Strigolactones as a new plant growth regulator

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Abstract: In the rhizosphere, strigolactones exuded from plant roots function as host recognition signals for beneficial symbionts arbuscular mycorrhizal fungi and at the same time for detrimental root parasitic plants, Striga and Orobanche spp. In planta, these compounds act as a novel class of plant hormones inhibiting shoot branching and thus regulating aboveground plant architectures. So far, most of naturally occurring strigolactones have been shown to be active in these three biological systems. Some of these strigolactones are more active in, for example, germination stimulation, but less active in the other systems. Therefore, it is expected to develop new plant growth regulators that are specific to one or two of these systems regulated by strigolactones.

Keywords: Arbuscular Mycorrhizal Fungi, Plant Hormone, Root Parasitic Plant, Shoot Branching, Strigolactone

1. Introduction

Strigolactones were originally identified as germination stimulants for root parasitic plants, witchweeds (Striga spp.), broomrapes (Orobanche spp.), and Alectra, all belonging to the family Orobanchaceae. The seeds of these root parasites need to be kept in a warm moist (wet) condition for several days to break dormancy. However, the seeds will not germinate unless they are exposed to germination stimulants. Strigol, the first described strigolactone, was isolated from the root exudates of a false host of Striga, cotton [1,2] and then identified in genuine Striga hosts, sorghum, maize, and proso millet [3]. Therefore it was clearly shown from the beginning that not only host but also non-host plants of root parasites produce and exude strigolactones. To date, more than 10 strigolactones have been characterized as germination stimulants from various plant species [4].

An interesting question arose why plants produce strigolactones that help the enemies locate their targets. Therefore, it was suggested that these compounds should play other roles that outweigh the potential risks of parasitism. Then such a beneficial role of strigolactones was unveiled by the finding that these compounds function as branching factors for symbionts arbuscular mycorrhizal (AM) fungi from which plants benefit [5]. Under appropriate temperature conditions, the spores of AM fungi germinate and their hyphae elongate. When AM fungi perceive strigolactones, hyphal branching occurs and then they prepare for symbiosis with host plants. The hyphal branching is a critical step in the host recognition process, and this phenomenon can be observed only in the vicinity of roots of host plants. Both of the root parasites and AM fungi are obligate heterotrophs and incapable of completing their life cycle without connecting to and residing in their host roots, respectively. Since the symbiosis between AM fungi and plants evolved 460 million years ago, and more than 80% of land plants form symbiotic relationship with AM fungi [6], strigolactone production was thought to evolve concomitantly with the symbiosis. The root parasites, which evolved later, could develop a detection system for strigolactones as the cues of living host roots in the vicinity. However, non-hosts of AM fungi such as Arabidopsis [7] and white lupin [8] have been shown to produce strigolactones, suggesting that strigolactones would play other unknown pivotal roles in plants for their normal growth and development.

Very recently, two groups independently identified strigolactones, or their further metabolites, as a novel class of plant hormones regulating shoot branching [9,10]. Mutants with phenotypes of excessive shoot branching in pea (rms), rice (htd and d), and Arabidopsis (max) have been characterized by a deficit either in strigolactone biosynthesis or its perception. In addition, these studies have confirmed that strigolactones are derived from carotenoids in plants as proposed by Matusova et al. [11]. However, enzymes involved in the biosynthetic pathway and the intermediates are largely unknown.

In this paper, structural diversity of strigolactones and their distribution in the plant kingdom are summarized. In addition, structural requirements for the three biological activities are discussed along with the possibility to develop new plant growth regulators.
2. Structural diversity of strigolactones and their distribution in the plant kingdom

Some of natural strigolactones isolated to date are shown in Fig. 2 [4]. All of these strigolactones contain a tricyclic lactone (ABC part) that connects via an enol ether bridge to a butenolide group (D-ring). These compounds have one or two methyl groups on the A-ring and one or more hydroxy or acetyloxyl groups in the A/B-ring moiety. Therefore, 5-deoxystrigol (1) is thought to be the common precursor of these strigolactones. Indeed, 5-deoxystrigol (1) has been detected in root exudates of various plant species, both monocots [12] and dicots [8]. An allylic hydroxylation of 5-deoxystrigol leads to strigol (2, R=H) or orobanchol (5, R=H) and the third hydroxy-strigolactone, sorgomol (3, R=H) [13], is produced by the hydroxylation on the homoallylic position. These hydroxy-strigolactones may be acetylated, and conjugations with sugars and amino acids may occur. Further oxidation of the hydroxymethyl group of sorgomol and the subsequent decarboxylation affords sorgolactone (4) [14].

