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EDITORIAL

Molecular biology of chemical defenses

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Producing chemicals is the primary way plants cope and thrive in diverse environments. Countless studies have examined the ingenious ways plants use chemistry, sometimes as direct weapons and other times as signals. This Special Issue provides some of the most recent developments in the study of plant chemical defenses. Our editorial team surveyed broad areas of research covering both basic and applied plant sciences. Subjects extended from single molecules to organisms and evolution, as well as areas involving responses to abiotic and biotic stresses, using either model or non-model plant species. Of these, 20 insightful articles were chosen and are presented here grouped into nine reviews and eleven primary research articles.

Schenck and Busta (2021) begins with a discussion of comparative and phylogeny-guided studies to understand metabolic pathways and the evolution of specialized metabolism. Highlights include the power of such approaches in the backdrop of exponentially increasing multi-omics data, especially in many intractable non-model species. A review by Deng et al. (2021) showcases the application of phylogenetic reconstructions for the independent evolution of phenolic sucrose esters in monocots and dicots. While more detailed studies are needed to understand their biological functions, the inducibility of those compounds through pathogens and stress-related phytohormones strongly imply their involvement in defense. Shoji et al. (2021) reviews efforts to use information gathered from large sets of genomics data to investigate how domestication has contributed to the evolution of defense metabolites. There is evidence that mutations in transcriptional regulators form the molecular basis for many cases of metabolite elimination.

Several research papers examine the specialization of diverse defense metabolites in different plant species and stress contexts. Acylsugars produced in the trichomes of *Nicotiana benthamiana* were found to provide protection against desiccation and herbivory by hemipteran and lepidopteran insects (Feng et al. 2021). The group identified two acylsugar transferases and created loss-of-function mutants by CRISPR-Cas9 genome editing. The resulting lines lacked acylsugar and were more susceptible to herbivory. The group discusses the potential of this method as a useful transient gene expression platform to test other genes for their roles in acylsugar biosynthesis and for conferring resistance to insects. Moreover, the short chain fatty alcohol, 1-octen-3-ol, is one of the volatiles emitted from plants confronted with fungal pathogens or insects. Ntoruru et al. (2021) detected large amounts of its glycoside precursor 1-octen-3-yl β-primeveroside in the young leaves of soybeans. Damage to leaves caused rapid release of the 1-octen-3-ol volatile at the expense of its primeveroside precursor suggesting the hydrolysis of the existing precursor glycoside was used for the quick volatile release. This is reminiscent of the fast deployment of isothiocyanate by the myrosinase-glucosinolate system in Brassicaceae. An article by Li et al. (2022) reports the identification of enzymes catalyzing the formation of key intermediates in lignin and flavonoid biosynthesis. Flavonoids represent the largest group of plant polyphenols and are implicated in diverse protective roles against environmental stresses and diseases. The enzymes they identified are from tea plants (*Camellina sinensis*), which is known for a rich flavonoid content that benefits human health. Wound and UV-B-inducible patterns of their genes are consistent with the general defensive roles of flavonoids. Tsuzuki et al. (2021) proposes the application of a menthol derivative, called ment-Val, that can boost the expression of defense genes to reduce pest damage in soybean plants and other crops. Their findings could usher in a change from harmful chemical pesticides to sustainable and environment-friendly alternatives. Articles by Dangol et al. (2022) and Tiwari et al. (2021) discuss the occurrence and biological function of serotonin and its derivative melatonin

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in plants. These indoleamine compounds are better known for their roles as vital neurotransmitters involved in diverse mental and physiological processes in animals. Melatonin is reported to play diverse roles in plants, but Tiwari et al. (2021) focuses on recent evidence of the protective roles it plays against microbial pathogens and oxidative stresses by acting as a signaling molecule and powerful antioxidant. Tryptophan is the common precursor of serotonin and melatonin in both plants and animals, and while similar enzymes in plants and animals catalyze a two-step conversion from serotonin to melatonin, the upstream pathways leading to serotonin synthesis from tryptophan are distinct. Dangol et al. (2022) identified the genes encoding tryptophan decarboxylase and tryptamin 5-hydroxylase from *Setaria viridis* that produce resistance against aphid feeding. One of the many challenges that arise because plants are sessile is the need to deal with the pollutants in the soil in which they grow. Toxic metals are not only a problem for plants but also a danger for human health through food consumption. Uraguchi et al. (2021) discusses how plants deal with organic and inorganic mercury by activating a phytochelatin-mediated metal detoxification pathway.

