Plant–Plant Interactions

Plants lack familiar sense organs, such as eyes and ears, and often mistakenly have been thought to be insensitive. Throughout much of history, plants were considered to be the passive subjects of the actions of others, such as pathogens and herbivores, but the 20th century brought an awareness of the many ways that plants sense and respond to threats and opportunities conferred by others. This lecture examines how plants perceive and respond to other plants, how these plant–plant interactions affect the growth and productivity of individual plants, and their broader effects on plant communities. Although the community-level effects of plant–plant interactions have been recognized and studied for years, their molecular underpinnings are relatively recent discoveries and continue to be debated and examined. In this lecture, we will introduce well-established and more tentative, emerging models of plant–plant interactions. We start with brief definitions of some key terms.

KEY DEFINITIONS AND CONCEPTS

Phenotypic Plasticity

Phenotypic plasticity is the capacity of an individual (or a genotype) to exhibit a range of phenotypes in response to variation in the environment. It specifically refers to processes that are selected from alternative choices, based on information perceived. In animals, examples include the production of a defensive helmet by Daphnia in the presence of predators and temperature-dependent sex determination in reptiles and fish. When considering phenotypic plasticity in plants, it is helpful to consider that, unlike animals, plants continually produce new organs (e.g., leaves and roots) and that there is considerable redundancy in these organs. Examples of phenotypic plasticity are the proliferation of roots at the site of localized nutrient abundance or the selective senescence and shedding of a shaded branch.

Allometry

Allometry is the study of the relative size, scale, or growth rate of parts and the consequences of allometric scaling. In many organisms, the proportions of body parts change during development. Human babies are born with heads that are huge relative to their body size. As babies grow, their proportions change due to differences in relative growth rate of their body parts. A plant’s proportions and activities also change with growth (ontogenetically), independently of environmental factors. Studies of phenotypic plasticity must differentiate between ontogenetic or allometric and environmental contributions.

Signals and Cues

Plants sense their environment and neighbors through many cues and signals. Generally, a distinction can be made between cues and signals, although the precise definitions are not always agreed upon. “Signals” serve as intended information broadcasts, while “cues” are without intention. Information internal to an organism, delivered by, for example, a hormone, can be assumed to be a signal. External information might be a cue or a signal. Physical and chemical information (such as water or a mineral nutrient) is clearly conveyed by cues. Some biological information might be conveyed by cues (not intended for broadcast to neighbors) or a signal. Generally, external biological information should be considered a cue unless proven otherwise. Ethylene and strigolactones are hormones that serve as both internal and external information vectors.

Plant Behavior

Plant behavior has been defined as what a plant does in the course of its lifetime “in response to an event or change in the environment” (Silvertown and Gordon, 1989). The ability of a plant to respond to environmental challenges or opportunities is restricted by its reduced mobility compared with animals, and so much of what we define as plant behavior is necessarily limited to developmental, growth, and physiological responses. A familiar example of a plant behavior is the phototropic curvature of a plant toward a light source, first recorded by Theophrastus (371 to 287 BC), the so-called father of botany. Physiological behaviors can be immediate and short term, such as a change in the expression of a nutrient transporter gene or pathogen response gene. Morphological, growth-based behaviors are slower to take effect and are more permanent. Growth provides costs as well as opportunities. Allocating resources to one organ means less is available to another, and retreating from an already grown organ might have substantial costs. Optimal plant behavior also requires the integration of information about the spatial and temporal scales and gradients of environmental conditions. For example, is a change in the light intensity indicative of a shading tree or a cloud or bird passing overhead? Is the concentration of a nutrient in the soil increasing or decreasing relative to the direction of root growth? Because most responses, especially those that involve growth, require time, the functional outcomes of any response will only materialize in the future. Accordingly, plants are selected to respond not only to their current environment but also to cues and signals that contain sufficiently reliable information about their future environment.

Case Study: Heterophylly and Leaf Plasticity in Response to Submergence

Semiaquatic plants often can produce two or more forms of leaf, which are determined by the levels of submergence. Frequently,
the leaves that form underwater are thinner, sometimes elongated, and do not produce cuticles or stomata. Heterophyll in response to submergence occurs in a wide range of plants, suggesting convergent evolution. The hormone abscisic acid and blue light are signals and cues for the aerial leaf form in many plants. As with all plastic responses, not every genotype is similarly plastic, and the degree of plasticity of the submergence response tends to vary with the susceptibility of the plant’s natural environment to flooding.

COMPETITION FOR LIGHT

Many of life’s most intriguing behaviors arise due to competition. As Charles Darwin pointed out, organisms that are the most similar and “fill nearly the same place in the economy of nature” are also the most competitive. For example, you compete more with your siblings and classmates than you do with your cat or your teacher. Because most plants have the same basic needs for water, space, and a substrate for growth, mineral nutrients, and light, the competition for these resources can be intense (although, as discussed later, competition is not always necessary). Plants respond directly to these nutrients and to competing plants, which they perceive through cues that include nutrient gradients and changes in the light environment. Responses to competition can include avoiding competitive environments, tolerating the competitor, or aggressively confronting the competitor (i.e., fighting back).

