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Bouwmeester, H.

DOI
10.1126/science.aav8482
Publication date
2018
Document Version
Final published version
Published in
Science

Link to publication

Citation for published version (APA):
Bouwmeester, H. (2018). Can witchweed be wiped out? *Science*, *362*(6420), 1248-1249. https://doi.org/10.1126/science.aav8482

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AGRICULTURE

Can witchweed be wiped out?

A potent stimulant induces parasitic plant germination that causes it to die

By **Harro Bouwmeester**

Root parasitic weeds of the *Orobanchaceae* such as broomrapes and witchweeds form a serious threat to agriculture in many countries around the world (*1*). They cause large yield losses in crops such as sorghum, millet, maize, rapeseed, tomato, sunflower, and legumes (*1*). These obligate parasitic plants are dependent on a host for survival, using them to grow and reproduce on. Therefore, they only germinate in the presence of a germination stimulant exuded by the host root (*2*). On page 1301 of this issue, Uraguchi *et al.* (*3*) reveal the discovery of a potent synthetic germination stimulant. Their discovery provides the basis for the development of an agrochemical that may be used to germinate parasitic weeds in the absence of a host (so that they will die, called suicide germination) and gives insight into what may be determining host specificity of these parasites.

"...SPL7 can induce suicidal germination of Striga in soil and thus reduces Striga infection of maize..."

The tight control of germination of these root parasitic plants is caused by their ability to respond to germination stimulants (*4*). These are secreted by the roots of host plants and induce seed germination. Although several compounds, from different chemical classes, in the root exudate have been identified as germination stimulants, the most important class is the strigolactones (*5*) (see the figure). The first discovered strigolactone, strigol, was isolated from the root exudate of cotton and induced germination of the root parasitic plant *Striga*

Swammerdam Institute for Life Sciences (SILS), University of Amsterdam, Science Park 904, 1098 XH Amsterdam, Netherlands. Email: h.j.bouwmeester@uva.nl

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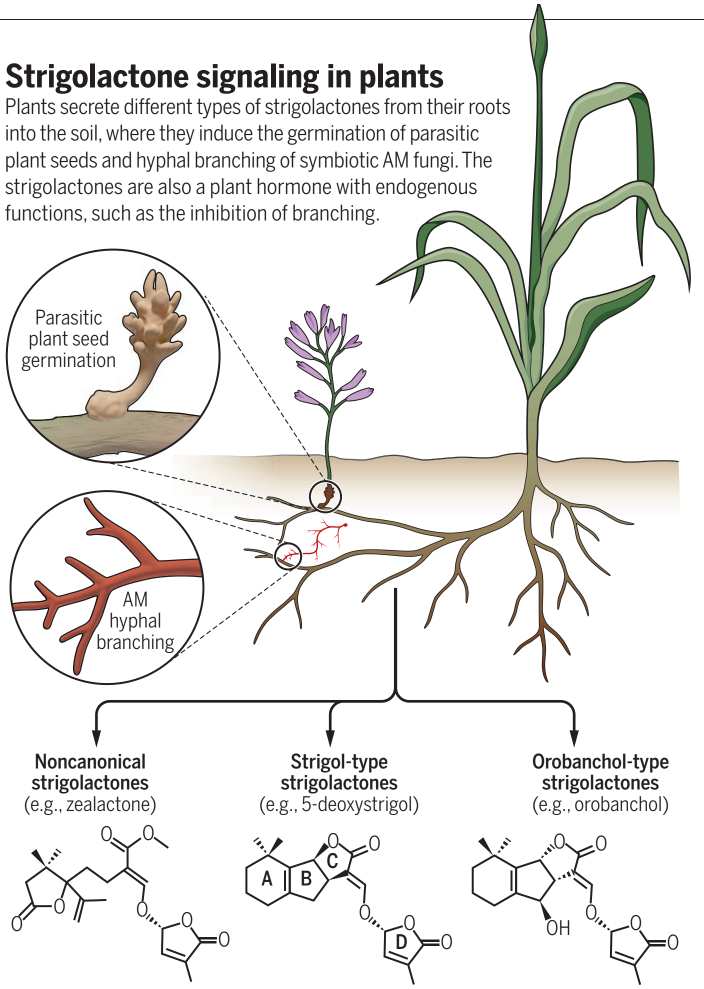
Strigolactone signaling in plants

Plants secrete different types of strigolactones from their roots into the soil, where they induce the germination of parasitic plant seeds and hyphal branching of symbiotic AM fungi. The strigolactones are also a plant hormone with endogenous functions, such as the inhibition of branching.



lutea (6). At least 25 other strigolactones have been identified in root exudates of different plant species and shown to be germination stimulants of root parasitic *Striga*, *Orobanche*, *Alectra*, and *Phelipanche* spp. (5, 7).