Many of the articles presented touch on the importance of gene transcription for the expression and regulation of the defensive traits of plants including the already mentioned by Shoji et al. (2021) Research by Valea et al. (2021) takes a closer look at the basic helix–loop–helix (bHLH) family transcription factor RERJ1 that is found in rice. RERJ1, in many ways, resembles the major bHLH transcription factor, OsMYC2, that is known to regulate jasmonic acid (JA)-responsive gene expression in rice, and in fact, they physically interact with one another. But RERJ1 also seemed to regulate terpene synthesis, and its defect renders increased susceptibility to insect herbivory and bacterial blight infection in the mutant plants. Tünnermann et al. (2022) discuss how plants and pathogens compete for nitrogen rich amino acids and how that contest most often centers on membrane transporters of amino acids. Both seek to gain control by manipulating the expression of these transporters at the site of invasion. They present cases involving several transporters that provide insights to this less understood form of chemical defense. Zhuang et al. (2021) examined the dynamics of genome-wide transcriptional changes in rice during an attack of leaf folder insects (*Cnaphalocrocis medinalis*). Time series transcriptomics data revealed the enormously complex gene expression changes that are clearly linked to the release of defense compounds. Using mass spectrometry, the authors generated a time-dependent JA metabolite profile in these plants. Mutants defective in JA signaling are characterized in greater detail regarding gene expression, antinutritive proteins, phenolamides, and insect bioassays to show the extent to which JA signaling pathway exerts its control over the diverse defense responses in rice against leaf folder insects. Despite the dominant role of JA in many defense responses, Shinya et al. (2021) provides evidence of other oxylipins acting as major signaling molecules in some other contexts. They found that 12-oxo-phytodienonic acid (OPDA), most likely in form of amino acid derivatives rather than JA-derivatives, synergistically stimulate chitin oligosaccharide-elicited phytoalexin production in rice cells. Measurements of diverse amino acid conjugates of OPDA and JA in cells derived from oxylipin biosynthetic mutants treated with combinations of chemical elicitors provoke interesting questions surrounding this branch of OPDA-specific signaling pathway.

In the upstream of oxylipin biosynthesis and signaling are cellular messengers such as membrane potential changes, reactive oxygen species, pH changes and calcium ions that relay extracellular and environmental information to downstream cellular responses. However, these messengers are shared by multiple signal transduction pathways and it is unclear how information encoded in these common messengers can induce specific downstream responses corresponding to each stimulus. Heyer et al. (2021) discusses plant-specific calmodulin-like (CML) proteins involved in decoding of signal information carried by calcium during insect, pathogen and drought responses. They report two CMLs acting antagonistically in such capacities.

A plant's exquisite ability to tailor its responses to complex external cues has been evolving for a long time and must not remain static. To be successful, those signal transduction pathways need to constantly adapt to changing environmental challenges. A review by Jones et al. (2021) reflects on how chemical elicitors/effectors from insects and matching responses from plants have characterized the evolution of the two enormously diverse and prolific species. Several examples are given that warn against a simplified view of insect-derived chemicals as mere elicitors/effectors of plant defense responses, but rather as also influencing insect species at the same time. Concise analysis provides a comprehensive list of known elicitors and effectors in diverse plant–insect interactions that calls for a more holistic approach that includes ecological dimensions. Furthermore, the review by Baez et al. (2022) focuses on the currently available knowledge regarding the plant cell wall maintenance mechanism, discusses pattern triggered immunity and highlights how both mechanisms could modulate jointly adaptive responses to changes in the environment. They present knowledge deriving both from *Arabidopsis thaliana* and other plant species to show the extent of conservation of these processes across the plant kingdom.

The final output of plant defense responses is the sum of many signaling pathways that influence one another. Grover et al. (2020) analyzed levels of several hormones in an inbred line of sorghum (*Sorghum bicolor*) that has a high tolerance against sugarcane aphids. The highly interconnected nature of signaling networks makes it almost impossible to isolate defense pathways from other signaling pathways including those governing plant growth. Antagonistic crosstalk creates growth-or-defend dilemma for plants as discussed in-depth by Sestari and Campos (2021). They compiled published reports on the inverse relationship between the elevated chemical defenses and growth in diverse plant species, and contemplate the evolutionary past based on the prevalence of the phenomenon among land plants. They then provide new evidence that departs from some of the traditionally held views of the phenomenon as a mere resource reallocation problem. Uncovering the molecular details of this relationship could help with efforts to alleviate some of the yield penalties associated with developing stress resilient crops by decoupling defense response from growth. Ganie et al. (2021) discusses an alternative solution to enhance both plant growth and tolerance by using endophytes. They put forward several known cases of plant growth promoting microbes offering protection against abiotic stresses such as salinity and drought as well as against biotic aggressors. They discuss the underlying molecular mechanisms and share their perspectives on exploiting them for sustainable rice production.

The immensely diverse variety of plant-based chemicals has only begun to be explored. This Special Issue has drawn our attention to the defensive and informative roles of these compounds that is one of the strongest driving forces behind the chemical diversification and expansion in plants. We want to thank the authors for their truly insightful and visionary reviews and fascinating research stories. We deeply appreciate their hard work and dedication which has made this Special Issue a resounding success. The editors hope that the readers will find these papers enjoyable to read, as we did, and useful to their own scientific endeavors. We also acknowledge all the peer reviewers and staff members for their valuable input and contributions.

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