes than at sea level (see Figure 16.5). Certain other parts of the solar spectrum vary across Earth's surface to a much greater degree than does PPFD. In particular, ultraviolet B (UVB) radiation, which is damaging to plants and dangerous as well to other organisms, including people, is up to ten times as great at high elevations in the tropics than at low elevations in Arctic environments. The ozone layer in the stratosphere absorbs UV radiation (see Box 16C). UV radiation passes through much more ozone before reaching the ground in the Arctic than in equatorial regions, because the path of solar energy through the atmosphere to Earth's surface is much longer in the Arctic than in the tropics (see Chapter 16). However, several types of man-made chemicals began to destroy the stratospheric ozone layer that protects organisms at the surface of the Earth from UV radiation, creating an "ozone hole" that was particularly severe in the Southern Hemisphere. Global cooperation in reducing these chemicals has been effective in considerably reducing this danger. While these problems still exist and this requires continued efforts and commitment, as of the time of writing this, the ozone hole is in the process of healing.

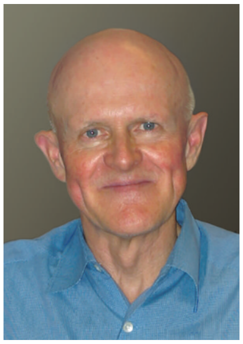


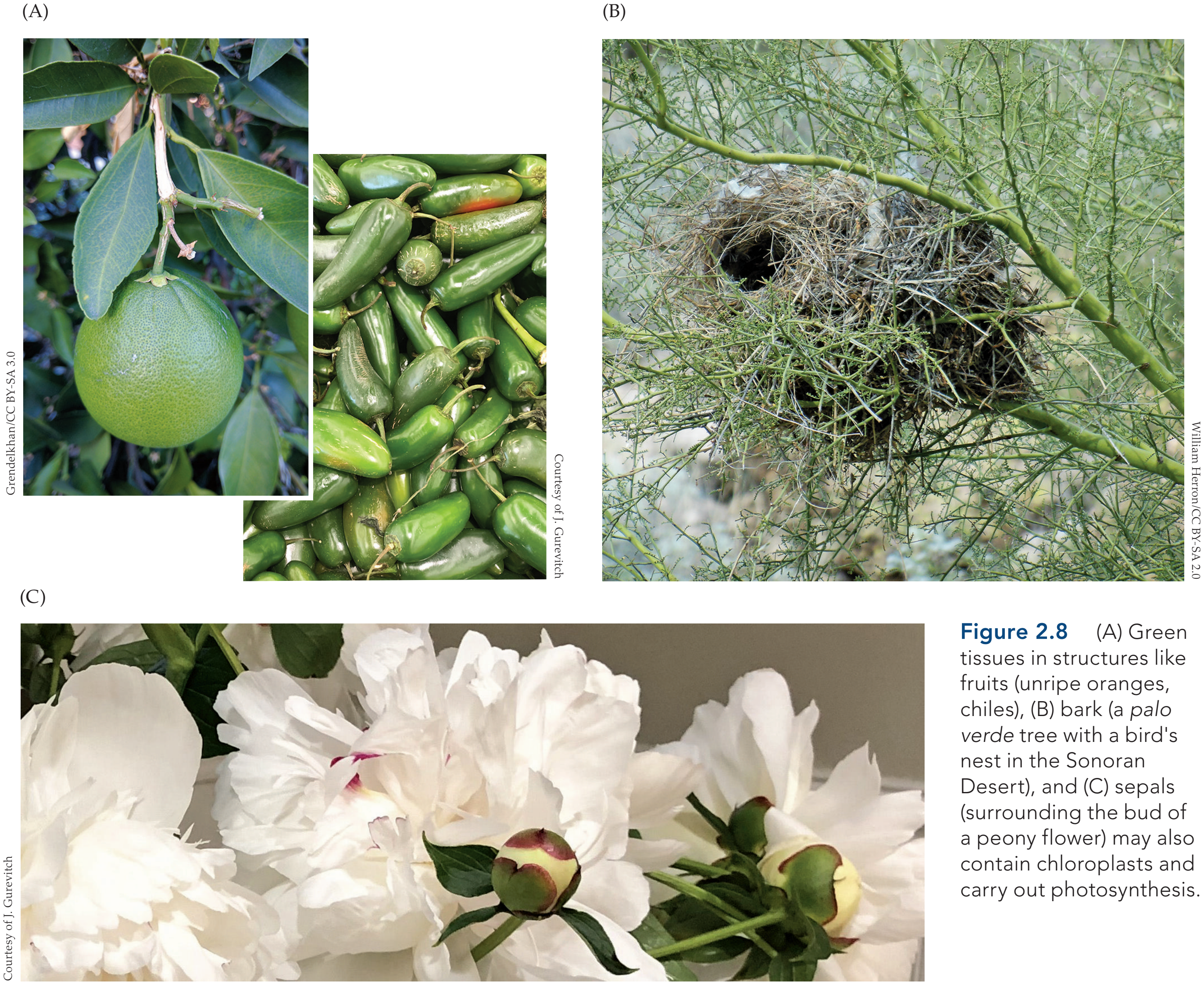
Photo by Donna Chambers. Courtesy of Martyn Caldwell