With a very few exceptions, plants completely depend on light energy to drive photosynthesis and fuel all of the plant’s energetic needs. Photoreceptors enable plants to monitor their light environment, to gauge and differentiate to what extent they are shaded by other plants or by inanimate objects, and to anticipate imminent shading. Some plants respond to vegetative shading through stem elongation to reach above the shading neighbor or growing away from the shade. This common and well-known response, often called the shade avoidance syndrome, is a developmental scheme that is both an avoidance strategy and also a confrontational strategy; plants that succeed in shooting up above their neighbors often end up winning the battle for light.

Other plants do not compete for light but are adapted to tolerate shade and thrive in low-light conditions. However, even understory plants compete among themselves for the available light and thus are expected to be responsive to similar-sized neighbors but not to very tall canopy trees they have no chance of overcoming.

Light Perception: Photoreceptors Sense Light Intensity and Spectral Quality

Plants, like animals, have several photoreceptors that are sensitive to light quality (wavelength or color) and intensity. Visible light comprises photons with a wavelength range from ~390 to 760 nm. The energy of a photon is inversely correlated with its wavelength, so per-quantum energy drops off proportionally with increasing wavelength. Photons of short, UV wavelengths carry sufficient energy to damage DNA, whereas long-wavelength infrared light is merely warming. All land plants have similar photosynthetic machinery that can use photons with wavelengths of 400 to 700 nm, known as photosynthetically active radiation (PAR). Longer wavelength photons pass through the leaf or are reflected off of it. Thus, light that passes through or reflects off a leaf is depleted in PAR (~700 nm) and is relatively rich in far-red light (~700 nm) compared with sunlight.

Phytochromes are a group of photoreceptors that detect red and far-red light and are particularly important for the optimization of photosynthesis, perception of day length, and the perception of other plants. Phytochromes detect photons on both sides of the boundary between PAR and far-red light. They do this by existing in two alternative conformations that preferentially absorb photons at ~660 or 730 nm. When activated by red photons, phytochromes change their conformation into a form that is capable of absorbing far-red light, known as Pfr. When Pfr absorbs far-red light, it switches back to a conformation known as Pr that can absorb red light. Thus, phytochromes are switches that toggle back and forth, like a light switch. In a cell that contains hundreds of thousands of phytochrome molecules, the proportions of both forms will depend on the relative abundance of red and far-red photons, in other words, the red to far-red (R:FR) ratio. The Pfr form initiates downstream responses, such as chlorophyll accumulation and leaf expansion, through changes in gene expression and hormone responses. Plants have additional photoreceptors that are sensitive to blue and UV light (cryptochromes, phototropins, and UV receptors), which also contribute to the regulation of plant light responses.

Through its photoreceptors, a plant perceives information about its environment. At the crudest level, the plant perceives the relative quantity light of different wavelengths, but there is considerable data to indicate that the information perceived is much richer. For example, photoreceptors are present throughout the plant body, allowing the plant to sense the quantity and quality of light coming from different directions, as well as spatial and temporal light gradients. Light perceived by a plant from different directions conveys valuable information about the presence and location of neighboring plants, even when those neighbors are still small and remote.

Shade Avoidance Syndrome

One set of responses to vegetative shading or to the possibility of future shading is the shade avoidance syndrome. These responses affect many aspects of plant behavior and can include an inhibition or delay of seed germination, increased stem and leaf elongation, a more vertical orientation of the leaves (hyponasty), a decreased number of branches (i.e., stronger apical dominance), and accelerated flowering. The elongation responses may enable the plant to confront a competing plant and increase its chances to rise above it. Beyond light cues, there is now evidence that touch and volatile compounds, including the hormone ethylene, serve as anticipatory cues that contribute to shade avoidance, at least in *Arabidopsis thaliana*.

Case Study: *Portulaca oleracea*

Shade avoidance does not necessarily involve upwards growth. Plants with a prostrate growth habit can sense and anticipate shading and orient their direction of growth to avoid it. As an
example, the spreading succulent *P. oleracea* grows and branches in a way that minimizes both self-shading and anticipated shade of neighboring plants, and the growth pattern is attributed to the R:FR ratio of the light reflected by neighbors and other parts of the same plant. When subjecting young *P. oleracea* seedlings to contrasting light cues, they become recumbent and grow away from sources of far-red light even when that means growing toward a region of less photosynthetic light. In other words, for young seedlings, low R:FR sunlight, a cue for future competition for light, is a strong deterrent. The plant chooses to forgo more light now to increase its potential to receive more light during the rest of its life.

**Shade Tolerance**

Plants respond in different ways to vegetative shading, and many do not respond through a shade avoidance response. Some species, known as shade-tolerant species, have evolved to thrive in the low-light environment beneath the forest canopy; the amount of PAR at ground level can be as little as 2% of that that hits the top of the overlying forest canopy. Although shade tolerance can take many forms, a few characteristics are frequently found among these species. Note that some of these features can be adopted by sun-loving plants growing in the shade, but others are restricted to shade-tolerant plants.

