Plants Are Not Alone

The social networks of plants are pervasive and profound. Plants participate in communities that include beneficial and pathogenic microorganisms, beneficial and herbivorous insects and other animals, and conspecific (same species) and heterospecific (different species) plants. Over millions of years plants have evolved mechanisms by which they partner with other organisms to enhance their nutrient uptake, disperse their pollen and seeds, and ward off their attackers. Stable relationships between plants and their partners that have been established for millions of generations are now under threat by changes caused by human activities.

Many of these interactions have been recognized by naturalists and ecologists for centuries, but through the modern biologists’ toolkit, we are learning about the molecular events that underlie them. Recent findings have included an appreciation for the chemical signals that plants emit continuously or conditionally, including air-borne volatile compounds and root-exuded compounds. Some of these compounds attract beneficial partners, while others deter harmful organisms or competitors. Plants also perceive the chemical signals emitted by the organisms that surround them and use this information to respond appropriately. Light intensity and wavelength also inform plants’ social interactions.

This article introduces the social networks in which plants participate and the challenges brought to them by our human actions. We will examine each of these types of interactions in more detail in subsequent lectures.

MUTUALLY BENEFICIAL INTERACTIONS

An interaction between members of different species that benefits both is called mutualism. Some mutualistic interactions are transient, for example, that between cleaner fish and the parasites. Others are extremely stable and persistent, for example, the partnerships between algae or cyanobacteria and fungi that constitute lichens. The interactions between angiosperms and their pollinators or the fruit-eaters that disperse their seeds are forms of mutualism, as are the symbioses between plants and mycorrhizal fungi or nitrogen-fixing bacteria.

Pollinators

Gymnosperms and angiosperms produce desiccation-resistant pollen that allows the enclosed sperm cell progenitor to move between flowers or between individuals. Gymnosperms and many angiosperms are primarily wind-pollinated, but most angiosperms (~90%) rely upon animal pollinators for maximum pollination success, and some are completely dependent on insect pollinators. Insects, including honeybees, bumblebees, wasps, beetles, moths, flies, and butterflies, are the most important pollinators. Vertebrate pollinators include hummingbirds, bats, mice, and lizards.

Plants and their pollinators have coevolved in mutualistic relationships in which the pollinator is rewarded by eating some of the protein-rich pollen or a sugary nectar treat. In the well-studied partnership between yucca (Yucca spp) and yucca moth (Tegeticula spp) the reward is deferred; the moth lays its eggs in the flower and the larvae eat some but not all of the seeds. Fig trees (Ficus spp) and their pollinators have evolved similar but even more complex arrangements.

Some flowers and pollinators are generalists and others are highly specialized, but either way the insects use chemical and visual cues to recognize their partners. Genetic methods are allowing hypotheses about these cues to be tested and confirmed experimentally. Nectar and emitted volatile compounds are complex mixtures of chemicals that convey information about the plant’s fitness as well as its identity. The shape, size, color and surface texture, and iridescence of flowers attract and facilitate the interaction with pollinators. Bee-pollinated flowers are often closed, but the weight of the pollinator landing opens the flower; this trait is easily seen in snapdragon (Antirrhinum majus). The slightly bumpy surface texture of the landing site helps bees to grip onto it. Bees are thought not to see red except in contrast with other colors, but they see pigments that absorb light in the UV and that appear ivory or off-white to us. Bees are also attracted by large flowers with bright color patterns. Nocturnal moths are attracted to scented flowers and pollinate white flowers that are more visible in the dark. Hummingbirds are attracted to red flowers and flowers that produce abundant nectar.

