

CURRENT OPINION IN CHEMICAL ECOLOGY

Phytochemicals Link Heaven and Earth: Induced Plant Responses Mediating Interactions Between Root and Shoot Herbivores

Although mankind may like to think that plants produce phytochemicals mainly for human benefit, one of the primary roles of these so-called secondary metabolites is to defend their producers against attacks of herbivores, pathogens and other phytophages (Fraenkel, 1959; Harborne, 1989). Many plants indeed increase the production of defensive compounds in response to phytophage attack (Karban and Baldwin, 1997; Agrawal et al., 1999). These induced defenses can directly affect phytophage by increasing their mortality or decreasing their growth rates (van Dam et al., 2000; van Dam et al., 2001). Additionally, attacked plants may produce indirect defenses, such as volatile compounds or extra-floral nectar. Indirect defenses attract predators or parasitoids to the damaged plant, which increases the probability that the phytophages are found and consumed by their natural enemies (Dicke and Sabelis, 1988; Wäckers and Wunderlin, 1999). Eventually, the plant may benefit from both direct and indirect induced responses if they decrease loss of biomass and increase net seed production (fitness) compared to plants that do not induce their defenses.

So far, the chemical-ecological aspects of induced responses in plants have been studied almost exclusively on above-ground phytophages and their natural enemies. There is, however, ample evidence that root phytophages, such as nematodes, bacteria, fungi or arthropods, also induce defensive plant responses. Similar to their aboveground counterparts, root-induced responses may also affect root phytophages and their soil-dwelling natural enemies (van Tol et al., 2001; van Dam et al., 2002). Both root and shoot phytophages may

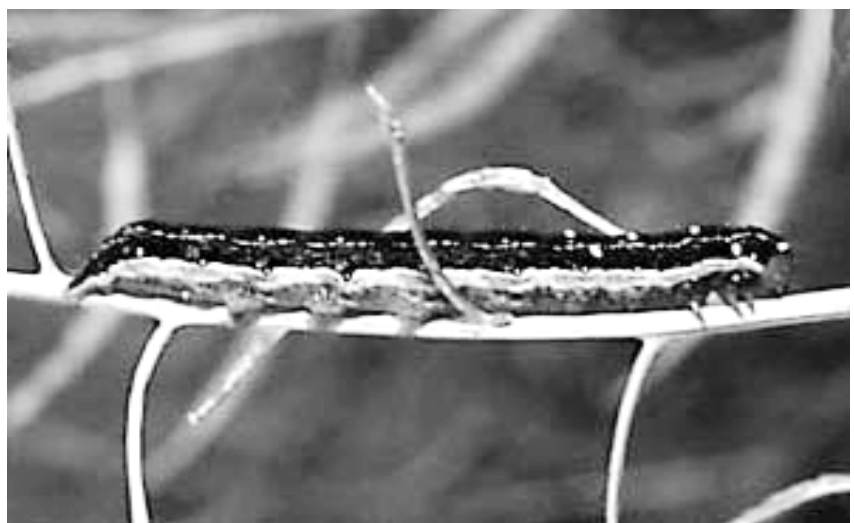
elicit systemic responses if the signaling compounds that are produced are transported throughout the entire plant and alter chemical profiles of undamaged organs (Karban and Baldwin, 1997; Agrawal et al., 1999). Thus, by inducing the plant's defensive responses, root feeders may alter host quality for shoot herbivores, and vice versa. Eventually, such interactions may affect the performance of above-ground (AG) and below-ground (BG) phytophages - and their natural enemies - and consequently, the eventual amount of damage the plant will suffer.

Because there are no explicit studies yet on how inducible compounds mediate interactions between AG and BG phytophages, I can only support the idea that they do by combining separate studies on shoot or root induction processes. As an example, I will use the induction of glucosinolates in the Brassicaceae. Glucosinolates are a very diverse class of plant compounds known to deter feeding by generalist insect herbivores, pathogens and nematodes

(Fahey et al., 2001). When plant cells are ruptured, the glucosinolates that are stored in the vacuoles are metabolized by the enzyme myrosinase that is stored in specialized storage cells. This enzymatic reaction yields toxic products such as isothiocyanates and nitriles, that are even more potent feeding deterrents against a wide range of phytophages (Brown and Morra, 1997; Rask et al., 2000). Both myrosinase and glucosinolate levels increase systemically after herbivore feeding, pathogen infection or after application of induction hormones such as jasmonic acid and salicylic acid (Bodnaryk, 1994; Ludwig-Müller et al., 1997).