A fundamental requirement for survival in dim light is the ability to maximize the net rate of energy gain. Often, this means that the leaves of shade-tolerant plants are relatively thinner but with a larger area for light capture than those of sun-loving plants. Shade leaves also usually have a higher ratio of chlorophyll *b* to chlorophyll *a*, as a consequence of an increased size of light-harvesting antenna complexes relative to reaction centers. Similarly, compared with sun-loving plants, shade-tolerant plants have a lower stomatal density and lower abundance of the carbon-fixing enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase in the chloroplasts. Taken together, these features mean that in shade-tolerant plants, the rate of photosynthesis saturates at a lower light intensity (the light saturation point is lower) than in sun-loving plants. At the same time, shade-tolerant plants typically have a higher ratio of photosynthetic tissues (e.g., leaves) to nonphotosynthetic tissues (e.g., twigs, branches, and roots), which contributes to a lower rate of respiration in the dark per unit leaf area in shade leaves. As a consequence of this, the light compensation point (light intensity at which CO₂ uptake = CO₂ evolution) is lower in shade-tolerant plants. Collectively, these morphological and physiological traits enhance carbon accumulation in low-light conditions.

Optimization of carbon gain alone does not fully explain the basis of shade tolerance; responses to abiotic and biotic stresses have to be considered as well. Typically, compared with sun-loving plants, shade-tolerant plants have longer-lived leaves and invest more energy into protecting their leaves by increasing expenditures into defense against herbivores and pathogens. Furthermore, mechanisms of shade tolerance are constrained by the availability of water and the length of the growing season. For example, morphological adaptations to shade (large leaves) and drought (large root systems) might be achievable in a tropical plant, with a year-round growing season, but not in a temperate plant that only achieves a positive carbon balance during a few months of the year.

Finally, shade-tolerant species typically show a reduced stem elongation response to vegetative shading compared with sun-loving plants; nevertheless, these shade-tolerant plants might compete with their similar-sized understory neighbors. In terms of competitive behaviors, plants of shaded habitats often tolerate low light and avoid confrontational stem elongation responses that are likely to be futile, sun-loving plants tend to be confrontational, and plants that are typical to sparse, competition-free stands tend to avoid confrontation.

The light environment of plants is extremely information-rich, and plants are likely to perceive subtle information about the position, height, and growth rates of their neighbors through absolute amounts of light of different wavelengths, the angle of incidence of the light, light gradients, and time-of-day light information, perceived through interactions with the biological clock. Strong shade at midday followed by more light in the late afternoon might be the result of shading from a much taller tree and thus trigger an adaptation to enhance light collection within the understory rather than confrontational growth elongation. In addition, a plant might be more responsive to a vertical light gradient, where a plant encounters more light as it grows upwards and which indicates light competition by plants of similar stature than to homogenous shade, in which light intensity does not increase with increasing height and which indicates much taller and, thus, unbeatable neighbors.

Of course, as described below, the information conveyed by the light environment is augmented by chemical and other cues produced and affected by neighbors. The more we learn about the interactions between plants, the more sophisticated we recognize them to be. Is it any surprise that organisms that have competed with each other for space and resources for more than 400 million years are pretty good at sizing up their competitors?

**Germination Plasticity**

The global dominance of seed plants is attributable to their ability to wait out hard times as stable, dormant seeds. One of the most important choices a plant makes is when to germinate and shift from a safe to a vulnerable state. Getting the timing right means the difference between success (surviving to reproduce) and total failure (dying before reaching reproductive age). Although they appear inert, seeds are extremely sensitive to their external environment. Some of the cues that seeds are responsive to include light (with far-red light strongly suppressing the germination of seeds of many sun-loving plants), moisture, heat, smoke, etc.

Some but not all seeds require light for germination. Classic studies of seed germination, by Flint and McAlister (1935 and 1937), subsequently reproduced by Borthwick et al. (1952), used a light-sensitive variety of lettuce (*Lactuca sativa*). Their experiments showed that white light or red light stimulates germination but that far-red light is strongly inhibitory. These studies further demonstrated that the germination response was photoreversible, with far-red and red light reversing each other’s
effects, an early and clear demonstration of the nature of phytochrome. In such light-sensitive seeds, exposure to vegetative shading promotes a continued state of dormancy, avoiding a competitive environment.

Smoke and heat are other cues that can promote germination. Fire-responsive plants, including many endemic to the fire-prone regions of Australia, germinate or sprout following fire. Fires can open the canopy to reduce the competition for light but also generally result in improved growth conditions. Fires reintroduce nutrients into the soil, so fire-induced germination helps plants avoid competition for nutrients as well as light. In some cases, the response is to the heat of the fire, which can remove germination inhibitory compounds from the soil. Recently, a family of germination-promoting compounds called karrikins was identified from the smoke of burned plant materials. (The name karrikin is derived from karrik, a word for smoke used by a group of Aboriginal people of Australia.) Karrikins are stable in soil and very potent promoters of germination of many plant species, not only of fire-adapted species. Interestingly, karrikins and their signaling pathway closely resemble strigolactones and their signaling pathway. Strigolactones are plant hormones that also have additional roles in plant cueing and signaling between organisms.

