Strigolactones: A Cry for Help Results in Fatal Attraction. Is Escape Possible?

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Abstract

During evolution, plants have adapted an ecological balance with their associates, competitors, predators, and pests. Keeping this balance intact is an active process during which the plant needs to respond to many different stimuli in order to survive.

For example, plants have developed an array of physiological and biochemical responses to phosphate deprivation. One of these responses is the production of isoprenoid-derived molecules called strigolactones. Strigolactones are used to stimulate the formation of symbiotic associations

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of plant roots with arbuscular mycorrhizal (AM) fungi. AM fungi colonize the root cortex to obtain carbon from their host while assisting the plant in phosphate acquisition. However, strigolactones also stimulate the germination of root parasitic plant seeds. Only upon perception of the presence of a host through its strigolactone production, seeds of the parasites germinate and attach to the roots of many plant species. In contrast to a mutual symbiotic relationship, where both partners benefit from the affiliation through an exchange of resources, the host is heavily exploited by a parasitic plant and suffers strongly from the interaction because it is robbed from its assimilates, water, and nutrients.

In this chapter, we focus on the knowledge about the biosynthetic origin of the strigolactones, their ecological significance, and physiological and biochemical regulation. We finally point at recent scientific developments which may explain why a nonmycorrhized plant like Arabidopsis is still producing strigolactones.

Keywords

Strigolactones • Germination stimulants • Parasitic plants • Arbuscular mycorrhiza • Phosphate starvation • Hormones • Shoot branching

14.1 Introduction

Plants produce a large variety of chemicals for which no role has yet been found in growth, photosynthesis, reproduction, or other "primary" functions. These chemicals are generally called secondary metabolites. It has been estimated that 15–25% of plant genes are dedicated to plant secondary metabolism (Pichersky and Gang 2000). The chemical structures of secondary metabolites are extremely diverse; many thousands have been identified and can be subdivided in several major classes. One of those classes is represented by the terpenoids, an abundant and structurally diverse group consisting of more than 40,000 different chemical structures. They are of great importance to plants because of their multitude of functions in signaling and defense, and they enable plants to communicate with their environment.

Terpenoid secondary metabolites occur across a wide range of plant tissue types and are often emitted at particular times or under specific conditions related to their function. In the rhizosphere, plants secrete terpenoid-derived molecules, the so-called strigolactones, from their roots to establish a symbiotic relationship with the arbuscular mycorrhizal fungi such as *Gigaspora* and *Glomus* spp. However, unfortunately for the host plant, these molecules are also recognized by the seeds of root parasitic plants. In this case, strigolactone perception triggers germination of the parasitic plant seeds hereby ensuring the close vicinity of a host plant which is a prerequisite for survival of the parasitic plant seedlings.

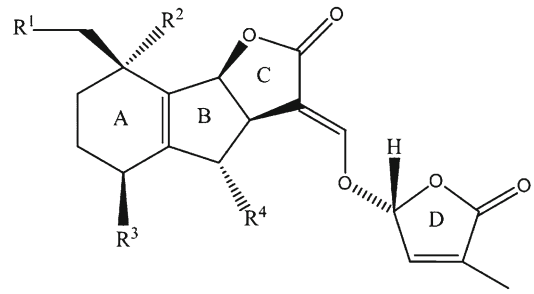
14.2 Parasitic Plants

Root parasitic plants such as *Orobanche* and *Striga* spp. derive all or most of their sustenance from the host plant. They are geographically widespread, occupying all major ecosystems on the planet (Press and Graves 1995). In some species of parasitic plants, the ability to obtain sugars from a host is believed to have led to decreased selection pressure on retaining a functional photosynthetic apparatus. This is reflected in reduced ability to photosynthesize, alterations to

the structure of the plastid genome (Revill et al. 2005), or even complete disappearance of chlorophyll, for example, in the *Orobanchaceae*. Although the evolution of parasitism seems to require complex metabolic, developmental, and anatomical adaptations, parasitism has evolved independently at least ten times within the angiosperms and is found in approximately 4,000 plant species among 22 families (Nickrent et al. 1998).