A homoallylic hydroxylation of orobanchol (5, R=H) and orobanchyl acetate (5, R=acetyl) leads to 7α- and 7β-hydroxyorobanchol (6, R=H) and their acetates (6, R=acetyl), respectively (Xie et al., unpublished). These are oxidized to 7-oxo derivatives (7) [15] or dehydroxylation and migration of methyl group result in the formation of didehydro-orobanchol derivatives [16] whose structures have not yet been confirmed. These didehydro-orobanchol may then be converted to solanacol (8, R=H) [16] through a similar sequence of reactions. Structure of solanacol was revised recently as shown in Fig. 2 [17].

Among the three hydroxy-strigolactones, orobanchol (5, R=H) has been found in root exudates from various plant species and thus appears to be distributed most widely in the plant kingdom. In addition, various strigolactones that may be derived from orobanchol have been isolated as described above.

All the natural strigolactones shown in Fig. 2 have the 2'-((R) stereochemistry except for solanacol whose stereochemistry has not yet been determined. It was thus a surprise that 2'-epiorobanchol (9) was isolated from tobacco [16]. Furthermore, fabacyl acetate (10), the first ent-strigolactone was found in pea root exudate from which neither ent-2'-epi-5-deoxystrigol nor ent-2'-epiorobanchol, precursors of fabacyl acetate, were detected [18]. One of major strigolactones in rice plants (Oryza sativa cv. Nipponbare) was 2'-epi-5-deoxystrigol but orobanchol was also detected, indicating that the plants would produce both 2'-epimers [10]. These results suggest that the coupling of the D ring to the ABC part may not be a stereoselective process and only one epimer might be released to the rhizosphere.

Strigolactone profiling of the Fabaceae plants suggests that plants produce many strigolactones at highly variable levels so that only parts of them can be detected in root exudates and in plant tissues. For example, sorgomol (3, R=H) and orobanchyl acetate (5, R=acetyl) but not orobanchol (5, R=H) were detected in the root exudate of white lupin [8]. Since orobanchyl acetate appears to be formed by the acetylation of orobanchol, it is likely that white lupin produces orobanchol and its precursor 5-deoxystrigol. Therefore, the conversion of 5-deoxystrigol to orobanchyl acetate via orobanchol would proceed quickly in this plant. By contrast, conversion of sorgomol to sorgolactone or sorgomyl acetate seems to be quite slow.

Although precise data have not yet been published, we have already confirmed that trees (Japanese pine trees, Eucalyptus spp., etc) and a moss (Physcomitrella patens) also produce strigolactones (Akiyama et al.; Xie et al., unpublished). Therefore, strigolactones are distributed more widely in the plant kingdom than once expected and it
is likely that many novel strigolactones remain to be characterized. Since plants produce strigolactones in extremely low quantities and they are unstable during purification process, purification and structural determination of these novel strigolactones would not be straightforward.

3. Structural requirements for biological activities

1) Seed germination activity

In germination stimulation of root parasitic weed seeds, extensive studies on structure-activity relationship (SAR) of strigolactones were conducted, and the C–D ring moiety has been identified as the essential structure for exhibiting germination stimulation activity. Indeed, natural and synthetic strigolactones carrying this moiety have moderate to potent germination activity. Hydrolysis of this structure in the synthetic strigolactone GR24 affording the ABC part and the D-ring moiety resulted in a complete loss of germination activity (Akiyama et al., unpublished).

Other parts of strigolactone also affect germination activity and in particular the presence of 4-hydroxyl group seems to enhance the activity. In general, hydroxy-strigolactones are about 10–100-fold more active than their acetates (and probably also other conjugates) [19,20] and strigolactones carrying two or more hydroxyl groups, for example, 7-hydroxyorobanchol (6, R=H), appeared to be only weakly active in in vitro germination assay due to their instability. These results, however, do not exclude the involvement of these compounds in the germination stimulation; these or further metabolites might be the true active form(s).