Martyn Caldwell

Plants have numerous biochemical adaptations to high UVB radiation (Searles et al. 2001). To avoid UVB damage, plants increase the leaf concentration of compounds that absorb UVB radiation, primarily flavonoids. They also limit damage by increasing concentrations of antioxidant enzymes and DNA repair enzymes. Martyn Caldwell (1968) found that high concentrations of these compounds were particularly common in plants that grow in high alpine environments.

Carbon uptake is limited by the ways plants respond to their environments

Plants take up CO_2 from the atmosphere as air moves through the stomata and into the intercellular spaces surrounding the photosynthetic cells within a leaf. Carbon uptake is driven by a concentration gradient of CO_2, set up by the biochemical reactions in the chloroplasts that remove CO_2 from the intercellular spaces. The uptake of CO_2 is regulated by conductance to CO_2 diffusion on the pathway from the surrounding air into the leaf and into the chloroplast. The concentration of CO_2 in the intercellular spaces depends on how rapidly CO_2 is removed by being fixed in organic compounds, and on how readily CO_2 comes into the leaf to replace that CO_2.



Grendelkhan/CC BY-SA 3.0

Courtesy of J. Gurevitch

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Courtesy of J. Gurevitch

Figure 2.8 (A) Green tissues in structures like fruits (unripe oranges, chiles), (B) bark (a *palo verde* tree with a bird's nest in the Sonoran Desert), and (C) sepals (surrounding the bud of a peony flower) may also contain chloroplasts and carry out photosynthesis.

The **leaf conductance** to CO_2 is the rate at which CO_2 flows into the leaf at a given concentration difference between ambient and intercellular CO_2. The inverse of conductance is resistance. Low conductance or high resistance at a particular point in the pathway of CO_2 will limit its movement along that pathway. If the overall leaf conductance to CO_2 is high and CO_2 concentrations in the intercellular spaces are being continually drawn down by the rapid reduction of carbon, then CO_2 influx from the air surrounding the leaf will be high.

The rate of CO_2 uptake can be modeled with a flux equation. **Flux equations** are used to model flow rates and are of the general form

$$\text{flux} = (\text{conductance}) \times (\text{driving force})$$

For CO_2 uptake, the driving force is a difference in CO_2 concentration, and the flux equation can be stated as

$$CO_2 \text{ uptake rate} = (\text{leaf conductance to } CO_2 \text{ diffusion}) \times (\text{difference in } CO_2 \text{ concentration between air and chloroplast})$$

or, using conventional symbols,

$$A = g_{\text{leaf}} \times (C_a - C_i)$$

The term A is the **assimilation rate** (in μmol/m^2/s); this is the rate at which CO_2 is taken up by the leaf. The terms C_a and C_i are the ambient and intercellular concentrations of CO_2, respectively, that is, its concentrations in the surrounding air and at the surface of the photosynthetic cell. The term g_{leaf} is the total conductance of the leaf to CO_2.

