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TEACHING TOOLS IN PLANT BIOLOGY™: LECTURE NOTES

Three-Way Interactions between Plants, Microbes, and Arthropods (PMA): Impacts, Mechanisms, and Prospects for Sustainable Plant Protection

Plants are surrounded by and interact with a diverse community of organisms. Examples include interactions with harmful organisms, such as herbivores and pathogens, but also interactions with beneficial organisms, such as plant growth-promoting microorganisms, mycorrhizal fungi, and pollinators. For instance, the interaction of a plant with a soil-borne microorganism may impact the plant's growth, development, and stress resistance properties (it's "phenotype"). Often this is mediated by microbially induced changes in plant gene expression. Subsequently, the altered properties of that plant (the "extended phenotype") can have knock-on effects on the functioning of other members of the surrounding community (e.g., an insect herbivore that shares the same host plant).

It is increasingly recognized that such three-way interactions between plants and their surrounding community members may benefit the plant. For instance, interactions of plants with beneficial microbes can enhance the plant's production of substances that are harmful to pests or pathogens as well as substances that attract natural enemies of these pests ("bodyguards"). Such interactions can be exploited to boost the plant's resistance to agricultural pests, while in natural systems such effects hold promise for application in conservation biology.

This lecture specifically addresses **cross-domain interactions**, focusing on three-way interactions between plants, microorganisms (including fungi, bacteria, and viruses), and arthropods (the large animal phylum that includes insects, spiders, mites, and a few other groups of invertebrates). We refer to these interactions as **PMAs (plant-microbe-arthropod interactions)**. Microbe-induced resistance to arthropod pests holds great promise for application in sustainable agriculture, reducing the needs of fertilizer and pesticide inputs. PMAs in natural ecosystems represent some of the "hidden" interactions with potentially large effects on the functioning of natural ecosystems.

In this Teaching Tool, we introduce PMA interactions with examples, explore their mechanisms of action, address their evolutionary origins and ecological consequences, assess their potential applications in agriculture, and discuss their relevance in the context of United Nations (UN) Sustainable Development Goals (SDGs).

INTRODUCTION TO PMA INTERACTIONS AND THE PHYTOBIOME

Plants do not live in isolation but are part of a larger living environment called the phytobiome that includes plants, their environment, and their associated communities of organisms, including insects, mites, fungi, bacteria, viruses, etc. These interactions occur across broad scales of space and time.

Interactions between two partners fall within the ecological continuum from beneficial to harmful relationships. They follow a defined classification that ranges from symbioses that provide mutual benefits to both parties (mutualism) to detrimental effects by antagonists (parasitism) and various kinds of competitive interactions. Communities that associate with a plant occur both inside (endophytes) and outside its tissues and in aboveground and belowground parts of the plant. The nature of the relationships may depend on the lifestyle of the associated organism, for example whether it lives inside or outside the plant, whether it depends on certain tissues for its development, and whether it is a specialist (that only interacts with a limited number of plant taxa) or a generalist (that may interact with a broad range of plant species or families).

In three-way interactions between plants, microbes, and arthropods, the effect of one actor may often be described by the impact it has on the interaction between the two others. For example, a microbe might make the plant more susceptible to an herbivore or more attractive to a pollinator. It should be noted, however, that the outcome of PMA interactions often strongly depends on environmental conditions such as soil type, nutrient availability, climate, and cultivation practices. This so-called "context dependency" of the outcome of PMAs indicates that their broad-scale application necessitates control of the factors involved in such dependency or the development of more tailor-made solutions.

Examples of PMA Interactions

It is increasingly recognized that PMA interactions cannot simply be predicted from the underlying two-way interactions. This is because, for instance, microbes alter the quality or suitability of their host plants for arthropods, so that the interactions between the host plant and the arthropod becomes contingent upon the presence of the microbe and vice versa. Below we give some examples.

Microbes Countering Herbivores, Directly and Indirectly

Entomopathogenic bacteria (i.e., bacteria pathogenic to insects) such as *Bacillus thuringiensis* (Bt) infect herbivorous arthropods and reduce the negative effect these may have on their host plants. Bt is a well-known example of an entomopathogen with a commercial value, and the Bt toxin is being directly applied in pest eradication programs. The gene that codes for Bt has been

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inserted into crops like maize, cotton, and soybean. Furthermore, many plant-associated beneficial microbes such as arbuscular mycorrhizal (AM) fungi, a group of obligate root symbionts, plant growth-promoting rhizobacteria (PGPR), and plant growth-promoting fungi (PGPF) can affect arthropod herbivores indirectly, by altering plant growth, plant nutrient composition, and/or the profile of root and leaf metabolites and by inducing systemic resistance that can result in enhanced mortality of arthropod pests, as shown for lepidopteran caterpillars on tomato.

