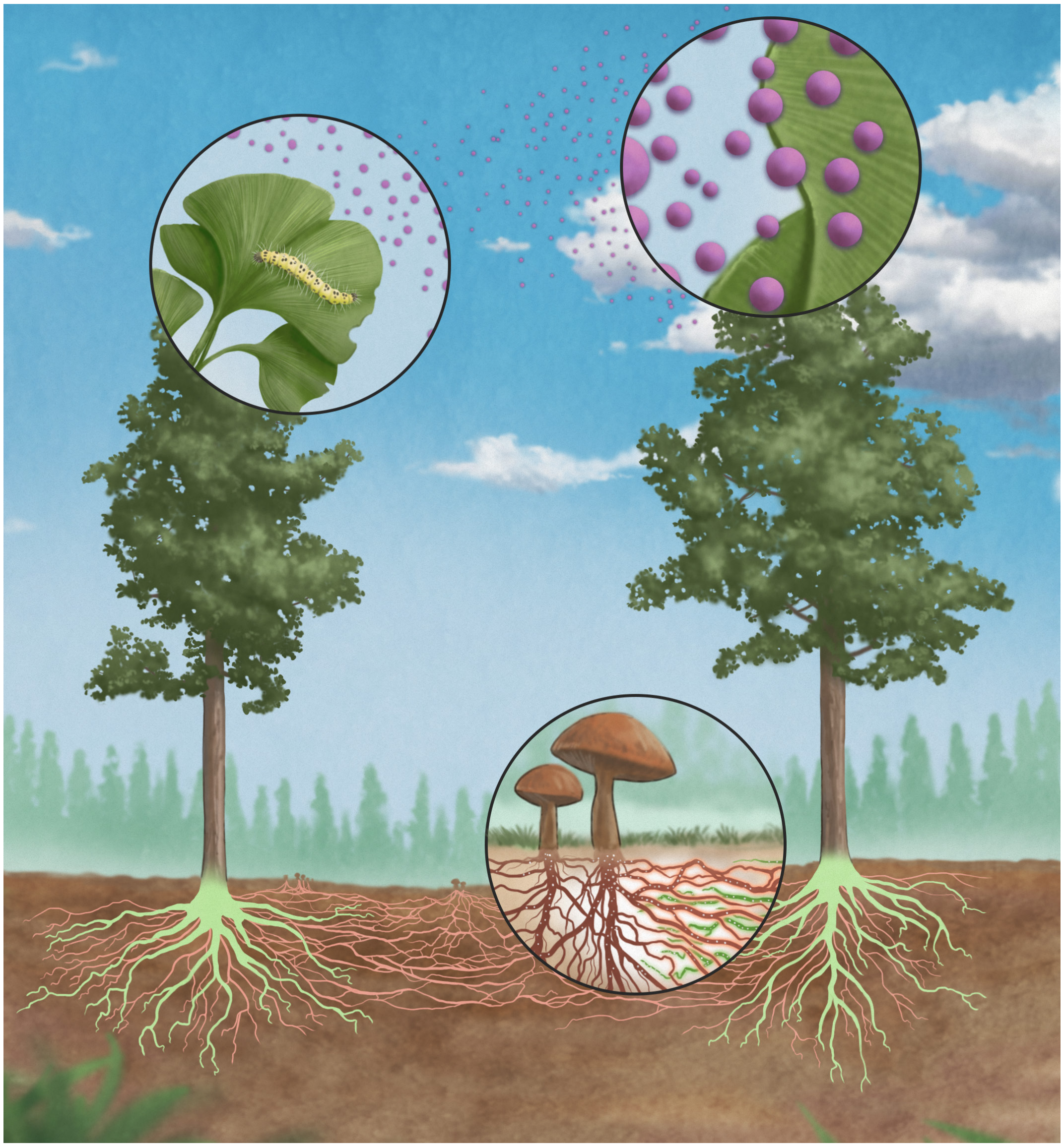
CONTENTS

respond to changes in position by reinforcing support structures and redirecting growth if the plant is tilted.

Although plants make their food—sugars—through photosynthesis, they require a variety of other elements to make the wide range of molecules needed for life. In addition to hydrogen from water and carbon and oxygen from carbon dioxide, plants need nitrogen for proteins, phosphorus for energy storage molecules, and potassium to control water movement in and out of cells. Plants also need calcium, magnesium (for chlorophyll), sulfur, boron, copper, iron, chloride, manganese, molybdenum, and zinc. Roots hunt through soil for these mineral nutrients, detecting them with specialized proteins on their tips. When detector proteins sense needed elements, plant hormones signal a proliferation of root hairs and turn on the absorption system. This moves mineral nutrients into the root, where they ascend the stem to nourish plant cells.



Plants produce and detect chemical signals—scents represented as purple molecules above—that are exchanged among plants, and between plants and fungal and animal partners. Mycorrhizal fungi (drawn in red) facilitate communication among root systems (in green).

Plants sense temperature with other proteins embedded in their cell membranes. These proteins change shape as temperature rises and falls, which stimulates a variety of responses in the plant cell. These proteins work together with light sensors to tell leaves when sunlight causes leaves to overheat and they must open their stomata to cool off. Temperature sensors in other parts of the plant help synchronize growth and other important activities with seasonal conditions.

Plants also sense touch. In animals, detecting pressure relies on specific nerve cells. Lacking nerves, plants perceive touch using springy proteins embedded in their cell membranes. When touched, these proteins change shape and signal physical contact. This mechanism is most important for plants that respond quickly to touch, such as the Venus flytrap (*Dionaea muscipula*), which snaps shut on an unsuspecting insect within seconds of contact. In this case, the plant responds to the fly's touch by sending waves of electrically charged calcium ions through the cell. This signals the plant to move water into cells on the outside of the trap, swelling them and folding the trap closed. In other cases, physical contact changes pressure inside the cell as a whole, triggering slower responses. In climbing plants, for example, a tendril feels the pressure of contact with a nearby surface. The touch causes the tendril to grow toward the pressure, eventually grasping a support.

Plants use other specialized proteins on their cell surfaces to detect specific chemicals. In animals, we call this smell. Like animals, plants sense and respond to compounds that travel through the air. For example, plants emit particular compounds when experiencing drought stress or insect attack. Nearby plants, or different parts of a large tree, detect these chemicals and respond by producing defensive compounds or adjusting water use. In grass, the familiar "new-mown lawn" smell is an alert signal to neighbors that leaves are under widespread assault. Roots also release chemical signals that invite connections with neighboring plants, direct the behavior of soil fungi, and alert neighbors of developing water stress. Plants release familiar chemicals—scents—that attract pollinators and seed dispersers. In many cases, the particular blend of compounds released can be complex and specific, a way for the plant to communicate its identity to a particular pollination partner. In other cases, generalized scents advertise sweet fruit to a variety of dispersers.

LIVING TOGETHER IN COMMUNITIES

In the mid-twentieth century, the new field of ecology debated whether plants lived together in highly interdependent communities or plant species co-occurred as neighbors of convenience. In 1916, Frederic Clements observed that regions were clearly defined by particular collections of species. Patterns emerged regionally and locally, with specific plant associations seen in spots with specific soil and climate conditions. In northeastern North America where he worked, Clements noted that when plants recolonized abandoned farm fields, they did so with a predictable pattern of successive species. First came grasses and herbs like asters (*Symphyotrichum*), ragweed (*Ambrosia artemisiifolia*), and goldenrod (*Solidago*). These were followed by sun-loving shrubs like blueberry and huckleberry (*Vaccinium*). Easily dispersed, hardy, and short-lived trees like pin cherry (*Prunus pensylvanica*) and aspen (*Populus*) germinated in the sunny meadows and quickly developed a canopy, which shaded the soil, reduced its temperature, and stimulated germination of longer-lived trees like sugar maple (*Acer saccharum*) and beech (*Fagus*). Deeper shade beneath this canopy fostered oaks (*Quercus*) and a variety of ferns. Clements argued that these species depended on each other to provide the conditions needed for germination and growth, so they must live as an interconnected community, vulnerable to the loss of any of its members. Henry Gleason offered a counterargument in 1917. He proposed that individual plant species simply followed their preferred environmental conditions. If particular species tended to be found together, it was because they all sought similar climates, soil types, moisture, and light environments.

Over the next decades, several important observations shifted thinking toward Gleason's view of plant communities. The species that recolonized an area after wildfire or clear-cutting differed depending on the type of disturbance. While grasses and herbs dominated abandoned farm fields, bracken fern greened areas cleared by wildfire. Moreover, paper birch (*Betula papyrifera*), not yellow birch (*B. alleghaniensis*), was the first tree to invade areas blackened by fire. However, the arrival of forest trees also depended more on the proximity of mature trees that could provide seed than on the particular species of the tree. These observations suggested that plant species responded to cues in their environment and the luck of dispersal, rather than following specific partners.

In Wisconsin, John Curtis described the slow dance between prairie and forest. In 1959, he reported that the boundary was dynamic and varied with climate, fire history, and dispersal as species from the forest ventured into the prairie and prairie species penetrated open spots in the forest. Fossil pollen preserved in the sediment of ponds throughout the eastern United States provided additional evidence. In 1958, Margaret B. Davis published her first paper on pollen deposited in ponds during the retreat of glaciers at the end of the most recent ice age. Davis's work documented 21,000 years of forests greening a landscape that had been scraped bare by ice. Over the next 20 years, Davis showed that tree species followed individual migration routes out of their glacial refuges. She realized that tree species living together today were those that happened to arrive at a spot where climate and soil conditions were right.

The final piece of evidence came from ecologists studying how North American forests responded to the chestnut blight of the early twentieth century. American chestnut (*Castanea dentata*) was one of the most abundant trees throughout the Appalachians until the late nineteenth century thanks to forest husbandry by Indigenous Americans. In Clements's view of interconnected plant associations, chestnut's loss would have ripped the forest community apart. Chestnut was abundant in the pollen record prior to the early twentieth century, then it suddenly disappeared as mature trees succumbed to a fungal disease introduced from Asia. By 1912, almost all mature chestnuts in North America were dead or dying. Instead of collapsing, however, other trees like maples and oaks filled the spaces left by the chestnuts. The forest communities changed but did not collapse. The evidence seemed clear that plants followed preferred soil and climate conditions and established wherever their seeds could find a space. Although canopy trees certainly changed the environment on the forest floor and influenced which species could live in their shade, the identity of canopy trees seemed to matter little.

Applying these ideas to the Mesozoic, paleobotanists recognize that plants have relatively simple needs that have remained the same over most of the history of plants on land: sunlight, water, mineral nutrients in soil, and space. The constancy of these needs means that many of the principles of plant biology derived from the study of modern plants apply easily to those that lived in the Mesozoic. And where details might differ, we have Mesozoic survivors—ferns, horsetails, conifers, *Ginkgo*, and cycads—with which to test the breadth of these biological ideas.

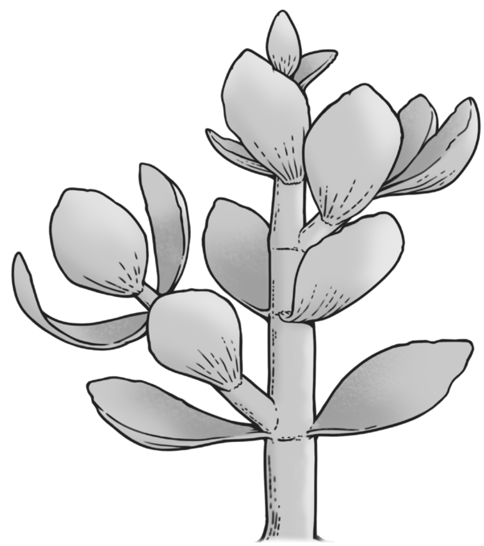
GROWTH

The differences between plants and animals begin with their cells. Both plant and animal cells have nuclei that contain most of the genetic instructions—in the form of DNA—needed to build and operate the organism. Plant and animal cells also share structures called ribosomes that translate genetic information into proteins that do the work of life, and mitochondria that use sugars for energy to power all the organism's activities. A flexible cell membrane encloses all these cellular structures and selectively allows water and other molecules in and out of the cell. This is where the differences begin. Plants have chloroplasts, the factories where photosynthesis takes place. Chloroplasts contain the pigments plants use to gather light, split water molecules, and package chemical energy. Chloroplasts also house the scaffolding where the photosynthetic enzyme rubisco grabs carbon dioxide and begins its transformation into sugar. The most consequential difference between plant and animal cells is the stiff cell wall that surrounds the cell membrane in plants. Plant cell walls are composed mostly of cellulose, the long molecule that gives cotton its string-making powers. Some cell walls, particularly those in water-conducting cells, are further reinforced with a virtually indestructible compound called lignin, which gives wood its woodiness.