The C-2′-(R) stereochemistry has repeatedly been reported to be another important structural feature for potent activity. This is true for strigol, sorgolactone, and GR24 [4,21]. However, 2′-epiorobanchol (9) is slightly more active than orobanchol (5, R=H) on seed germination of O. minor and Phelipanche ramosa (O. ramosa) [16]. The presence of a 4-α-hydroxy group appears to enhance the activity, in particular, in 2′-epi-strigolactones. Indeed, solanacol (8, R=H), 4-α-hydroxy-7,8-dimethyl-GR24, is far more active than GR24 [16], while the introduction of a methyl group at C-6 or C-8 did not affect germination stimulation activity [21].

Germination stimulation activity of strigolactones on one root parasitic plant species may be different from that on the other species. Under laboratory conditions, sorgomol (3, R=H), originally isolated from sorghum root exudates is more active on Striga than on Orobanche [13].

2) Hyphal branching activity

The natural strigolactones identified so far have been examined for their activity on hyphal branching in AM fungus Gigaspora margarita and all of natural strigolactones are active as branching factors. Although structural requirements for activity are very similar to those for germination stimulation of root parasites, some noticeable differences have been observed. For example, 3,6′-dihydro-GR24 was totally inactive as a germination stimulant but still showed distinct activity on hyphal branching [Akiyama et al., unpublished].

3) Shoot branching inhibition

The natural and synthetic strigolactones have been examined for their effects on shoot branching mainly in rice plants. Since the duration of treatment period is long and relatively large amounts of samples are required for the shoot branching bioassay, only a few of natural strigolactones have been tested so far. Therefore, structural requirements for shoot branching inhibition are not yet well understood. All the natural and synthetic strigolactones examined so far are active in bioassays for shoot branching inhibition. Therefore, it is likely that other natural and synthetic strigolactones that induce parasite seed germination also inhibit shoot branching. To clarify bioactive form(s) of this hormone, if they are different from strigolactones, rapid and sensitive bioassays need to be developed.

4. Development of novel plant growth regulators

Plants produce mixtures of strigolactones and release them into the rhizosphere. Therefore root parasite seeds and also AM fungi are exposed to strigolactones if they are located close to a living root of any plant species. However, both seed germination of parasites and hyphal branching of AM fungi are often reduced in the vicinity of non-host roots. Therefore, not only strigolactones but also other signaling chemicals which are synergistic or antagonistic to strigolactone action are involved in the seed germination of root parasitic weeds and hyphal branching of AM fungi. Indeed, we observed both synergistic and antagonistic interactions on seed germination activity with mixtures of two strigolactones. In addition, interactions among strigolactones and other plant hormones would influence biological responses in plants.
As described before, it may be possible to design strigolactones or related compounds that are active only on one or two of the three biological systems; parasite seed germination, AM fungi hyphal branching, and inhibition of shoot branching.

In addition to GR24 (Fig. 3), the standard strigolactone, GR7 and GR5, both carrying the essential structure, have also been developed as germination stimulants (Fig. 4). Zwanenburg and his colleagues at Nijmegen University, the Netherlands, have developed Nijmegen-1 which is less active but more stable in the soil than GR24 [22]. Sasaki and his colleagues at Kobe University, Japan, modified the structure of GR24 and developed imino analogues (II) with promising activity [23]. So far, their effects on hyphal branching in AM fungi and on shoot branching have not yet been described, these compounds would be good leads for new type of plant growth regulators (PGRs).

Alternative approach to new PGRs would be the molecular design of biosynthetic inhibitors. In fact, as described before, strigolactones are derived from carotenoids and thus fluridone and norflurazon, herbicides inhibiting carotenoid biosynthesis (inhibitors of phytoene desaturase) could reduce strigolactone production [11]. Since these compounds are herbicidal, it is preferable to develop compounds inhibiting later steps of the strigolactone biosynthetic pathway, for example, inhibitors of CCD7, CCD8, and/or MAX1 (Fig. 5) [9,10]. CCD inhibitors affecting strigolactone production have recently been reported [24].

Further study is needed to clarify why plants produce so many different strigolactones and how each strigolactone contributes to the host recognition by root parasites and by AM fungi and to the inhibition of shoot branching. For example, to establish an affordable management strategy of root parasitic weeds, we must take into consideration that strigolactones are host recognition signals for both symbiosis and parasitism and inhibitors of shoot branching.

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References