Some parasitic plants, particularly those in the Scrophulariaceae, are economically important weeds, causing dramatic losses in crop yield (Stewart and Press 1990; Parker and Riches 1993). The hemiparasitic *Striga* spp. infects important crops such as maize, sorghum, pearl millet, finger millet, and upland rice, causing devastating losses in cereal yields in sub-Saharan Africa and, therefore, obstructing food supply in many developing countries (Joel 2000; Scholes and Press 2008). Several of the holoparasitic *Orobanche* spp. are the most damaging parasitic weeds in Mediterranean areas and Central Asia, parasitizing important agricultural crops such as legumes, crucifers, tomato, sunflower, hemp, and tobacco (Joel 2000; Press et al. 2001; Shen et al. 2006; Yoneyama et al. 2010).

All parasitic plants penetrate the tissue of their host, subsequently develop feeding structures known as haustoria that allow rapid removal of solutes (Hibberd and Jeschke 2001; Seel and Jeschke 1999). However, species differ in the type and amount of solutes that they remove. Some, such as *Striga,* feed on the host xylem (Dörr 1996), while others, for example, members of *Cuscuta* and *Orobanche*, are highly specialized phloem feeders (Jeschke et al. 1994; Hibberd et al. 1999). Upon vascular connection, the parasitic plants continue to develop, emerge from the soil, flower, and finally set seed. The seeds of the parasitic plants are tiny and contain few nutrient reserves. After germination, they must attach to a host root within days or they will die. To prevent the seeds from germinating too far from the host, these parasites have evolved a mechanism by which parasitic plant seeds only germinate upon perception of a specific germination stimulatory signal produced by the root of the host plant.



$R^1 = R^3 = R^4 = H$, $R^2 = CH_3$: 5-Deoxystrigol;
$R^1 = R^4 = H$, $R^2 = CH_3$, $R^3 = OH$: Strigol;
$R^1 = R^3 = H$, $R^2 = CH_3$, $R^4 = OH$: Orobanchol;
$R^1 = R^3 = H$, $R^2 = CH_3$, $R^4 = OAc$: Orobanchyl acetate;
$R^1 = R^2 = R^3 = R^4 = H$: Sorgolactone;
$R^3 = R^4 = H$, $R^2 = CH_3$, $R^1 = OH$: Sorgomol;

Fig. 14.1 Common structure of strigolactones. The strigolactone backbone is decorated with various side groups (R) that are characteristic for the different strigolactones

14.3 Strigolactones Are Germination Stimulants for Parasitic Plants

Germination stimulants are secreted by the roots of the host plant in very low amounts. Several different strigolactones have been detected in the root exudates of a wide range of plant species, including mono- and dicotyledonous plants. Even different cultivars of one crop species may produce different strigolactones and/or mixtures (Bouwmeester et al. 2007; Yoneyama et al. 2008). It has been proposed that 5-deoxystrigol, which does not have any hydroxyl substituent, could be the precursor of all the different strigolactones (Rani et al. 2008; Matusova et al. 2005).

The structural core of the strigolactone molecules consists of a tricyclic lactone (ABC part) which connects via an enol ether bridge to a butyrolactone group (the D-ring) (Fig. 14.1). All known strigolactones have one or two methyl substituents on the cyclohexyl A-ring and various combinations of hydroxyl or acetate substituents around the A- and B-rings. The C- and D-rings remain constant, except for the enol ether bridge for which also an *epi* orientation has been reported. It has been suggested that the biological

activity of the strigolactones resides in this enol ether bridge (Magnus and Zwanenburg 1992). According to the putative modifications that could take place in the A- and B-rings, over a hundred strigolactone derivatives can be predicted to exist in the plant kingdom (Rani et al. 2008; Matusova et al. 2005; Yoneyama et al. 2010; Xie et al. 2010).

An interesting question is whether these small changes have an effect on putative receptor binding in the parasitic plant seeds and hence on host-parasite specificity. The recognition of the germination stimulant is a crucial moment in the life cycle of the parasitic plants. Here, a strong selection pressure is present that should ensure that the seeds of the parasites only germinate in the presence of a true host and enabling them to complete their life cycle. Germination experiments with seed batches collected from *S. hermonthica* and *O. ramosa* plants parasitizing several different host species show that the parasites develop a preference for the exudate of the host species they were growing on (Matusova and Bouwmeester 2006).

