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Plant diversity. Vegetation types. The first plant life moves onto land. Evolution and diversification of land plants. Energy flow. Membranes. The origin of eukaryotes. Photosynthesis. The oxygen revolution. The ozone layer. Plants and climate. The biosphere.

FIGURE 1.1 Flowering plants now dominate the land. Some, like this enormous saguaro (*Carnegiea gigantea*), are even able to tolerate the lack of moisture on this hot hillside in the Sonoran desert. (Photograph of saguaro cactus and author by Cathy Keddy, Phoenix, Arizona, 2007.) Saguaro cacti are introduced in Section 7.2.1, while deserts and barrel cacti are discussed in Chapter 10.

1.1 Introduction: The Importance of Plants

1.1.1 Plants Are Abundant and They Support Other Life Forms

Plants occur in almost every imaginable habitat on Earth – exposed on wind-swept mountain tops, submerged under water on lake bottoms, perched perilously on branches in the rain forest canopy or simply withstanding the sweltering desert sun. Moreover, they can be many sizes, from microscopic oceanic plankton to towering giant sequoias and eucalypts. Let me begin by introducing you to just three plants that illustrate some of the larger terrestrial species, and the topics we will explore in this book. The saguaro cactus (Figure 1.1) is seen in many films but in reality occurs only in the Madrean deserts of the New World. This one was photographed just outside of Phoenix, Arizona. The remarkable sausage tree (Figure 1.2) grows naturally only in the tropics of Africa, where it depends upon bats to pollinate its flowers. The sacred fir (Figure 1.3) is restricted to just a few mountains in Central America, where it provides a winter home for monarch butterflies. As we proceed through this book you will meet many more unusual plants and vegetation types. We will explore the factors that control their abundance and consider the challenges of managing habitats for conservation.

There is a very practical reason for learning about plants. They comprise more than 99 percent of all the Earth's living matter. That is to say, Earth is not a world of lions and whales, but a world of conifers and angiosperms. We can also say with confidence that the biosphere – including the oxygen you are breathing as you read this paragraph – is largely the consequence of the origin and diversification of plants. Without plants, conditions on

FIGURE 1.2 The world's tropical regions have an enormous number of flowering trees. One example is this sausage tree (*Kigelia africana*) on the edge of a savanna in Uganda. The flowers open at night for pollination by bats and moths. The fruit is consumed by mammals including elephants. (Photograph from Wikimedia Commons)

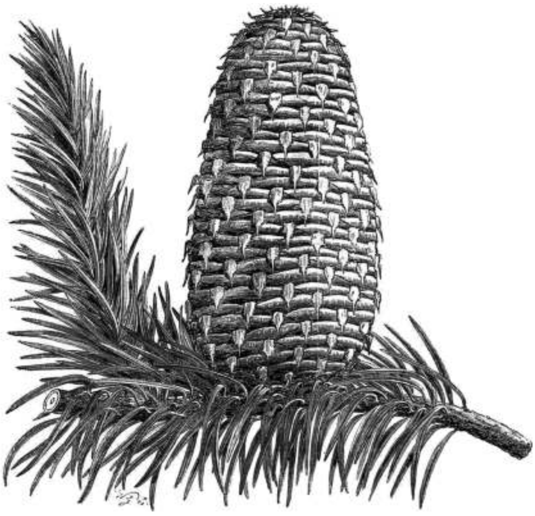

FIGURE 1.3 *Abies religiosa*, or sacred fir, is one of several conifers found in the mountains of Central America at altitudes of 2,000 to 4,000 metres. A single cone is typically greater than 10 cm long and typically produces 300 to 400 seeds. This is also the preferred tree in which overwintering monarch butterflies hibernate. (Worthington Smith, 1887, Peter H. Raven Library/Missouri Botanical Garden)