Serotiny is another trait that allows plants to exploit postfire opportunities. Prevalent in many gymnosperms and some angiosperms, serotiny is a condition in which seeds are stored for prolonged periods in closed cones or fruiting structures, often in the canopy (rather than the soil). Serotinous structures remain closed with encapsulated seeds protected from predators until the heat of a fire opens them, sometimes by melting a resinous coating. Some other fire-responsive plants are induced to sprout or flower following fire, including the fire lily (Cyrthanthus ventricosus), which survives as an underground bulb and only flowers after a fire. Ethylene released from burning material may contribute to this response. Fire thus provides many cues that inform plants about the potential release from competition from other plants. This leads us to the question of what happens if the strongest competition comes from the plant itself, a phenomenon known as somatic competition.

**Somatic Competition**

The modular nature of plants means that they can produce many redundantly functioning organs. Growth often includes the addition of more leaves, branches, roots, flowers, and fruits, as well as the expensive growth of any or all of them. More often than not, this growth redundancy results in somatic competition among organs of the same plant. That is, one branch or leaf might shade another from the same plant. Nevertheless, the outcome of somatic competition is increased performance of the entire plant. The plant can explore many microenvironments and allocate more resources to organs that grow in the most favorable conditions. For example, a successful branch will not only grow faster than a less successful branch on the same plant, it will also induce the differentiation of more vascular strands toward itself at the expense of vascular connections to other, less successful (i.e., shaded), branches on the same plant. Ultimately, the outcompeted branch may be shed, a phenomenon made apparent by the absence of branches at the base of the trunk of any tree, especially tall trees growing in dense stands. The integration of cues and signals that leads to some organs “winning” and others “losing” is referred to as correlative inhibition. Somatic competition also occurs in the root system and the reproductive organs, in which limited resources are allocated only to the best-performing flowers and seeds.

Clearly, light and photosynthesis contribute to the dominance of one branch over another, but plasticity is also under the control of endogenous signals. Numerous studies of small, short-lived plants (including *Pisum* and *Arabidopsis*) indicate that the control of bud outgrowth is under hormonal control. The axillary bud that forms in each phytomer may or may not grow out. Apical dominance is the suppression of lateral bud outgrowth by the flow of auxin from the shoot apex. The hormones auxin, cytokinin, and strigolactones as well as nutrient availability all contribute to apical dominance and correlative inhibition.

**Case Study: Two-Shoot Peas**

In a classic paper by Snow (1931), the interactions between two shoots on a single plant were investigated. He germinated peas and then decapitated them. Two side branches initiated from the cotyledonal axillary buds, making an ideal system in which to investigate somatic competition. Snow showed that when one of the two shoots was cut off and the other was growing in the dark, the darkened shoot could survive and further develop using the nutrients reserves in the cotyledons. However, when one shoot was placed in the dark and the other in the light, the shoot in the dark died. Nutrients were preferentially allocated to the more successful shoot, at the expense of the weaker shoot. The results of Snow’s studies demonstrated that the growth of each shoot is not independent but that they are correlated with each other: that allocation of resources depended on both local conditions under which each shoot developed but also on the success of other shoots on the same plant.

**BELOWGROUND COMPETITION**

**Root Plasticity and Behavior: Nutrient Foraging**

In most environments, plant growth is limited by nutrient availability. Vascular plants take up nutrients usually through their roots, which forage for nutrients. Foraging behavior includes changing the rate and direction of growth of individual roots as well as the timing and positioning of new root initiation and root hair initiation and root death. Factors that affect root growth and architecture include the volume of soil, the level and heterogeneity of any of at least 20 essential mineral nutrients, water availabilities, the presence of other roots and organic molecules produced by other plants, and the presence and activity of microorganisms (e.g., mycorrhizal fungi, nitrogen-fixing rhizobia, and various pathogens).
According to the optimal foraging theory, plants will behave in such a way to maximize their net gain of energy and resources. When a root encounters a locally rich resource patch, it often invests resources, through root proliferation or nutrient transporter activity, to increase resource uptake and assimilation. At the same time, when soil resources are scarcer than light, plants allocate relatively more of their biomass to their roots; scarce, widely distributed nutrients force the plant to invest more resources in the root system to explore a larger soil volume. Cues that inform root behavior include nutrient availability as well as other, less well understood cues that indicate the presence of other roots.

Most plants (~90% of species) can recruit the aid of symbiotic mycorrhizal fungi for more effective foraging. Under conditions of nutrient limitation, root-exuded strigolactones are released into the soil and recruit the fungal partners. The plant provides the fungi with photosynthate, and the fungi increase the surface area for nutrient uptake, particularly phosphate. Most legumes similarly can recruit nitrogen-fixing rhizobia, which provide these plants with a competitive advantage (at the expense of photosynthate) in nitrogen-limited environments.