The cell wall gives plants many advantages. First, they are stiff and resilient. Plants do not need bones or shells to hold their bodies together and upright on land. Cell walls also protect plant cells from invasion by ever-present microbes and make them a little less palatable to predators. Of course, both microbes and plant predators have evolved strategies to deal with these defenses. For example, one group of fungi found the biochemical key to digest lignin. The protective cell wall also comes at a cost: after they lay down their walls, plant cells cannot move. In animal growth and development, cell movement is vital. Most animal cells are specialized for a particular function—for example, becoming muscle, blood, bone, or a reproductive cell—soon after they arise and must move to the appropriate part of the animal body to function. This strategy will not work for plants. Instead, plants retain pockets of generalized cells throughout their body, allowing them to spring into developmental action and transform into specialized cell types whenever needed. In practical terms, when you prune your shrubs, the plant can activate generalized cells near the site of the cut and immediately build new water-conducting, sugar-transporting, structural, or photosynthetic parts. Most animals, in contrast, struggle to replace important cells when they are lost or damaged.

MODULAR GROWTH IN PLANTS

Plants build their amazing variety of forms from a simple building block, creatively modified and repeated over and over. To understand this design, consider a familiar houseplant like the jade plant (*Crassula ovata*). Look closely at a straight part of the stem. You will notice that leaves emerge, generally in pairs, at defined points along the stem, with successive pairs oriented at right angles to the pair above and below. Between the leaf pairs, the stem is straight and smooth—or perhaps wrinkly and textured in older stems. The point where the leaves emerge is called a node. The straight stem between is an internode. In an unbranched jade plant, the node-internode building blocks stack one on top of the other like children's snap-together bricks to form a straight stem with pairs of leaves all along. Growth begins with a cluster of generalized cells tucked between the topmost pair of leaves. These cells retain the ability to transform into any cell type that the plant needs. The generalized cells at the growing tip produce a plant hormone called auxin, which directs the proliferation of cells and helps the new cells become organs, such as leaves at the edges of the stem or water-conducting cells toward the center. When all the needed module cells are ready, a second family of hormones, gibberellins, signal cells to elongate by filling with water and stretching, just before the stiff cellulose cell wall forms. Once the final shape of the cell is cast by the cell wall, the new cell is ready to begin its work. In a plant instant, a new shoot extends from the growing tip, the straight internode elongates, and leaves unfurl. The



Crassula ovata illustrates the node–internode design found in most land plants. Leaves and branches emerge from nodes. Between nodes—the internode—the stem elongates.

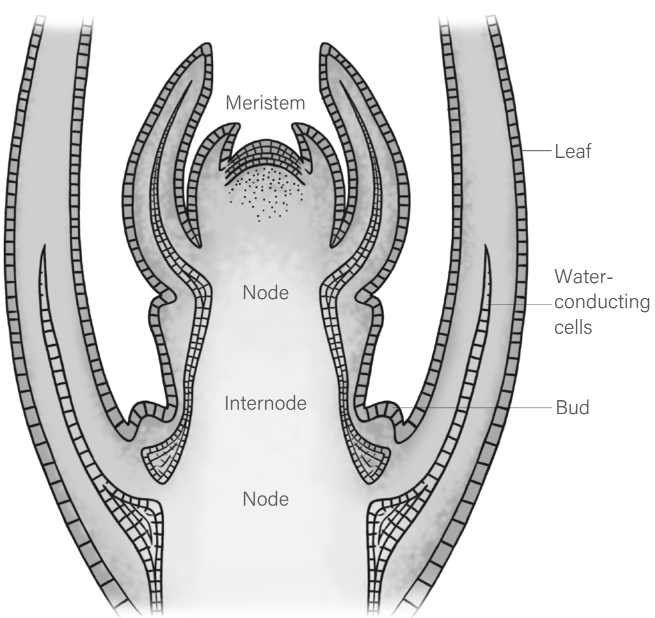
plant has added a new node–internode module, and the leaves at the growing tip have moved just a bit closer to the light. During the phase when gibberellins direct cell elongation, the plant's light-sensing system samples the environment to determine whether the growing tip is in sun or shade. If phytochrome detects shade, gibberellins pour into the cells, and the internode stretches as far as it can in search of better light conditions. If phytochrome detects the red wavelengths of full sunshine, gibberellins fade and the plant produces a short internode.

Take a pair of pruning scissors and cut through the jade plant's internode just above any pair of leaves and you will see another key part of the plant growth strategy. Nestled in the node, just above the place where the leaf attaches, is another cluster of generalized cells, a bud. When growth is focused at the tip of the stem, auxin produced by cells at the top of the plant keeps the buds below in a state of suspended animation. They remain able to develop, but they do not. However, remove the tip of the stem, and the auxin supply disappears. Now, the generalized cells closest to the topmost remaining pair of leaves spring into action and begin to pump out their own auxin. Auxin stimulates development of a new branch—long, straight internode and leafy node—that emerges from the spot just above the topmost remaining leaf. In addition to becoming branches, the generalized cells at each node can become reproductive structures like flowers or cones when the plant senses that the time is right.

Now return to the cutting you removed from the jade plant. Place it in water, and the generalized cells at the node just above the cut will recognize that something dramatic has happened and respond by transforming into roots. Once roots emerge, the new plant can be transferred to soil, where it will continue to grow upward from the shoot tip and downward as roots from the bottommost node. In nature, wind or a passing animal might knock branches off the wild jade plant. Once on the ground, the node closest to the break will send out roots that sense gravity and dive downward in the hope of reestablishing a connection to the lifegiving soil. The shoot tip also senses gravity and turns to grow upward. This ability to respond to damage allows the plant to proliferate in spots where the parent thrives.

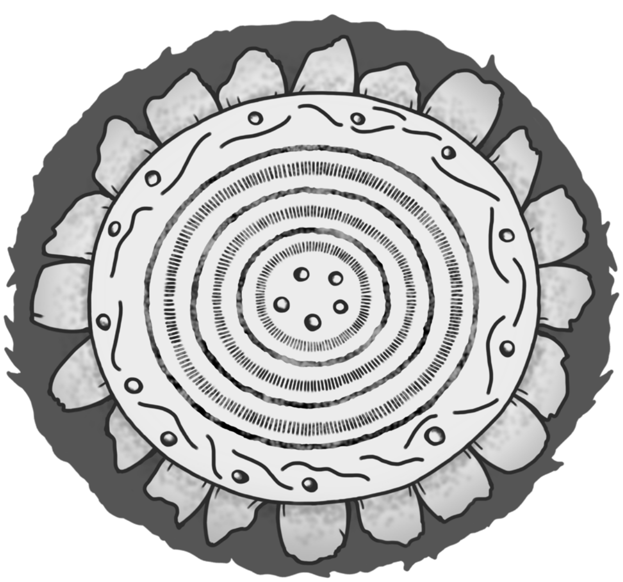
BUILDING THE VARIETY OF PLANT FORM WITH NODES AND INTERNODES

Although a jade plant provides a useful example of basic plant growth, many plants look quite different, with less obvious nodes and internodes. Even so, they use the same succession of modules, with a few modifications, to produce their varied architecture. Consider a conifer like eastern white pine (*Pinus strobus*). When a seed germinates, the embryo's root tip emerges first. Starch granules in the root cells sense gravity, and the tip dives for the cover of soil. Meanwhile, the shoot wriggles free from the seed coat and displays a tuft of needles. Phototropins immediately look for the blue light that will point the shoot skyward. Once upright, the cluster of generalized cells nestled within the first lock of needles produces growth-stimulating auxin, and new modules develop. If phytochrome detects shade, the seedling's best chance of survival will be to devote energy to producing as many new leaves as possible. Therefore, successive internodes will be



The growing tip or meristem of the plant contains cells that can develop any plant tissue, giving the plant flexibility to replace lost or damaged parts.

extremely short, with needles produced at each node. So that needles do not shade each other, they emerge in a spiral around the cylindrical shoot, creating a bottle-brush array. Because the internodes are short, the seedling does not grow taller during this early phase. Over time, the forest canopy might open, allowing red-enriched sunlight to strike the pine seedling. Phytochrome senses the change and signals gibberellins to stretch the internodes so that the seedling can shoot up quickly. Pines, like most conifers, depend heavily on their topmost growing tip to regulate their shape, and as that growing tip moves farther away from the nodes below, the buds at these lower nodes feel the apical tip's auxin less and begin to stir. When the growing tip is just the right distance from the buds below, they produce new branches. For many conifers, branches arise at regular intervals along the straight, central stem as the tree grows taller. For pines growing in a forest where the only red light is from above, lateral branches may see shade, which triggers growth to stop and the branches to die and fall off. This creates the tall, straight, branchless trunks that characterize conifers in dense forests.



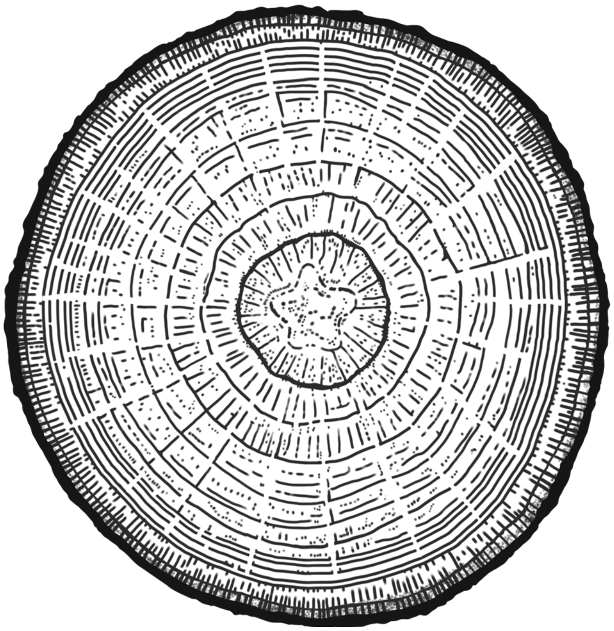
This cross section shows how cycads build sturdy trunks. Their strength comes from a thick outer bark and woody leaf bases. Cycads produce little or no wood.

Some ferns and grasses take a different approach to nodes and internodes. The green clumps of ferns or the grass blades between our toes are only the leaves of the plant. Dig down a bit and you will find the leaf clusters, produced on very short internodes, attached to a specialized stem that grows horizontally just below the soil surface. For the underground stem, the dark of the soil environment stimulates the internodes to elongate as the growing tip explores for soil nutrients or a patch of light. Once the growing tip detects a suitable spot, gibberellin production slows, internodes shorten, buds spring into action, and a new tuft of leaves grows skyward. For these plants, their growing tips and the generalized cells that control plant growth are hidden safely below the surface of the soil, protected from animals who gobble up the leaves.

To build even more exotic plant bodies, evolution has modified the basic module even further. In the squat trunks of many modern cycads, internodes fail to elongate, and whorls of leaves and the woody scales that support them pile on top of one another to form a spiky mound. Precious generalized cells are protected inside the armored trunk while only leaves face a world full of herbivores. Vines like kudzu (*Pueraria montana*) take the opposite approach. The fast-growing invasive from subtropical regions of South and East Asia can grow up to 30 cm (12 in) a day by maximizing cell elongation in its internodes. Vines combine this extraordinary elongation ability with their light-sensing and support-grabbing powers to locate sunlight and climb toward it.