It took more than 50 years to answer why plants are producing and secreting strigolactones (obviously not to induce germination of parasitic plant seed). In 2005, it was reported that strigolactones induce hyphal branching in arbuscular mycorrhizal (AM) fungi (8). AM fungi engage in a symbiotic interaction in the roots of most land plants: They supply water and nutrients in return for assimilates produced from photosynthesis. Later, it was discovered that the strigolactones are also a plant hormone that regulate plant branching (9, 10). Further studies discovered that strigolactones also regulate other aspects of plant development, including root architecture and leaf senescence (4).

Since these discoveries, strigolactone biosynthesis was partially elucidated (11)—although our knowledge is far from complete (5). Strigolactone perception was also investigated, including the discovery of the strigolactone receptor, D14 (12). In the root parasitic broomrapes and witchweeds, however, a receptor homologous to D14, HYPOSENSITIVE TO LIGHT (HTL), was shown to have duplicated and evolved new ligand binding specificity, allowing these parasites to germinate upon perception of strigolactones secreted by their host (13, 14). Intriguingly, the exact role and ligand of HTL in other, nonparasitic plants remains elusive (12).

Uraguchi *et al.* used *Striga hermonthica* (witchweed) HTL, ShHTL7, as a sensitive biosensor for germination stimulants. In a chemical screen using *Striga* germination as a readout, they identified a molecule that had considerable potency. Serendipitously, most of the activity was due to the presence of a synthetic impurity, which had the classical D-ring that is also present in all strigolactones (see the figure). Upon further optimization of this molecule, the authors generated sphynolactone-7 (SPL7), a molecule with an affinity for ShHTL7 that is comparable with the affinity of the most potent natural strigolactone known, 5-deoxystrigol. However, intriguingly, experiments in which amino acids outside the ligand binding pocket of ShHTL7 were mutated suggest that the interaction of SPL7 with ShHTL7 involves different amino acids than for 5-deoxystrigol. Although the authors do not show what the mechanism underlying this difference is, it is now clear that amino acids outside the ligand binding pocket are important in ligand specificity. This will help direct investigations into the causes of strigolactone specificity in these parasites.

This result was further underpinned with experiments in which the effect of SPL7 was compared with that of GR24 (a synthetic strigolactone with a similar D-ring as that of SPL7). SPL7 did not have the hormonal effect that GR24 has—for example, in inhibiting shoot branching or inducing root hair elongation in *Arabidopsis thaliana*. SPL7 also hardly affected AM fungi hyphal branching, in contrast to GR24. This suggests that through the structure of the rest of the molecule SPL7 has a high affinity for ShHTL7, whereas its affinity for other strigolactone receptors, such as D14 in *A. thaliana* and the as yet unknown receptor in AM fungi, is very low. Last, the authors showed that SPL7 can induce suicidal germination of *Striga* in soil and thus reduces *Striga* infection of maize that is sown afterward.

The work of Uraguchi *et al.* confirms the crucial importance of the D-ring for the biological activity of the strigolactones. Importantly, the authors touched on a phenomenon so far hardly addressed in the field: Does specificity in germination contribute to target host specificity (5)? A number of *S. hermonthica* hosts produce quite different strigolactones (5, 7). Sorghum produces mainly strigol-type strigolactones, such as the 5-deoxystrigol that was also used by Uraguchi *et al.* (3, 5, 7). Millet produces mainly orobanchol-type strigolactones, whereas maize produces noncanonical strigolactones (5, 7). Yet, all three are severely infected by *S. hermonthica*, albeit by different strains. Whether selectivity to the strigolactones produced by these hosts plays a role in this strain preference, and whether ligand specificity of the different ShHTLs is important, is a conundrum.

SPL7 is an interesting lead for the development of suicide germination stimulants that could be used to clear fields from *Striga*, before a crop is planted. There are, however, several challenges that need to be overcome. For application in the African continent, the molecules must be extremely cheap, if not free. In addition, the application on a field and sufficient penetration into the soil will probably need large amounts of water (15). Clearly, a lot of research is still needed to bring this finding to the field. However, the study of Uraguchi *et al.* may lead to new approaches, such as engineering of the strigolactone profile of the crops, which could also result in solutions for this tremendous agricultural problem that causes hardship for millions of African farmers. ■

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10.1126/science.aav8482

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