**Root Plasticity and Behavior: Interactions between Roots**

How do roots recognize other roots? Like many questions about roots, our understanding lags behind our understanding of the same phenomena in shoots, largely because roots are more difficult to study. The studies and findings we present here are intriguing, but in some cases their meanings remain open to interpretation and ongoing discussions. The story of how roots perceive and interact with each other is not yet clear.

**Competition between Roots of Different Species and Genotypes**

The results of many studies indicate that a competing root can suppress the growth of another. One mechanism for the suppression of growth by a competing root is that when two roots compete for limiting nutrients, their growth rates can be reduced due to nutrient limitation. An alternative, non-mutually exclusive mechanism is the production of root-exuded allelochemicals (chemicals that affect others) by one or the other root.

Many plants are known to produce allelochemicals. These small molecules can be produced by various tissues and can affect seed germination as well as root growth. Two of the most studied allelochemicals are juglone, produced by black walnut (*Juglans nigra*), and sorgoleone, produced by sorghum (*Sorghum bicolor*). Because of their specificity, several allelochemicals have been investigated as natural herbicides. For agricultural applications, allelochemical-producing plants can be desirable crops because they effectively suppress competing weeds, but they have to be managed carefully because they also can leave chemical residues in the soil that affect subsequent crop cycles.

Allelochemicals can act directly or indirectly, through effects on soil microbes. In the US, the aggressive invasive species garlic mustard (*Alliaria petiolata*) produces allelochemicals that inhibit mycorrhizal fungi, which most plants rely upon for efficient nutrient uptake. Like other crucifers, garlic mustard does not associate with mycorrhizal fungi, so the allelochemicals it produces do not affect its own growth. Furthermore, its impact is much lower in Europe, where it is native, than in the Americas, suggesting that following their long coevolution, the European mycorrhizal fungi are less susceptible to it, supporting the “novel weapon hypothesis” whereby invasive species can dominate an environment, the species of which haven’t had enough evolutionary time to evolve mechanisms to deal with the aggressive traits they bring.

**Do Plants Perceive and Discriminate between Self, Non-Self, and Kin?**

Studies in social animals support a role for kin selection and even seeming altruism in some behaviors, such as the shared rearing of infants by chimpanzees and elephants or the division of labor seen in social insects like bees and ants. An unresolved question in our understanding of plant–plant interactions is to what extent the relatedness of the competing plants matters. Although this question remains unanswered, some recent studies suggest that plants can discriminate between kin and non-kin, and self and non-self, but how this information is used is less clear.

In one study, pairs of rice (*Oryza sativa*) plants of the same or different genotypes were grown in clear gels and the extent of overlap between root systems measured. Roots of different genotypes tended to avoid each other and showed less overlap than root of the same genotype. This avoidance might arise from the production of different chemical exudates by roots of different genotypes.

Another study using peas investigated the responses of plants to other individuals of the same species and genotype, in an effort to determine if root foraging might minimize somatic competition (competition between roots of the same individual). The results of this study indicated that roots compete more (as measured by mass and directional growth) with other individuals than with self. When the connections between the roots of the same plant were severed, the roots lost some ability to recognize each other as belonging to the same plant/self. A similar result was found using *Buchloe dactyloides*. Taken together, these and other studies suggest that plants can recognize self and kin, though the precise signaling underlying these phenomena is yet to be revealed.

**Case Study: Parasitic Plants**

Parasitism can be considered an extreme form of competition. About 1% of angiosperms have evolved the ability to parasitize other plants: that is, to penetrate into their tissues and extract water and nutrients from them. Most parasitic plants are facultative opportunists, but a few have become completely dependent on their hosts as nutrient sources. In some tropical regions, such as the savanna agriculture in Africa, parasitic plants are major agricultural pests and can impact the food security of more than 100 million people. Much of the damage is
caused by parasitic witchweed (Striga spp) and broomrape (Orobanche spp and Phelipanche spp).

Parasitism is a complex trait that requires specific recognition of suitable hosts, evasion of their defense responses, and extraction of nutrients from them. Invasive structures called haustoria, analogous to those formed by pathogenic oomycetes and fungi, penetrate the host’s shoot or root and serve as conduits through which nutrients and water are transferred to the parasite. Some parasitic plants have evolved a strong dependency on their host, even to the point of losing their ability to perform photosynthesis, including the loss of many chloroplast-encoded photosynthetic genes.

Host recognition involves both chemical and tactile cues. Flavonoids released into the soil by host plants are important cues for some parasitic plants, as are the strigolactone hormones that were first characterized based on their ability to promote germination in Striga. Striga parasitism is prevalent in the low-input, unfertilized fields that are common in parts of Asia and Africa to a large extent because the nutrient-limited crops release strigolactones that are signals perceived both by beneficial mycorrhizal fungi and by parasitic plants. It has been shown that Striga parasitism is decreased when the crop plants are provided with exogenous fertilizers or grown with companion crops that enrich the soil.

COOPERATIVE/FACILITATIVE BEHAVIORS

There is increasing evidence to suggest that the interactions between plants are not only competitive, but that plants can benefit each other’s survival, growth, and performance. Positive interactions can include facilitation, in which both partners benefit, and commensalism, in which one benefits and the other neither benefits nor is harmed. Here, we will introduce three well-documented cases of beneficial interactions in plants: modulation of the abiotic environment, enhanced nutrient availability, and stress cueing.