MANY WAYS TO BUILD A TREE

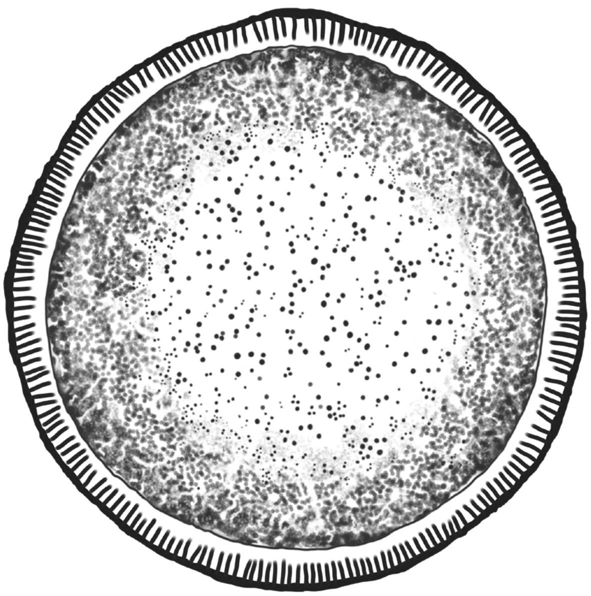
Imagine taking your childhood sweetheart to a favorite tree to enjoy a first kiss. You might—but really shouldn't—commemorate that first love by carving your initials into the tree's bark. Decades later when you return to reminisce, what will you see? The letters, now broad and distorted, remain at child's height, even though the tree is now much taller than it was when you visited long ago. The increase in trunk diameter is only one of the ways plants become trees sturdy enough to withstand storm winds and hold up a canopy full of leaves.



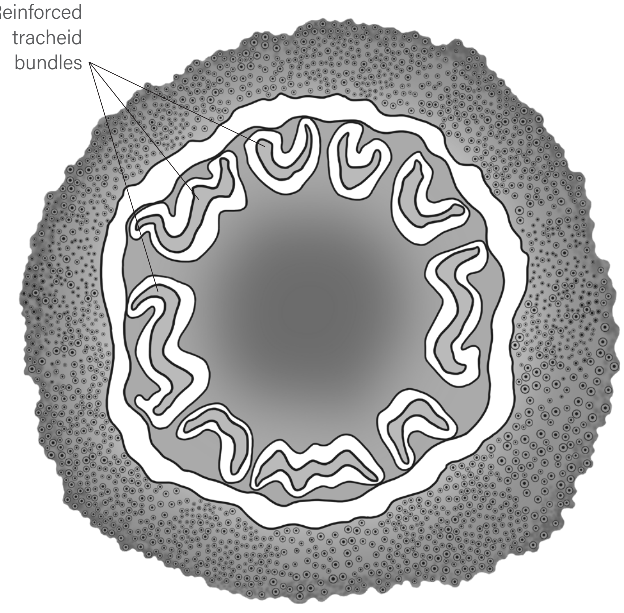
Many seed plants produce woody trunks with a thin layer of growing cells that proliferates just under the bark in this cross section. In seasonal climates, alternating periods of growth and dormancy produce rings.

Tree size has evolved in all groups of land plants that have tracheids to conduct water. When similar traits are seen evolving repeatedly in different groups, it is a good bet that the trait offers a significant benefit for the lineage that possesses it. For plants, light is a vital resource, and it only comes from above. Mesozoic plants found several solutions to the challenge of becoming tall.

The most common way to become a tree is to make wood. Wood is simply abandoned water-conducting cells. In conifers, ginkgos, some cycads, and many closely related extinct groups from the Mesozoic, the tree maintains a layer of generalized cells just under their bark. These cells, called the cambium, divide, with the cells toward the outside of the layer becoming the sugar-transporting phloem cells, and the cells on the inside becoming the water-conducting cells, or xylem. In seasonal climates, cambium cells begin dividing at the beginning of the growing season, creating a new layer of large, water-conducting cells that jump-start leaf expansion in the canopy high above. Cambium cells continue to divide throughout the growing season until they quiet as the tree becomes dormant. This pattern of activity and dormancy creates the familiar tree rings



Palms, a group of flowering plants, build sturdy trunks with a combination of thick woody bark and sturdy fibers that run up and down the trunk providing strength and flexibility.



Tree ferns mantle their stems in fibrous roots that give the trunk strength and flexibility. Within the stem itself, bundles of water-conducting cells are reinforced to make the trunk stiff.

that characterize wood formed in seasonal climates—in both warm–cold and wet–dry seasons. Trees that experience a year-round growing season continually make new conducting cells and do not produce rings. Making new wood and the resulting increase in trunk diameter helps the tree in two ways. First, growth replaces water-conducting cells that no longer function because their water chain has been broken. Second, continually adding wood means that the tree's trunk grows stronger as its canopy enlarges and becomes heavier.

Most angiosperms build trees with a cambium, a skill they inherited from a common ancestor with the other seed plants. However, palms evolved a different approach. Instead of a cambium layer, palms cluster all their growing cells at the top of the plant where the leaves emerge. The palm stem contains bundles of water-conducting cells scattered throughout the trunk rather than ringed wood. The multitude of conducting bundles, combined with lignin-reinforced fibers, give the palm trunk the strength and flexibility to withstand tropical cyclones. Palm seedlings grow by first expanding laterally to achieve their adult diameter. This produces a low, squat trunk topped with a shock of leaves. This early phase requires a lot of energy and explains why tree-sized palms prefer sunny spots. In contrast, shade-loving palms generally remain small and slender. After widening, the generalized cells of the palm heart continue to divide and elongate but shift toward upward growth. Also, because palms cannot replenish their water-conducting cells with new growth from a cambium, they cannot recover when the water in their conducting cells freezes. Consequently, palms have reliably indicated warm climate for their 85-million-year history.

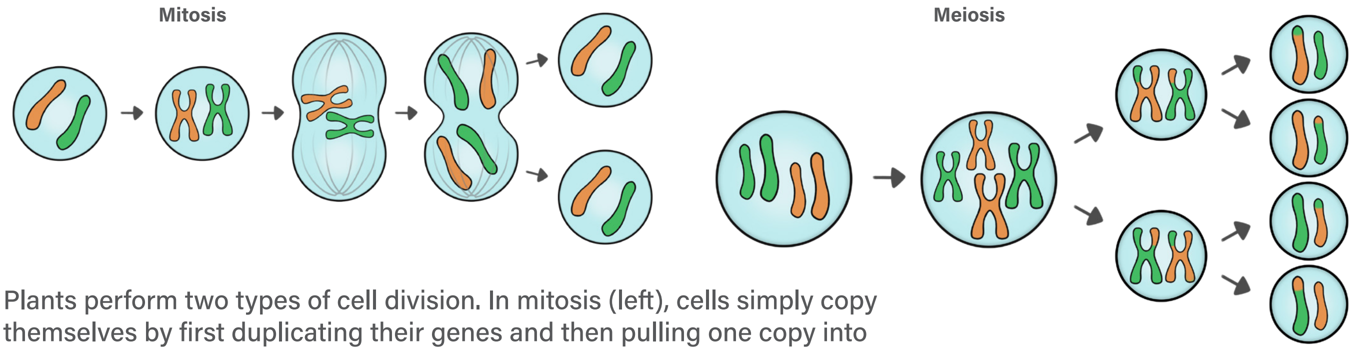
Ferns also lack a cambium and those that become trees use a strategy like that of palms. Tree fern trunks have complex, netlike webs of thick-walled conducting cells, lignin-reinforced, rodlike fibers, and sturdy leaf bases that remain on the trunk to provide extra support. Many tree ferns also swaddle their stems in a mantle of special roots that add more support. Ferns have another trick to help keep their leaves in the canopy as their trunk grows taller: they extend their leaves on the plant equivalent of a selfie stick. As a tree fern's growing cells begin to sense shade, phytochrome turns on the gibberellins in the leaf's petiole to extend it from a modest 50 cm (about 1.5 ft) to more than 300 cm (over 9 ft), simply by making individual cells longer. This allows the leaves to reach the encroaching canopy even if the trunk cannot grow fast enough. Eventually, however, the tree fern may be overtopped by faster-growing neighbors and adjust to life in the shade.

EVOLVING IN RESPONSE TO THE ENVIRONMENT

HOW EVOLUTION HAPPENS

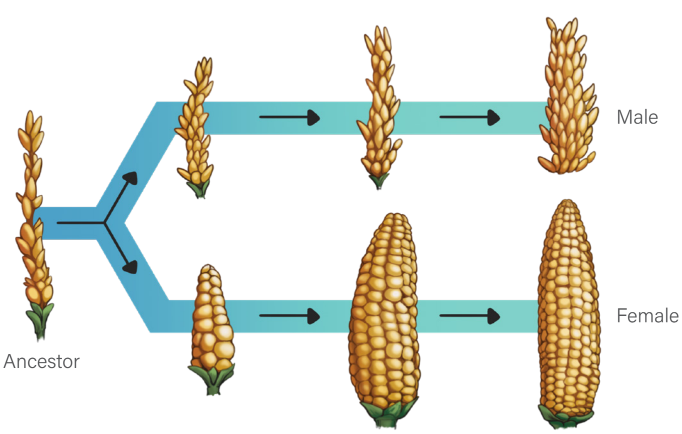
Genetic Variation and Natural Selection

Evolution means changes in a lineage that happen over many generations. In addition to time, evolution requires individuals to differ from one another genetically. Like animals, plants generate genetic variation through mutations—changes in the DNA sequence—that happen when cells copy their genes as they divide. Because animal cells specialize very early in development, the only mutations that travel into the next generation are those that happen in egg cells and sperm. Mutations in any other part of the body perish with the animal. Plants have more possibilities. Because each of a plant's growing tips retains generalized cells that can become eggs and sperm, mutations that happen in any of a plant's many growing tips can be passed down to the next generation. For large, long-lived trees, the thousands of growing tips in a single canopy may each contain a different suite of mutations that can become



Plants perform two types of cell division. In mitosis (left), cells simply copy themselves by first duplicating their genes and then pulling one copy into each of the newly divided cells. In meiosis (right), cells exchange genes along the strings of DNA to create different genetic combinations. After a second division, these cells become eggs and sperm.

part of the tree's evolutionary heritage. Next, sexual reproduction adds to genetic variability by shuffling the genes of the parents to produce new combinations in offspring. Plants and animals both do this, but plants have a few additional tricks for amplifying the variation generated by sex. Plants can combine and multiply all of their genes at once—a catastrophic genetic "error" that would be fatal to most animals. This allows plants to combine more traits and generate new species with novel features. The duplication of the plant's genes that happens during these events can also boost useful traits. For example, a number of weeds have evolved resistance to common commercial herbicides by simply adding more copies of the gene targeted by



An ancestor of modern maize (above left) produced separate pollen- and seed-producing flowers that looked similar. Over time, farmers chose those individuals that made larger ears with more grain.

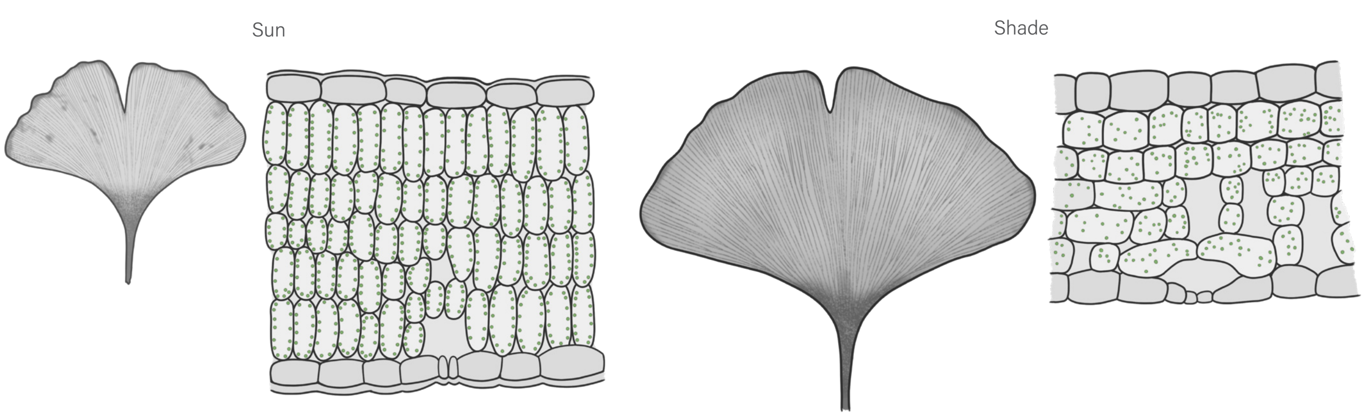
RIGHT: Wild teosinte grows in branching clumps. This species contributed genes to domestic maize.

the chemicals. Generating tremendous genetic variety quickly allows plants to evolve rapidly.