We can separate leaf conductance into its two major components, g_a and g_s—the conductances to CO_2 through the boundary layer of air surrounding the leaf and through the stomata, respectively—and then

$$\frac{1}{g_{\text{leaf}}} = \frac{1}{g_a} + \frac{1}{g_s}$$

Generally, g_a is large, since CO_2 readily passes through the boundary layer and so does not contribute much to regulating CO_2 flux. The conductance to CO_2 through the stomata (g_s), however, is highly variable and is under the control of the plant. Stomatal conductance regulates leaf CO_2 flux under most conditions. Thus, plants do not act as merely passive recipients of CO_2, but regulate its uptake closely. This regulation occurs over short time scales (seconds to minutes), as stomata are opened or closed, and over longer time scales (days to months), as leaf morphology and chemistry are altered. Over even longer time scales (years to millennia), natural selection acts to alter the capacity of plant populations in different environments to take up carbon under different conditions as morphology, physiology, and other plant characters evolve (see Chapter 9).

Why would plants ever restrict their uptake of CO_2? We examine this question in more detail in Chapter 3, but briefly, mostly it is because CO_2 gain is linked inextricably with loss of water through the same stomatal openings in the leaf where CO_2 is taken up.

A different formulation for photosynthetic rate is sometimes employed to describe net photosynthesis at **light saturation**, A_{sat}, the light level at which the maximum photosynthetic rate is reached, when stomata are wide open and CO_2 uptake is not limited by stomatal conductance:

$$A_{\text{sat}} = g_m \times (C_i - C_c)$$

where C_c is the compensation point for CO_2 (the CO_2 concentration at which net photosynthesis is zero), C_i is as defined above, and g_m is the **mesophyll conductance** or **intracellular conductance**, the conductance to CO_2 through the leaf mesophyll cells and cell walls.

An enormous amount of air must be processed by the leaf in the course of photosynthesis. To make a single gram of the carbohydrate glucose, a plant needs 1.47 g of CO_2, which is the amount in about 2500 L of air. Looked at another way, the air needed to fill a structure the size of the current largest sports stadium in the world, the North Korean Rungrado 1st of May Stadium located in Pyongyang, could supply enough CO_2 to synthesize about 5000 kg of glucose (if there were no fans present breathing out CO_2). (In contrast, the Astrodome, the world's first superdome, had enough air to synthesize 600 kg of glucose.)

When the stomata of a leaf are fully open, its conductance to CO_2 is generally high. The exact value depends on the number and size of the stomata, and it varies among species, individual plants, and even leaves on the same plant. (We will return to this issue in Chapter 3.) When the stomata are closed, leaf conductance to CO_2 approaches zero, although sometimes small amounts of CO_2 may "leak" through the cuticle.

Stomata are often very dynamic. The guard cells that determine the degree of stomatal opening are continually in motion, widening and narrowing the stomatal pores to regulate CO_2 entering the leaf and water leaving it. Some of the stomata may begin to close while others remain open (Figure 2.9). Such patchy stomatal closure may be more common when plants are experiencing stress (Beyschlag and Eckstein 2001). The guard cells are under a complex set of controls that respond to both internal and external factors.

Photosynthetic rates can vary among species in different habitats

Plant physiological ecologists have been able to study photosynthetic gas exchange and other physiological processes in natural environments, leading to considerable progress in our understanding of how these