Microbes Enhancing Pollination

Plant-associated microbes can also have profound positive effects on the interaction of plants with arthropods. For instance, plants that associate with AM fungi often show enhanced visitation rates by pollinators. Such three-way interactions are not only important in natural systems but also in cropping systems, where AM fungi can be applied to prevent malformation of strawberries that occurs when flowers are not sufficiently pollinated.

Microbes Attracting Predators of Herbivores

Beneficial plant microbes can also alter the profile of so-called herbivore-induced plant volatiles that plants produce when they are attacked by pests. The microbe-induced changes in these volatile profiles have been shown to enhance the plant's attraction of the natural enemies of their crop pests, such as predatory mites that prey on spider mites, a significant pest in several crop species.

PMAs Are Not Always Beneficial for The Plant

Above we described some examples of PMAs that potentially benefit plants. However, PMAs can also negatively affect plants. First, in several systems, it has been shown that beneficial microbes that enhance resistance against leaf-chewing arthropods often reduce resistance to sap-sucking arthropods such as aphids and may even increase pest fecundity. Second, arthropods are often vectors of diseases, as is the case for the xylem-sucking bug *Philaenus apumarius*, which carries the devastating bacterial pathogen *Xylella fastidiosa* that infests several fruit tree crops, including olives, plums, cherries, and grapes. In such cases, the PMA interaction thus reinforces the harmful effect of the arthropod on its host plant rather than providing a benefit. Third, insect-associated bacteria often benefit pest insects by enhancing their ability to exploit host plants, providing protection against the arthropod's natural enemies, or by suppressing plant defense.

THE MECHANISMS BEHIND PMA INTERACTIONS

The mechanistic scenarios most commonly invoked to explain plant-mediated interactions between microbes and arthropods involve (1) changes in nutrient content and primary metabolism of the plant, (2) changes in plant morphology, and (3) the activation of defense-signaling pathways and subsequent metabolomic alterations.

Mechanism: Primary Metabolism and Nutrition

Beneficial root-associated microbes, such as mycorrhizal fungi or rhizobia, can improve plant nutrition, primarily through an enhanced uptake of phosphorus and nitrogen. This increases plant size, vigor, and nutrient levels, thus potentially improving herbivore development. Similarly, attacks by plant aggressors such as pathogens and herbivores also affect plant primary metabolism, including quantity and quality of nitrogen and concentrations of carbohydrates. Following shoot herbivory, plants can preferentially allocate resources to roots as an important mechanism conferring tolerance. Such changes in resource allocation can affect the root exudation patterns and the host quality for root pathogens and symbionts, altering the communities of microbes interacting with the roots.

Mechanism: Architecture and Morphology

The attack by herbivores and microbial pathogens and the establishment of plant-microbe mutualistic associations can induce changes in plant architecture and other morphological traits, such as the density and type of trichomes (hairy outgrows of epidermal cells that function in defense), leaf morphology and thickness, leaf color, and leaf toughness. Like changes in the primary metabolism, plant morphological changes also influence subsequent interactions. Examples of microbe-induced morphological changes that change arthropod performance and behavior are the yellowing of some virus-infected plants that increases their visual attractiveness to whitefly vectors and the curling of leaves infected with some viruses that provides shelter for aphids.

Mechanism: Plant Defense Responses

The activation of plant defense pathways by insect herbivores and microbial pathogens strongly influences subsequent plant interactions. To ward off an attack by enemies, plants have evolved a whole array of constitutive and inducible defenses. **Constitutive defenses** are always present and include many structural barriers, such as cell walls, waxy epidermal cuticles, thorns, and bark, as well as many bioactive compounds. In addition, plants can detect an attack by enemies and respond with a diversity of structural or chemical **inducible defenses** that are expressed at the site of the attack (locally) but also in distal tissues (systemically). Systemic induction of plant defenses can confer plant protection to still undamaged tissues.

Plant defenses can also be classified as direct or indirect. **Direct defenses** include any plant traits that by themselves affect the susceptibility of host plants to pathogen or insect attack, including the production of toxic chemicals, defense proteins, physical barriers, and the activation of cell death. **Indirect defenses**, on the other hand, include plant traits that by themselves do not affect plant susceptibility but can serve as attractants to natural enemies of the attacking insects and thus reduce plant tissue loss. For example, upon herbivory, plants produce and release a blend of volatiles that can attract predators, parasites, and other natural enemies of the herbivore, reducing its population and, as a result, reducing plant damage.