14.4 Biosynthetic Origin of Strigolactones

The strigolactones were originally identified to be sesquiterpene lactones (Butler 1995; Yokota et al. 1998), but there is also some structural similarity to higher-order terpenoids/isoprenoids such as abscisic acid and other compounds, which are derived from the carotenoid pathway (Parry and Horgan 1992; Tan et al. 1997; Bouwmeester et al. 2003; Matusova et al. 2005; Matusova and Bouwmeester 2006).

To verify the biosynthetic origin of the strigolactones, Matusova et al. (2005) studied the effect of chemicals that affect several different isoprenoid biosynthetic pathways on the production of germination stimulants by the roots of host plants. In parallel to this biochemical approach, several mutants in the predicted biosynthetic pathways were examined for germination stimulant production. The isoprenoid-pathway inhibitors mevastatin (inhibitor of the cytosolic MVA pathway) and fosmidomycin (inhibitor of the plastidic MEP pathway) only had a minor effect on germination stimulant formation, possibly because of the exchange of IPP that has been shown to occur between the two pathways, particularly upon the use of these inhibitors (Hemmerlin et al. 2003). However, the carotenoid pathway inhibitor fluridone reduced maize root-exudate-induced germination by about 80% compared with untreated seedlings, suggesting that the germination stimulants produced by maize are derived from the carotenoid pathway (Matusova et al. 2005). Subsequently, the root exudates of several maize carotenoid mutants *y10, al1, al1y3, vp5,* and *y9* (Fig. 14.2)

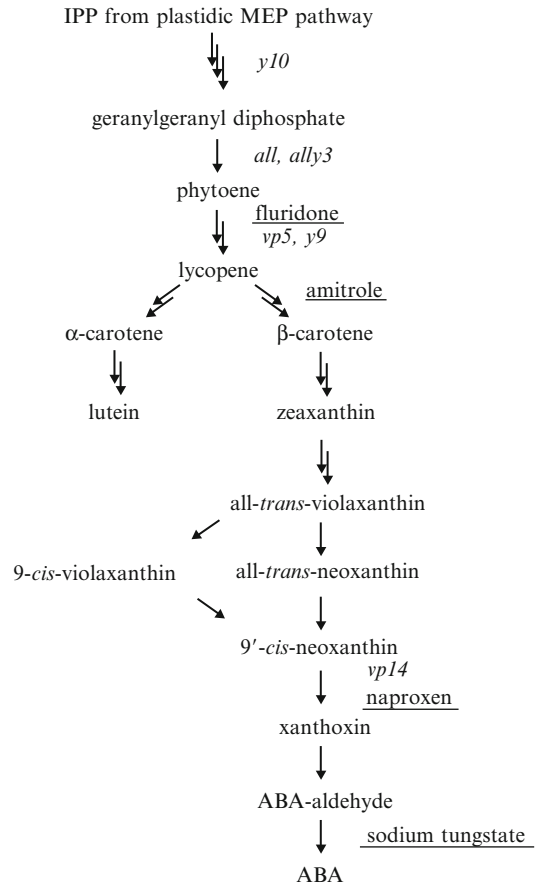


Fig. 14.2 Schematic representation of the carotenoid and abscisic acid biosynthetic pathway. Carotenoids maize mutants (*italics*) and inhibitors (*underlined*) at different steps in the pathway are indicated (From Matusova and Bouwmeester 2006)

were tested for induction of *S. hermonthica* seed germination. The carotenoid biosynthesis inhibitor fluridone blocks the activity of phytoene desaturase, which corresponds to the maize *vp5* locus (Li et al. 1996; Hable et al. 1998). Both fluridone-treated maize and *vp5* mutant root exudates induced significantly lower germination of *S. hermonthica.* In addition to this, also treatment with the herbicide amitrole that blocks lycopene cyclase in maize seedlings (Dalla Vecchia et al. 2001) resulted in lower germination of *S. hermonthica* seeds than induced by control seedlings. The results in germination bioassays with root exudates of amitrole-treated plants suggest that the germination stimulants are derived from the carotenoid pathway below lycopene (Fig. 14.2) (Matusova et al. 2005). Also, the seedlings of all other mutants that were tested induced lower germination of *S. hermonthica* seeds in comparison to their corresponding wild-type siblings (Matusova et al. 2005). The branching point from the carotenoid pathway for strigolactone biosynthesis could not be identified.