Earth – including temperature, types of rocks, the composition of the atmosphere and even the chemical composition of the oceans – would be vastly different. And, of course, plants provide for human sustenance, with the spread of human civilization being linked to the first discovery of agriculture. Global exploration (and wars) were driven by the search for spices, including pepper and cinnamon, which came from tropical trees. And then there are the many other products such as rubber, cotton, silk, quinine, tobacco, wine, potatoes, sugar cane, soybeans and heroin, all of which had, and continue to have, enormous impacts upon human individuals and human civilization (Laws 2010). Along the way we shall also meet asteroids, burning cliffs, dinosaurs, poisonous plants, seed-carrying ants, carnivorous plants and wild orchids. And we shall visit, briefly, locations including the Andes Mountains, the Amazon River basin, the Sonoran desert, South African deserts, Socotra Island in the Middle East, the Galapagos Islands in the Pacific Ocean and the forested mountains of southern China. You will also meet an array of early scientists who actually did the research that made a book such as this possible.

The world will always need botanists and plant ecologists. Many of the students on my courses seem to want to use their skills to protect wild animals and improve the human condition, but I often find it necessary to explain that it is rarely possible to be effective at these tasks without some understanding of botany and ecology. If you want to contribute to ecology, or to conservation, or to many kinds of human welfare, you have to know something about plants first. Those of you planning to work in fields including forestry, zoology, fisheries management, geography, planning or environmental studies (not to mention molecular biology and medicine) may find it helpful, if not absolutely necessary, to know something about plant ecology. Indeed, one could suggest further that there is little point in going on a tropical holiday if you are unable to appreciate the remarkable plants and vegetation found there. If this book inspires you to continue with the study of plant ecology, and provides some resources to guide you in doing so, it will have succeeded. Equally, however, if it enriches another scholarly discipline that you intend to follow, or at least helps you better appreciate parts of the world that you one day visit, then it will have succeeded in another way. With the increasing specialization of many sub-disciplines in ecology in particular, and biology in general, I also think there is a need for a book that synthesizes the big picture in a way that will allow specialists to pursue their selected field more effectively. Hence this is also a book for fellow professionals and, if the early parts of each of the chapters seem somewhat basic, you will find in the later sections of each chapter enough depth and subtlety to challenge even the expert.

1.1.2 Fundamentals and Overview

While plant ecology is generally defined as "the study of relationships between plants and the environment" plants do not, as this definition implies, merely inhabit environments. Plants also create environments, and they may even control them. Where, then, should one begin a book on plant ecology? The answer is clearly genesis – the origin of plants and the processes that created the current biosphere. As we all learned in our first biology course, plants live by capturing sunlight. The first chemical process we were likely expected to memorize may well have been photosynthesis. This was a world-changing process and we will look at it in some detail.

Most newer students that I teach – including graduate students – appear to know relatively little about global processes and geological time scales. I will therefore start with the story of plants and the origin of the biosphere in a quite general way, emphasizing long-term consequences for the atmosphere, the oceans and the land. The list of further readings will allow you to pursue a deeper understanding of the impacts of plants on biogeochemical cycles, energy flow and the greenhouse effect. In Chapter 2 we will examine global patterns in plant distribution and some of the explorers who made these important discoveries, which might inspire you to visit new areas of Earth and explore them yourself. Then and only then will we encounter the material with which most text books begin: resources and plant growth. In Chapters 4 to 7 we will work our way through the processes by which plants interact with other plants, fungi and animals (including competition, herbivory and mutualism), and the ecological consequences of these interactions. In Chapter 8, we will return to time, including the impacts of meteor collisions and ice ages upon plants and vegetation. Chapters 10 through 12 have more advanced work on patterns in vegetation and how they are studied. We will conclude, in Chapter 13, with the large scale again: the growth of the human population and its consequences for the biosphere and the Earth's plants and vegetation.

But first, a brief introduction to plants and vegetation types as they exist today.