Plant Defense Response: Recognition

The induction of plant defenses relies on successful recognition of the invading organism. Potentially harmful organisms are recognized by the presence of molecules that have structures or chemical patterns unique to them and thus are perceived by the plant as nonself/foreign. These molecules are referred to as pathogen-associated molecular patterns (PAMPs), microbe-associated molecular patterns (MAMPs), herbivore-associated molecular patterns (HAMPs) or nematode-associated molecular patterns (NAMPs), depending on the group of organisms they respond to. In addition, plants can also perceive endogenous molecules (such as signal molecules or fragments from membranes or cell walls) that are released or produced by the plant after the attack, known as damage-associated molecular patterns (DAMPs).

These "danger" molecules are detected by pattern recognition receptors on the surface of the host plant cell, leading to PAMP-triggered immunity, HAMP-triggered immunity, or wound-triggered immunity. Successful attackers can evade this immune response through the action of effector molecules that, upon delivery into the host cell, suppress the defense response. However, some plants acquired a second line of defense in which resistance proteins mediate the recognition of these effectors, resulting in effector-triggered immunity.

Plant Defense Response: Immune Signaling Network

Upon perception of an attack, the activation of plant defenses involves complex reiterative transduction networks with extensive signal amplification and crosstalk, in which plant hormones act as central players. Salicylic acid (SA) and jasmonic acid (JA) together with their derivatives are recognized as the major defense regulators. Hormones such as ethylene, abscisic acid, brassinosteroids, auxins, cytokinins, gibberellins, and reactive oxygen and nitrogen species function as regulators of the plant immune signaling network. The activation of the SA defensive pathway is typically (but not exclusively) effective against microbial biotrophic pathogens (including viruses and biotrophic bacteria and fungi) and against sucking insects. On the other hand, the defenses regulated by the JA pathway are mostly effective against necrotrophic pathogens and chewing insects.

Moreover, antagonistic and synergistic interactions between diverse hormone signal transduction pathways add another layer of defense regulation. This so-called hormonal crosstalk provides the plant with a powerful regulatory capacity to fine-tune its immune response to the attacker. The most studied interplay between hormonal pathways is the negative crosstalk between the SA and JA pathways. As plants in nature are simultaneously or sequentially attacked by multiple enemies with different lifestyles, SA-JA crosstalk represents a powerful mechanism to prioritize one specific pathway over the other, according to the sequence and the type of attackers encountered. Indeed, tradeoffs between SA-dependent resistance to biotrophs and sap-sucking insects and JA-dependent defense against necrotrophs and leaf-chewing insect herbivores shape cross-effects in multiple PMA interactions, as we will describe below. Moreover, hormonal crosstalk has also been implicated in adaptive responses to abiotic stresses. Hence, in addition to their regulatory role in induced defenses after the perception of specific stresses, phytohormone interactions function as integrators of developmental and environmental cues, fine-tuning plant adaptation to the ecological context.

Plant Defense Response: Defense Priming

An interesting plant strategy for improving its defensive capacity against enemies is the phenomenon of defense priming, which leads to an enhanced capacity for the induction of defense mechanisms. Different stimuli from microbial pathogens, arthropods, beneficial microbes, or abiotic cues can bring the plant's immune system to a state of alert that allows the plant to respond faster or stronger to subsequent attack. This first stimulus, known as the priming stimulus, triggers a transient activation of defenses and, even more interestingly, leaves a "stress memory" in the plant. Upon subsequent challenge, the plant effectively mounts a faster and/or stronger and/or more enduring defense response, resulting in enhanced resistance. Defense priming is considered as an adaptive, low-cost defensive measure, because defense responses are not, or are only slightly and transiently, activated by a given priming stimulus. Instead of maintaining a costly elevated level of defenses, defense responses are deployed in a more efficient manner following the perception of a later attacker. Defense priming is suggested to be durable, representing a type of plant immunological memory that can strongly shape PMA interactions throughout the plant's life cycle.

MECHANISMS BY WHICH MICROBES CAN ALTER THE OUTCOME OF PLANT-ARTHROPOD INTERACTIONS

Plant-arthropod interactions can be modulated by both plant-associated and arthropod-associated microbes, which do not all necessarily benefit the plant. Interactions with microbes that affect every trophic level in the plant-associated trophic interaction network are not uncommon. As discussed, certain plant-associated microbes induce/prime plant defenses, mediating phenotypic changes (morphological, physiological, and/or biochemical) in the plants. Those changes can subsequently affect their attractiveness and suitability as a host plant for arthropods by inducing the production of additional bioactive compounds. The effect of these changes in higher trophic levels is most commonly mitigated through arthropod "counter" responses to the changes, sometimes assisted by arthropod-associated microbes. The next sections summarize study cases of such complex PMA relationships and the regulatory mechanisms behind them.