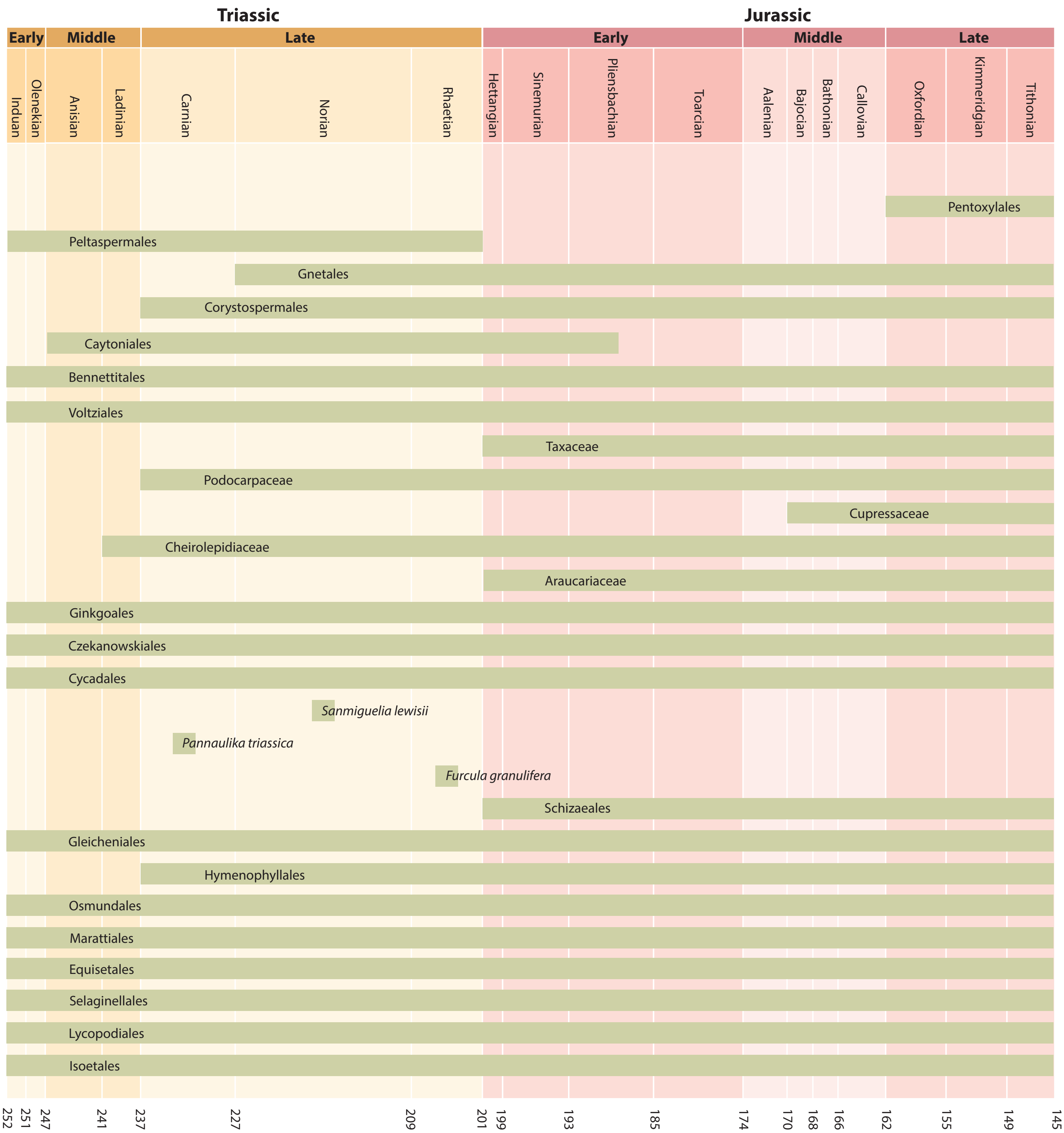
The environment tests the traits produced by genetic variability through a process that Charles Darwin called "natural selection." In developing this idea, Darwin riffed on a practice that farmers have used for millennia: they chose traits that they liked and encouraged individuals possessing those traits to reproduce. Over generations, breeders could sculpt plants and animals with the traits they preferred. The evolution of domestic maize (*Zea mays*), also known as corn, illustrates the process. A wild grass that is likely extinct today produced a few popcorn-like seeds that caught the attention of Indigenous Americans in what is today central Mexico. They began to save seeds and plant them in their gardens. However, the ancestral plant was not particularly productive. In a chance event about 5,000 years ago, pollen from a related wild species accidentally combined with early maize and brought with it new genes that produced a compact cob with many more kernels. An observant Indigenous farmer recognized the potential in the new combination and began to grow it, choosing the largest ears in successive generations. Over time, selective breeding of individuals with large and nutritious seeds produced the crop that became a staple throughout the Americas. Darwin proposed that the environment governed which organisms produced offspring, much like a farmer selected traits. Over long stretches of time, this process could produce all the variety observed in the biological world.

Evolution for Flexibility

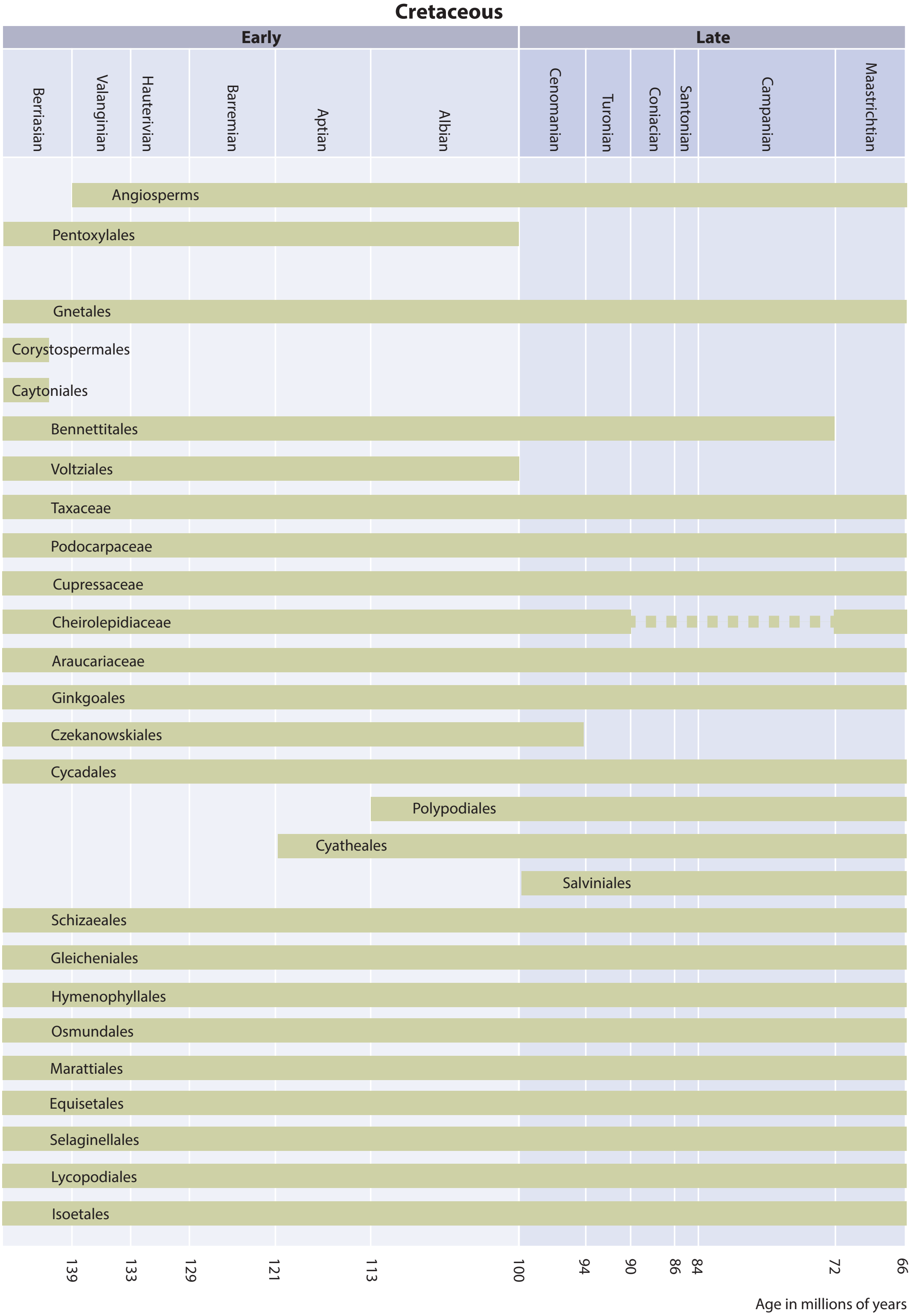
In animals, new species commonly evolve as organisms specialize to share key resources. Plants have simple needs—light, water, a handful of common minerals, carbon dioxide, and space to grow—that cannot be easily divided to generate new species. Instead, new plant species explore different strategies for acquiring a limited resource. Light, for example, generally comes from above, so any trait that allows plants to move skyward, whether through climbing or growth upward on sturdy branching stems, will be favored by natural selection. Similarly, plants are rooted in place throughout their lifetimes. Therefore, selection favors strategies for flexibility in changing conditions, rather than increasing specialization. For example, most plants can adjust the configuration of their leaves to accommodate differing light conditions throughout their lifetime. For instance, plants that live on the forest floor experience shade until a gap in the canopy opens above them.



Leaves of modern *Ginkgo biloba* demonstrate that leaves developing in full sun (left) are smaller and, in microscopic section, thicker with elongated photosynthetic cells. Leaves grown in the shade, even on the same tree (right), are larger and thinner.



Time ranges for major groups discussed in the text. The dotted line indicates that the group was absent from the fossil record for a time but not yet extinct.


Cretaceous
Early
Late
Berriasian
Valanginian
Hauterivian
Barremian
Aptian
Albian
Cenomanian
Turonian
Coniacian
Santonian
Campanian
Maastrichtian
Angiosperms
Pentoxylales
Gnetales
Corystospermales
Caytoniales
Bennettitales
Voltziales
Taxaceae
Podocarpaceae
Cupressaceae
Cheirolepidiaceae
Araucariaceae
Ginkgoales
Czekanowskiales
Cycadales
Polypodiales
Cyatheales
Salviniales
Schizaeales
Gleicheniales
Hymenophyllales
Osmundales
Marattiales
Equisetales
Selaginellales
Lycopodiales
Isoetales
139
133
129
121
113
100
94
90
86
84
72
66
Age in millions of years

Now intense sunlight floods the forest floor, damaging delicate chloroplasts in leaves tuned for shade. Most plants have the ability to shed these damaged leaves and grow new ones calibrated for their new light environment. When the canopy closes again and the plant finds itself back in shade, it will shed its sun leaves and make a new set of shade leaves. Neither the sun- nor shade-type leaves have been specifically selected by this patchy environment. Instead, plants that had flexibility to change with the environment were more likely to survive longer and reproduce more. Evolution favored resilience in a constantly changing environment. The simplicity of a plant's environmental needs also means that many pathways lead to survival. For example, if rain is rare, some plants evolve strategies for storing water, others conserve it, and others develop seed dormancy in which they germinate, grow, and reproduce quickly in the few weeks following a rainstorm. All these strategies will allow their bearers to successfully weather drought and send offspring into the next generation—the definition of evolutionary success.

Yucca filamentosa has evolved an exclusive pollination relationship with a single species of tiny moth, *Tegeticula yuccasella*.

Although the rule in plant evolution is flexibility, angiosperms provide an exception. One key to the tremendous diversity of flowering plants is the complex relationships with pollinators and seed dispersers. Flowers evolved colors, shapes, and scents to attract specific pollinators because a plant produces the most seeds when pollinators only visit other members of its species. In this case, the advantages of specificity are worth extra energy to the plant. A yucca (*Yucca filamentosa*) produces a scent attractive only to a single species of yucca moth (*Tegeticula yuccasella*) and times its flowering to the season when adult moths emerge and begin to look for mates. Yucca moths seek out the flower and deposit a few eggs within, picking up pollen as they do. They then seek out another flower of the same species to lay more eggs, spreading pollen as they go. When the moth larvae hatch, they eat a few of the developing seeds, a small price for the plant in exchange for having pollen faithfully delivered. Flowering plants have also evolved to cater to the tastes of specific dispersers. Apples, for example, evolved first in a dispersal partnership with birds in what is today China. These early apples were bright red, a color birds easily recognized amid a sea of green foliage, with small, hard, bitter fruit that suited birds that swallowed the fruit whole. As the lineage migrated into central Asia, it left its bird partners behind and developed dispersal relationships with mammals. Mammals have a notorious sweet tooth and were looking for more substantial meals. The new relationship favored trees that produced the large, sweet fruit that we enjoy today. In these cases, angiosperms adopted the animal pattern of dividing recourses—pollinators and dispersers—among many different species to multiply their own diversity and become the most varied lineage of plants in Earth's history.