Orchids produce some of the most sophisticated and specialized flowers. The earliest flowers to evolve were radially symmetrical, but orchids and some other flowers have evolved a bilateral symmetry that can enhance the efficiency of pollination. Some orchids have spring-loaded anthers that are hidden until a pollinating insect lands upon the landing pad, at which point it is ambushed by a load of pollen. There are even orchid flowers that look and smell like the females of the pollinating species, attracting their pollinators by deception. The male pollinator is attracted to the flower and attempts to mate with it and through his actions moves pollen between flowers, obviously a system that works for the plant but isn’t beneficial for the pollinator.

Plants also face the challenge of protecting their precious pollen and nectar resources from thieves that take the reward without effectively pollinating. Ants are notorious pollen thieves because they are small enough to reach nectar and pollen sources without brushing against other reproductive structures.
Many plants produce volatile compounds or compounds in their nectar that deter unwanted visitors. Pollinator deception, pollen thievery, and nectar robbing reveal that mutualistic interactions can degenerate into exploitation.

The Status of Bees

Approximately 84% of commercial crops depend to some extent on pollination by insects, mostly by honeybees (Apis mellifera). The production of some foods, including almonds and raspberries, depends absolutely on bees. For the past several years, bee populations have been declining in North America, Europe, and Asia. Factors contributing to bee losses may include habitat loss, dietary deficiencies, pesticide and herbicide use, diseases, and parasites.

The external parasite varroa mite (Varroa destructor) is the most serious threat. Varroa feed on the blood of larval and adult bees, weakening them and spreading diseases. Early in the 20th century, varroa expanded its host range to include honeybees and has since spread widely around the world. Thanks to strict quarantine laws, Australia has managed to exclude the mite and also has experienced no signs of bee decline. In North America, it is a common practice to transport bee hives from field to field as a mobile pollination service, but this practice has hastened the spread of the mites. Efforts are underway to identify control agents against Varroa that are not harmful to bees as well as to implement better diagnostic and quarantine practices. Bees are also susceptible to several viral and fungus-like microsporidian pathogens that have been correlated with declining bee populations.

A widely used class of neonicotinoid insecticides used to protect plants against aphids and other sucking insects may be contributing to bee decline. Although there is no direct proof that use of this insecticide increases bee mortality in the field, under laboratory conditions it is quite toxic to bees. These compounds cannot be used when plants are flowering and bees are present, but many people worry that this safeguard is not sufficiently rigorous. Use of these pesticides is being reevaluated in the US and in Europe and has been banned in some countries.

These diverse threats to bees occur at a time when the demand for bee-pollinated foods has been increasing rapidly relative to demand for other foods, exacerbating the problem. This confluence of events has gotten the world’s attention and raised our awareness of our own dependence on these little pollinators and reminds us that bees have needs too. A report by the United Nations Environment Program reminds us that “Pollination is not just a free service, but one that requires investment and stewardship to protect and sustain it” (United Nations Environment Program, 2010). It has been argued that our species would persist even if honeybees ceased to exist, but perhaps this is the time to ask ourselves if we are willing to risk a world without bees.

Mutualistic Symbionts

Symbiosis is the condition in which two organisms live together in a relationship that may or may not be mutually beneficial. As organisms capable of photosynthesis and ready sources of energy and sugars, plants are desirable partners for symbions. In return for sugar, the plant may gain access to nutrients or water, or protection. Symbiosis has contributed to the colonization of land by plants and is still helpful or necessary to most terrestrial plants.

Single-celled algae and photosynthetic bacteria engage in symbiotic relationships with diverse organisms in which they are the smaller partner. They can live as lichen in partnership with fungi, but also live within coral, jellyfish, or even, to a limited extent, invertebrate sea slugs (Elysia chlorotica), which are not truly symbionts because they only retain their partner algae’s chloroplasts and digest the rest of the cell. Chloroplasts in eukaryotic plant cells probably originated in a very similar way.

Multicellular land plants participate in mutualistic symbioses with fungi and bacteria, in which the plant acts as the larger, dominant partner. Two of the best understood forms of plant symbiosis involve mycorrhizal fungi and nitrogen-fixing bacteria. Mycorrhizal associations are ancient and phylogenetically widespread, but symbiotic nitrogen fixation is relatively recent and only occurs in a narrow range of species. Both are hugely important contributors to natural and agricultural ecosystems.