Plant-Associated Microbes May Contribute to Plant Defenses

Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are states of enhanced defensive capacity that confer long-lasting protection against a broad spectrum of biotic stresses. Both ISR and SAR are central to arthropod-microbe interactions. They differ mainly in the identity of the organisms triggering this enhanced resistance and the main signaling pathways regulating them.

The onset of SAR requires accumulation of the signal molecule SA and pathogenesis-related proteins that often result in distinctly localized hypersensitive responses. SAR can be triggered by avirulent or attenuated pathogens, and its induction commonly increases resistance to a number of pathogens and pests. Generally, SAR is most effective against biotrophic and hemibiotrophic pathogens that thrive on live plant tissues, whereas it is considered less protective against necrotrophic pathogens that kill the plant. This is usually related to the negative crosstalk between the SA and JA pathways.

ISR is another important defense mechanism induced by some beneficial microorganisms such as PGPR and PGPF that are commonly found in the rhizosphere. These microbes prime the entire plant (see section on defense priming above), leading to enhanced systemic resistance against a broad range of pathogens and insect herbivores. A large variety of root-associated microbes, including *Pseudomonas*, *Bacillus*, *Trichoderma*, and mycorrhizal fungal species, prime the plant's immune system to become more resistant against pathogens without directly activating the production of costly defense chemicals.

ISR is mostly associated with the activation of JA and ethylene. Unlike SAR, ISR does not depend on activation of the SA pathway and it does not entail higher basal accumulation of pathogenesis-related proteins in systemic tissues. Although ISR is often regulated through SA-independent mechanisms, several PGPR have been reported to trigger an SA-dependent type of ISR that resembles pathogen-induced SAR, suggesting that SAR and ISR are not completely separate phenomena. Indeed, they may share some common elements, as shown in Arabidopsis, where they share the common regulator protein NONEXPRESSOR OF PATHOGENESIS-RELATED GENES1.

Belowground defense priming activated by plant-associated microbes has also been documented in multiple studies. For example, when tomato is colonized by the AM fungus *Funneliformis mosseae*, a reduction in the performance of the chewing bollworm *Helicoverpa arimigera* is observed. This effect coincides with induced levels of defense compounds and increased expression of several plant-associated defense genes, including those coding for proteinase inhibitors that negatively affect the insect digestion of plant tissues.

Besides modulating the expression of plant defense genes, plant-associated microbes can supplement plant protection by producing bioactive compounds that directly or indirectly affect arthropod performance. Then, by providing additional features to the host plant, the microbe genotype complements the plant genotype, providing new functions such as the synthesis of additional defensive compounds. Thus, the combination of plant and microbe can be considered as the extended phenotype (comprising the expression of plant and surrounding microbial genomes). There are several examples of plant-associated microbes that produce compounds, toxic or deterrent for the arthropod. Some compounds are constitutively produced by the microbe (inside the plant tissue), whereas others may only be activated under specific conditions in which they are needed, thus supplementing the plant defensive arsenal. For example, the production of an insect deterrent alkaloid (peramine) by an endophytic fungus is induced in response to herbivory in the grass *Lolium perenne*.

Remarkably, as plant-associated microbes can contribute to plant defense by priming plant defenses or producing additional defensive compounds, attacked plants try to recruit those microbes by altering root exudation to attract them, in a belowground "cry for help."

Arthropod-Associated Microbes May Affect Plant-Arthropod Interactions

Just as plant defense against arthropods can be mediated by plant metabolites that act as feeding deterrents or toxins that impede the digestion of plant tissues, the gut microbiota of insect pests may play an active role in the detoxification of these secondary metabolites, such as monoterpenes and diterpenes, alkaloids, and IRIDOID glycosides. Antibiotic-treated insects (devoid of bacterial microbes) are generally less effective in the degradation of some of these toxic compounds.

Defense compounds are costly for the plant to produce, so it is common that defense compounds are kept at a constitutively low level. They are induced only after damage is inflicted, for example, in response to wounding. Some herbivore-associated microbes actively assist the herbivore in overcoming plant defenses by targeting the plant's main resistance signaling pathways and, thereby, their ability to induce the production of defense compounds.

Plant wounding and the presence of arthropod digestive secretions generally elicit a plant defense response, usually coordinated through JA signaling. Remarkably, this can be altered by the presence of certain microbes within the arthropod. For example, symbiotic bacteria in the oral secretion from Colorado potato beetle (*Leptinotarsa decemlineata*) larvae contribute to a suppression of the JA-regulated defense responses, thus favoring larval performance. After treating leaves with antibiotics that removed bacteria from the oral secretion of Colorado beetles, an upregulation of plant defense genes was demonstrated, suggesting that microbes in the beetle saliva activate the SA-signaling pathway and downregulate the JA-signaling pathway through their negative crosstalk. This leads to the reduction of the plant's response to damage, thus facilitating the herbivore.