ENVIRONMENTAL FORCES SHAPING PLANTS

Water and the Climate that Delivers It

To plants, temperature is simply an index of water availability. In a cold season, for example, ice crystals form in conducting cells, disrupting the chain of water molecules on the way to the leaves. The leaves experience the loss of water, not the cold directly. Similarly, in a hot, dry season, leaves open their pores to allow water to escape, taking excess heat with it. This pulls hard on the column of water molecules along the stem and may break the chain. Once again, the leaves experience a water shortage. In both hot and cold climates, when the change is seasonal, long-lived plants evolved the ability to sense the oncoming change and drop their leaves before water runs short. By acting preemptively, the tree can harvest valuable nutrients like nitrogen, potassium, and magnesium from leaves before they are shed and store them in the roots until favorable growing conditions return.

Plants have evolved other features to thrive in a range of climates. In rainy regions, the leaves of flowering plants have pointed tips that help shed accumulated water so that it does not clog pores and restrict airflow into and out of the leaf. In dry climates, small, chunky leaves with a thick, waterproof covering retain limited moisture. In the early 1900s, Irving Bailey and Edmund Sinnott observed that broadleaf trees in cool climates tended to produce leaves with serrated edges. Researchers do not understand how this feature aids the tree's survival, but even if the function of all the plant's features cannot yet be explained, there is no question that plants are exquisitely adapted to the climate where they grow. Wladimir Köppen's global climate classification scheme published in 1884 was fundamentally a mapping of vegetation types. Later, when meteorological measurements became available worldwide, the vegetation zones correlated almost perfectly with temperature, precipitation, and seasonality patterns.

Disturbance

Environmental disturbance was ubiquitous in the Mesozoic. Warmer climates contributed to frequent wildfire, even in a time when atmospheric oxygen levels were somewhat lower than those of today. Warm climates also intensified storms that shattered limbs and downed trees. Triassic monsoons in what is today the western United States generated floods that swept away hundreds of trees at a time. And during the Jurassic and Cretaceous, large dinosaurs crashed through the vegetation. Unable to run or hide, plants were burnt, uprooted, swept away, or crushed by a myriad of Mesozoic disasters. And in addition to the everyday disturbances of Mesozoic life, plants passed through three animal mass-extinction events that were each characterized by catastrophic disruption of the physical environment. Even if extinction events did not wipe out as many groups of plants as animals, the conditions responsible for widespread extinction certainly killed uncountable individual plants and disrupted their communities.

Disturbance acted as a powerful selective agent, killing many individual plants. Those that survived, and thus passed on their traits to subsequent generations, possessed a variety of features that helped them cope with disturbance. Plants adapted to fire shelter pockets of generalized cells safely below the soil surface. When aboveground stems burn, these buds activate and grow new shoots. Other plants protect seeds in sturdy cones that remain clenched until the wildfire's heat melts resins on the cones' surface and allows them to open. For these plants, the fire also removes organic matter and competitors from the soil surface, making a perfect bed for the seeds that drop from the newly opened cones. Other species make seeds that can persist in the soil for long periods and germinate when their phytochrome senses detect that the canopy has been removed. Other trees like the coast redwood (*Sequoia sempervirens*) evolved thick, fire-resistant bark to insulate their delicate living cells from the heat of a blaze. *Sequoia* also sheds most of its low branches as it reaches its full height so that wildfire cannot climb into the canopy and destroy vulnerable foliage.

Many of the innovations that make flowering plants so successful may have begun as adaptations to disturbance. The high angiosperm photosynthetic rate may have its roots in quick responses to a changing light environment in their ancestral forest floor habitat. Likewise, fast growth and reproduction may have allowed flowering plants, germinating on the banks of frequently flooded rivers, to complete their life cycles before they were swept away. This ability allowed angiosperms to occupy a piece of the landscape unavailable to slower-growing species. In a world with limited space to grow, this strategy helped angiosperms leave more offspring in the next generation. Fast growth also helped flowering plants recover from trampling and colonize ground churned by passing dinosaurs, conditions that slower-growing seed plants could not exploit.

Predators, Pathogens, Partners, and Dispersers

For animals like us, plants are resources—food, shelter, and, perhaps, beauty. Plants, on the other hand, have evolved a myriad of ways to coax animals to work for them. Some plants surround their seeds in sweet and nutritious fruit to encourage animals to consume and transport their seeds, depositing them in a pile of ready-made fertilizer. Plants advertise such seeds and fruits with colors and scents tuned to the animal partner's senses. Other plants evolved seeds with hooks to catch fur, skin, and feathers for a free ride to a new spot. Plants also use some of their surplus sugar to offer sweet rewards for animals who visit their reproductive structures and carry pollen from plant to plant. And to encourage fidelity, natural selection tuned the colors and scents to the preferences of a specific set of animal partners. For example, the flower of the hammer orchid (*Drakaea*) smells exactly like a female thynnine wasp. The male lands on the flower and becomes covered with pollen as he attempts to mate. He then flies off in search of a new partner, carrying pollen to the next orchid as he goes.

Plants cannot evade predators by running or hiding. Instead, they protect themselves with physical and chemical defenses. The Mesozoic introduced many new plant predators to the evolutionary stage: large (herbivorous dinosaurs), small (voracious mammals), and minuscule (several new groups of insects). Some lineages like conifers and cycads evolved armor—investing their long-lived leaves with the sturdy molecule lignin and imbuing them with sticky and bitter resins. Although this challenged delicate mouths and sensitive tummies, many large dinosaurs, particularly the long-necked sauropods, seem to have specialized on tough foliage. They may have evolved a style of digestion similar to that of modern cows, sheep, goats, deer, and camels, which consume indigestible plant material and let the microbes in their gut do the biochemical work. Some paleontologists speculate that the largest herbivorous dinosaurs may have done the same.

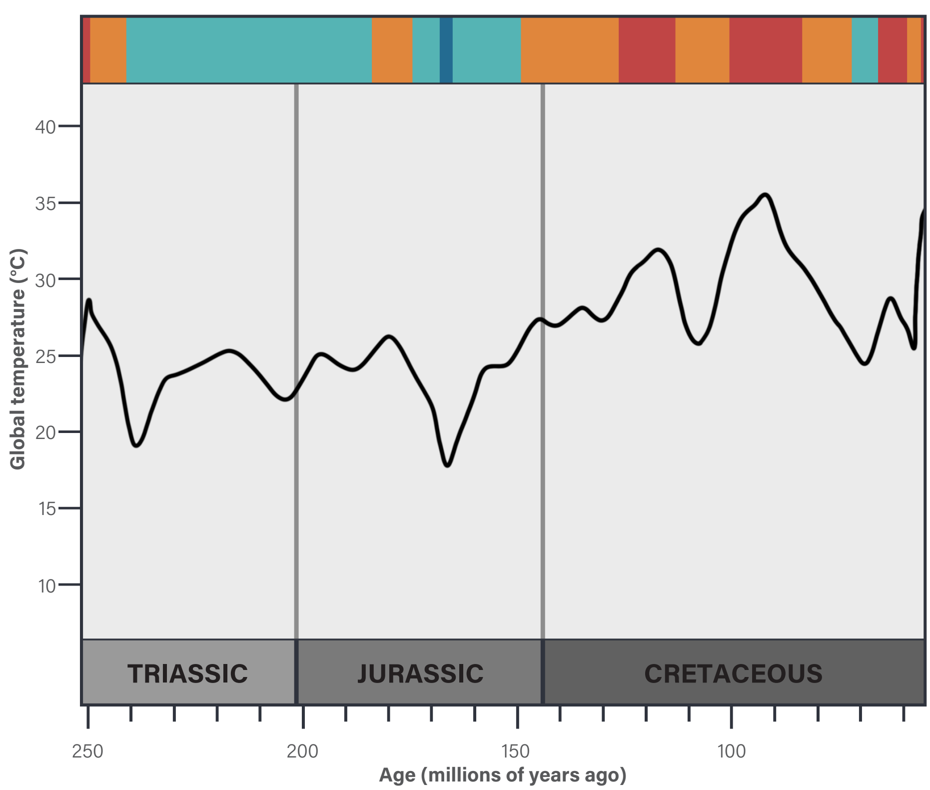
Plants have also evolved a wide variety of biologically active molecules that they use to defend against predators. Most of these chemicals began in biochemical pathways evolved to deal with plant waste products. Since plants lack a liver, kidneys, and lymphatic system to remove waste products from their cells, they eliminate wastes at the cellular level by making unwanted or toxic molecules into something harmless to the plant. When left in leaves, some of these molecules are toxic (or just bad-tasting) to the animals that sample them. Plants with the widest range of such chemicals persisted in the predator-filled Mesozoic forests. Over time, evolution sculpted these defensive chemicals to mimic biochemical pathways in the animals that consumed them. For example, caffeine, a compound made by a number of flowering plants, stunts the growth of insects that consume the leaves or fruits that contain it. Another molecule stashed under the bark of willows (*Salix*) offers antimicrobial protection for the tree, and for humans, who use it in traditional medicine and in Western medicine as a pain reliever and in over-the-counter acne treatments. Plants produce chemicals that, when consumed by animals, stimulate appetite, control blood sugar, stop or start the heart, kill cancer cells, alter brain function, and much, much more.

Plants evolved molecules to signal neighboring plants and other partners. At the most basic level, plants produce chemicals to entice pollinators and seed dispersers. Other sophisticated chemical signals attract soil fungi. Fungus and root each release specialized chemicals that stimulate mutual growth and interconnection. The fungus releases defensive chemicals that ward off parasites and helps the plant gather water and minerals from the soil. The plant reciprocates with sugary food for the fungus. Some call these interconnections the "wood wide web" because the underground network of roots and fungal cells seem to transmit information through the soil. Plants starved for light send chemical signals through the fungal network to larger neighbors that then coax fungi to share sugar, with the fungus taking a bit for its trouble. Although science is just beginning to explore these subsurface connections, early research leaves little doubt that in healthy soil, plants, fungi, and a variety of soil microbes form complex, dynamic partnerships in which all parties benefit. Plants also use their communication chemicals to signal one another. When plants are attacked by a herbivore, they emit chemical signals that waft through the air and trigger neighbors to produce defensive chemicals. Although plants do not act with altruistic intent, sensing and responding to an antipredator signal would enhance reproductive success and therefore persist in a predator-filled world.

MESOZOIC CLIMATE SHAPES PLANTS

EARTH'S ATMOSPHERE AND CLIMATE EQUILIBRIA

The Mesozoic climate fluctuated with the quantity of so-called greenhouse gases in the atmosphere. Greenhouse gases take their name from their ability to act like the glass in the windows of a greenhouse. On a summer's day, the sun's visible rays shine through transparent windows and heat up surfaces within. Warm surfaces radiate energy in infrared wavelengths—heat—that raise the temperature of air inside the greenhouse. The same happens with Earth's atmosphere. Visible light speeds through the atmosphere to warm Earth's surface. Warm surfaces radiate heat that raises the temperature of the air around them. Some heat escapes back to space, but some gases in the atmosphere—mainly water vapor, carbon dioxide, and methane—act like closed windows, preventing heat from escaping. This property of our atmosphere makes Earth habitable. Without the atmospheric greenhouse, Earth's average surface temperature would be about –18°C (0°F), too cold for liquid water and most life. Earth's vast oceans mean that water vapor will always be abundant in the



Mesozoic temperature history with icehouse (dark blue), coolhouse (light blue), warmhouse (orange), and hothouse (red) equilibrium states marked. In 2025, the global average temperature was 15°C.

atmosphere. Other greenhouse gases, like carbon dioxide and methane, have varied considerably, and these changes drive Earth between its four stable climate equilibria: hothouse, warmhouse, coolhouse, and icehouse.