1.1.3 The Number of Species and Their Classification

There are now some 350,000 species of plants in total, spread from coastal mangrove swamps to mountain peaks. Many plants are found in deserts. Some even grow in shallow water, including shallow salt water, although none of these represents ancestral plants. Contemporary wetland plants are species that have re-invaded wetter habitats from terrestrial ancestors. In this book we shall focus a good deal of time on flowering plants, or **angiosperms**, because they are the most common. However, this does not mean we can safely ignore the other groups of plants. A brief introduction to the others is given, following Table 1.1, from the bottom to the top. The second most common group is the **gymnosperms**, with seeds, and often in cones, but plants with no flowers or fruits. They appeared much earlier in evolutionary history, and are common in the fossil record. Those of you familiar with plants will know that the gymnosperms are a somewhat artificial group, since they contain four divisions: Coniferophyta, Cycadophyta, Ginkgophyta and Gnetophyta. The latter three are quite uncommon, although of considerable botanical and evolutionary significance. They may show up from time to time in this book, but you will survive if you realize that when I refer to gymnosperms, I am mostly referring to conifers, but trying to remind you that they are not the only seed-bearing plant that lacks flowers. The last group, a small proportion of the numbers and biomass, is the spore-producing plants that represent some early evolutionary stages, pteridophytes and other early vascular plants. Some of these (such as *Lepidodenron*, see Figure 1.7) were enormous, but only relatively small species survive today, with the notable exception of the tree ferns. Lastly there is the Bryophyta. They most likely represent the earliest stage of land colonization and still remain relatively common in wet habitats, often as epiphytes. And yet there is one exception: possibly the most abundant plant in the world by weight is *Sphagnum* moss (see Figure 10.13), the plant that forms vast northern peat bogs.

Table 1.1 The main groups of flowering plants (kingdom Plantae) and the classification used in this book.[a] We will return to this table again late in the book in Box 8.1.

Group	Division
Bryophytes	Bryophyta (mosses and liverworts)
Vascular plants	
Seedless plants	Lycopodiophyta (club mosses)
	Equisetophyta (horsetails)
	Pteridophyta (true ferns)
	Psilophyta (whisk ferns)
Seed plants	
Gymnosperms	Cycadophyta (cycads)
	Ginkgophyta (ginkgo)
	Pinophyta (conifers)
	Gnetophyta
Angiosperms (flowering plants)	Magnoliophyta (flowering plants)
	Class Magnoliopsida (dicots)
	Class Liliopsida (monocots)

[a] Note that newer classifications are available, but not necessarily helpful from the perspective of plant ecology. For example, the *Tree of Life*, based on Kenrick and Crane (1997a) combines the last three divisions of seedless plants into one group, the Polypodiopsida, as a single clade. It also calls the entire group of plants in this table Embryophtes. The Angiosperm Phylogeny Website of the Missouri Botanical Garden (www.mobot.org/MOBOT/research/APweb) puts many of the above divisions into orders, and has a more complicated breakdown of the Magnoliophyta. Sometimes the name Lycophyta is used instead of Lycopodiophyta, and so on. While systematics thrives on such changes, for readers of this book and most practising ecologists, this table is quite sufficient.

Now, obviously, this is quite a broad series of generalizations. I would encourage you to revisit a book of basic botany and evolution to remind yourself of the different main groups of plants. It will make this book more interesting, and account for the occasional digression into topics such as gametophytes. At a minimum, I shall assume that you know what an angiosperm, conifer and fern are, and I shall, when necessary, use more technical names when it is appropriate.

1.1.4 Vegetation Types and Climate

One of the most useful general principles in plant ecology is this: all the major types of plant communities on Earth are controlled by two main factors: temperature and rainfall. In general, the warmer it is, and the wetter it is, the more abundant plants will be and the more kinds of species there will be. This is why, for example, the world's rain forests are huge reservoirs of plant species. There are, as we shall see, more than ten thousand species of trees in the Amazon basin alone, not counting the orchids and bromeliads that grow on the branches of these trees. And there are more kinds of orchids than any other group of flowering plants. So Figure 1.4 is an important, one might say, foundational, figure. It was first presented by Helmut Lieth in German and later adapted in English by Whittaker in his (1975) book *Communities and Ecosystems*.

You have likely already seen a version of Figure 1.4 in a basic ecology book, but let us have a short review. If you follow the upper line in the diagram, you are moving along a gradient of increasing temperature and rainfall. You pass through four major vegetation types, tundra (arctic plants), boreal forest (conifers and cold grasslands), temperate rain forest and tropical forest. Those of you reading this book in Europe or eastern North America, for example, are in the temperate forest region of the world, a region where many tree species are deciduous.

