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Review

Review: Implications of non-specific strigolactone signaling in the rhizosphere

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ABSTRACT

Strigolactones produced by various plant species are involved in the development of different plant parts. They are also exuded by plant roots to the rhizosphere, where they are involved in the induction of seed germination of the parasitic plants *Striga* and *Orobanche*, hyphal branching of the symbiotic arbuscular mycorrhizal fungi (AMF), and the symbiotic interaction with *Rhizobium*. In the present discussion paper, the essentialness of strigolactones as communication signals in these plant interactions is discussed in view of the existence of other plant-derived substances that are able to promote these plant interactions. In addition, the importance of strigolactones for determination of interaction specificity is discussed based on current knowledge on strigolactone composition, perception and delivery. The different activities of strigolactones in plant development and in the rhizosphere suggest their possible use in agriculture. However, despite efforts made in this direction, there is no current, practical implementation. Possible reasons for the encountered difficulties and suggested solutions to promote strigolactone use in agriculture are discussed.

Contents

1. Introduction

Strigolactones have recently become the focus of research in various disciplines. These groups of substances, produced by various plant species, consist of an ABC-ring system connected via an enol ether bridge to a butenolide D ring (Fig. 1; [1–5]). Strigolactones are derived from the carotenoid-synthesis pathway [6–8] by the activity of several known enzymes [7,9–14]. Strigolactones are also produced in the Embryophyta and Charales [15]. Approximately 15 strigolactones have been structurally characterized to date [16]; several different types of these molecules can be produced by a single plant species in different quantities. The produced strigolactone mixture may also differ in type and quantity among different varieties of the same plant species [1,2].

Strigolactones are involved in the development of different plant parts. They suppress outgrowth of preformed axillary buds in the shoot [17,18], induce secondary growth in the stem [19] and suppress adventitious-root formation [20]. They are also involved in determining plant height [21]. Strigolactones induce root-hair elongation [22] and promote cell numbers in the primary-root meristem [23,24]. They suppress lateral-root formation under conditions of sufficient phosphate, but they induce it under limiting phosphate [22,23].

Abbreviation: AMF, arbuscular mycorrhizal fungi.

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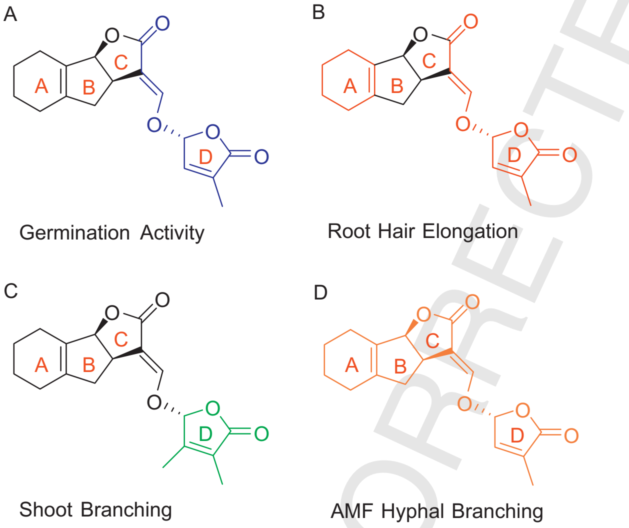
Before strigolactones were identified as plant hormones [4], they were known as substances exuded by plant roots that induce germination of seeds of the parasitic plant species *Striga* and *Orobanche* spp. [25,26]. Strigolactones stimulate hyphal branching in the symbiotic arbuscular mycorrhizal fungi (AMF; [27,28]) and promote plants' symbiotic interaction with *Rhizobium* [29]. The half-life of strigolactones varies greatly depending on pH [3], and they are perceived at very low quantities; for example, the synthetic strigolactone GR24 induces AMF branching at 10^{-11} M and the natural strigolactone sorgolactone induces AMF branching at a concentration as low as 10^{-13} M [30]. This high sensitivity to strigolactones guarantees the AMF response in the presence of host roots, which occurs despite the relatively short lifetime of strigolactones in aqueous medium [3,27,31] and in the relatively complex, hydrophilic mixture of substances in the rhizosphere [27].