Hothouse climates are the warmest and least stable of the climate equilibria. In the hothouse climate, Earth lacked polar ice, and global average temperature may have been more than 10°C (18°F) warmer than today. So-called hyperthermals also characterized the hothouse. During hyperthermals temperature rose rapidly—geologically speaking—to inhospitable levels in response to small changes in greenhouse gases. These geologically sudden heat waves may have lasted tens of thousands of years and devastated some biological communities. Organisms were pushed past their heat tolerances, resulting in mass migration, pest and pathogen plagues, local die-off, or, in extreme cases, extinction.

Warmhouse climate is the most stable climate equilibrium and prevailed for most of the Mesozoic. The warmhouse world also lacked persistent polar ice as global average temperatures hovered 5°C (9°F) or more above today's values. During the warmhouse, forests grew at polar latitudes, and although the poles experienced a freezing season, snow melted with spring and climate remained temperate. Warmhouse climates were generally humid, with ample rainfall to support lush forests.

Coolhouse climate featured the development of polar ice that persisted all year. Snow-white surfaces reflected the sun's energy back to space and further cooled the poles. While tropical temperatures stayed steady, colder polar conditions created a large temperature difference between equator and poles that dried climate in the middle and high latitudes.

The icehouse climate equilibrium was marked by thick, persistent ice sheets at the poles that periodically advanced into the middle latitudes. These so-called "ice ages" characterized the last two million years or so of Earth's history, with the advance and retreat of continental glaciers driven by minute variations in Earth's orbit and amplified by changes in snow cover and greenhouse gases. Although the waxing and waning of continental ice created wild swings in climate that triggered widespread migration of plants and animals on land, these fluctuations happened at regular intervals and over timescales that allowed ecosystems to respond. So, unlike climate instability in hothouse hyperthermals, icehouses produced relatively few extinctions.

ESTIMATING CARBON DIOXIDE LEVELS IN THE MESOZOIC ATMOSPHERE

Over its long history, Earth has moved among these climate states in response to changes in greenhouse gases, primarily carbon dioxide. Despite the importance of carbon dioxide in the climate equation, geologists struggle to estimate how much of the gas was present in the atmosphere of the past. Scientists can directly sample the atmosphere of the last 800,000 years or so by measuring gases trapped in air bubbles in glacial ice. Beyond this, geologists rely on a variety of indirect methods that measure something correlated with atmospheric carbon dioxide. For example, the chemistry of some minerals in soil

Gas exchange pores, stomata, on the underside of a Mesozoic *Ginkgo* leaf reveal the history of carbon dioxide in Earth's atmosphere. When carbon dioxide levels are high, plants produce fewer stomata.

tracks atmospheric carbon dioxide. Geologists also estimate the amount of carbon dioxide emitted from volcanoes and locked up in coal and other sedimentary rocks to model changes in carbon dioxide through time. Paleobotanists recognized another correlation between the number of stomata produced by some plants and atmospheric carbon dioxide. Stomata, specialized leaf pores that control gases moving into and out of the leaf, allow carbon dioxide into the leaf for photosynthesis, so plants have evolved to adjust their number to prevailing conditions. During times of high carbon dioxide, plants make leaves with fewer stomata to allow sufficient carbon dioxide in while minimizing the amount of water that escapes. When carbon dioxide is low, plants need more stomata to allow sufficient carbon dioxide in. However, none of these estimates are precise, and approximations of Mesozoic carbon dioxide vary widely. Nonetheless, a general picture of Mesozoic climate has emerged.

CARBON DIOXIDE LEVELS TRANSLATE TO CLIMATE

At the beginning of the Triassic, carbon dioxide may have been as low as 420 ppmv, a value on par with early-twenty-first-century levels. Geological indicators suggest that during the Early Triassic, Earth was firmly gripped by a warmhouse climate and there is no evidence for polar ice. Carbon dioxide rose steadily through the Triassic and into the Early Jurassic, when levels likely reached 1,000 ppmv or higher. A drop in deep-ocean oxygen concentrations in the Early Jurassic Toarcian age suggests a geologically brief period, when carbon dioxide may have exceeded 2,000 ppmv.

Carbon dioxide levels fell through the Middle and Late Jurassic. Climate shifted from warmhouse to coolhouse, allowing polar and mountain ice to accumulate before the return to a stable coolhouse. Estimates suggest that carbon dioxide levels remained near 1,000 ppmv through much of the Cretaceous, with geologically brief intervals of much higher temperature about 120 million years ago during the Aptian, 105 million years ago during the Albian, and 100 and 94 million years ago during the Cenomanian. These temperature spikes may have been driven by a rapid release of methane from seafloor sediment. By the end of the Cretaceous, carbon dioxide levels settled at about 700 ppmv, comfortably in the warmhouse.

Most climate indicators agree that the Mesozoic was generally warmer than today, with much lower temperature differences between equator and poles. Seasonality in both temperature and rainfall was also much less than today, with most of the world, except for the interiors of the great continent of Pangaea and then Gondwana, receiving ample precipitation that supported lush forests that produced extensive mid-latitude coal deposits, which are today used for fuels. Moreover, the moisture that these trees pulled from the soil and released through their stomata helped to maintain humid conditions. As forests do today, Mesozoic trees modified and moderated the global climate.

COMPLEX CONTROLS ON GREENHOUSE GASES

Over long stretches of geological time, three processes control atmospheric carbon dioxide: the amount of the gas added by volcanic activity, the amount removed by rock and soil weathering, and the amount stored in rock as fossil fuel and other forms of geological carbon. Most people think of charismatically explosive mountains like Mount Vesuvius or Mount Saint Helens when they think about volcanoes. While eruptions from volcanoes like these can influence climate by adding cooling particles to the upper atmosphere, they contribute little carbon dioxide. Most volcanic carbon dioxide comes from the mid-ocean ridges that bisect many ocean basins. These are zones where Earth's crust pulls apart and new seafloor forms as lava spills out from great rifts. The activity of these ridges varies through time, and the Mesozoic was a particularly active time. Also, a series of especially large lava outpourings, so-called large igneous provinces, punctuated the Mesozoic. These events erupted millions of cubic kilometers of lava and with it came an array of gases, including carbon dioxide. For example, the Siberian Traps at the dawn of the Mesozoic erupted 1–2 million cubic kilometers (240,000–480,000 cubic miles) of lava. The Central Atlantic event during the Early Jurassic contributed

2–3 million cubic kilometers (480,000–720,000 cubic miles) of lava. The Ontong Java Plateau spewed more than 8 million cubic kilometers (1.9 million cubic miles) of lava during the Aptian age of the Early Cretaceous. And the Deccan Traps closed the Mesozoic with another million cubic kilometers (240,000 cubic miles) of lava. These episodes corresponded roughly with intervals of high carbon dioxide and warming climate.

Weathering is the chemical breakdown of rock and soil on Earth's surface. Most weathering occurs in slightly acidic water produced when carbon dioxide in the atmosphere dissolves in raindrops. When the atmosphere contains more carbon dioxide, drops naturally become a bit more acidic. When they fall on rocks, chemical reactions transform minerals in rock into the mineral nutrients plants need, such as calcium, potassium, and phosphorus. In the process, the carbon dioxide transforms from a gas in the atmosphere to minerals dissolved in water. In this way, weathering removes carbon dioxide gas from the atmosphere. These reactions occur faster when carbon dioxide is abundant, conditions are warm, and mountain-building has exposed fresh rock to the rain.

On shorter timescales, the photosynthetic work of plants also modulates atmospheric carbon dioxide. Photosynthesis takes carbon dioxide from the atmosphere and transforms it into organic molecules that become the plant's body. In the process, plants release oxygen. In the normal cycle of photosynthesis and decomposition, which consumes oxygen and releases carbon dioxide, the system remains balanced. However, if organic matter produced by photosynthesis is buried in sedimentary rocks, the associated oxygen stays in the atmosphere. Likewise, if organic matter is removed from Earth's crust and burned, that carbon dioxide returns to the atmosphere and a corresponding amount of oxygen is removed.

OXYGEN, TEMPERATURE, AND WILDFIRE

Plants require oxygen for respiration just as animals do. However, plants produce their own oxygen as they split water during the light reactions of photosynthesis. Therefore, plants are much less sensitive to the amount of oxygen in the atmosphere than are animals, with two exceptions. The first involves photosynthesis itself. The enzyme responsible for capturing carbon dioxide during photosynthesis can also capture oxygen. When oxygen binds with this enzyme, a junk molecule results. Plants recycle this molecule but that takes energy, making photosynthesis less efficient under high-oxygen conditions. Since most estimates suggest that atmospheric oxygen during the Mesozoic was a bit to substantially lower than today's 21%, plants benefitted from a boost in photosynthetic performance.

The amount of oxygen in the atmosphere also influenced the frequency and intensity of wildfire, an important disturbance affecting plant communities. Lightning provided ample ignition throughout all of Earth's history. Relatively low atmospheric oxygen rendered fire infrequent throughout the Triassic and most of the Jurassic. However, as oxygen levels and temperatures crept up in the Late Jurassic and Cretaceous, wildfire became more common, coincidentally at the time flowering plants probably first appeared.

CLIMATE, WILDFIRE, AND THE FLOWERING PLANT REVOLUTION

Earth changed dramatically as flowering plants diversified and began to invade existing communities during the Early Cretaceous. The earliest members of the angiosperm lineage grew in the understory of wet tropical forests. Broad swaths of wet lowland tropical and subtropical forest growing during the Jurassic provided ample ground for these first flowering plants. In addition, brief bursts of hothouse heat in the Early and mid-Cretaceous may have helped angiosperms spread. Rapid warming put significant stress on the conifers that dominated the canopies of mid- and high-latitude forests during the Cretaceous. As they died back, fast-growing, fast-spreading angiosperms took the opportunity to invade. Studies of fossil pollen from North America revealed the poleward march of flowers during the middle and Late Cretaceous. In one spot in Utah, studies of fossil pollen revealed a forest community that included conifers, ginkgos, ferns, and a few flowering plants. However, sediments from a small pond yielded only angiosperm leaves. The pond sediments were deposited during one of the brief hot spells at the beginning of the Cenomanian age and suggest that flowering plants sought out ephemeral habitats like this during their scramble to the poles.

Warm Cretaceous climate also contributed to an increase in wildfire frequency, which nudged the evolution of remarkable disturbance tolerance in flowering plants. Wildfire also provided some of the oldest flower fossils yet discovered: minute flowers preserved in charcoal from Valanginian- and Barremian-age sediments of Portugal. The fossils captured the delicate structure of these ancient flowers in three-dimensional detail and revealed the surprising diversity already present by that time. Moreover, their preservation in charcoal showed that early flowering plants thrived in fire-prone environments.

A GUIDED WALK THROUGH THE MESOZOIC FORESTS

Time travel is the stuff of science fiction, but geology offers clues to past environments. Coupled with an understanding of living plants and ecosystems—and a little imagination—the fossil record allows us to take a stroll through ancient landscapes.

TRIASSIC AND JURASSIC

Your geological time ship lands first in the midlatitude lowlands of Pangaea, about 252 million years ago. Craggy Appalachian peaks to the south are shrouded in cloud. You open the door to a silent world. The end-Permian extinction event is over, but the insect world was so decimated that the only sound is the wind rustling the leaves of the *Pleuromeia* lycophytes that extend in dense stands as far as you can see. Their stout, unbranched stems grow straight from a beanbag-like base. These must be *Pleuromeia sternbergii*, as the tallest are about 2 m (6.5 ft) high. Their stems are covered in thin, straight leaves that give the impression of giant green bottle brushes. A single, cone-like structure about the size of your fist perches atop some of the tallest plants. The air is hot, heavy, and humid, and the narrow *Pleuromeia* leaves provide little shade. There are virtually no other types of plants here. A few fern clumps grow in a sheltered nook beside an enormous, rotting log. Some tall, dead trees stand amid the stubby *Pleuromeia* forest. One, which sports the flat, shelflike fungus, is surrounded by a ring of slender shoots. The fan-shaped fringed leaves reveal that it is a ginkgo of some sort. A closer look reveals that the leaves are attached directly to the stem rather than on a short stalk as in living *Ginkgo biloba*. This tree might be *Sphenobaiera*, one of the Late Permian ginkgos that survived the runaway warming at the end of the period. Gingkos, after all, retain buds at the base of their trunk, ready to sprout if the main trunk dies.