Whiteflies are the main vectors of *Tomato yellow leaf curl virus*, and when this pathogenic virus infects the plant, it alters the nutritional content of the leaf tissue and phloem sap to benefit the whitefly performance, thereby improving viral dispersion. Besides the nutritional effect, the presence of the virus in the plant also has an indirect impact on arthropod performance by suppressing the JA-mediated plant defenses against the whitefly by inducing SA signaling.

Examples of More Complex PMA Interactions

An increasing number of studies report about the complex network of interactions involving various groups of microbes with importance for plant-arthropod interactions. Herbivory-induced plant volatiles, for example, make caterpillars more susceptible to their natural viral and bacterial pathogens. Such changes in susceptibility have been associated with the gut microbiome of the caterpillar. Another example of the complexity of PMA interactions involves polydnaviruses, a group of symbiotic viruses that facilitate the development of some braconid and ichneumonid parasitic wasps by suppressing the immune system of the insect hosts. It has been found that parasitized caterpillars (*Helicoverpa zea*) are less effective at inducing plant defenses than their nonparasitized counterparts. These differences have been linked to a reduction of elicitors in the saliva of the parasitized caterpillars, thus involving a trophic cascade of events across four trophic levels that silence plant defense and simultaneously promote herbivore fitness and proliferation of the virus.

EVOLUTION AND ECOLOGY OF PMA THREE-WAY INTERACTIONS

Interactions with Microbes Have Strongly Shaped Plant Evolution

Terrestrial plants evolved from an ancient and continuing symbiosis between semiaquatic green algae and aquatic fungi. This idea is supported by genetic evidence proving that alga-like ancestors coexisted with early fungi. Indeed, the very evolution of plants was only possible through such mutualistic partnerships. The earliest fossils of plant-fungal associations are documented for small-sized plants with rhizoid root systems that formed symbioses with several types of endomycorrhizal fungi. These were discovered in the 407-million-year-old Early Devonian Rhynie chert deposit known for its extraordinarily detailed fossils. Currently, ~72% of all plants form symbioses with AM fungi that share common ancestry with these fossil fungi and that enhance mineral nutrition of their host plants in exchange for carbon obtained from the plant.

Interactions with Microbes Have Shaped Plant-Arthropod Interactions

Similar to plants coevolving with microbial symbionts, arthropods also coevolved with microbial communities that enabled them to exploit new host plants and evolve novel feeding styles, resulting in diversification into the wide variety of arthropod lineages with their associated microbiomes that we see today. Indeed, the acquisition of endosymbiotic microorganisms by arthropods often appears to be the starting point of evolutionary radiation of major arthropod families.

For instance, ~250 million years ago, bacterial endosymbionts of the genus *Sulcia* enabled the evolution of a sap-feeding lifestyle among arthropods. Later, in the Tertiary era, another bacterial endosymbiont of the genus *Baumannia* also enabled arthropods such as sharpshooters (Cicadellidae) to adopt a xylem-feeding lifestyle. Sap from xylem and phloem lacks several of the essential amino acids that are necessary for the development of arthropods and that are partly produced by their endosymbionts. In some cases, the complementary loss of genes involved in amino acid production in the insect and endosymbiont over evolutionary time has led to an obligate symbiosis, where partners can no longer survive without each other, indicating that insect-microbe symbioses affect the evolution of both the host's and the symbiont's genomes.

Other symbioses are facultative, that is, endosymbionts provide additional nutritional or defensive benefits without (yet) being essential for survival. Studies manipulating the presence of such facultative endosymbionts in stinkbugs have elegantly shown that these microbes can enhance the arthropod's opportunities for the exploitation and utilization of novel host plants, demonstrating their role in the insect's ecological opportunities and adaptation to different host plants. Together, these studies yield a broad picture of the symbiotic origins that may have contributed to the evolutionary and ecological diversification of arthropods.

Species Continuously Adapt within Three-Way Interactions

The evolved associations of both plants and arthropods with their symbiotic microbes have ecological and evolutionary consequences for three-way interactions between plants, microbes, and arthropods. This can be seen, for instance, in contemporary evolutionary responses of spider mites to plants associating with AM fungi. The association of plants with AM fungi alters their nutritional and defense status. Arthropod herbivores such as spider mites respond to such AM-induced changes in the quality of their host plants. Interestingly, it has been shown that in the course of several generations on AM-associated plants, spider mites evolve traits that enable them to attain higher fecundity on plants colonized by AM fungi, indicating that they evolutionarily respond to the "holosymbiont," that is, the plant including its symbiotic partner. This illustrates how three-way interactions can steer the evolutionary responses of organisms. It also illustrates that when three-way interactions occur, we need to identify them in order to understand evolutionary responses in, for instance, plant-arthropod interactions.