The different types of glucosinolates are known to differ in induction profiles and biological activities. Here I will focus on the role of 2-phenylethyl glucosinolate (nasturtiin) which is found in the roots and shoots of several economically important *Brassica* species (Kiddle et al., 1994; Ludwig-Müller et al., 1997).

continued on page 10



The Bertha Armyworm causes severe damage to canola and other crops

continued from page 9

Nasturtiin and its breakdown products are known to be nematicidal, fungitoxic and inhibit microbial growth (Potter et al., 1999). Shoot treatment with jasmonic acid - which is widely used to mimic induced responses after insect feeding - also increased root levels of nasturtiin (Ludwig-Müller et al., 1997). This indicates that shoot herbivores may very well alter the suitability of the roots as food for nematodes feeding on the same plant. Whether the reverse is true so far remains unexplored, but studies with nematodes on cultured tobacco have shown that nematode feeding indeed may increase shoot levels of defensive phytochemicals, such as nicotine (Davis and Rich, 1987). If nematodes indeed increase shoot glucosinolate levels, this may even affect above-ground natural enemies of specialist herbivores on Brassica plants that use these compounds for their own defense (Müller et al., 2001). If these specialist herbivores, that are not deterred by the induction of glucosinolates, become more resistant to their own enemies, inducing plants may eventually suffer more damage than non-inducing plants.

The above example, and a few

other examples of well-studied biologically active phytochemicals (van Dam et al., 2002) show that there is a significant potential for induced responses to mediate interactions between above- and belowground phytophages and their natural enemies. This awareness will not only change our views on which natural selection pressures have played a role in the evolution of induced chemical defenses in plants, but also will have consequences for the application of induction hormones for 'plant immunization' in agricultural systems. Therefore, it is about time that those studying induced responses 'go underground' to include root-induction processes and their interactions with shoot-induced responses in their studies. This is publication 2948 NIOO-KNAW Centre for Terrestrial Ecology, Heteren, The Netherlands

Agrawal AA, Tuzun S and Bent E (1999) Induced plant defenses against pathogens and herbivores. APS Press, St. Paul, Minnesota
Bodnaryk RP (1994) *Phytochemistry* 35:301-305
Brown PD and Morra MJ (1997) *Adv Agronomy* 61:167-231
Davis EL and Rich JR (1987) *J Nematol* 19:23-29

Dicke M and Sabelis MW (1988) *Funct Ecol* 2:131-139
Fahey JW, Zalcman AT and Talalay P (2001) *Phytochemistry* 56:5-51
Fraenkel, GS (1959) *Science* 129:1466-1470
Harborne JB (1989) *Introduction to ecological biochemistry*. Third edn. Academic Press, London
Karban R and Baldwin IT (1997) *Induced responses to herbivory*. University of Chicago Press, Chicago, Illinois, USA
Kiddle GA, Doughty KJ and Wallsgrove RM (1994) *J Exp Bot* 45:1343-1346
Ludwig-Müller J, Schubert B, Pieper K, Ihmig S and Hilgenberg W (1997) *Phytochemistry* 44:407-417
Müller C, Agerbirk N, Olsen CE, Boevé JL, Schaffner U and Brakefield PM (2001) *J Chem Ecol* 27:2505-2516
Potter MJ, Vanstone VA, Davies KA, Kirkegaard JA and Rathjen AJ (1999) *J Nematol* 31:291-298
Rask L, Andréasson E, Ekbom B, Eriksson S, Pontoppidan B and Meijer J (2000) *Plant Mol Biol* 42:93-113
van Dam N, Harvey J, Wäckers F, Bezemer T, van der Putten W and Vet L (2002) *Basic Appl Ecol* (in press)
van Dam NM, Hadwich K and Baldwin IT (2000) *Oecologia* 122:371-379
van Dam NM, Hermenau U and Baldwin IT (2001) *Ecol Entomol* 26:578-586
van Tol RWHM, van der Sommen ATC, Boff MIC, van Bezooijen J, Sabelis MW and Smits PH (2001) *Ecol Lett* 4:292-294
Wäckers FL and Wunderlin R (1999) *Entomol Exper Appl* 91:149-154

Nicole M. van Dam
Netherlands Institute of Ecology
The Netherlands
dam@cto.nioo.knaw.nl



A parasitic wasp laying eggs on a canola leaf