Strigolactones, by increasing AMF hyphal branching, may promote symbiosis. This is since increasing AMF hyphal branching may increase the probability of AMF meeting their host roots [32]. The strategy of hyphal branching has been suggested to play a part in the evolutionary success of AMF in entering into symbiotic associations [32]. Strigolactones are also produced and exuded by charophyte green algae of the order Charales [15]. The presence of strigolactones in algae suggests that their appearance predates the first AM symbiosis [15]. This further suggests that strigolactones evolved in plants as a hormone, and it is only later in evolution, upon emergence on land, that these hormones were utilized for communication with other organisms [15]. Parasitic plants must have evolved the use of this "hormonal flag" to detect their host plant, although not all strigolactone-producing plants are necessarily hosts for AMF or parasitic plants. For example, cotton is a non-host for *Striga* and *Orobanche* spp. despite its strigol production [26]. However, as attractive as these hypotheses might be, there are still several questions challenging them, namely, how essential are strigolactones as communication signals in these plant interactions? Are strigolactones important for determinations of specificity between host and symbiont/parasite?



Germination Activity

Root Hair Elongation

Shoot Branching

AMF Hyphal Branching

Fig. 1. Suggested sites of natural strigolactones' specific activity. A standard strigolactone structure is illustrated to demonstrate sites of specific activity [3,51,70]. However different organisms may respond differently to the various strigolactones, and therefore generalizations should be made with caution. (A) For strigolactones to induce seed germination of parasitic plants, the α,β-unsaturated carbonyl moiety (C ring) should be connected via an enol ether unit with the D-ring; in the case of an extra methyl on the D-ring (not shown), activity is reduced (marked in blue; [51,53]). (B) The C–D structure (marked in red) is important for *Arabidopsis* root-hair elongation induced by strigolactones; however this activity, unlike germination, is sensitive to substitutions on the A ring of the molecule [52]. (C) The D-ring (marked in green) is important for repression of shoot branching, at least in pea. In this case of strigolactone activity, an extra methyl on the D-ring has a boosting effect for inhibition of branching activity in pea [53]. (D) For strigolactone activity as branching factors of AMF hyphae, not only the extra methyl on D compromises the activity, but simpler molecules lacking A, B or C are inactive. The enol ether bridge between C and D is also essential (marked in orange) [27,53].

2. How essential are strigolactones as communication signals in plant interactions?

Upon closer examination, strigolactones do not seem to be essential for AMF symbiosis. Both spore germination and some degree of AMF hyphal development and branching occur without their host or its root exudates in the vicinity [33]. Indeed, extensive hyphal growth of AMF is evident in the presence of high levels of CO$_2$ and flavonols [34]. As a result, even in the absence of root exudates (and strigolactones), encounters between the developing hyphae and the host root are still possible. Strigolactones are only needed for AMF symbiosis in the pre-symbiotic stage, and not for intracellular fungal development. This is concluded based on genetic studies in *Petunia hybrida* of a mutant deficient in a putative strigolactone transporter [35]. Hence, strigolactones may not be essential for mycorrhization. Strigolactones are positive regulators of rhizobium nodulation in pea, and are required for optimal nodule number. However, they are not required for nodule formation per se [29]. Hence, similar to the case of AMF symbiosis, strigolactones do not seem to be essential for the occurrence of rhizobial symbiosis.

Other compounds, such as ethylene, dehydrocostus lactone and glucosinolate breakdown products, can also induce seed germination of parasitic plants [36–38]. Moreover, root exudates are only needed for the germination of obligatory root parasites [36]. Further, 7-hydroxylated simple coumarins (unsaturated lactones) from sunflower have been suggested to play a defensive role against *Orobanche cernua* parasitism, by preventing successful germination, its penetration, and/or the establishment of a connection to the host vascular system [39]. Together, these results suggest that compounds additional to strigolactones may induce parasitic plant seed germination and that the balance between inhibitors and inducers might be important.

To conclude, while strigolactones are important for enhancing associations with AMF, rhizobia, and parasitic plants, they may not be essential for these associations. These biological systems (like many others) are likely to be much more complex than more definite concepts, such as response of one organism to one stimulus (e.g., root response to gravitropism). For example, strigolactones may be important for the recognition between host plants and AMF, but still both host and nonhost may have similar composition of strigolactones. It might be that the combination of the presence of inhibitors and certain strigolactones is the one to determine the efficiency of the symbiosis. It is doubtful that there is AMF unique branching, or symbiotic capacity or highly specific AMF-host pairing (as AM symbiosis is by its nature is with low level of specificity).

3. Are strigolactones important for determination of specificity between host and symbiont/parasite?

3.1. The importance of strigolactone composition for determination of specificity between host and symbiont/parasite

Strigolactones are differentially produced and secreted as different mixtures by different plant species, sometimes even by different cultivars within a species [1–3]. This suggests that there is a strigolactone "fingerprint" for each plant [28]. It is tempting to speculate that this "fingerprint" allows identification of a certain plant type by its interacting organism. The present manuscript is

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