All the regions below these four main types are produced by low rainfall. On the far right, that is in warm climates, as one moves from top to bottom it becomes drier, from tropical rain forest to tropical seasonal forest (with a pronounced dry season), to subtropical desert. Finally, in the intervening area lies a rather complex mixture of shrubland and grassland. In this region, generalizations may be more difficult. This is likely because other factors

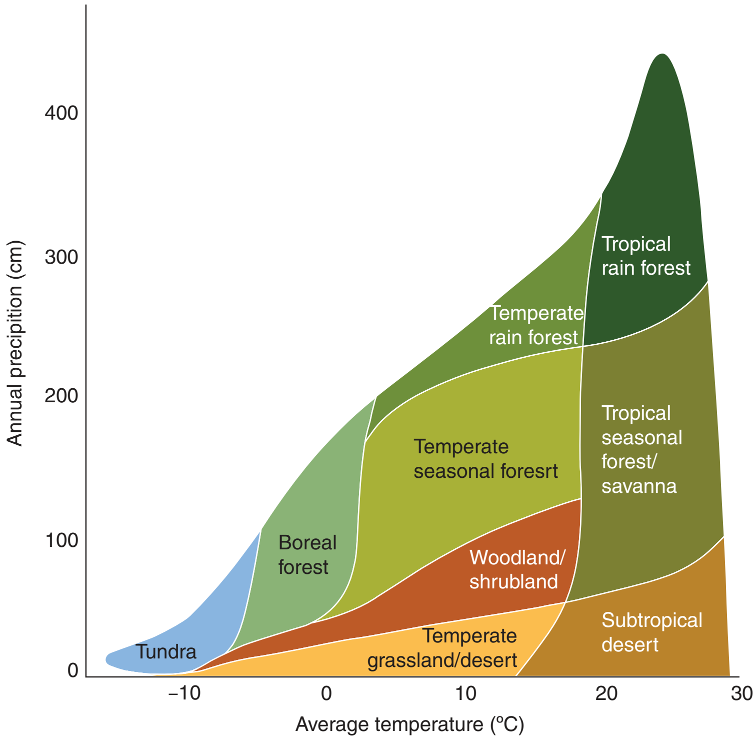

FIGURE 1.4 World vegetation types are produced by just two main factors: precipitation and temperature. We all live somewhere inside this envelope. Identify the location of your home. (From Ricklefs 2001 after Whittaker 1975)

such as fire and grazing animals have a pronounced effect on these vegetation types. Hence one has to consider factors such as disturbance (Chapter 5) and herbivores (Chapter 6) to understand what is happening. It is possible for herbivores to change grassland to shrubland by removing grasses; it is also possible for herbivores, particularly with human assistance, to turn grassland into desert (Figure 10.8). One might regard this region of the diagram as an area of lower predictability and multiple stable states. Often there can be quite abrupt thresholds to switch from one state to the other, a topic to which we will return in Chapter 13. Thus while this diagram shows the main relationships between climate and plants, other factors become important in specific situations.

1.2 The First Land Plants

The land was apparently colonized about 400 million years ago (Niklas et al. 1985; Taylor 1988; Stewart and Rothwell 1993). So far as one can infer from the known fossil record, both plants and animals colonized the land at about the same time, give or take 50 million years. It is not clear why there was a long delay before life forms were able to colonize terrestrial habitats. One hypothesis is that it took that long for there to be sufficient oxygen in the atmosphere for respiration. Another suggestion is that it took that long for ozone to accumulate and shield the Earth's surface.