Matusova et al. (2005) postulated a hypothetical biosynthetic pathway leading to the formation of all known strigolactones suggesting that they are produced by oxidative cleavage of a carotenoid substrate through the action of a 9-*cis* epoxycarotenoid dioxygenase (NCED) or carotenoid cleavage dioxygenase enzyme (CCD) (Fig. 14.3). The NCED/CCD family is composed of nine different members in Arabidopsis and 12 in rice, and they can be grouped into six different clusters (Bouwmeester et al. 2007). NCEDs are involved in the production of the plant hormone abscisic acid (ABA), which is derived from *cis*-neoxanthin (Taylor et al. 2005). Matusova et al. (2005) and López-Ráez et al. (2008) have shown that the ABA-deficient mutants *viviparous14* (*vp14*) in maize and *notabilis* in tomato, with a null mutation in the genes *ZmNCED* and *LeNCED1,* respectively, induce less germination of parasitic plant seeds of *S. hermonthica* and *O. ramosa*, respectively. Moreover, for tomato it was demonstrated using LC-MS analysis that this reduction in germination stimulatory activity correlates closely with a reduction in the exudation of strigolactones. This shows that either NCED1 is directly involved in strigolactone biosynthesis or exerts a regulatory role on strigolactone production through ABA. In the latter case, the reduced production of strigolactones in the mutants *notabilis* and *vp14* is due to the reduced ABA content observed in these mutant lines. Hence, it is clear that NCED(s) is involved in the biosynthesis of strigolactones, although further research is required to determine whether their involvement in this biosynthetic pathway is direct or indirect (López-Ráez et al. 2008; López-Ráez et al. 2010).

14.5 Strigolactones Are Branching Factors for AM Fungi

A puzzling question that was asked when the strigolactone germination stimulants were first discovered was: why do plants produce these signaling molecules while they induce germination of one of their worst enemies?

The work of Akiyama and coworkers (2005, 2006) shed some light on this aspect when they demonstrated that these secondary metabolites are involved in signaling between plants and the symbiotic arbuscular mycorrhizal (AM) fungi. AM fungi are obligate symbionts that need to grow in association with a host plant to survive and complete their life cycle (Harrison 2005; Paszkowski 2006). Their spores can germinate spontaneously and undergo an initial asymbiotic stage of hyphal growth. If these fungal hyphae do not encounter a symbiotic partner, they will stop growth and retract. When there is a host plant root in the vicinity of the germinating spore, signaling molecules released by the roots into the rhizosphere – shown by Akiyama et al. (2005) to be strigolactones – reach the hyphae, and the fungus responds to this with increased growth and intensive hyphal branching. This intensive branching is expected to increase the probability of the root and fungi to find each other and to establish a symbiosis (Paszkowski 2006; Besserer et al. 2006). Despite this apparently important