Modulation of the Abiotic Environment

Beneficial associations between plants that help them to withstand harsh physical environments are widely documented. These can include acting as wind breaks, increasing the retention of soil moisture, changing the physical characteristics of soil, increasing soil oxygenation in water-logged environments, and decreasing soil salinity. Another example comes from nurse plants, which are adult plants that shelter seedlings as they establish. As an example, saguaro cactus (Carnegiea gigantea) seedlings are not very heat or desiccation tolerant but can survive under the shade of another plant, which is often the palo verde (Parkinsonia spp). Unfortunately, it is not uncommon for the saguaro to eventually outcompete its former nurse, in what is a classic case of succession. Nurse plants can belong to the same or to different species as the seedlings they protect, can confer protection from heat, excess radiation, desiccation, and even herbivory, and often have been described in challenging arid or alpine environments. The positive impacts that plants can have on the environment and, thus, other plants may also affect larger scale, population- and community-level interactions, as described further below.

Enhanced Nutrient Availability

Although all plants have the same basic requirements, some are better at meeting these needs than others. In such cases, different plants can benefit from the strengths of others. In agroecosystems, facilitations can result in greater yields when two crops are grown together (intercropping) than when either species is grown in monoculture. Legumes are known to increase the availability of fixed nitrogen for intercropped partner plants. They may also indirectly increase the availability of phosphorous for those plants, through soil acidification. Intercropping may also enhance the availability of minerals such as calcium, iron, nitrogen, and water through a process known as hydraulic lift, in which a deep-rooted species bring water up toward the surface where it can be used by a shallow-rooted species. Indirect facilitation can occur through effects on rhizosphere microorganisms or through shared mycorrhizal networks. A recent study showed that a C4 plant, Sorghum, which assimilates carbon very efficiently, provides carbohydrate to a common mycorrhizal network that greatly facilitates the growth of the intercropped flax, a C3 plant. Thus, in some of these systems, the community benefits from each according to its abilities. Carbohydrate sharing also occurs through naturally occurring root grafts, which can provide life support to a plant whose ability to assimilate carbohydrates is limited by shading or logging; at the same time, it can present a significant burden to the donor plant.

Case Study: Community-Level Effects of Phenotypic Plasticity in Rooting of Quercus douglasii

How do phenotypic plasticity and facilitative interactions affect plant communities? Plant ecologists have documented a wealth of community-level interactions between plants, and we urge the reader to explore this topic further. Here, we mention one study that looked at the blue oak Q. douglasii. The architecture of the oak’s roots shows a high degree of plasticity, and depending on whether they can access deep water reserves, they can vary root density near the soil surface. Trees that produced a large biomass of shallow roots competed more effectively with nearby plants, reducing the biomass of understory plants by about half compared with nearby open grasslands. By contrast, trees with deeper roots had a facilitative effect on nearby understory plants that had about twice the biomass compared with plants in the nearby open grassland. Thus, through phenotypic plasticity, environmental heterogeneity at the scale of the individual tree can be translated into higher level effects on populations and communities.

Stress Cues

Many animals produce alarm signals, which warn their kin, clan, troop, or flock of danger, which is usually a predator. In some
cases, the alarm conveys information about a predator, such as whether it is threatening from above or below (e.g., a hawk or a snake). There is growing evidence that plants also produce alarm signals or cues through the release of volatile chemicals. Whether these have evolved to elicit responses in the emitting plant itself or in other individuals remains an open question, but it is clear that plants can eavesdrop on each other and respond to the cues they perceive. Some of these compounds may have evolved primarily to convey information to herbivores and/or the enemies of the herbivores. As examples, wild potato (Solanum berthaultii) can produce an aphid alarm hormone that scares away herbivorous aphids, and many plants respond to herbivory by producing volatile compounds that attract parasitoid or predatory arthropods.

Evidence that plants can perceive and respond to chemicals released by others comes from many growth chamber and field studies. Early studies were criticized as being unrealistic, but more recently there is accumulating evidence that plant–plant communication occurs in natural settings. A now classic study compared tobacco (Nicotiana attenuata) plants near sagebrush (Artemisia tridentata) that had been mechanically wounded (clipped) or not. The tobacco near the clipped sagebrush showed an elevated level of the antinutritive polyphenol oxidase and a lower level of herbivory than those near the unclipped sagebrush plants, indicating that some information had been conveyed from the sagebrush to the tobacco.

Since this landmark study, much effort has gone into identifying the components of interplant cues, their stability once released from the emitting plant, whether they convey specific information, how far they travel, what plants perceive them, and how the information is recognized and transduced. There is good evidence to support information-carrying roles for the volatiles methyl jasmonate, methacrolein, and trans-2-hexenal. Mounting a full defensive response involves costs and reduced growth rate. Plants receiving these cues don’t activate a full antiherbivore defense response, but instead become primed (i.e., increase their readiness to more readily respond to future attack). Priming seems to involve the accumulation of signaling intermediates that enable the plant to respond faster and more vigorously should they themselves become infested with pests in the future.

