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Self defense by plants

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Plants have evolved elegant and complex chemical systems to defend themselves against the pathogens and herbivores that attempt to consume them. The current exponential growth in interest and experimentation in this area provided the motivation to hold this colloquium.

Some plant chemical defenses are constitutive, providing built-in physical or biological barriers against the invading organisms, but others are active, being induced by the attacking foe. The responses can be local or can extend systemically through the plant. In the inducible systems, signal and receptor mechanisms are present that rival the complexity and sophistication of signaling systems of animals. Many of the chemicals used by plants for self defense have been called "secondary plant metabolites," since they are products of specialized biosynthetic pathways. However, some macromolecules active in defense can also have primary roles in the plant, examples being proteinase inhibitors and lectins that act as storage proteins in seeds and structural complexes such as lignin and surface waxes.

Following survival against an initial pathogen attack, plants can become immune to subsequent attack by a wide variety of fungal, bacterial, and viral pathogens. This response is known as "systemic acquired resistance." For example, tobacco plants infected on one leaf with tobacco mosaic virus can produce local lesions that restrict the virus infection. When this occurs, entire plants become resistant not only to new infections by the same virus but to other pathogens as well. This sort of response involves the production of a set of new extracellular "pathogenesis-related" or PR proteins. It has been determined that the systemic signal for this response is salicylic acid. The PR proteins that are systemically induced by pathogen attack can also be induced by exogenously applied salicylic acid. While aspirin is useful for humans, its close relative may be even more important for plants.

A different sort of systemic immunity is induced by grazing herbivores or chewing insects. When leaves of some plant species are consumed, the plants manage to render themselves unpalatable to and/or indigestible by the herbivores. In 1972, specific defensive proteins (protease inhibitors) were demonstrated to be synthesized in tomato and potato leaves throughout the plant within a few hours of even one leaf being attacked by chewing insects. A signal is produced at the damage site that travels to distant leaves of the plant. The signal is clearly not salicylic acid, and studies in several laboratories have implicated at least three possible alternatives: an 18-amino acid polypeptide called "systemin," the perfume methyl jasmonate, electrical signals, or various combinations thereof.

In another somewhat different strategy of inducible plant defense, plants can respond by releasing constitutive chemicals, while at the same time mobilizing inducible defenses. Conifers, for example, when attacked by beetles that carry an infectious fungus in their mouth parts, release large amounts of resin from attack sites that flow out onto the attackers, embalming the creatures for posterity. Meanwhile, the tree

mobilizes its defenses against the pathogenic fungus that the intruder has deposited at the wound site.

In another kind of plant–insect interaction, it has been found that some plants appear to call for help—attracting predators of their predators. For instance, in response to attacks by specific insect larvae, some plants release volatile signals, attracting wasps parasitic on the larvae. The wasp injects its eggs into the herbivore, dooming the plant predator to a timely end while propagating its own species. The plant benefits because the feeding life of the herbivore is shortened, and its reproduction is terminated. In another type of recruitment, some plants provide beneficial soil organisms with a suitable environment surrounding their roots by secreting specific nutrients. The soil microorganisms, in turn, produce antibiotics that control pathogenic soil organisms that would otherwise attack the plant.

For centuries, agricultural crops have been bred for increased resistance against various pathogens. Numerous resistance traits, most of them due to single genes, have been identified, but the chemical bases for the genetic traits have not been known. Identification and analysis of resistance genes using DNA technology has been a major goal of many laboratories throughout the world, and progress in this area has been impressive. Less than two years ago, the first of the resistance genes that have so long been recognized by breeders was isolated. Since then, several more resistance genes have been isolated and characterized. These genes will provide not only fundamental knowledge of the function in disease resistance but also the capability of inserting resistance traits in crop plants through genetic engineering.

The manuscripts that follow are the summaries of lectures presented at the colloquium "Self Defense of Plants: Induction and Signaling Pathways." The presentations focused on the signaling molecules that govern known plant defensive responses and the intracellular and extracellular events associated with the various strategies of plant defense against pathogens and herbivores. The isolation of several resistance genes was reported. The characteristics of the deduced gene products suggest that many if not most of the resistance genes code for components of signaling pathways. Signaling systems that involve interactions between plants and their predators were also reported that provide new opportunities for fundamental and applied approaches to the understanding of self-defense mechanisms in plants. The positive response of those invited was impressive. The contributions of the speakers were well received, with lively comments and discussions by the audience of more than 100 scientists. The professional and personal attention of Carrie Huntley and Norman Lawson of the staff of the Beckman Center provided an environment for the meeting that was exceptional. We thank Jack Halpern and the colloquium selection committee of the Academy for providing the opportunity for this colloquium and the National Academy of Sciences for financial support. We are indebted to Kenneth R. Fulton for his gracious help in all phases of the planning, to Frances R. Zwanzig and her staff of the Proceedings Office for their efforts in publishing the colloquium papers, and to Karen Maartens of Washington State University for her efforts in coordinating the conference details.

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