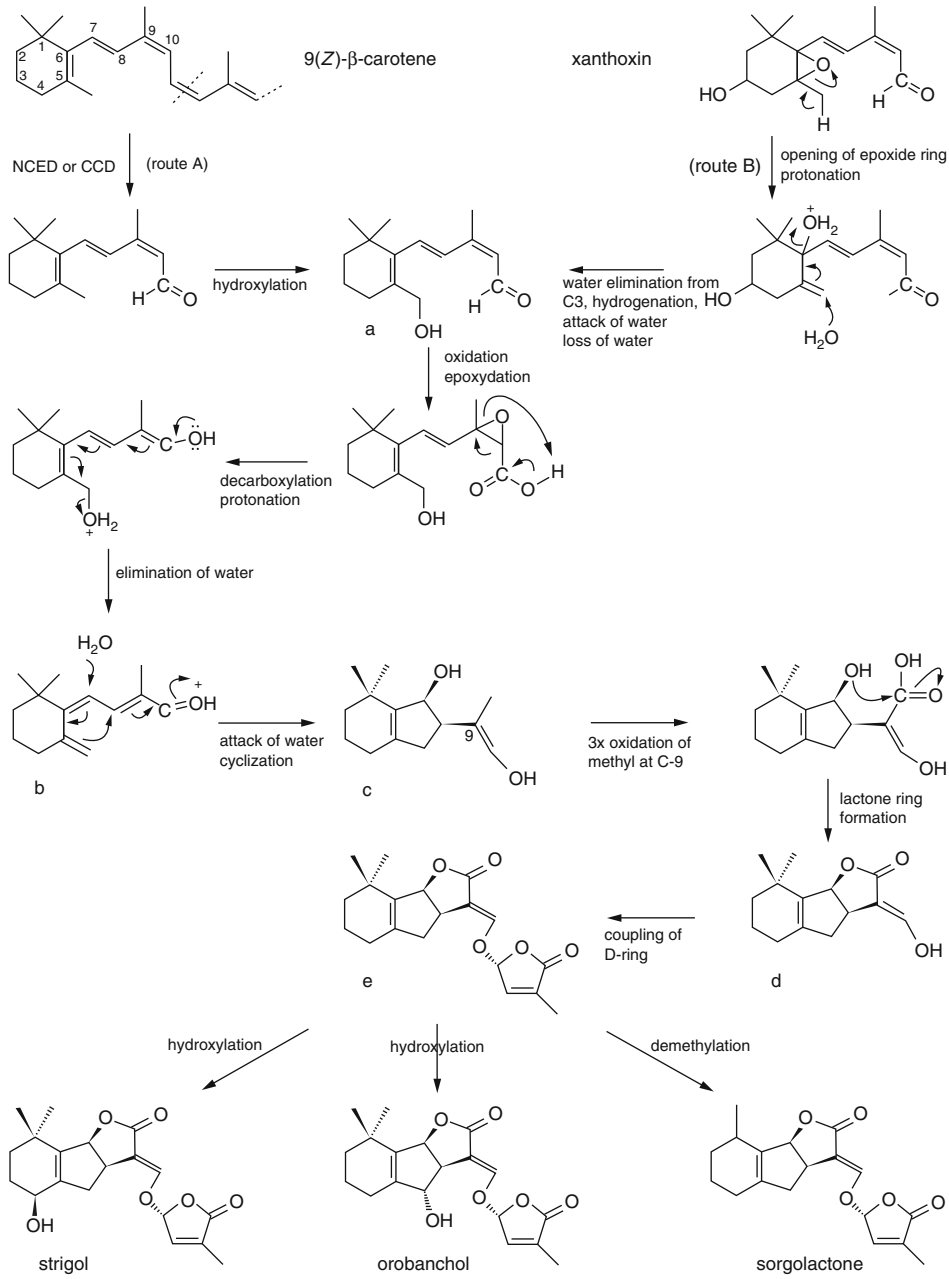


Fig. 14.3 Putative biogenetic scheme for the formation of strigol, orobanchol, and sorgolactone. *CCD* carotenoid cleavage dioxygenase (From Matusova et al. 2005)

function, it is not yet fully understood how essential strigolactones are for the establishment of the symbiosis and/or whether they also play a role in subsequent steps of the interaction (López-Ráez et al. 2009).

14.6 Regulation of Strigolactone Production

One of the primary roles of AM fungi in the symbiotic relationship with plants is the delivery of