Mycorrhizal Fungi

About 80% of plant species, from moss to tree, participate in symbiotic associations with mycorrhizal fungi (mycorrhizal means fungus root). Fossil evidence indicates that this interaction has occurred since plants first colonized the land more than 460 million years ago and may have been essential for plants to establish themselves in the terrestrial environment. In the early plant-mycorrhizal symbioses, as well as those ongoing with bryophytes, the plants are rootless; the nutrient- and water-absorbing functions of the fungi fulfill some of the functions associated with roots in vascular plants.

There are two types of mycorrhizal associations: ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM; sometimes called endomycorrhizal). In both cases, the association of the plant or root with the mycorrhizal fungi dramatically increases the surface contact with the soil, facilitating nutrient absorption. The plant benefits from increased access to water and other nutrients, and the fungus gains photosynthetically derived sugars.

Only ~3% of plant species (~8000) form associations with ECM fungi, but this includes most species of forest trees. Familiar ECM trees are gymnosperms, such as pine (Pinus) and spruce (Picea), and angiosperms, such as poplar (Populus), eucalyptus (Eucalyptus), beech (Fagus), and birch (Betula). The fungal partners are phylogenetically diverse, and their ability to form symbiotic associations with plants has arisen independently several times over the past 180 to 150 million years. These fungi can live independently and symbiotically; their association is facultative. ECM fungi form a dense network called a Hartig net that surrounds the plant root and to a certain extent penetrates in between root cells. Unlike AM fungi, ECM fungi do not enter the plant cells. The genomes of two ECM, Laccaria bicolor and Tuber melanosporum Vittad (the valuable
Périgord black truffle), were sequenced in 2008 and 2010, giving insights into the molecular nature of their symbiosis.

Although AM fungi constitute a small monophyletic group of fungi (the Glomeromycota), they colonize 80% of plant species. AM fungi are obligate symbionts. Spores can germinate to produce hyphae in the soil, but they do not grow much until they perceive a nearby plant root. In 2005, the strigolactone plant hormones were shown to be root-exuded signals recognized by AM fungi. Upon perceiving strigolactones, the fungal hyphae branch extensively, facilitating contact with the root. The fungus produces a structure called an appressorium that enables it to penetrate the plant root and produces a signal that is recognized by the plant and prevents the plant from initiating its defense responses. AM fungi form a highly branched tree-shaped structure inside the root cortex cells across which nutrients and sugars are transferred. Experiments have demonstrated that plants benefit tremendously from these associations. Some, like orchids, are completely dependent upon their mycorrhizal associations, and their tiny seeds do not germinate in the absence of their fungal partner.

**Symbiosis with Nitrogen-Fixing Bacteria**

Our atmosphere is 78% nitrogen, which is in the form of nitrogen gas, N\(_2\), an unusually stable molecule. To become biologically available, nitrogen gas has to be reduced to ammonia (NH\(_3\)) or nitrate (NO\(_3^-\)).

Symbiosis with nitrogen-fixing bacteria form symbiotic associations with plants. *Frankia* bacteria associate with a small number of plants, but the most abundant nitrogen-fixing plants are legumes, which associate with a diverse group of bacteria collectively called rhizobia.

Legumes such as soybean (*Glycine max*), pea (*Pisum sativum*), lentil (*Lens culinaris*), alfalfa (*Medicago sativa*), peanut (*Arachis hypogaea*), and beans (*Phaseolus* spp and *Vigna* spp) have important roles in human nutrition and farming practices. Because they can fix nitrogen symbiotically, legumes can produce seeds that are high in nitrogen-rich protein. Legumes have traditionally been a staple of the human diet, although in some regions they have been largely supplanted by meat or other animal products. Legumes are also an important component of the food given to farm animals.