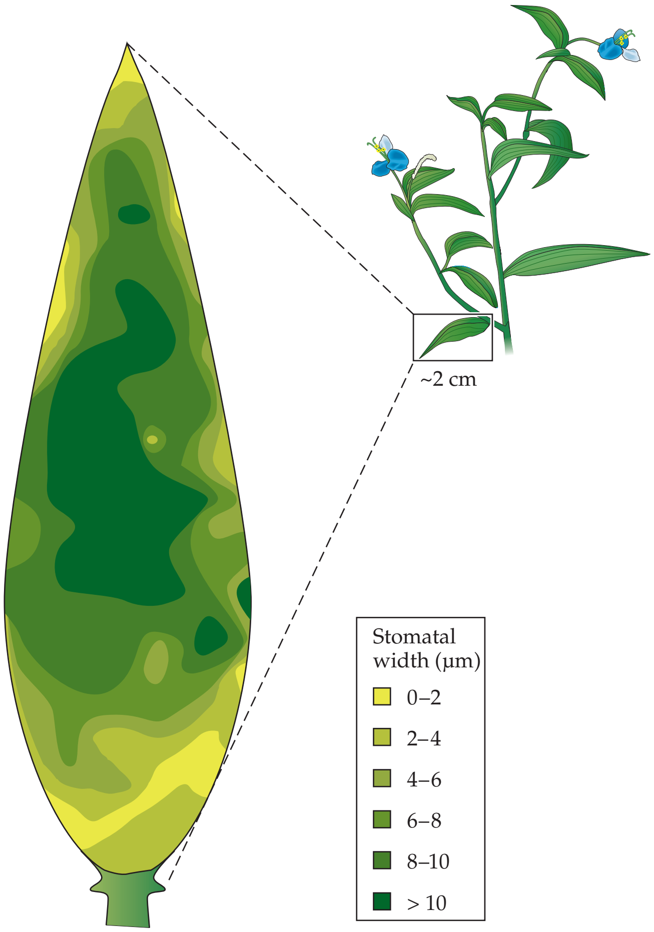

Figure 2.9 Stomatal widths in different parts of a leaf of *Commelina communis* (dayflower, Commelinaceae) at midday. Some stomata are wide open, while others are partially open or fully closed. (After W. Larcher. 1995. *Physiological Plant Ecology*, 3rd ed. Springer: Berlin; S. Smith et al. 1989. *Plant Cell Environ* 12: 653–659.)

processes function in nature (see Box 3A). Photosynthetic rates sometimes vary among plants within a habitat, and across habitats, in ways that seem to make sense because they are correlated with species composition, habitat preferences, or growth rates. In other cases, photosynthetic rates may have little role in determining population processes or species distributions. Even growth rates may be minimally related to photosynthetic rates. The total carbon accumulated by a plant depends not only on the rate of photosynthesis on a leaf area basis, but also on the total leaf area of the plant, as well as on other factors, such as the length of time the leaves are maintained and are photosynthetically active.

In the study of northern forest understory species discussed above (Rothstein and Zak 2001), maximum photosynthetic rates were correlated with the growth environments of the three species studied (see Table 2.1). The spring ephemeral, *Allium tricoccum* (wild leek, Amaryllidaceae), which grew only in the highest-light period, had the highest maximum photosynthetic rates overall. During spring, the summer-green *Viola pubescens* (downy yellow violet, Violaceae) had intermediate photosynthetic rates, and the evergreen *Tiarella cordifolia* (foamflower, Saxifragaceae) had the lowest rates. In midsummer, when light levels were lowest, photosynthetic rates declined substantially for both *V. pubescens* and *T. cordifolia*, but *T. cordifolia* still had the lower rate of photosynthesis. In autumn, only *T. cordifolia* was photosynthetically active, and its maximum photosynthetic rate increased again in the higher-light environment. These differences among species and seasons were positively correlated with leaf levels of rubisco (the enzyme that catalyzes the initial capture of CO_2; see below), as well as patterns of plant growth and the duration of time that each plant was photosynthetic. The spring ephemeral, *A. tricoccum*, gained all of its biomass during the spring high-light period and lost biomass after that time. The other two species also gained biomass rapidly during spring but continued to increase in biomass during summer. *V. pubescens* sharply declined in biomass from late summer through winter, while *T. cordifolia* continued to accumulate biomass through early winter. Only 25% of the biomass gain for *T. cordifolia* occurred during the low-light period of summer.

2.3 There Are Three Photosynthetic Pathways: C_3, C_4, and CAM

Plants fix carbon using one of three different photosynthetic pathways: C_3, C_4, or CAM (crassulacean acid metabolism; see below). C_3 photosynthesis and C_4 photosynthesis are named for the three-carbon and four-carbon molecules that are the first stable products of photosynthesis in these pathways, while CAM is named after the plant family Crassulaceae (the stonecrops), in which it was first discovered. The vast majority of plants use C_3 photosynthesis, and C_3 plants are found everywhere that plants exist. C_3 photosynthesis was the first pathway to evolve and the first to be understood by scientists. C_4 and CAM photosynthesis are modifications of C_3 photosynthesis and evolved from it.

C_3 photosynthesis is the most common and original type of photosynthesis

C_3 photosynthesis is found in the largest number of plant species, and C_3 plants dominate many parts of the Earth, from the oceans' phytoplankton to the vast northern coniferous forests and tropical rainforests. In the Calvin-Benson cycle of **C_3 photosynthesis** (see Figure 2.4), CO_2 is joined with a five-carbon molecule, RuBP (ribulose bisphosphate), to form a six-carbon compound that instantly separates into two three-carbon molecules (phosphoglycerate; 3PGA). In C_3 photosynthesis, therefore, the first stable product of carbon reduction is a three-carbon chain.