Some typical early land plants are shown in Figure 1.5. These fossils of *Asteroxylon* and *Rhynia* were found in Scotland by Kidston and Lang (1921), preserved in chert that formed in the early Devonian, about 410 million years ago. These two examples appear typical of early land plants – small erect shoots

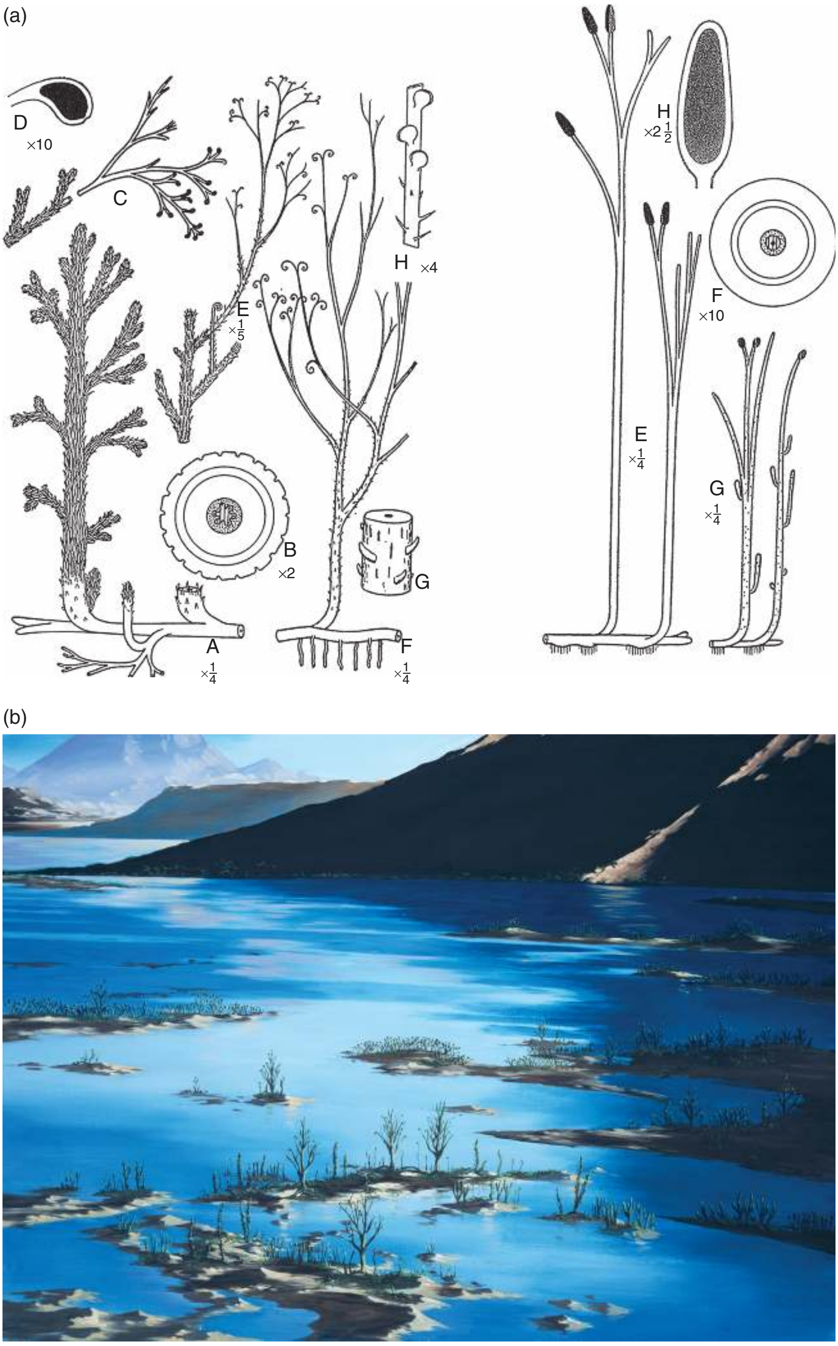

FIGURE 1.5
(a) Reconstructions of three early land plants discovered in the Rhynie chert in Scotland including an *Asteroxylon* species (left A–E), *Psilophyton princeps* (middle F–H) and a *Rhynia* species (right E–H). Sections B and F show stem cross-sections with a central vascular bundle. D and H give a longitudinal section of a typical sporangium. (From Sporne 1970)
(b) Artist's impression of an early Silurian landscape (ca. 440 million years ago) showing populations of early land plants beside freshwater pools. (© Natural History Museum, London)

with horizontal rhizomes – lacking roots, leaves, seeds and woody tissues (Stewart and Rothwell 1993; Kenrick and Crane 1997a,b). Some similar genera still alive today include *Psilotum, Lycopodium* and *Selaginella*. The ancestors of such plants were probably horizontal in growth form with the gametophyte stage dominant, similar to modern liverworts. Fossilized spores of such ancient liverworts have been found in rocks approximately 460 million years old in Argentina; this could place the earliest land plants in the Ordovician era, on the western margin of the Gondwana paleocontinent (Rubenstein et al. 2010).

