



The smartest plant?

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Received: 19 November 2022 / Accepted: 21 December 2022
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Keywords Rapeseed · Broomrape · Soil microbiota · Isothiocyanate · Pesticide treadmill

Plants perceive and have the capacity to adaptively respond to environmental signals, both aboveground and belowground. Early on Charles Darwin (1880) acknowledged this capacity to respond to belowground signals when he wrote “The tip of the root having the power of redirecting the movements of the adjoining parts acts like the brain of one of the lower animals receiving the impressions of sense organs and directing the several movements”. It is clear then that questions of plant intelligence should find their place in Plant and Soil.

However, not all plant signalling belowground seems *prima facie* adaptive. Most plants exude through their roots compounds that act as germination stimulants for parasitic plants of the Orobanchaceae. This behaviour seems suicidal rather than intelligent. This riddle (why do plants behave suicidally?) was solved when Akiyama et al. (2005) reported that these compounds, known as strigolactones, induce hyphal branching in an arbuscular mycorrhizal (AM) fungus, and subsequent work by Besserer et al. (2006)

showed that a synthetic strigolactone stimulated spore germination in two other species of AM fungi. This interplay between plants and their mutualistic fungi is crucial for plant fitness. Orobanchaceae, therefore, have been able to hijack this very old communication system between plants and their belowground friends, to the detriment of some plants, wreaking havoc in cropping systems, especially under nutrient-poor conditions. The capacity to use strigolactones as germination stimulant implies, inevitably it seems, that plants that do not release these strigolactones in the rhizosphere, such as the non-mycorrhizal Brassicaceae (Auger et al. 2012), would escape from parasite infestation. However, the parasitic *Phelipanche ramosa* (L.) Pomel has been reported from brassicaceous hosts where it causes major losses in rapeseed (*Brassica napus* L.). Currently, the problem seems restricted to France, but with the increasing importance of rapeseed oil as a sustainable biodiesel source, it is likely that the parasite will spread. It is not clear when this ability to attack non-mycorrhizal plants evolved; however, widespread damage in rapeseed has only been reported during the last 30 years.

Phelipanche ramosa consists of two interfertile genetic groups, with a further subdivision of group 2 in two subclades (Stojanova et al. 2019). Members of both groups 2a and 2b have a broad host range, including rapeseed, hemp (*Cannabis sativa* L.), tobacco (*Nicotiana tabacum* L.), and tomato (*Solanum lycopersicum* L.). Members of group 1 also have a broad host range, including rapeseed, weeds in

Responsible Editor: Hans Lambers.

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rapeseed cropping systems, tobacco, sunflower (*Helianthus annuus* L.) and melon (*Cucumis melo* L.), but have not been recorded from hemp. Only members of group 1 have a high germination success with rapeseed. Apparently, this genetic group has retained the ability to respond to strigolactones, but it also evolved the ability to respond to other germination stimulants, more specifically isothiocyanates, through the same receptor, the KAI2 protein, that perceives strigolactones (De Saint Germain et al. 2021). These isothiocyanates, coming from the degradation of glucosinolates in planta and in the soil, are highly toxic to several soil organisms, including AM fungi. In the soil. This transformation is caused by a number of microorganisms that produce the enzyme myrosinase. This transformation has been considered beneficial as the production of isothiocyanates contributes to biological control of several soil-borne pathogens and weeds (Gimsing and Kirkegaard 2009), while also inhibiting AM fungi (Lankau et al. 2011).

In this issue of Plant and Soil, Martinez et al. (2023) report a number of elegant assays that demonstrate that this microbial conversion of glucosinolates to isothiocyanates stimulates germination of *P. ramosa*. They first characterised, through metabarcoding, bacteria and fungi occurring in rapeseed fields that were infested by *P. ramosa*. They then tested the effects of these microbial assemblages on seed germination of *P. ramosa* and observed that germination was much faster in the presence of these assemblages than in soil extracts with a 0.22 µm filter that effectively should have eliminated these microbes. Not only was seed germination affected, but there was a carry-over effect on subsequent attachment on rapeseed roots. An additional soil microbial effect on haustorium-inducing compounds might have been important as well. A direct germination test in 96-well plates indicated no germination of *P. ramosa* seeds with soil extracts; however, if gluconasturtiin (the main glucosinolate of rapeseed) was added to soil extracts, germination was very high, whereas addition of only gluconasturtiin did not result in seed germination of *P. ramosa*. The best explanation for this effect is that it is the microbial conversion of gluconasturtiin by soil microbes into isothiocyanates that causes successful germination. Based on the results of metabarcoding and subsequent isolation of some fungal and bacterial strains, Martinez et al.

(2023) suggest a number of candidate species that are responsible for the conversion of gluconasturtiin into isothiocyanates.

Genetic group 1 of *P. ramosa* can benefit from plants that form AM symbioses by responding to strigolactones, and its simultaneous response to glucosinolates allows it to extend its parasitic portfolio outside these AM plants. And where AM fungi protect AM plants against parasites of the Orobanchaceae by downregulating strigolactone exudation upon successful colonization, the microbiota in the agro-ecosystems with rapeseed even enhance the parasitic behavior by *P. ramosa*. Through that latter mechanism, this smart plant has the potential to create positive feedbacks between rapeseed monocropping, stimulation of myrosinase-producing microbes, and seed germination of *P. ramosa*, thereby bringing bad news for sustainable oilseed production. Martinez et al. (2023) write: “To a larger extent, these microbial driving forces, as well as rapeseed cropping intensification, may eventually contribute to host specialization of *P. ramosa* on *B. napus* in western France. These findings also disclose a dilemma for Brassicaceae cropping in an agroecological context. Indeed, although isothiocyanates act as biofumigants and suppress soil-borne pathogens, Brassicaceae are likely to promote broomrape infestation and suppress mutualist symbiosis for the next crop.”

If members of the Brassicaceae likely increase broomrape infestation, this cropping system may well become an example of a further pesticide treadmill (Bakker et al. 2020). Fighting *P. ramosa* likely needs herbicides as the use of microbes to kill *P. ramosa* seeds is likely insufficiently effective. And because rapeseed would also be sensitive to these herbicides, this practice would then demand genetically-modified rapeseed that is herbicide-resistant. This would not only increase selection pressure towards herbicide resistance in *P. ramosa*, but the use of such genetically-modified races of rapeseed would also create a lock in (Vanloqueren and Baret 2009), as escape from continuous monocropping of rapeseed would become increasingly unlikely. From that perspective this smart plant, which benefits not only from the need of plants to communicate with AM fungi, but also from the toxic substances generated by non-mycorrhizal plants, tells us a clear lesson that we need much smarter cropping systems.

Acknowledgements I am grateful to Hans Lambers for his invitation to provide a commentary on this paper, and for conversations about smart arbuscular mycorrhizal fungi and plants.

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