Motion catches your eye. Turning quickly, you see a pair of lizard-like creatures scatter from a hollow at the base of another of the dead trees. Behind them, *Moschowhaitsia*, front paws and snout covered in black mud, emerges from the labyrinth of decomposing logs. This four-footed carnivore has a stout body and a head longer than your hand. It must be a juvenile because you recall that the animal's Permian-age ancestors grew much larger. You notice the *Moschowhaitsia*'s sparse coat of spiky fur and recall that it is warm-blooded. Its meal having escaped, the *Moschowhaitsia* locks eyes with you briefly, bears its menacing yellow fangs, and clambers over the downed trees in search of other prey. You latch the door of your time ship and set the date to 167 million years ago to survey the world fully recovered from the extinction.

Landing in the Middle Jurassic, you step out into a coastal forest just as the sun is about to slip below

Spiky tree-sized lycophytes called *Pleuromeia* were among the first large plants to recolonize marshy areas after the end-Permian environmental collapse. These small trees were descendants of the giants of the Paleophytic and persisted for only the first few million years of the Triassic period.

By the Jurassic, cool, moist climates allowed conifers, ginkgos, cycads, and ferns to reign. These plants presented tough, resinous, and toxic forage for the large herbivores of the time.

the western horizon over the young Atlantic Ocean. This part of Pangaea has been drifting apart for about 70 million years. Your time ship has landed amid the tall, straight trunks of giant conifers. A deep-green carpet of moss coats their rough bark. You crane your neck and squint into the upper branches, hoping to identify the trees. Perhaps they are *Araucarites*, their leaves spoon-shaped and with spiked tips that warn they are tough and sharp. Right, you think. This is the time of long-necked sauropods that can browse the uppermost branches. You also notice the scaly, gray-green leaves of *Brachyphyllum* high in the canopy, but the conifers grow so closely together it is hard to tell which leaves belong to which trunk.

Stepping onto the soft carpet of decomposing leaves beneath your feet, you breathe the spicy-sweet smell of conifer pitch. The air is cooler than during the Early Triassic and buzzes with the twilight song of crickets. At your feet you notice a cluster of needlelike leaves attached to a sturdy branch. They look a little like pine needles, but softer, brighter green, and more flexible. Picking up the branch, you notice a string of delicate, scallop-shaped structures about the size of a coin dangling amid the fringe of leaves. This is not a pine but *Czekanowskia*, a relative of the ginkgos, and these are its seeds. A closer look at the tall trunks reveals subtle differences in their bark. There are so many kinds of trees here but they all have the tall, straight trunks. As the sun dips toward the horizon, the understory grows dark. You set off toward a patch of lingering light in the distance, threading carefully through the tufts of deep-green cycad leaves nestled in the spaces between the conifers. Running your fingers across the soft, furlike covering of the cycad seed cones, you notice they are swarming with beetles. Probably pollinating. Wait! Some of the cycad-like trunks display stout, flowerlike structures. A ring of sturdy, pale pink, leaflike scales surrounds a central sphere where the egg-bearing structures hide among a protective armor of woody barbs. This is a member of the Bennettitales, one of the many Jurassic seed plants that is experimenting with flowerlike reproductive structures tailored by natural selection to attract insect pollinators.

As you approach the edge of the forest, ferns become more numerous. You wade into the waist-deep fern foliage at the forest's edge and emerge at a slow-flowing river, its sandy banks covered with a thick stand of horsetails. Crashing through the ferns to the river's edge, you surprise a *Stegosaurus*, drinking just a few meters upstream. It mistakes you for a carnivorous *Proceratosaurus* and raises its spiked tail in defense. It seems best to stay out of sight until the *Stegosaurus* lumbers away. As your heart slows, you notice a surprising diversity of ferns: *Angiopteris*, *Aspidistes*, and *Todites* growing in lush, tangled clumps. *Dicksonia* tree ferns line the edge of the forest and tilt their large fronds toward the open sky like satellite dishes. A shrub emerging from the fern scrum is the one you were looking for—*Caytonia*. This enigmatic plant also evolved features similar to those of flowering plants. Its compound leaves have a slender petiole from which four tongue-shaped leaflets extend like the fingers of a chubby hand. The veins of the leaves intertwine in a complex network that can efficiently supply water across the photosynthetic surface. This one has seeds dangling like tinsel from the base of leaves on the lower branches. Each fertile strand has seven to ten pairs of globular balls on short stalks, with each ball formed from a flap of tissue wrapped tightly around four egg-bearing ovules. Pollen, or perhaps a pollinating fly, could slip into the tiny gap in the enrolled flap, but the nutritious ovules themselves are hidden from insect predators. This seems like a good evolutionary investment, because some of the older leaves are riddled with holes made by hungry herbivorous arthropods. Toward the top of the shrub, similar strands sport pairs of tubular pollen organs that dust your fingers with bright yellow grains. With your magnifying hand lens, you note that the pollen looks very conifer-like.

As the last light fades, you return to your time ship and set course for the Early Cretaceous.

EARLY CRETACEOUS

Your time ship lands next on the eastern shores of North America, 125 million years ago. The ancient Appalachian Mountains still dominate the landscape. Great rivers capture the rain that falls on their highlands and meander across coastal plains to the sea. Although puffy clouds drift overhead, they drop little of their rain on the coastal plain. You landed on a bluff above the river. Here, conifers bearing *Hirmeriella* foliage grow in patchy stands. The growing tips of these conifers have small, scalelike leaves that press tightly against branching twigs. Tender bits at the tips form a spiky tuft at the end of each branch. *Hirmeriella* makes a sparse canopy, and dappled light bathes the forest floor. There, squat cycads and the dried foliage of ferns bake in the sun. You dig the toe of your boot into the soft, sandy soil and kick up a cloud of dust—it is the dry season. The trunk nearest you bears scars of a past fire. Damaged bark has begun to curl around the charred wood beneath in the tree's slow effort to cover the wound. The fire must have been some time ago, because the ground is now covered with a thick layer of dry leaves. The day is hot but not particularly humid. Even so, sweat beads on your nose. As you wipe it away, you jump with a dozen sharp pinches around your ankle. Your boot has disturbed an ant colony, and they are not pleased. You shoulder your pack, stamp your foot free of ants, and head down the hill toward the river below. Scrambling down a north-facing slope, you plunge into a cascade of ferns. A thicket of the drought-tolerant fern *Dryopteris* rims the gully. Descending farther into the cool shade, tree ferns bearing *Thyrsopteris* and *Cladophlebis* foliage reach for the sky. Beneath them, *Aspidium*, *Gleichenia*, and *Anemia* ferns cascade down the slope. On the flat floodplain below, tall, straight *Sequoia* trunks tower above the cypress and yew that have colonized wetter hollows in the landscape. Still more ferns dot the forest floor, and flies buzz annoyingly around your head.

The fern thicket grows dense around the edge of a pond formed where a meandering branch of the river separated from the main channel. The water is still, riffled only by fish breaking the surface to grab an insect. A turtle basks on a nearby log. Across the pond, the beady eyes of a submerged crocodile peer at you over a floating water lily. It is the first flowering plant you have seen so far. You pick your way slowly along the edge of the pond, aware that another croc might be waiting in ambush. You are about the size of one of the croc's favorite prey, the midsized dinosaur *Archaeornithomimus*. You have heard that the carnivorous theropod dinosaur *Acrocanthosaurus* also prowls these forests, but the dense cypress thickets are probably difficult for the 10 m (33 ft) long predator. The much smaller and even more ferocious *Deinonychus* might be another matter, so you pause between steps to listen for movement in the vegetation.

Soaked in sweat, you finally emerge at the river's main channel. Scanning the sandy bank, you find both shores lined with angiosperms. Herbs, vines, and small shrubs of a dozen species festoon the riverbank, basking like the crocodiles in the bright sun. Their leaves are broad and net-veined and come in a variety of shapes. The leaves seem flimsy compared to those of the ferns and conifers on the floodplain behind you, and insects have riddled them with holes. Some riverside plants display tiny flowers swarmed by clouds of pollinating thrips. Butterflies drift above the scramble of greenery looking for a nectar treat. Other plants display clusters of fire-engine red fruits to potential dispersers. A rustle beneath the foliage makes you jump. Too small for *Deinonychus*, so you drop to your knees and search. Lifting a large leaf, you spy *Argillomys*, a shrew-sized mammal, sitting frozen in fear with a seedpod clenched in its tiny jaw. With a smile, you gently lower the leaf and hear the mammal scurry away. You have been so focused on discovery you did not notice that the morning's puffy white clouds have turned gray and ominous. Wind rises and cold air from the approaching thunderstorm flows over you. It feels wonderful on the hot afternoon, but you do not want to be caught out. Storms in the hothouse world are violent. You feel the hairs on the back of your neck rise, and before you can think to take cover, a bolt of lightning strikes one of the conifers at the top of the bluff. Flammable resin explodes, and the dry debris quickly catches fire. A line of low flames and thick smoke spread westward, driven by the storm winds. Time to get going.

LATE CRETACEOUS

The next stop on your time ship is the eastern shore of North America's western landmass, Laramidia. You check your chronometer before heading out—66

Warming and drying climate, coupled with frequent disturbances like wildfire, allowed flowering plants to spread out of the understory of tropical forests and begin to migrate toward the poles and into a wide range of habitats. During the early Cretaceous, angiosperms were mostly still confined to streamsides and other unstable habitats.

million years ago. Glancing up, you notice that the midday sun is dusky red. You remember that the Deccan volcanoes on the other side of the globe have been erupting for more than 100,000 years now. Moreover, a line of explosive volcanoes dot the western edge of Laramidia. Who knows when one of those last spewed ash into the stratosphere?

To the east, at the edge of your vision, you see a ribbon of white sand and the glimmering blue of the Cretaceous Western Interior Seaway. The sea extends from the Gulf of Mexico to the Arctic, dividing North American into two landmasses. Turning to the west, you see the low ridges of the Rocky Mountains and below you to the north a wide, brown river winding slowly toward the sea. The river is full of sediment washing down from the rapidly eroding Rockies. A flock of pigeon-sized *Ichthyornis* rest on a sandbar. These fish-eating birds are usually found much closer to the sea, but they may have followed the spawning gar upstream. A few meters upstream from the resting birds, three large *Edmontosaurus* duck-billed dinosaurs tug at a patch of water lilies growing in a quiet bend of the river. A fourth, much larger *Edmontosaurus* stands guard on the levee above the resting birds.

The landscape is a patchwork of greens. Swatches of deep-green cypress and *Glyptostrobus* dot the low, marshy parts of the landscape. On drier parts of the river's floodplain, a low woodland of emerald and apple green drapes over the rolling hills. Unlike the straight trunks of Jurassic and Early Cretaceous conifers, most of these trees are gnarled and irregular, with the globular crowns of angiosperms. Many of these trees have large leaves, suggesting that rainfall is plentiful. However, their leaves are relatively thin, a trait common among plants evolved for climates cool enough to encourage trees to shed their foliage periodically. Beyond winter, it makes good evolutionary sense for the trees to refresh their foliage periodically, because butterflies flutter everywhere above the woodland canopy, and their hungry larvae lurk below. The irregular carpet of trees is studded here and there with the tall, straight trunk of the dawn redwood (*Metasequoia occidentalis*) and an occasional *Ginkgo*. These elders of the Mesozoic have now become rare. Amid the woodland are other gray-green patches of fern thicket where the trees have been temporarily knocked back by some disturbance. The patches of bare brown earth amid the ferns provide a clue. Perhaps these are wallows for herds of *Triceratops* that munch their way through the coastal woodlands. There are no *Triceratops* in sight today and that is good. The large predators that feast on these three-horned herbivores are probably following the herds. It might be safe to descend into the forest.

Where the Jurassic forests were an orderly cathedral of straight trunks, the Late Cretaceous forest is a tangle of irregular branches. Trees sporting compound leaves with slender, serrated *Dryophyllum* leaflets and heart-shaped *Celastrus* leaves are common. Spiky palms scrabble through the understory, and fruit drips from many branches. The forest floor is also different, here covered in a thick layer of decomposing leaves. Tree ferns stretch for the canopy, too, extending their long petioles to compete for light with the fast-growing angiosperm trees. A rare *Nilssoniocladus* cycad shelters in their shade. In a bit of irony that makes you chuckle, an inconspicuous tuft of green nestles at the roots of the cycad. It is one of the early grasses that will—millions of years from now—diversify and dominate this place. In the latest Cretaceous, though, they are newcomers. Scrabbling through the undergrowth, you reach the edge of one of the fern thickets and push through the dense tangle of *Vitis* vines that line the clearing. As you scan the clearing, a smear of light in the southern sky catches your attention. It's too low to be the moon and you remember: Today is the day the Cretaceous—and the Mesozoic—will end in a fiery burst of white-hot rock—impact day. You look around for one last moment. The *Edmontosaurus*, *Triceratops*, and *Tyrannosaurus* will all be gone soon. The trees will be stripped of their foliage by the force of the blast and many killed. But this vegetation is accustomed to disturbance, even cataclysmic disturbance. And the Earth will green again soon. You, however, are too big to survive the catastrophe. No animals larger than 25 kg (55 lb) remained after the impact. You return to your time ship and leave the Mesozoic.