The initial step in which CO_2 is captured—the **carboxylation** of RuBP—is catalyzed by the enzyme RuBP carboxylase/oxygenase, which is mercifully nicknamed **rubisco**. Rubisco is probably the most abundant protein on Earth but is curiously inept at capturing CO_2. This is particularly strange considering how important this task is for primary productivity on Earth—one might have expected a more efficient process to have evolved and replaced it in plants long ago. Not only does rubisco have a relatively low affinity for CO_2, it also has an alternative function that competes with its role in capturing CO_2. Besides catalyzing the initial step of photosynthesis, rubisco can also catalyze a process called **photorespiration**, in which oxygen is taken up instead of carbon dioxide (see Box 2B). At higher temperatures, rubisco increasingly favors the oxygenation reaction over carboxylation, or photorespiration over photosynthesis. Likewise, the higher the concentration of O_2 and the lower the concentration of CO_2 reaching the chloroplast, the more O_2 is taken up in preference to CO_2. These properties of rubisco limit photosynthetic CO_2 uptake.

The limitations of rubisco are not especially important for plants whose leaves are shaded, because in their case photosynthesis is limited mainly by light levels, rather than by the efficiency of CO_2 uptake. However, for plants growing in warm, bright environments, the limitations posed by the properties of rubisco can have major ramifications for photosynthetic rates, and ultimately for growth. Even under the best conditions, C_3 plants must maintain large quantities of rubisco to support adequate rates of photosynthesis. Rubisco, like all enzymes, contains a substantial amount of nitrogen. Between 10% and 30% of the total nitrogen in the leaves of C_3 plants is in rubisco.

Because of the limitations of rubisco, photosynthetic rates are also limited by the concentration of CO_2 in the atmosphere. Consequently, at elevated CO_2 concentrations, C_3 plants can achieve higher photosynthetic rates, all else being equal. Plant growers sometimes make use of this response by growing plants in greenhouses with artificially high concentrations of CO_2 in the air. Plants evolved under atmospheric CO_2 levels very different from those of today, as we will see shortly. The current rapid increases in atmospheric concentrations of CO_2 caused by human activities may have long-term consequences for CO_2 uptake by plants. We return to this issue in Chapter 16.

BOX 2B Photorespiration

Plants have mitochondria, of course, which carry out cellular respiration much as those of animals do, consuming O_2 and releasing energy to be used by the cells. Plants also carry out another kind of respiration, called photorespiration. Like ordinary cellular respiration, photorespiration consumes O_2 and releases CO_2, but unlike cellular respiration, it depends on light. It takes place in cells that contain chloroplasts, but it involves two additional organelles: mitochondria and peroxisomes.

The enzyme rubisco catalyzes the initial capture of CO_2 in the Calvin-Benson cycle, but rubisco also has another, competing function. Rubisco also catalyzes the binding of O_2 to ribulose bisphosphate (RuBP) in the process of photorespiration. Photorespiration competes with photosynthesis not only for rubisco, but also for RuBP, the substrate of both reactions. Photorespiration results in large losses of previously captured CO_2 to the atmosphere, making photosynthesis much less efficient (without releasing usable energy as ordinary cellular respiration does). Conditions that favor photorespiration in place of photosynthesis are low CO_2 concentrations, high partial pressures of oxygen, and warm temperatures. C_4 photosynthesis is highly efficient because it overcomes all of these factors by concentrating CO_2 and separating the Calvin-Benson cycle in the bundle sheath cells away from atmospheric O_2. Another mechanism partially reduces photorespiratory carbon loss: C_2 photosynthesis. C_2 photosynthesis has been detected so far in only a small number of plant species. In C_2 photosynthesis, CO_2 that has gone through photorespiration is trapped and refixed in the Calvin-Benson cycle instead of diffusing out to the atmosphere. This is accomplished by spatially separating the oxygenation of rubisco (in chloroplasts in the mesophyll cells) from glycine decarboxylation (in mitochondria in the bundle sheath cells). The CO_2 released in these internal bundle sheath cells builds up to high levels, allowing recapture in the Calvin-Benson cycle in chloroplasts in the bundle sheath cells. In a few cases (such as in the genus *Flaveria*), C_2 photosynthesis appears to be a precursor to the evolution of C_4 photosynthesis.