Plant production of volatile compounds can benefit the emitting plant directly by acting as a systemic priming signal for distant or disconnected tissues. The emitting plant can also benefit from the enhanced resistance of its neighbors if this leads to a local decrease in pest or pathogen activity, but only if these benefits are greater than the cost of helping potential neighboring competitors. Are these stress-induced volatiles cues, or are they signals, released with the intention of conveying information to others? Along the same lines, there is some evidence that plants are more perceptive to cues from kin, but how universal and specific these stress cues are remains an open question.

Case Study: Communication of Drought Stress

Do plants communicate other types of stress? Recent data suggest so. To investigate whether drought cues can move from plant-to-plant, two-root plants were planted such that some shared the soil with a drought-stressed plant and others did not. Following drought stress of a single induced plant, the width of the stomatal pore decreased in both the stressed plant and the plants that shared soil with the induced plant, suggesting that they were anticipating drought. Interestingly, the stress cues seem to be relayed even by unstressed plants via the root system. Plants that shared no root connections to the stressed plant showed no response, indicating that the signal is not likely to be a shoot-emitted volatile compound such as those involved in herbivore warning but rather, yet unidentified, root exudates.

PUTTING KNOWLEDGE TO WORK

Far from an esoteric pursuit, understanding the interactions between plants could have enormous value for improving the way that humans interact with and take advantage of plants. As examples, we will briefly describe three applications: invasive species mitigation, intercropped and allelopathic crop plants, and exploiting plastic responses to light quality.

Invasive Species Mitigation

Biological invasions are an important cause of global biodiversity loss. Some of the most economically important invasive species today are water hyacinth (Eichhornia crassipes), kudzu (Pueraria lobata), Japanese knotweed (Fallopia japonica), leafy spurge (Euphorbia esula), giant hogweed (Heracleum mantegazzianum), and mile-a-minute weed (Polygonum perfoliatum). Each is a fascinating tale of good intentions and mistakes. Each also provides vital information as we try to avoid introducing plants into environments in which they will become pests. It is estimated that 1 in 10 species moved into a new environment will survive to reproduce in it, and 1 in 10 of those might become pests (see Richardson and Pysek [2006] for the caveats). Many of those that become pests are armed with novel chemical weapons, such as an allelochemical that attacks other plants, chemicals that affect the mycorrhizal fungi needed by the native plants, or a chemical deterrent that protects the invader from herbivores or pathogens. Many invasive species have greater phenotypic plasticity than the natives they are displacing, but this is not a hard-and-fast requirement for invasiveness. Besides this, small seeds, a short generation time, and large numbers of seeds produced are frequently associated with invasiveness, but none are requirements. Therefore, it is difficult to identify and anticipate potential problems. However, there is an increased tendency for alien species to become pests in disturbed environments, particularly those in which light and/or nutrient resources are abundant, such as deforested regions and lands downstream of fertilized fields. These correlations can only remind us to try to tread lightly in our actions toward the natural environment.

Case Study: Japanese Knotweed, from Prize Winner to Pariah

Japanese knotweed and its hybrid Fallopia × bohemica (Bohemian knotweed) is listed by the World Conservation Union
as one of the 100 most invasive species. It was widely distributed as a prizewinning ornamental plant in the mid-19th century, but now is a serious pest. It outcompetes native plants partially through the production of allelochemicals. It grows from underground rhizomes, so regenerates quickly, making its removal difficult. Millions of dollars are spent annually on control efforts, but it continues to spread. Although allelochemicals produced by Japanese knotweed have not been identified yet, a recent study showed that their harm could be mitigated by the presence of activated charcoal in the soil, which adsorbs and neutralizes the harmful chemicals. Another study found a way to fight fire with fire; in other words, to use an allelochemical-producing plant bog myrtle (Myrica gale) as a biocontrol agent with which to inhibit the growth of Japanese knotweed. Other studies have shown that knotweed exhibits highly plastic responses to salt, which is thought to contribute to its competitive success in salty environments.

Case Study: Backfiring Biocontrol of Invasive Knapweed?
Spotted knapweed (Centaurea stobe ssp micranthos, also known as Centaurea maculosa) is native to Europe and was introduced to North America in the 1890s. It is a noxious weed that competes very effectively with native plants and has ruined millions of acres of rangeland and native habitat throughout the western US and Canada. Biological control efforts, using herbivores imported from Europe, were started in the 1970s, with mixed results. In some studies, the negative effects on native plants were greater in the presence of the herbivore-infested knapweed than the uninfested knapweed. Possibly, herbivory induces defensive allelochemicals in the knapweed that negatively affect native plants or beneficial soil microbes.