Legumes enrich agricultural soils because not all of the nitrogen they fix is harvested in the seed. This is the basis for the practice of crop rotation, in which a field alternates between a nitrogen-withdrawing crop such as maize (*Zea mays*) or wheat (*Triticum aestivum*) and a nitrogen-fixing legume. Sometimes a legume crop isn’t harvested but just grown to enrich the soil, in which case it is referred to as green manure. Legumes are sometimes grown between other crop plants as a nitrogen-enriching companion crop, although this practice is not common in fields that are mechanically harvested.

Symbiosis requires extensive communication between plant and rhizobium. This process has been best characterized in pea and alfalfa. The plant root exudes flavonoid compounds that are perceived by the bacteria, which in turn synthesize and secrete a nodulation (nod) factor. When a plant perceives the nod factor produced by its appropriate symbiont, it initiates cell divisions in the root that will give rise to the nodule. The bacteria can enter the root through a gap in the surface associated with an emerging lateral root or through a root hair, which curls around the bacteria and provides an entry channel. Recent evidence shows that the early stages of plant-rhizobial interactions are remarkably similar to those of plant-mycorrhizal interactions, raising the interesting possibility of ancient gene transfer from mycorrhizal fungi to rhizobial bacteria.

Nodule morphology is diverse as is the form of nitrogen exported from the nodule to the plant. Within a nodule, the bacteria often differentiate into bacteroids and begin to express nitrogenase, a multisubunit nitrogen-fixing enzyme. The plant provides the energy for the nitrogen-fixing reactions, and in some nodules, the plant produces leghemoglobin, which binds to oxygen and provides the anaerobic environment necessary for nitrogen fixation. Leghemoglobin is similar to hemoglobin in red blood cells of vertebrate animals, requires iron as a cofactor, and has a reddish color which is clearly seen in many nodules.

A long-standing goal of plant scientists is to introduce the genes needed for symbiosis and nitrogen fixation into non-leguminous crop plants like maize (*Zea mays*), rice (*Oryza sativa*), and wheat. Achieving this goal would have the dual benefits of improving human nutrition and decreasing the need to produce, transport and apply synthetic fertilizers.

**PATHOGENS AND PESTS**

Pests and pathogens not only deprive people of food, but do so after significant land, labor, and water resources have been expended into the production of the food. Improvements in agronomic practices, development of more specific and less toxic pesticides and fungicides, and genetic approaches to enhance plant resistance to these destructive pathogens and pests in order to reduce crop and food losses is one of our most pressing global challenges.

As sedentary food sources, plants depend on an arsenal of physical and chemical defense mechanisms for survival. Most plants resist attack by most organisms through their thorns, cell walls, sticky secretions, and an enormous range of toxic chemicals. Generally, a healthy plant is more resistant than a stressed or wounded plant; many microorganisms are unable to penetrate through the plant’s protective coverings other than through a wound site. Like humans, plants in high-density populations are more prone to diseases because the pathogen can easily spread from host to host. Local environmental conditions have a significant role in determining whether a plant succumbs to disease. Many pathogens thrive in moist environments, and disease outbreaks are often correlated with wet weather.

In an undisturbed, natural environment, plants generally are protected from pests and pathogens as a consequence of thousands of generations of coexistence. An evolutionary innovation in the pest or pathogen will be met by an innovation in the plant’s defenses, maintaining a balanced system. Human activities and agricultural practices have introduced plants into
new environments and introduced new pests and pathogens into previously unexposed ecosystems, leading to regular outbreaks of devastating diseases. Well-known historical plant epidemics include the chestnut blight disease (Cryphonectria parasitica), a fungus introduced to North America from Asia that devastated American chestnut tree (Castanea dentata); potato late blight (Phytophthora infestans), an oomycete that destroyed crops throughout Europe but was particularly devastating in Ireland in the mid-19th century; and, in the late 1960s, an epidemic of Southern maize leaf blight (Bipolaris maydis) that destroyed the more than 85% of maize plants growing in the US carrying the cms-T cytoplasmic male sterility trait.