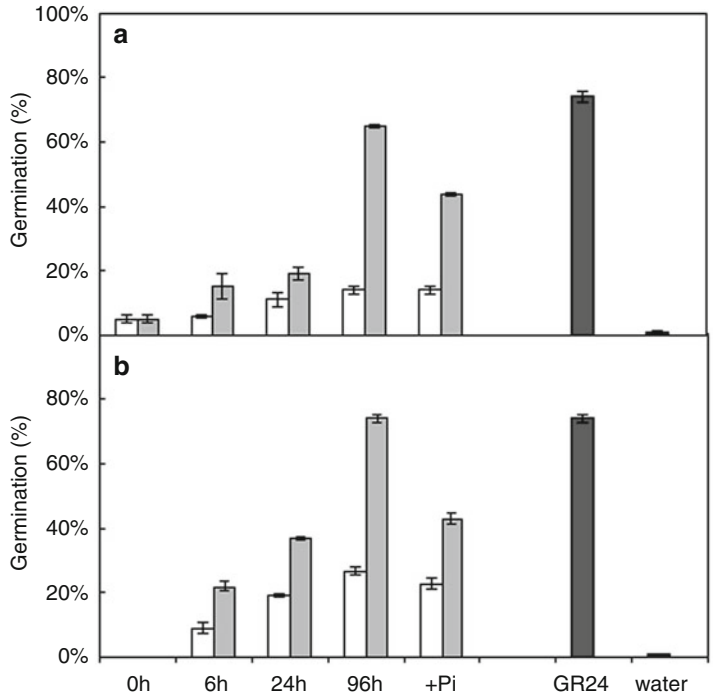


Fig. 14.4 Effect of inorganic phosphate (Pi) availability on the production of germination stimulants by tomato roots. Plants were grown for 3 weeks on half-strength Hoagland's nutrient solution and then transferred to the same solution with 0.2 mM Pi (*open bars*) or without Pi (*gray bars*) and grown for an additional 0, 6, 24, or 96 h. After 96 h, Pi was added back to the remaining plants of the Pi starvation treatment (+Pi). Germination bioassays with *O. ramosa* seeds were carried out using (**a**) root exudates or (**b**) root extracts. GR24 (10^{-9} M), and demineralized water were used as positive and negative controls, respectively. Within each experiment, the concentrations of root exudates were equalized by dilution to the same ratio of volume of exudates to root fresh weight. Bars represent the average of three independent replicates ± SE (**a**) or the average of three replicate disks ± SE (**b**) (From López-Ráez et al. (2008). Reprinted with permission of New Phytologist copyright 2008)

mineral nutrients and particularly phosphate (Karandashov and Bucher 2005). The availability of phosphate is limiting plant growth in many areas of the world, not the least in the African continent. AM fungi can help to improve the uptake of phosphate and hence improve agricultural production in these areas (Johansson et al. 2004; Bagayoko et al. 2000; López-Ráez et al. 2011).

In agreement with their role in the uptake of phosphate, it was shown that root exudates produced by phosphate-limited plants are more stimulatory to AM fungi (Nagahashi and Douds 2004). Indeed, low phosphate conditions also stimulate the exudation of the strigolactone orobanchol by red clover (Yoneyama et al. 2007a).

López-Ráez et al. (2008) investigated whether the increase in the germination stimulant activity under Pi starvation observed in tomato was caused by an increase in the exudation by the roots or by de novo production of germination stimulants. A germination bioassay was performed with either root extracts or root exudates (Fig. 14.4). The increase in germination stimulation by Pi starvation, as observed in root exudates, was also found with root extracts, suggesting that the increase in germination stimulant activity is mainly caused by de novo biosynthesis of strigolactones rather than by an increase in the exudation only.

Yoneyama and coworkers recently described that not only phosphorous but also nitrogen deficiency promotes the production and exudation of 5-deoxystrigol in sorghum. They suggest that the response in strigolactone production and

exudation to nutrient availability varies between groups of plant species. Legumes that can establish symbiosis with *Rhizobia* and acquire nitrogen from root nodules only respond to phosphate deficiency with enhanced strigolactone production to attract AM fungi, whereas in nonleguminous plant species, both phosphate and nitrogen starvation enhance the production of strigolactones (Yoneyama et al. 2007b).

14.7 Interaction Between Parasitic Plants and AM Fungi

In a number of studies with the parasitic plant *S. hermonthica*, it was demonstrated that maize and sorghum have a 30–50% reduction in the number of *S. hermonthica* shoots after inoculation with AM fungi (Gworgwor and Weber 2003; Lendzemo et al. 2007). AM fungi may confer resistance to other biotic stresses as well. For example, there are a number of reports showing that plants colonized by AM fungi are protected against subsequent infection with nematodes and plant pathogenic fungi (Borowicz 2001; Johansson et al. 2004). This protection has been suggested to be due to improved nutritional status of the host, but there is ample evidence that this cannot be the (only) explanation (Johansson et al. 2004; Harrison 2005). Several studies have shown that during mycorrhizal symbiosis, the expression of defense-related genes is induced (Pozo et al. 2002; Kuster et al. 2004). However, improved defense is not likely to be the only possible explanation for the lower infection of mycorrhizal sorghum and maize by Striga. Sun et al. (2008) have shown that the exudates of maize roots, colonized by AM fungi, induce less germination of Striga seeds than control root exudates (Fig. 14.5). Control experiments, in which the synthetic strigolactone analog GR24 was mixed with exudates of AM colonized maize, showed that this effect was not due to the presence of inhibitors. Similar results were obtained with root exudates of mycorrhized sorghum plants and Striga seeds (Lendzemo et al. 2007). These results suggest that the reduction of Striga infection of sorghum and maize, when colonized by AM