Although photorespiration is often considered to be disadvantageous because it competes with photosynthesis, it may have a protective function. Photorespiration may “soak up” excessive electron flow in bright light, thereby protecting photosystem II from damage when the leaf’s carboxylation capacity is not capable of keeping up with the energy captured in the light reactions (e.g., when drought forces stomata to close partially or fully, limiting or cutting off the supply of CO_2).

There is an evolutionary "solution" to the dilemma posed by photorespiration and the limitations of rubisco as a catalyst for CO_2 uptake. That solution is C_4 photosynthesis.

C_4 photosynthesis is a specialized adaptation for rapid carbon uptake in warm, bright environments

C_4 photosynthesis and CAM are specializations that evolved from C_3 ancestors. Like C_3 photosynthesis, **C_4 photosynthesis** ultimately depends on the Calvin-Benson cycle to convert CO_2 into carbohydrates. However, C_4 photosynthesis contains an additional step that is used for the initial capture of CO_2 from the atmosphere (Figure 2.10). In this additional step, a three-carbon molecule called PEP (phosphoenolpyruvate) is joined with CO_2 to form a four-carbon acid, OAA (oxaloacetate). The first product of carbon reduction in C_4 photosynthesis is a molecule with four carbons. The initial capture of CO_2 is catalyzed by the enzyme **PEP carboxylase**, which functions only to fix CO_2. It has a much higher affinity for CO_2 than does rubisco. Because it does not also catalyze photorespiration, PEP carboxylase can maintain high rates of CO_2 uptake even at warm temperatures as long as there is enough sunlight energy for carbon capture.

After its formation, the four-carbon molecule is decarboxylated (the CO_2 is removed), and the CO_2 is then incorporated into organic molecules via the Calvin-Benson cycle. Rubisco functions to fix this internally liberated CO_2 molecule in C_4 plants, just as it acts to fix CO_2 coming in from the external atmosphere in C_3 plants. There are three different subtypes of C_4 photosynthesis, each with its own enzyme for decarboxylation: NADP-ME, which uses NADP-malic enzyme; NAD-ME, which uses NAD-malic enzyme; and PEPCK, which depends on PEP carboxykinase.

C_4 photosynthesis depends on specialized leaf anatomy (Figure 2.11). In the typical Kranz (German for "wreath") anatomy found in C_4 plants, there is a spatial separation of the C_4 and C_3 reactions. The initial capture of CO_2 from the atmosphere takes place in the mesophyll cells just under the epidermis and adjacent to the substomatal cavities, while the incorporation of CO_2 into carbohydrates via the Calvin-Benson cycle takes place deep inside the leaf in the bundle sheath cells. In C_3 plants, the concentration of oxygen in the chloroplasts is typically about 1000 times greater than the concentration of carbon dioxide, resulting in substantial rates of photorespiration. In C_4 plants, rubisco is located (along with the other enzymes of the Calvin-Benson cycle) in the bundle sheath cells, which are not exposed directly