By the late Cretaceous, flowering plants had evolved a wide range of sizes including woody trees and shrubs, and small herbs. They also formed the backbone of most plant communities. Conifers and ginkgos still thrived, but in isolated stands or specialized habitats. And a new group of ferns, the Polypodiales, diversified in the deep shade of the new flowering forests.

IF FLOWERING PLANTS HAD NOT BECOME DOMINANT...

Looking at the history of life on Earth from the vantage point of the present day, the evolution of the organisms and ecosystems we see around us seems inevitable. The reptiles and dinosaurs of the Mesozoic must have been inferior to the mammals that fill the same ecological roles today. Despite their 165-million-year run as the most important large animals on land, "dinosaur" remains the term for something that is not up to the rigors of the modern world. However, from a Mesozoic perspective, it would be hard to imagine that the tiny, ratlike creatures scuttling in the underbrush would someday evolve into lions, bats, wolves, antelope, giraffes, apes, elephants, and whales—the tremendous variety of modern mammals. The happenstance of the end-Cretaceous extinction removed dinosaurs and opened the evolutionary door to mammals. Catastrophic extinction events like those that started and ended the Mesozoic are unpredictable and reset the evolutionary stage, opening opportunities for new lineages at unexpected moments. Or so it goes with animals. The Mesozoic plant story is different.

Many species of Paleozoic plants perished during the end-Permian extinction, but most major groups survived and diversified again in the Triassic. Another extinction event at the end of the Triassic wiped out many more plant species, but again, most major groups persisted to generate still more diversity in the Jurassic. Again, at the end of the Cretaceous, a major extinction event wiped out a host of plant species, but the fundamental nature of Late Cretaceous plant communities changed little as the Cenozoic began. Instead, the Mesozoic botanical transformation happened over tens of millions of years between the second and third animal extinctions. A new lineage born in the steamy understory of the Mesozoic tropical forests, the flowering plants, evolved a suite of features that together allowed them to outcompete Triassic and Jurassic dominants, particularly when it came to exploiting disturbed sites. Given that many Jurassic seed plants independently evolved features like those key to angiosperm success, it would be easy to imagine that some upstart plant would eventually put all the features together and begin the revolution. But that perspective comes from looking backward. During the Mesozoic, there was no such guarantee. Without the lucky combination of pollinator relationships, high photosynthetic rates, and rapid growth and reproduction, the remarkable diversity and ecological dominance of flowering plants would not have been possible. What might the world be like without them?

FLOWERING PLANTS AS RESOURCES FOR ANIMALS

Flowering plants pack their seeds with high-energy deliciousness (carbohydrates, fats, and protein) to sustain their embryos through long periods of seed dormancy and during the early days of growth in the understory where the photosynthetic capacity of the youngest leaves might not be enough to support rapid growth. Many angiosperms also wrap their seeds in sweet and nutritious fruit to attract and reward seed dispersers. In addition, the super-charged photosynthetic system of angiosperms renders their leaves higher in protein than the foliage of other plants. And many flowering plants store their photosynthetic harvest in their roots as starch, which provides another animal food source. Flowering plants provide more calories and more nutrition bite for bite than the plant groups that preceded them.

For Triassic and Jurassic herbivores, the hunt for food was about processing ever larger quantities of low-quality forage. In dinosaurs, groups like the sauropods evolved large size to become gigantic fermentation tanks where microbes broke down indigestible cellulose. As flowering plants became more numerous in the mid-Cretaceous, many herbivorous dinosaurs shifted toward forms that foraged closer to the ground, where most of the early flowering plants grew and fruit fell. Without flowering plants, the great herds of Cretaceous horned herbivores could probably not have found enough to eat. Energy-hungry mammals also took advantage of the plentiful resources offered by angiosperms. Mammals needed the abundant high-energy food provided by flowering plants to fuel their own evolutionary diversification. While the extinction of dinosaurs may have been necessary to open ecological opportunities for mammal evolution, the extinction alone was not sufficient. Without the abundant calories provided by angiosperms, we might not be here. Without flowering plants, the end-Cretaceous extinction might have ushered in the Age of Turtles and Crocodiles, rather than the Age of Mammals.

MESOZOIC PLANT CONSERVATION

Most of the plants we eat and the plant-derived medicines we use come from flowering plants. When asked which non-angiosperms humans regularly consume, most people in Western cultures struggle to name even a few. Anthropologists estimate that humans have domesticated about 200 plant species for food, virtually all of them flowering plants, and 90% of our plant-based calories come from just 30 angiosperm species.

Indigenous and traditional cultures also see the botanical world as a pharmacy, with angiosperms making up most of the healing diversity. Western medicine has co-opted some of these plants, learned their biochemical secrets, and formulated commercial versions of these medicines. Among the most common examples of angiosperm-derived medicines are aspirin, from willow (*Salix*) bark, natural opioid medicines like morphine and codeine, prepared from the poppy species *Papaver somniferum*, and the heart medication digitalis, extracted from foxglove (*Digitalis purpurea*). Quinine, from the bark of the cinchona (*Quina*) tree, was used in the nineteenth and early twentieth centuries to treat and prevent malaria, and in the late twentieth century, artemisinin, produced from the sweet wormwood (*Artemisia annua*), became the standard of care for the disease. Vincristine and vinblastine, made from Madagascar periwinkle (*Catharanthus roseus*), revolutionized chemotherapy for lymphoblastic leukemia, non-Hodgkin lymphoma, and testicular, ovarian, breast, bladder, and some lung cancers in the 1960s. Their introduction increased the survival rate of several childhood cancers from 10% to nearly 95%. Despite the dominance of flowering plants in the human pantry and medicine cabinet, some Mesozoic survivors hold important economic and cultural significance and continue to thrive through partnerships with people.

TAXUS: A TREATMENT FOR CANCER

One conifer from an Early Cretaceous lineage provides a potent anticancer drug. The Pacific yew (*Taxus brevifolia*) produces paclitaxel (known by the trade name Taxol), used to treat and prevent recurrence of several types of breast, ovarian, esophageal, cervical, pancreatic, and lung cancer. Paclitaxel was first isolated in 1962, and its anticancer properties were described in 1971. The U.S. Food and Drug Administration approved the first commercial formula for clinical use in 1993. Some considered it the most important chemotherapeutic drug introduced in the last 50 years. When Taxol first came to market, it could only be isolated from the bark of wild Pacific yew. Because harvesting bark destroys the growing cells beneath, paclitaxel production killed the trees. Yew populations quickly came under significant pressure, and because they grow slowly, trees could not be harvested sustainably to meet the tremendous demand for the life-saving drug. A single cancer patient, for example, required the bark of approximately eight 60-year-old yew trees for their initial therapy. Within a few years, many wild populations were threatened.

Taxus brevifolia grows in the forest understory and along exposed coastal hillsides in the Pacific Northwest of North America, along the coast from northern California to southernmost Alaska and following river valleys inland into southeast British Columbia and northern Idaho. Preferring moist soil, it tends to establish along streamsides or in areas with abundant precipitation, like the coastal rainforests of Oregon, Washington, and British Columbia. Since the US FDA approved paclitaxel, an estimated 30% of the wild populations have been depleted. Moreover, several decades of climate change have produced hotter and drier summers across the tree's home range and increased the frequency of wildfire. *Taxus brevifolia*'s thin bark and ground-hugging growth habit make it particularly vulnerable to fire, and its seeds seldom survive to germinate after adult trees burn. Today, the tree is threatened across much of its range, prompting efforts to find other ways to produce the life-saving medicine.

Drug manufacturers have taken several approaches to providing a sustainable supply of paclitaxel. In 1994, researchers succeeded in synthesizing paclitaxel in the laboratory. However, the process was complicated, and yields remained low, rendering the process uneconomical. The trees themselves remained the best source. Next, researchers explored the other 11 living *Taxus* species for new sources of paclitaxel. However, none could match the potency of *Taxus brevifolia*. Scientists also experimented with harvesting paclitaxel from yew leaves rather than bark and, in the process, discovered a fungus that had acquired the ability to make paclitaxel. However, the fungus proved difficult to culture in the lab and yielded only a little paclitaxel. In Europe, competing research teams developed partial synthesis strategies, starting with a natural plant chemical derived from *Taxus* leaves and finishing the synthesis in the lab. Using natural compounds derived from European yew (*Taxus baccata*), several methods emerged. And because the starting products are abundant in yew leaves, commercial-scale manufacture required less plant material than that needed to extract paclitaxel directly. Today, most paclitaxel is manufactured with the partial synthesis method, using yew leaves or the same natural chemicals derived from laboratory cell cultures. Both methods significantly reduce the pressure on wild populations of yew and allow trees to slowly recover. Human ingenuity is allowing a plant that has given so many the gift of life an opportunity to thrive too.

The bark of *Taxus brevifolia*, the Pacific yew, contains a powerful cancer-fighting chemical.

CYCADS: ANCIENT CULTURAL CONNECTION AND MODERN EXPLOITATION

Cycads were so abundant and diverse that the Triassic and Jurassic are called the "Age of Cycads." However, slow growth and reproduction doomed them during the Flowering Plant Revolution. Today, about 300 species remain. Many of the species that maintain healthy populations in the wild have found partnerships with humans. Genetic and ethnobotanical evidence suggest that humans have tended wild cycads as food and cultural resources since humans first inhabited the Ryukyu Islands of Japan more than 35,000 years ago. In the South Pacific nation of Vanuatu, people traditionally plant and tend cycads to mark important historic and ritual sites, and cycad leaves symbolize reconciliation and authority. Indigenous cultures in Central Mexico use the seeds of several species of *Zamia*, *Dioon*, and *Ceratozamia* in shamanic rituals, where participants consume preparations made from the toxic seeds to enter altered states of consciousness. Seeds and pollen of *Encephalartos* are used in a similar way in the Limpopo region of South Africa, where illegal harvest for cultural and recreational use puts some populations in peril.

For *Macrozamia communis*, known in the Dharug language as *burrawang*, a partnership with the Aboriginal peoples of southeast Australia allows the plant to thrive in the face of development and environmental change. When prepared in a way that removes toxic cycasin, the seeds of *Macrozamia communis* provide a starchy flour that traditionally provided a seasonal food for Aboriginal peoples and today provides an important cultural touchstone. Like many cycads, *Macrozamia communis* tends to synchronize production of male and female cones to encourage crossbreeding among individuals. Aboriginal peoples understand that they can stimulate this mass production of seeds using cultural burning, the practice of lighting low-intensity fires on the landscape to manage vegetation. By carefully timing burning, Aboriginal peoples produce an abundant crop of seeds and allow seedlings to germinate and grow large enough to withstand the next cycle of fire. Cultural burning also manages flammable debris on the ground to reduce the risk of intense wildfire that would kill the ancient plants. Tens of thousands of years of this management has allowed *Macrozamia communis* and all the other plants and animals in the region to thrive.

However, not all cycads have attentive human caretakers and many are critically endangered or functionally extinct. For example, *Encephalartos woodii* can no longer be found in the wild. The species was discovered by John Medley Wood in 1895 on a steep, south-facing slope in oNgoye Forest in KwaZulu-Natal, South Africa. Wood described four large stems that probably represented growth from a single, much older, root system. In 1899, botanists collected several shoots from these wild stems for Kew Gardens in the United Kingdom, and in 1903, more shoots were transplanted to the Durban Botanic Gardens, where Wood was curator. After several instances of poaching, the last surviving stem was transplanted to Pretoria in 1916; it died in 1964. Today, the species grows in botanical gardens around the world, but all these plants originated from the single wild individual—a male. No seed-producing plants have been found. While clones from the wild plant may live for centuries in captivity, the species will

The cycad *Encephalartos woodii* is among the rarest of living plants. Only a single pollen-producing individual has ever been found in the wild, making the species functionally extinct.

(continued...)

INDEX