Plant Defense Strategies and Traits: Resistance, Tolerance, and Avoidance

Plants basically master three defense strategies to protect themselves from damage by harmful organisms: they make use of resistance, tolerance, and avoidance strategies. **Resistance** strategies limit pest growth and reproduction by means of mechanical and chemical protection. When resistance traits confer a fitness benefit to the plant, these traits are considered defense traits. **Tolerance** refers to the ability of plants to maintain their performance and fitness despite the inflicted damage (e.g., by a pattern of resource allocation that enables the plant to regrow and partly or fully compensate the damage caused by an antagonist). Empirical evidence in natural populations reveals that individual plants allocate resources simultaneously to both strategies; thus, plants exhibit a mixed pattern of defense. A third, underappreciated, type of protection is provided by **avoidance** strategies that reduce damage by escaping harmful organisms by means of developmental, morphological, spatial, and temporal strategies to grow out of their reach.

Plant Defense Is Costly

Because the resources that are used by plants for growth and defense are usually limited under natural conditions, plant investment in any of these defense strategies can come at a cost of lower investment in either growth and reproduction or in other defense strategies. Two types of cost can be discerned. **Allocation costs** refer to the tradeoff between defense and growth, which builds on the observation that the production of defense metabolites or structures is metabolically costly, and when resources are used to build up protection the plant will have less resources left to grow. **Ecological costs** consider tradeoffs between different types of defenses that are effective against different types of attackers. For instance, investments in traits that confer resistance against sap-feeding aphids can trade off against investments in traits that confer resistance to chewing arthropods.

Tradeoffs may also occur between types of activation of defenses. Defense metabolites and structures can be produced constitutively (independent of attack), be induced (only produced in response to attack), or be primed (not produced in response to the first attacker but produced faster or stronger in response to subsequent attack). The risk of damage and the costs of activation are considered important drivers of which type of activation is favored under various environmental conditions. Tradeoffs between constitutive and induced resistance have been long predicted, since individuals or species that are already well defended by high constitutive resistance are expected to benefit only marginally from further induction. However, empirical evidence for such tradeoffs is still scant. This is partly because studies often include a limited set of genotypes or species or have used cultivated species that had been subject to artificial selection. In cultivated plants, the selection pressures maintaining tradeoffs may be alleviated because cultivated plants are artificially protected from pests or because breeding has broken up tradeoffs.

How Does Domestication Affect Defense?

A frequent hypothesis explaining the high susceptibility of many crops to pests and diseases is that, in the process of domestication, crops have lost defensive traits and genes, resulting in a low resistance to pests and diseases. The domestication of wild crop relatives has altered plant genomes through a number of human-induced processes during artificial selection of crop traits. Human-induced hybridizations, alteration of reproductive strategies, and ploidy (genome number) have resulted in genotypes and phenotypes that differ substantially from the original wild relatives. Artificial selection has, for obvious reasons, prioritized plant genotypes that show high growth or yield and low toxicity or low concentrations of specialized compounds detrimental for human consumption or handling. At the same time, intensification of agricultural practices and the use of pesticides have made crops less dependent on their own defenses. Most of these actions are thought to have contributed to varieties with low resistance to pest and diseases.

Costs and Benefits of Defense in PMA Three-Way Interactions

As discussed, the association of plants with beneficial microbes alters their growth and nutritional quality and can induce or prime particular defenses, altering the metabolic and ecological costs and benefits of defenses against arthropod pests compared with when the plants do not associate with these microbes. For example, enhanced nutrient acquisition by beneficial microbes may partly alleviate tradeoffs between plant growth and defense, as it will increase the plant's overall resource acquisition.

Elaborating on this, consider plants with high resistance to caterpillars. In a simple two-way interaction, the benefits of high resistance to caterpillar feeding in the presence of caterpillars may be offset by allocation costs in the absence of caterpillars as well as by ecological costs in the presence of aphids. However, in a three-way interaction, in the presence of microbial symbionts, these costs and benefits will be altered as a result of, for instance, enhanced resource acquisition, priming of caterpillar resistance, and concomitant enhanced susceptibility to aphids by reinforced ecological costs. This indicates that the evolution of defenses in PMA three-way interactions can considerably differ from that in two-way interactions.

Given the ability of beneficial microbes to alleviate tradeoffs between growth and defense and to fortify particular types of defenses, we could benefit from breeding plants for traits that promote their association with beneficial microbes and make them more efficient in exploiting the soil microbiome to enhance pest resistance as an additional strategy to resistance breeding. However, whereas numerous studies show genotypic variation in the ability of plants to recruit and form functional associations with beneficial microbes, such attempts have only been started very recently.