Plant pathologists are currently combatting hundreds of different pathogens that affect food production globally. Some are bacteria, including Xanthomonas spp that causes at least 350 different plant diseases, such as rice bacterial blight, and Ralstonia spp that affects more than 200 host species. Fungi such as Pyricularia oryzae, the fungus that causes rice blast, and various oomycetes (including Phytophthora) also cause severe diseases on a large number of different crop plants. Root-knot nematode, Meloidogyne incognita, infects 1700 plant species and is a major threat to soybean production. Tomato spotted wilt virus is a major viral threat to food production that affects more than a thousand species and is responsible for more than a billion dollars in crop losses annually. Pathogens affect nonfood plants also. In Europe, a disease that affects European ash trees is spreading rapidly and is expected to kill 90% of ash trees. The fungal pathogen, thought to spread by the wind as well as by the transport of infected seedlings, was unknown prior to the 21st century.

Plants can perceive the presence of a pathogen and initiate a defense response against it. Perception occurs through recognition of the double-stranded RNA of viruses, cell wall degradation, digestion products released by fungi, some bacteria, and some insects, and chemical signatures conserved among pathogens, including bacterial flagella and fungal cell walls.

Some pathogens produce effector proteins that interfere with the plant’s defense responses, and in turn some plants produce resistance (R) proteins (encoded by R genes) that respond to the effector proteins and further stimulate the plant’s defense responses. Many R genes have been identified, often from wild relatives, and introduced into crop plants. The effectiveness of a single R gene is readily overcome by further pathogen evolution. Many cultivars have been bred to carry multiple stacked R genes to lower the possibility of microbial resistance, and fields are sometimes sown with plants carrying different R genes to help prevent catastrophic epidemics.

Phytophagous (plant-eating) insects harm plants at all stages of their life cycle and attack roots, stems, leaves, flowers, and fruits. Some of the most destructive are aphids, thrips, whiteflies, mites, weevils, locusts, and caterpillars. Each of these groups includes tens to thousands of species, some of which feed on a single plant host and others that are more opportunistic feeders. Some eat any or all parts of the plant, but most specialize (e.g., as leaf chews, leaf miners, stem borers, or sap suckers). Besides their direct physical damage, insects also spread diseases and by wounding the plants make them more vulnerable to infection by pathogens.

Characterization of plant defenses to insects is challenging because of the tremendous diversity in these interactions, involving at least four million insects and 230,000 flowering plant species. Physical defenses include physical barriers like the waxy cuticle and bark that cover the stem and leaves as well as calcium oxalate and silica deposits that form sharp needle-like crystals, trichomes (epidermal hairs), and thorns. Plants also produce chemical compounds that deter or poison herbivores. Glandular trichomes on plants like stinging nettles (Urtica dioica), poison oak (Toxicodendron diversilobum), and poison ivy (Toxicodendron radicans) combine the physical deterrence of trichomes with chemical irritants. Often, chemical defenses are stored in the vacuole or kept in an inactive form that becomes toxic or repellent upon exposure to air or contact with an herbivore.

Some defenses are induced by herbivore activity. Induced defenses include the production of antinutritive compounds (e.g., proteinase inhibitors), strengthening of physical barriers (calllose production and cell wall fortification), and deterrent compounds. Systemic signaling induces defense gene expression in distant tissues as well as those under direct attack, and volatile compounds can also induce defense responses in nearby plants. Some carnivorous insects recognize these volatile compounds as an indication that herbivorous insects are feeding, attracting them to the site to do a little feeding of their own.