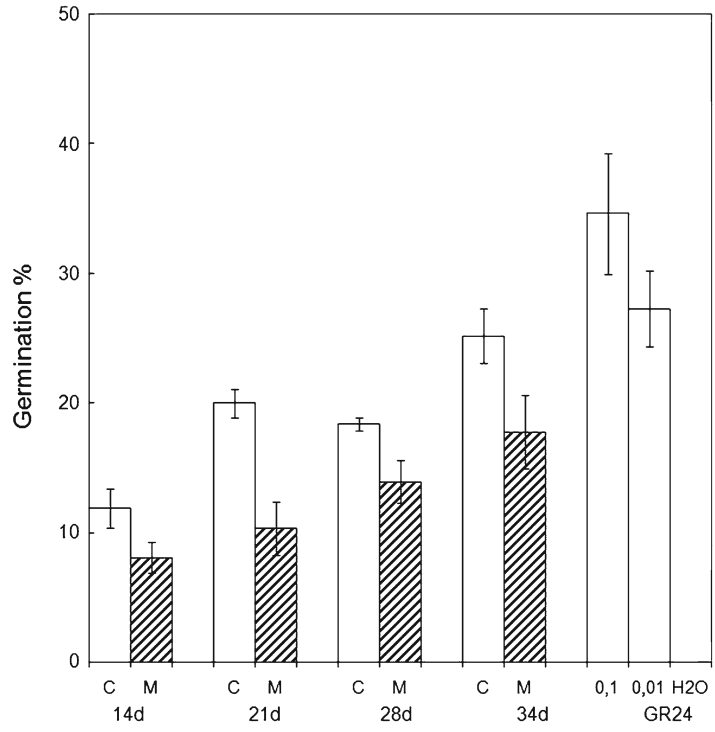


Fig. 14.5 Effect of colonization by *Glomus intraradices* of maize roots on the induction of *Striga hermonthica* seed germination. Root exudates from four plants per treatment (C, noncolonized control plants; M, plants colonized by *G. intraradices*) were collected separately for 24 h in demineralized water at 14, 21, 28, and 34 days after inoculation. The exudate of each plant was diluted to the same concentration of g root fresh weight per mL of root exudate, and induction of *S. hermonthica* germination was assessed. GR24 was used as positive control and demineralized water as negative control. Error bars indicate standard error (n = 4) (From Sun et al. 2008)

fungi, is caused at least partly by a decrease in the formation or secretion of strigolactone germination stimulants. It will be of special interest to find out if the downregulation of strigolactone production could be explained by a regulatory mechanism other than improved plant fitness and/or nutritional status.

14.8 Strigolactones and the Inhibition of Shoot Branching

If the persistence of strigolactones through evolution would be explained solely by their role in the process of mycorrhization, it is hard to explain their presence in nonmycorrhized plants like Arabidopsis as was found by (Goldwasser et al. 2008; Machiguchi et al. 2009).

Therefore, strigolactones may have additional functions. Two recent publications shed some new light on this aspect (Gomez-Roldan et al. 2008; Umehara et al. 2008). In their hunt for the identification of the CCD/NCED genes responsible for the cleavage of the apocarotenoid carbon backbone in the strigolactone biosynthetic pathway, both research groups discovered that mutations in the CCD7 and CCD8 genes of garden pea and rice are involved in this pathway.

In these studies, it was shown that root exudates of *P. sativum* carrying *ccd7* or *ccd8* mutations had significantly reduced activity in promoting fungal hyphae branching and that this could be restored with exogenous strigolactone (Gomez-Roldan et al. 2008). Furthermore, root exudates of mutant plants promoted less germination of parasitic plant seeds when compared with wild-type exudates. In accordance with this finding, *ccd8* mutant pea plants were infected by fewer parasitic *Striga* plants (Matusova et al. unpublished results) (Fig. 14.6).

While two different strigolactones were detected in wild-type root exudates, root exudates of *ccd8* mutant plants did not contain any detectable strigolactones.