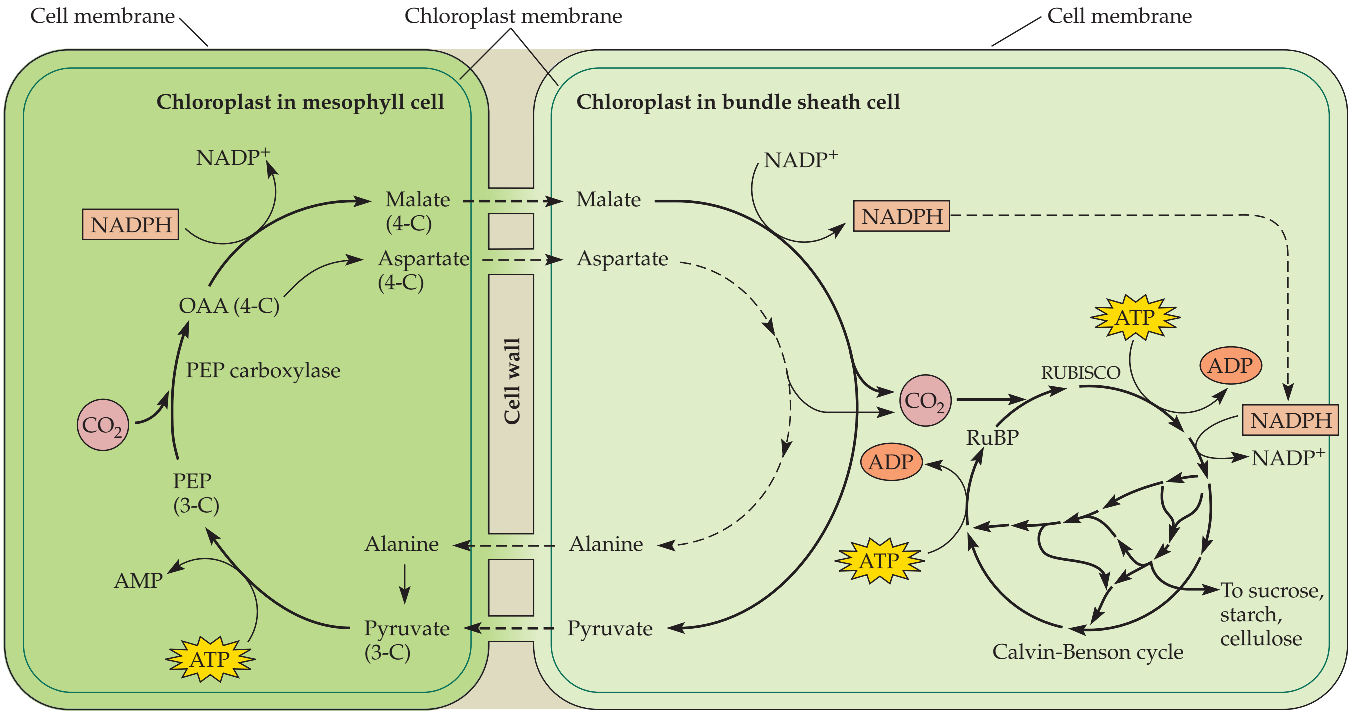

Figure 2.10 The C_4 photosynthetic pathway. The biochemical steps that take place in the chloroplasts of the mesophyll cells are shown on the left, and those that take place in the chloroplasts of the bundle sheath cells are shown on the right. The Calvin-Benson cycle functions in the bundle sheath cells in the interior of the leaves, where oxygen concentrations are low.