INTERACTIONS WITH OTHER PLANTS

Competition

Interspecific and intraspecific competition for light, nutrients, and water has been a driving force for plant diversification for millions of years. The scarcity of water in the terrestrial environment gave early vascular plants a great advantage over nonvascular plants and gave seed-bearing plants an advantage over those that relied on desiccation-sensitive spores for reproduction. Competition for light energy can be fierce. In dense forests, competition for light drives plants upwards, and some tree crowns can reach more than 100 meters above the forest floor. Other plants hitchhike to the light-rich canopy by growing epiphytically, on top of their neighbors. Epiphytes include mosses and lichen, ferns, and flowering plants, including orchids, the familiar tropical bromeliads, and Spanish moss (which is a bromeliad).

Some plants respond to being shaded by another plant by inducing a stem elongation response. Plants can detect an overlying leaf by a change in the spectrum of light that hits them: Leaves absorb most red light (they use it for photosynthesis) but transmit far-red light (which is not useful for photosynthesis). Thus, light filtered through, or reflected from, a green leaf has a decreased ratio of red to far-red light. Plants detect this altered red:far-red ratio with a system that uses a pigment called phytochrome and respond to shading by elongating their stems, as well as a host of other responses involving growth, germination, and reproduction. In temperate forests, small annual or bulb plants respond to temperature and daylength to germinate or sprout early in the spring. This adaptation gives them the
chance to collect much of their year’s worth of light energy before the overlying trees produce their leaves and shade them.

In some dense forests, the opportunity for seedlings to harvest sunlight only occurs occasionally, after fire removes overlying vegetation. Some plants, including some pine (Pinus spp) and Cyprus (Cupressus spp) species, store their seeds in tightly closed serotinous cones that open only in response to the intense heat of fire. Many indigenous Australian species, including acacias and banksias, are serotinous, and seeds of other Australian species require heat or smoke to promote germination. Small molecules called karrikins have been identified as smoke-borne germination stimuli.

Competition is just as fierce below ground. Some plants produce chemicals that inhibit growth and germination of other plants, called allelopathic (causing suffering to others) chemicals. Root-exuded allelopathic chemicals have been identified from wheat, rice, and sorghum (Sorghum bicolor) as well as other plants. One of the best-characterized allelopathic compounds is juglone, produced by black walnut (Juglans nigra). Allelopathic compounds are being investigated as possible herbicides because some are highly selective in their action and appear to have no harmful consequences to animals. Allelopathic plants can become very aggressive invasive plant species when introduced into new areas. This appears to be the case for spotted knapweed (Centaurea maculosa), which was introduced into North America in the late 1800s and has since become a serious pest and threat to native species.

Parasitic Plants

Parasitic plants are phylogenetically and functionally diverse. Some like dodder (Cuscuta spp) have mostly or entirely lost their photosynthetic ability. Some are obligate parasites (Orobanche aegyptiaca), whereas others can also be free-living (Mimulus guttatus). Some are shoot parasites, like the diverse mistletoe plants, whereas others parasitize their host plant’s roots. In each case, the root of the parasitic plant forms a specialized structure called a haustorium that penetrates into the host’s vascular tissues to withdraw water, nutrients, and sugars.

Parasitic plants that attack crop plants can be serious threats to agricultural productivity. Among these are witchweed (Striga spp) and broomrape (Orobanche spp), root parasites that can completely destroy crops and are extremely difficult to eradicate. When nutrient limited, many plant roots exude strigolactone hormones and other compounds that promote germination of parasitic plant seeds. This is consistent with the observation that these parasites are more abundant in nutrient-limited soils and has led to the use of fertilizers and/or copped legumes as a way to try to limit their germination. Dendrobium is a legume that also produces allelochemicals that interfere with Striga parasitism, providing two forms of protection. Genes that confer resistance to infection by Striga parasites have been identified. Details of the molecular interplay between host and parasite are being revealed, which will contribute to the elimination of parasitic pests and improve food security in the affected regions.