PMA INTERACTIONS FOR BIOCONTROL

The genetic improvement of crops in combination with the development of agrochemicals and improved irrigation systems initiated the Green Revolution that brought huge benefits for humans. Instead of being naturally surrounded by multiple organisms, crops could now be grown in cleaner and more controlled environments and yields were maximized. Half a century later, the drawbacks of the Green Revolution (including contamination of the environment and a false sense of security against pest outbreaks) have brought our attention to alternative agricultural practices. These practices consider the value of ecosystem services and, thus, positive feedback effects from the environment that surrounds plants.

Strategies for Biological Control of Pests

Although biological control of pests using arthropod-arthropod interactions (through the use of their natural enemies: predators and parasitoids) is widely applied in plant production systems, especially horticulture, three-way PMA interactions are rarely implemented in a grower's management strategies. However, research has revealed that PMA interactions have high potential for biological management of both pests and diseases in plant production.

Basically, there are two main ways to implement PMA in plant protection: (1) by environmental manipulation to promote beneficial interactions and (2) by the addition of biocontrol agents such as entomopathogens or resistance-inducing plant microbes.

Manipulation of the cropping environment to facilitate the colonization and multiplication of local biocontrol agents can, for example, take the form of organic matter amendment, intercropping, crop rotation, or reduced tillage. With use of these strategies, growers benefit from native ecosystem services by adapting their plant growth strategy to facilitate the colonization and abundance of naturally occurring beneficial organisms that may control potential threats (i.e., pests and or diseases).

The second method is to use inoculation or release of mass-produced biocontrol agents, which is a plant protection strategy that involves planning and knowhow at several levels. As a first step, biocontrol agents must be identified, tested, and registered, as described by Pliego et al. (2011) for PMA control of soil-borne diseases in avocado. Technical challenges in the use of PMAs for inoculation and release include (1) formulation of the biological product, (2) the development of cost-efficient mass-production methods, (3) the development of distribution and storage systems that ensure survival of the biological material, and (4) recommendation schemes that suggest relevant application processes and techniques to be used for inoculation and/or release of the biocontrol agent.

There are also cultural barriers to overcome before PMA pest-management strategies are preferred by farmers over traditional strategies. Although eco-friendly solutions are in demand, new strategies may also include investment in new procedures and/or infrastructures. Low damage levels may have to be tolerated when PMA methods cannot provide as efficient plant protection as chemical pesticides, for example, when abiotic conditions do not favor biocontrol, since biological interactions are more influenced by the abiotic context than chemical pesticides.

Examples of PMA Interactions for Crop Protection

However, with research and development, PMA interactions promise to be strong alternatives to crop protection with great potentials for modern agroecological farming. PMA interactions are currently mostly used for pest control; for example, fungal endophytes are used to control pests in grasses. At airports, this reduces the number of arthropods, so the area becomes less attractive to birds feeding on the insects, thereby reducing the risk of airplane accidents caused by birds. Other examples are entomopathogenic fungi such as *Beauveria bassiana* and *Metharizium brunneum*, which can be used to control peach aphids in sweet pepper as well as mealy bugs and grape leafhoppers in grapevine. Recently, the control of western maize rootworm by biocontrol nematodes has been shown to be improved by engineering the nematode's bacterial symbionts, demonstrating the potential of PMA interactions in bioprotection strategies.

PERSPECTIVE: PMA INTERACTIONS AND UN SDGS

The UN has launched initiatives to promote sustainability and equality to reach food security by 2030 in order to eradicate hunger and poverty. However, food security is underpinned by agricultural practices that are increasingly challenged. Current concerns may be classified as follows: (1) the need to supply plant production with nourishment in the context of nutrient shortages, climate change, and price volatility; (2) the need to consider environmental costs and benefits when evaluating yield from intensive plant production systems; and (3) the urge to provide actions to protect agrifood sectors in politically unstable regions.

To cope with these challenges, there is political and public understanding that traditional intensive agricultural practices, whenever possible, should be replaced with novel technologies more respectful to the environment. The concept of integrated pest management (IPM) was recently defined as "a holistic approach to combat plant pests using all available methods, with minimal applications of chemical pesticides." This concept has a long history that reaches far back into the 1800s, and the methods involved in IPM strive to combine resources to enhance plant health and yield through proactive actions. This IPM concept has gained new interest from governmental bodies that aim to establish guidelines for plant growers, suggesting a multi-scale and multi-method approach with the vision to minimize effects of pests and diseases, not just by killing them but through continuous actions and adjustments that keep their populations under limits for serious plant injury.