There is good reason to conclude that colonization of the land also required the evolution of symbiosis between plants and fungi. Much of the nutrient uptake by terrestrial plants is still accomplished by a mere 130 species of fungi in the relatively ancient genus *Zygomycotina* in the order Glomerales (Peat and Fitter 1993; Simon et al. 1993). Re-examination of fossil plants from the Devonian suggests that mycorrhizal fungi were associated with plant rhizomes as early as some 400 million years ago (Pirozynski and Dalpé 1989; Taylor et al. 1990). The fact that mycorrhizae are now found worldwide, and in groups including ferns, gymnosperms and angiosperms, is further evidence of their early origin. The fungi therefore appear to have diversified along with the terrestrial plants (Berbee and Taylor 1993; Simon et al. 1993).

The land produced intense selection upon plants. A whole new suite of traits, including a cuticle to reduce desiccation, stomata to control water loss but admit CO_2, sclerenchyma to strengthen stems for vertical growth, and water conducting tissues, arose out of the strong natural selection to cope with desiccation. Early land plants still betrayed their aquatic origins by having free-living sperm that swam from male to female organs. This is obviously workable in the ocean but not a terribly good trait for dry conditions (we return to this topic in Box 8.1). In fact, a recurring theme in many discussions of plant evolution is the way that terrestrial environments have driven modifications to plant reproductive systems to get around the constraints imposed by a terrestrial habitat (Raven et al. 2005). The gymnosperms appear to have been one of the first groups in which selection eliminated motile sperm and produced the

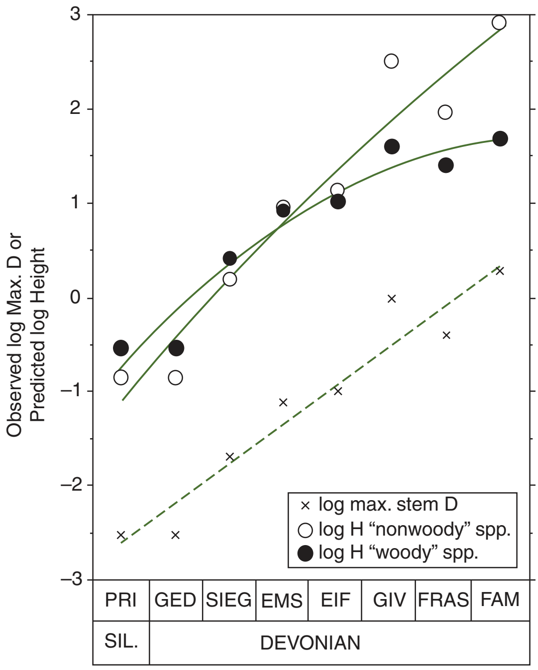

FIGURE 1.6 Plant height increased through the Devonian, as documented by stem diameters of early Paleozoic vascular plants combined with allometric equations for non-woody and woody species. (From Niklas 1994)

pollen tube (although free water is still required for the pollination droplets that capture the pollen). Further, the cycads, alone among the gymnosperms, still have sperm cells that swim down pollen tubes to fertilize the egg. The rest of the gymnosperms, and all of the angiosperms, have lost even this vestige of their aquatic origin; only nuclei move down the pollen tube.

Plant height increased steadily through geological time, presumably as a consequence of increasing competition for light (Figure 1.6). By the Carboniferous era, there were real forests. Trees such as *Lepidodendron* (Figure 1.7) reached a height of 30 metres with trunks a metre in diameter at the base (Bell and Hemsley 2000). Over the next 100 million years, these early vascular plants were replaced by ferns, and then by conifers (Figure 1.8). Then, just over 100 million years ago, the flowering plants (Angiosperms) arose – a topic we will explore further in Section 8.2.