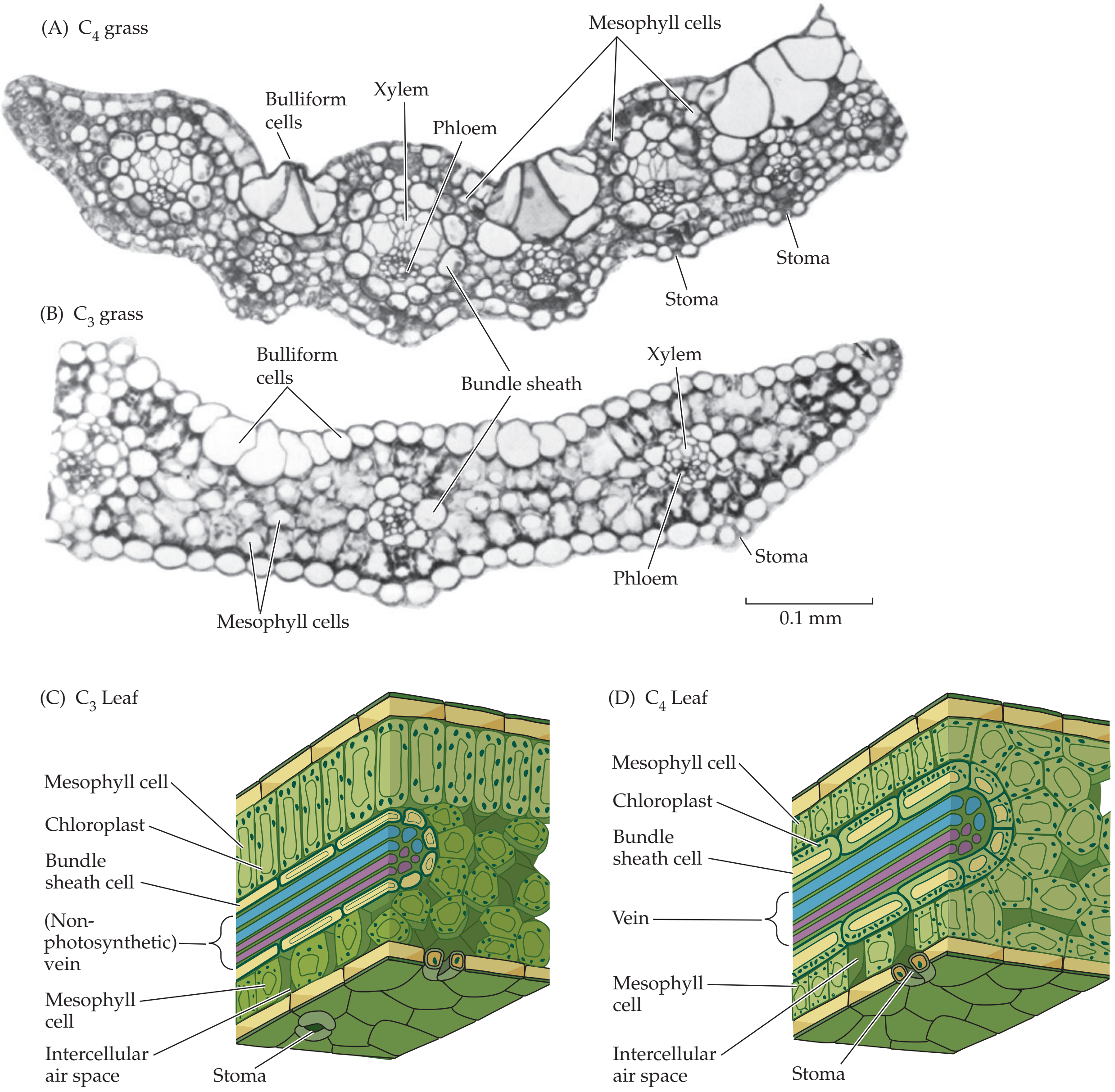

Figure 2.11 Anatomy of (A) a leaf of *Saccharum officinarum* (sugarcane, Poaceae), a C_4 grass, and (B) a leaf of *Avena* sp. (oats, Poaceae), a C_3 grass, both in cross section, showing the differences in their architectures. Note the tight packing of the mesophyll cells in the outer ring surrounding the bundle sheath cells of the C_4 leaf, which themselves tightly encircle the vascular bundle (xylem and phloem), in contrast to the more loosely packed photosynthetic cells in the C_3 leaf. There are large numbers of chloroplasts in the bundle sheath cells (clustered at the outer edge within each cell) as well as in the mesophyll cells of the C_4 leaf, in contrast with the absence of chloroplasts in the bundle sheath cells surrounding the vascular bundle in the C_3 leaf. The bulliform cells act as hinges to allow the leaf to roll up during drought (see Chapter 3). (C, D) Diagrams of C_3 and C_4 leaf anatomy, showing arrangement of photosynthetic cells, vascular bundles with xylem and phloem, and other structures. (A, B from K. Esau. 1977. *Anatomy of Seed Plants*. John Wiley: New York, NY © John Wiley & Sons, Inc.; generously contributed to K. Esau by J. Sass; C, D after T. J. Mabry, unpublished.)

to the external atmosphere and so are shielded from high oxygen levels. The four-carbon acid OAA travels directly through thin strands of living cells, called **plasmodesmata**, from mesophyll cells to bundle sheath cells, where it is decarboxylated. The concentration of CO_2 in the bundle sheath cells of C_4 plants is an order of magnitude higher than its concentration in the photosynthetic cells of C_3 plants, and the ratio of O_2 to CO_2 is greatly reduced. Rubisco is "fed" a concentrated stream of CO_2 molecules and kept away from high O_2, resulting in the effective elimination of photorespiration in C_4 plants.

The consequences for plants of overcoming the limitations of rubisco are enormous (Sage and Monson 1998). (See Box 2C for a less obvious consequence—an isotope signature that can tell whether living, dead, or fossil herbivores ate C_3 or C_4 plants.) C_4 plants generally have higher