LETTER TO THE EDITOR

Two Classes of Plant Antibiotics: Phytoalexins versus "Phytoanticipins"

Higher plants can produce a great diversity of chemicals that have antimicrobial activity in vitro. The group of plant-formed antibiotics that has probably received the greatest amount of attention is the phytoalexins, a term originally coined by K.O. Müller for those plant antibiotics that are synthesized de novo after the plant tissue is exposed to microbial infection (Müller and Börger, 1940). Müller's definition required that, to be considered a phytoalexin, an antimicrobial compound could not be preformed in the tissue or released from preexisting plant constituents (Müller and Börger, 1940; Müller, 1958). Thus, in contemporary terms, these antibiotics are produced in response to a microbial elicitor, and their production requires the expenditure of plant energy, generally in the form of new transcriptional and/or translational activity.

Another requirement of Müller's original definition was that to be called a phytoalexin, the antimicrobial compound must function as the basis of a disease resistance mechanism. Although disease resistance has been the assumed function of all plant antibiotics, it has been difficult to verify this function experimentally for any plant constituent with in vitro antimicrobial activity. Numerous redefinitions of phytoalexins have been proposed to resolve this and other perceived difficulties with the original definition (c.f. Ingham, 1973). In 1980, at a NATO Advanced Study Institute meeting on "Active Defense Mechanisms in Plants," a new working definition was arrived at by consensus that now appears to have gained general acceptance: "phytoalexins are low molecular weight, antimicrobial compounds that are both synthesized by and accumulated in plants after exposure to microorganisms" (Paxton, 1980, 1981). This definition essentially defined the group of compounds being called phytoalexins in 1980, but very importantly this definition avoided assigning the compounds a role in disease resistance.

Excluded from the above definition are those antibiotic compounds that are present in plant tissue prior to microbial infection and those that are produced from preformed constituents during infection. Although there have been previous proposals for names and definitions of antibiotic compounds that are produced as part of normal plant development (c.f. Ingham, 1973), none has become established. In addition, these definitions have often been hindered by the same problem that plagued the original phytoalexin definition—that is, the requirement that the compounds function as the basis of a disease resistance mechanism was incorporated into the definition. In the absence of an alternative name, there has been an increasing tendency to refer to all plant antibiotics as phytoalexins.

To counter this tendency and preserve the term phytoalexin for what we perceive as its more limited meaning, we propose a new name and definition for preformed plant antibiotics. This name and definition were conceived at a symposium on "Phytoalexin Hypothesis and Beyond" held in Dannenfels, Germany, to honor the 50-year anniversary of the phytoalexin concept. It was proposed that these compounds be known as phytoanticipins (name coined by J.W. Mansfield), with the following definition: "phytoanticipins are low molecular weight, antimicrobial compounds that are present in plants before challenge by microorganisms or are produced after infection solely from preexisting constituents." This definition is intended to parallel that proposed by the NATO group for phytoalexins and, like that definition, can be applied to compounds that have not yet been demonstrated to function as part of a defense mechanism. Thus, it may eventually be shown that, like phytoalexins, some phytoanticipins play a role in disease resistance whereas others do not.

It is important to point out that the distinction between a phytoalexin and a phytoanticipin is not based on its chemical structure but rather on how it is produced. Thus, the same chemical may serve as both a phytoalexin and a phytoanticipin, even in the same plant. For example, in the roots of red clover, the antimicrobial isoflavonoid derivative maackiain is present as the aglycone of a preformed glucoside and is released from injured plant tissue by the action of a preformed plant glucosidase during tissue decompartmentalization (Bredenberg and Hietala, 1961; McMurchy and Higgins, 1984). In this case, maackiain would be classified as a phytoanticipin. However, maackiain can also be synthesized de novo in this plant in response to microbial infection or other elicitors (Higgins and Smith, 1972; Dewick, 1975), making it, in this case, a phytoalexin.

Distinguishing plant antibiotics based on how they are produced may seem arbitrary, but this distinction is based on fundamental differences in the responses of plants to plant-associated microorganisms. For a phytoalexin to serve as the basis of a disease resistance mechanism, there must be an active response on the plant's part, in which communication between plant and microorganism redirects the plant's metabolic activity. However, for a phytoanticipin to serve as the basis of a resistance mechanism, the plant relies on preformed compounds and can be passive in its interaction with a potential pathogen. We hope that our proposed classification of

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plant antibiotics into these two classes will be helpful as we continue to define the role(s) these compounds play in the resistance of plants to microbial invasion.

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REFERENCES

Bredenberg J.B.-S., and Hietala, P.K. (1961). Confirmation of the structure of trifolirhizin. Acta Chem. Scand. **15,** 936–937.

Dewick, P.M. (1975). Pterocarpan biosynthesis: Chalcone and isoflavone precursors of demethylhomopterocarpin and maackiain in *Trifolium pratense*. Phytochemistry **14,** 979–982.

Higgins, V.J., and Smith, D.G. (1972). Separation and identification of two pterocarpanoid phytoalexins produced by red clover leaves. Phytopathology **62,** 235–238.

Ingham, J.L. (1973). Disease resistance in higher plants. The concept of pre-infectional and post-infectional resistance. Phytopathol. Z. **78,** 314–335.

McMurchy, R.A., and Higgins, V.J. (1984). Trifolirhizin and maackiain in red clover: Changes in *Fusarium roseum* "Avenaceum"-infected roots and *in vitro* effects on the pathogen. Physiol. Plant Pathol. **25,** 229–238.

Müller, K.O. (1958). Studies on phytoalexins. I. The formation and the immunological significance of phytoalexin produced by *Phaseolus vulgaris* in response to infections with *Sclerotinia fructicola* and *Phytophthora infestans*. Aust. J. Biol. Sci. **11,** 275–300.

Müller, K.O., and Börger, H. (1940). Experimentelle untersuchungen über die *Phytophthora*-resistenz der kartoffel. Arb. Biol. Reichsasnstalt. Landw. Forstw. Berlin **23,** 189–231.

Paxton, J.D. (1980). A new working definition of the term "phytoalexin." Plant Disease **64,** 734.

Paxton, J.D. (1981). Phytoalexins—a working redefinition. Phytopathol. Z. **101,** 106–109.