Cooperative Interactions

Cooperation between plants is more difficult to document. One form of plant cooperation involves a sharing of genetic resources within a species through cross-pollination. In this case, the cooperation occurs at the community level and benefits the next generation. Many plants have evolved mechanisms of self-incompatibility that prevent them from fertilizing their eggs with their own pollen-borne sperm. Thus, their reproductive success is at the mercy of other individuals of their own species. Other examples of shared community resources or other positive interactions have been observed. For example, communities can ameliorate some effects of harsh biotic environments, for example, by reducing transpiration from the soil, stabilizing soil, and protecting individuals from wind damage. Root grafts that form between related individuals can sustain a shaded or damaged plant through nutrient transfer, although these grafts also make plants sensitive to parasitism by their neighbors. Another form of community-level cooperation involves the production of volatile compounds upon pathogen or herbivore attack. These compounds may directly benefit the emitting plant, by promoting defense reactions in its own distant leaves. By producing volatile compounds that induce defense responses in nearby plants, the emitting plant benefits as well as its neighbors because the local population of pests or pathogens is maintained at a lower level when all the plants are resistant. In many cases, it is difficult to determine to what extent a plant’s fitness is enhanced directly as opposed to indirectly through cooperative effects.

PLANTS AND PEOPLE

Humans rely on plants for food, fresh water, clean air, medicinal compounds, wood, and other building materials and as sources of fiber for paper and clothing. What in return do plants get from humans? Other than the few species we selectively propagate, our effects on plants have been quite detrimental. Human actions have led to the destruction and erosion of many plant habitats and have brought about increases in atmospheric greenhouse gases that are contributing to rapid climate change.

Habitat Loss

During the past 10 thousand years, human activities have profoundly changed the abundance and distribution of plant life. Over the past 8000 years, half of the earth’s forests have been removed, and most of what is left is patchy and not capable of supporting the species richness of undisturbed forest. Replacing a complex forest ecosystem with agricultural lands is a major contributor to the decline in species diversity. The International Union for Conservation of Nature and Natural Resources lists 4000 plant species as endangered or critically endangered, but this is certainly an underestimate. With each species having a unique role in a network of community interactions, the loss of even a single species can have far-ranging effects.

Habitats are irreversibly degraded by air, soil, and water pollution. The release into the atmosphere of sulfur dioxide and nitrogen oxides gives rise to acid rain which has particularly harmed temperate forests. Fortunately, increased environmental awareness in the mid 20th century led to restrictions on
Climate Change

Atmospheric CO₂ levels are rising as a consequence of human activities and are currently ~40% higher than at any point in the preceding 200 million years. Although photosynthetic carbon fixation in some plants will benefit from elevated levels of CO₂, these benefits are usually small because plants are usually limited by water and nutrients as well as CO₂. Studies conducted at several Free-Air Carbon Dioxide Enrichment (FACE) facilities have examined the effects of CO₂ enrichment on plant growth rate and seed yields as well as photosynthesis, nitrogen assimilation, water use, and other plant processes. These studies show that although elevated CO₂ contributes to a small increase in photosynthesis in some plants, many topi cal grains that use fixation in some plants will benefit from elevated levels of CO₂, whereas specialist organisms face a more precarious future. Our understanding of the molecular communications and responses that these interactions involve. However, the complexity of plants’ interactions with other organisms is now magnified by a changing climate; we are trying to understand relationships that evolved over millions of years but are now being disturbed. Understanding and sustaining the ecosystems plants need for their survival is one of the biggest challenges we face.

SUMMARY AND FUTURE DIRECTIONS

Plants are not alone. Their survival depends on their ability to perceive and respond to countless other organisms, to fight off pathogens and pests, and to recruit beneficial partnerships. Our understanding of plants as components of ecosystems has contributed to our understanding of life at all levels and underlies the disciplines of ecology and evolutionary biology. Understand-