The latter was also shown for rice *ccd7* and *ccd8* mutants (Umehara et al. 2008). In line with such observations, strigolactone deficiency in the fast-neutron-mutagenized tomato mutant

Fig. 14.6 Two garden pea plants (*Pisum sativum*) both initially infected with an equal amount of seeds from the parasitic plant *Orobanche crenata*. (*left*) Wild-type pea and (*right*) *ccd8* pea mutant showing its branched phenotype. *Arrows* indicate early development of the parasitic plants on the root system of the wild-type pea plant (Matusova et al. unpublished results)

SL-ORT1 led to resistance to the parasitic weeds *Phelipanche* and *Orobanche* spp. (Dor et al. 2011), but plants were again parasitized after application of the synthetic germination stimulant GR24.

CCD7 and CCD8 are also known to be involved in the production of an as yet unidentified signal controlling the outgrowth of axillary buds (Foo et al. 2001; Morris et al. 2001; Sorefan et al. 2003; Booker et al. 2004; Zou et al. 2006; Arite et al. 2007; Mouchel and Leyser 2007).

Mutations in those genes result in enhanced shoot branching (Fig. 14.6). Other genes playing a role in the biosynthesis of this signal include a cytochrome P450 monooxygenase (Booker et al. 2005) and an F-box leucine-rich repeat family protein (Stirnberg et al. 2002). The latter is presumably involved in recognition and signal transduction and not in the actual production

of the signal itself. Umehara et al. (2008) and Gomez-Roldan et al. (2008) tested whether mutants in this F-box protein in rice, respectively pea, that also displayed the branched phenotype were capable of producing strigolactones, and indeed, substantial levels were detected. This is an extra indication that the reduced strigolactone levels seen in the *ccd7* and *ccd8* mutants are not a result from the aberrant phenotype and hormonal abnormalities observed in shoot-branching mutants.

Knowing that *ccd7* and *ccd8* mutants lack a branching inhibiting signal leading to excessive shoot branching and at the same time appear to be deficient in strigolactones raises, an intriguing question arises. Could it be that both carotenoid-derived compounds are related? Therefore, Gomez-Roldan et al. (2008) applied the synthetic strigolactone GR24 to the axillary buds of *ccd8* and F-box mutant plants in pea and Arabidopsis. Umehara et al. (2008) performed a similar complementation assay for *ccd8* and F-box shoot-branching mutants both in rice and Arabidopsis; however, in this study, GR24 was applied to the growth medium of the plants. In both studies, GR24 was found to contain shoot-branching inhibitory capacity, specifically in the *ccd8* mutant plants, but not in the F-box (receptor) mutant.

Therefore, it is proposed that either strigolactones themselves or closely related molecules produced from the administered strigolactones are the branching inhibiting signal which seems to be transported in the xylem (Kohlen et al. 2011).

Altogether, this puts the class of strigolactones in an entirely new perspective as this all points to the discovery of a new phytohormone. Evidence for additional roles in establishing root system architecture (Kapulnik et al. 2011; Koltai et al. 2010; Ruyter-Spira et al. 2011), seed germination (Tsuchiya et al. 2010), and light signaling (Shen et al. 2007; Tsuchiya et al. 2010) is accumulating at a fast pace.

14.9 Future Research

This also opens up a new era for strigolactone research.

A major challenge lies in the biochemical characterization of the bioactive form of the branch-inhibiting hormone and its link with the strigolactones. Although different strigolactones are all composed of the same building blocks as reflected by the A-, B-, C-, and D-rings, the diversity seen in the decorations of the ABC part is immense. It is far from clear what their functional biological significance is, how they are determined, and if there are any regulatory factors in this decoration process. And if strigolactones are closely related to the branch-inhibiting hormone, does this hormone itself also allow a great structural diversity to be functional?

When looking at the chemical structures of strigolactones, it is obvious that not all biosynthetic enzymes have been identified so far. Especially, the putative coupling of the D-ring to the ABC part is likely to be an enzymatic step calling for a corresponding responsible enzyme. So far, genetic loci of branching mutants in Arabidopsis did not result in a candidate, maybe as a result of redundancy.

It is now clear that strigolactones not only have a role underground in the establishment of a symbiosis with arbuscular mycorrhiza upon phosphate starvation but also have a role inside the plant in the regulation of plant development upon different environmental stimuli. Indeed, the decrease in bud outgrowth observed during phosphate starvation is indeed mediated through an increase in strigolactone production (Kohlen et al. 2011). In this respect, research aimed at the elucidation of the underlying regulatory processes and the interplay with (other) phytohormones will be of great interest, for instance, with the auxin status of the plant (Ruyter-Spira et al. 2011).

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