Case Studies: Intercropping, Crop Rotation, and Crop Allelopathy
Often, crop production can be enhanced by growing two or more crops in the same field at the same time (intercropping) or in alternating years (crop rotation). Yield gains occur when the crops are selected so that they facilitate each other’s growth, and competition is minimized. A familiar example is the intercropping of maize (Zea mays) and bean (Phaseolus vulgaris), or maize, bean, and Cucurbita spp, or squash (which have been referred to as the three sisters). This system of agriculture has been practiced since ancient times, probably first in Mexico where maize was domesticated. Maize provides a structure for the climbing bean vines, beans are nitrogen-fixing legumes that increase the availability of nitrogen to other crops, and squash’s large leaves growing near the ground may conserve soil moisture and suppress weeds. Legumes are also beneficial when grown in crop rotation, as the nutritional benefits they confer persist into the next growing season. The three plants have complementary shoot architectures, with maize being very tall, bean having small leaves that fit between the gaps of the maize leaves, and squash producing large leaves near ground level. In addition, a recent study found that the roots systems of legumes and maize are complementary in distribution, which minimizes their competition belowground.

Additional successful intercropping strategies have been identified more recently by examining the needs of the farmers as well as the needs and behaviors of the plants. A nice example is the push-pull system developed to reduce the impact of stem borer caterpillars on maize. In this system, the herbivores are pushed away from the crops by an intercropped plant, the legume Desmodium uncinatum, which produces repellent volatiles. The herbivores are pulled toward Napier grass (Pennisetum purpureum) planted at the perimeter of the field. An additional benefit of this system is that D. uncinatum also produces allelochemicals that interfere with Striga parasitism, protecting the crop from yet another pest. By intercropping, the farmer greatly increases the maize yield by minimizing herbivory and parasitism and also produces a nitrogen-rich legume crop as food for animals.

In Uganda, farmers have found that their coffee yields are improved when they are intercropped with banana trees, which provide some shade for the coffee plants. A particular benefit for the farmer is that the same land can produce a cash crop (coffee) and a food crop (banana), thus enhancing the farmer’s food security. Neither coffee nor banana is indigenous to Uganda, so this successful intercropping strategy could never have occurred without the input from humans.

Several cereals, including sorghum (Sorghum bicolor), wheat (Triticum aestivum), barley (Hordeum vulgare), oat (Avena sativa), and rice, are known to produce allelochemicals that suppress the growth of other plants. Efforts are underway to introduce these traits into cultivated varieties of these crop plants, which could reduce the need for chemical herbicide application and mechanical weed removal. Traditional and molecular breeding methods are being used. As an example, the biochemical pathway for the synthesis of an allelochemical from rice, momilactone B, has been identified, providing a molecular target for breeding and metabolic engineering studies.

Case Study: Manipulating the Light Environment for Increased Productivity
Understanding how plants respond to light intensity, quality, and gradients will provide us with opportunities to exploit these responses to alter their growth patterns and productivity. Greenhouses can be covered with colored filters to alter the spectral qualities of the light for various desired effects. For example, copper sulfate dyes filter out some red light but even more far-red light and can lead to a reduction in plant height or increase the production of axillary buds. Other filters can preferentially remove red light, leading to an increase in plant height. When sun-loving plants, such as tomatoes and roses, were grown under plastic sheeting with incorporated fluorescent dyes that increased R:FR ratios (by absorbing green light and emitting red light), the plants produced more fruits and flowers than control plants grown under clear covers. Similar results can be obtained using light-emitting diodes. It is conceivable that greenhouses could be programmed to provide plants with light customized to optimize their growth and architecture throughout development.
SUMMARY AND FUTURE DIRECTIONS

In many respects, the understanding of plant–plant interactions lags behind our understanding of other plant biotic interactions. Although phenomena such as the benefits of intercropping and allelopathy have been recognized for centuries, studies of the mechanistic bases for competitive and cooperative plant behaviors are relatively recent and ongoing efforts. A picture of plant interactions is emerging that is surprisingly sophisticated, in which plants perceive their neighbors through light and chemical cues, evaluate the extent to which these neighbors pose a threat, and respond appropriately.

It is likely that our understanding of these sensitive signaling and response systems can be manipulated to improve crop yields. For example, rather than manipulating light spectral qualities through filters, field-grown plants could be manipulated through an engineered phytochrome that could be induced to switch between Pr and Pfr forms by exogenous chemical signals. Thus, optimal architecture for crop production could be maintained, even in very densely planted fields. Genetically manipulating the responses of plants to the stress cues emitted by other plants or artificial preemptive treatments could effectively increase plants’ tolerance of pests or abiotic stresses.

Advances in metabolomic profiling and genomic and transcriptomic approaches may provide tools with which to decipher plant–plant interactions at the molecular level. Building up a predictive network from genes and environment through response and phenotype is important for modeling and managing natural and agroecosystems. The sustainable intensification of agriculture is necessary to feed the world’s population while preserving biodiversity and wilderness environments, but to achieve this goal scientists need to harness the power of plants to work with each other and limit their tendencies to act against each other.

Phenotypic Plasticity and Plant Behavior


Germination Plasticity


Root Plasticity and Competition Belowground


Hodge, A., and Fitter, A.H. (October 15, 2012). Microbial mediation of...


Facilitative Behaviors: Resources and Stress


Facilitative Behaviors: Information


Invasive Species