PMA Interactions as Eco-Tech Solutions

The urge to increase yields and guarantee food security with the help of eco-friendly practices has also engaged communities of plant growers and plant scientists to develop "eco-tech" solutions like the phytobiome initiative (http://www.phytobiomes.org/about/Pages/What-is-the-Phytobiome.aspx). PMA interactions provide a phytobiome strategy that fits well within the scope and ideas of IPM. For example, microbiome-plant interactions may have evolved originally as interdomain crosstalk and thus promise to offer ecosystem-sound methods for future plant protection. Through a positive feedback between a plant and its soil microbiome, plant production could be more resilient to variation in the growing environment.

In addition to enhanced yield, beneficial belowground interactions are also well known to enhance plant resistance to attackers both below and above ground. The potential to strengthen crops with pretreatments such as defense priming is a reasonably young field of research. To commercialize such efforts, several steps of optimization are required to guarantee safe and reasonable plant protection results.

However, in order to exploit PMA interactions as an environment-friendly technology in IPM strategies, integration of research knowledge at several scales, from the ecological to molecular scales, is needed, requiring close collaboration between scientists, farmers, and agro-suppliers. To facilitate the use of PMA in plant production, plant breeders should consider breeding for plant cultivars that naturally recruit beneficial organisms as a functional trait.

PMA Approaches Support UN SDGs

To move toward sustainable plant production including PMA interactions, attention must be given to environmental, economic, and societal benefits. Indeed, environmental health, social justice, and economic profit are three cornerstones of the goals suggested by the UN in the Agenda for 2030 SDGs (United Nations, 2015). The PMA concept naturally fits into the environmental health corner of the triangle, but potentially it also adds to both social and economic values by providing a healthier environment for plant production, leading to a safer and more economically stable working environment and food supply.

To achieve the UN's sustainability goals, the entire food production chain has to be considered: from legal regulations of the agroecosystem (from fields to ecozones) throughout the distribution chain to the end consumer. The food system has thus been considered the hub of the UN's SDG since 2015. The use of PMA interactions for crop protection is relevant to the UN goals, particularly to Goal 2 (Zero Hunger), Goal 4 (Quality Education), Goal 12 (Responsible Consumption and Production), Goal 15 (Life on Land), and Goal 17 (Partnerships for the Goals). The use of PMA interactions in sustainable agriculture thus agrees with the UN goals and supports future sustainable plant production.

SUMMARY

Plants in natural and managed systems interact with a plethora of beneficial and detrimental organisms, including microbes and arthropods. Many of these interactions have traditionally been studied as two-way interactions (i.e., interactions between plants and microbes or between plants and arthropods). However, plants usually interact with both types of organisms, either simultaneously or sequentially, leading to more complex three-way interactions.

Recent studies have provided fascinating insights into how plant-associated microbes alter the suitability of their host plants for arthropods and, conversely, how arthropod-associated microbes affect the ability of arthropods to exploit their host plants. These interactions represent two examples of the so-called PMAs, three-way interactions between plants, microbes, and arthropods. PMAs have far-reaching consequences for the functioning of plants and their associated organisms in natural and managed ecosystems that extend well beyond the simple sum of the two-way interactions between each of the pairs of organisms involved. They are therefore important to understand the functioning of natural communities and for managing our agricultural systems.

This Teaching Tool summarizes the current knowledge on impacts, mechanisms, evolution, and prospects for the application of such PMAs. In the past two decades, there has been a tremendous increase in our understanding of the mechanisms that underlie PMAs. These include, for example, microbial priming or repression of plant defense signaling pathways involved in activating defenses against arthropod herbivores, enhancement of plant growth and reconfiguration of plant primary metabolism that result in changes in plant nutritional quality, and the modulation of herbivore-induced plant volatiles involved in the attraction of natural enemies of arthropods.

Not surprisingly, the impacts of PMAs on plants range from highly detrimental (e.g., arthropods vectoring plant pathogens) to highly beneficial (e.g., microbe-enhanced pollinator service or microbe-induced pest resistance). The latter type of PMAs hold great promise for applications in more sustainable agriculture, horticulture, and sylviculture with reduced inputs of fertilizers and pesticides. Currently, there is wide application of insect-killing microbes (entomopathogens) and an increasing number of applications in the form of biostimulants and biofertilizers that contain growth-promoting microbes capable of inducing systemic pest resistance. However, full inclusion of PMAs in IPM programs is still in its infancy.

In order to exploit PMA interactions as an environment-friendly technology in IPM strategies, integration of research knowledge at several scales, from ecological to molecular, and close collaboration between scientists, farmers, and agro-suppliers are needed. Furthermore, plant breeders should consider breeding for plant cultivars that are better able to recruit beneficial organisms as a functional trait. PMA interactions are well suited to support the UN SDGs. The PMA concept naturally fits into these goals and potentially adds to both social and economic values by providing a healthier and more sustainable environment for plant production.

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