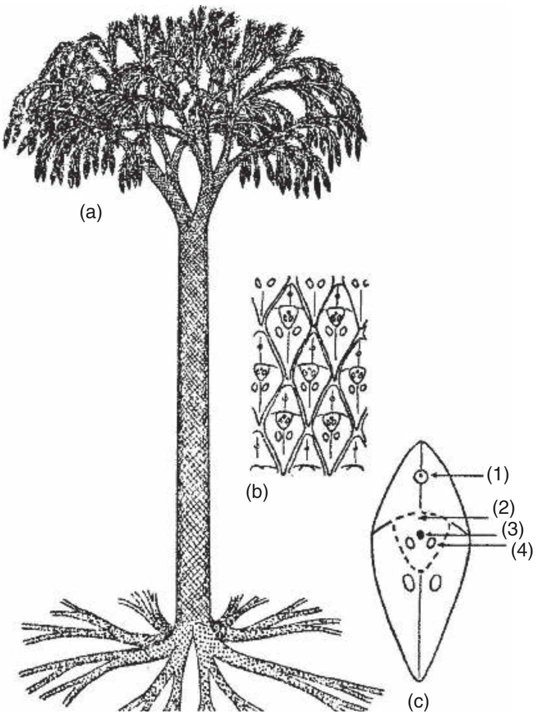

FIGURE 1.7 Reconstruction of *Lepidodendron* trees: (a) whole plant; (b) leaf scars; (c) leaf base (1 ligule pit, 2 area of leaf base, 3 vascular bundle, 4 parichnos scars). (From Sporne 1970)

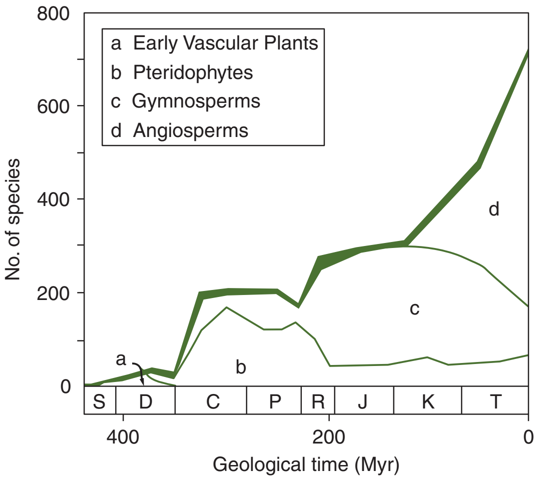

FIGURE 1.8 Trends in vascular plant diversity illustrated by the estimated number of fossil species in four major plant groups. (From Niklas et al. 1983)

We should note, in passing, that the spread of land plants probably had effects on the oceans. Before land plants appeared, there would have been very rapid rates of erosion, as rainfall spilled off the naked land directly into rivers and oceans. As plants covered more land surface, erosion would have decreased. Also, biologically essential nutrients such as phosphorus would have been selectively stored, either in living plants, or in their organic debris now accumulating as soil and peat. Hence those organisms in the ocean adapted to vast amounts of eroded material, or to higher dissolved nutrient levels, may have been replaced by other species better adapted to the new oceanic conditions.

Now that you have refreshed your familiarity with the diversity and origins of terrestrial plants, you have two choices available for the remainder of this chapter.

1. If time is limited and you want to move quickly through this book, you can wrap up the topic of plants in the biosphere by leaping ahead to Plants Affect Climate (Section 1.9).
2. If you are curious about what happened before plants arrived on land and how they created the atmosphere altogether, you can continue (Section 1.3, following) to read about the origins of photosynthesis, single-celled plants and the oxygen revolution.

1.3 Energy Flow Organizes Molecules

To understand the origin of plants, we must understand the origin of photosynthesis. For life to exist, energy flow is required. Such a requirement is met when a planet is situated near enough to a star for sufficient energy released by solar fusion to pass the planet before dissipating into outer space. This is the