Which are major players, canonical or non-canonical strigolactones?

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Scheme S1. Synthesis of racemic mixture of 7α- and 7β-hydroxy-5-deoxystrigol.

Fig. S1. 1H NMR spectrum of natural stimulant in dokudami root exudates.
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Fig. S4. LC–MS/MS chromatograms of synthetic 7β-hydroxy-5-deoxystrigol and natural
stimulant.
Highlight

The chemistry of canonical and non-canonical strigolactones and their distribution in the plant kingdom are summarized in relation to their biological activities in the rhizosphere and in plants.

Abstract

Strigolactones (SLs) can be classified into two structurally distinct groups: canonical and non-canonical SLs. Canonical SLs contain the ABCD ring system, and non-canonical SLs lack the A, B, or C ring but have the enol ether–D ring moiety which is essential for biological activities. The simplest non-canonical SL is the SL biosynthetic intermediate carlactone (CL). In plants, CL and its oxidized metabolites such as carlactonoic acid and methyl carlactonoate, are present in root and shoot tissues. In some plant species including black oat (Avena strigosa), sunflower (Helianthus annuus), and maize (Zea mays), non-canonical SLs are major germination stimulants in the root exudates. Various plant species such as tomato (Solanum lycopersicum) release carlactonoic acid, and poplar (Populus spp.) was found to exude methyl carlactonoate into the rhizosphere. These results suggest that both canonical and non-canonical SLs are active as host recognition signals in the rhizosphere. In contrast, limited distribution of canonical SLs in the plant kingdom and structure- and stereo-specific transportation of canonical SLs from roots to shoots suggest that plant hormones inhibiting shoot branching are not canonical SLs but are rather non-canonical SLs.

Key words: AM hyphal branching, canonical strigolactones, germination stimulant, non-canonical strigolactones, shoot branching inhibiting plant hormone.

Abbreviations

AM, arbuscular mycorrhizal; CL, carlactone; CLA, carlactonoic acid; 4DO, 4-deoxyorobanchol; 5DS, 5-deoxystrigol; GC–MS, gas chromatography–mass spectrometry; LC–MS/MS, liquid chromatography–tandem mass spectrometry; MeCLA,
methyl carlactonoate; NMR, nuclear magnetic resonance; SL, strigolactone
Introduction

Natural strigolactones (SLs) are carotenoid-derived plant hormones or their precursors that regulate plant growth and developmental processes through cross-talk with other hormones and also participate in plant–root parasitic plants and plant–microbe interactions in the rhizosphere (Xie et al., 2010; Al-Babili and Bouwmeester, 2015). SLs can be classified into two groups based on their chemical structures. Strigol (1) and related compounds that contain the ABC ring system connected to the methylbutenolide D ring via an enol ether bridge are called canonical SLs (Al-Babili and Bouwmeester, 2015). So far, 23 canonical SLs have been characterized from plant root exudates through bioassay-guided purifications (Xie et al., 2010; Xie, 2016). Most were isolated as germination stimulants for root parasitic weeds, except for 5-deoxystrigol (3) which was originally identified as the hyphal branching factor for arbuscular mycorrhizal (AM) fungi (Akiyama et al., 2005) (Fig. 1).

Extensive studies on the structure–activity relationships of SLs showed that the enol ether–D ring moiety was essential for biological activities (Yoneyama et al., 2009; Zwanenburg et al., 2009; Akiyama et al., 2010; Yoneyama et al., 2010; Boyer et al., 2012). In addition, stereochemistry, in particular at the 2′-position of the D ring, is important for high potencies (Thuring et al., 1997; Flematti et al., 2016). The introduction of a hydroxyl group on the A or B ring generally reduces stability and thus germination stimulation of Striga spp. (Gobena et al., 2017) but not Orobanche spp. (Kim et al., 2010).

Various synthetic SL mimics carrying the essential structural unit have been developed (Nefkens et al., 1997; Kondo et al., 2007; Zwanenburg et al., 2009; Cohen et al., 2013; Fukui et al., 2013; Boyer et al., 2014; Screpanti et al., 2016).

Recently, germination stimulants lacking the ABC ring structure but containing the D ring were characterized and are called non-canonical SLs. They are zealactone (methyl zealactonoate, 24) (Charnikhova et al., 2017; Xie et al., 2017), avenaol (25) (Kim et al., 2014), heliolactone (26) (Ueno et al., 2014), and two novel stimulants (27 and 28). The simplest non-canonical SL is carlactone (CL, 29) (Alder et al., 2012), a SL biosynthetic precursor. Its oxidized metabolite, carlactonoic acid (CLA, 30) (Abe et al., 2014), has been detected in root exudates from various plant species (Yoneyama et al., 2017). Some species such as poplar (Populus spp.) release methyl carlactonoate (MeCLA, 31) into the rhizosphere, which can interact with the SL receptor D14 (Fig. 2) (Abe et al.,
These results indicate that, in addition to canonical SLs, non-canonical SLs including CLA and MeCLA are likely involved in chemical communications in the rhizosphere (Yoneyama et al., 2017).

In this review, chemistry of canonical and non-canonical SLs and their distribution in the plant kingdom are summarized and discussed in relation to their involvement in parasite seed germination, AM fungi colonization, and shoot branching inhibition.

**Canonical SLs**

The canonical SLs characterized to date are strigol (1), strigyl acetate (2), 5-deoxystrigol (5DS, 3), sorgolactone (4), sorgomol (5), strigone (6), 4-hydroxy-5-deoxystrigol (ent-2′-epi-orobanchol, 7), 4-acetoxy-5-deoxystrigol (ent-2′-epi-orobanchyl acetate, 8), orobanchol (9), orobanchyl acetate (10), 4-deoxyorobanchol (4DO, 11), solanacol (12), solanacyl acetate (13), fabacol (14), fabacyl acetate (15), 7-oxoorobanchol (16), 7-oxoorobanchyl acetate (17), 7α-hydroxyorobanchol (18), 7α-hydroxyorobanchyl acetate (19), 7β-hydroxyorobanchol (20), 7β-hydroxyorobanchyl acetate (21), and medicaol (22) (Cook et al., 1969; Hauck et al., 1992; Yokota et al., 1998; Akiyama et al., 2005; Xie et al., 2007; Umehara et al., 2008; Xie et al., 2008; Xie et al., 2009a; Xie et al., 2009b; Chen et al., 2010; Kisugi et al., 2013; Tokunaga et al., 2015; Xie, 2016).

According to C ring stereochemistry, these canonical SLs can be divided into two groups: strigol- (1–8) and orobanchol-type SLs (9–22), which have a β- and an α-oriented C ring, respectively (Fig. 1) (Xie et al., 2013; Al-Babili and Bouwmeester, 2015). In general, plants appear to produce either strigol- or orobanchol-type SLs as major SLs; however, some species such as tobacco (Nicotiana tabacum) produce both (Xie et al., 2013). The three gymnosperms so far examined – Japanese black pine (Pinus thunbergii), cedar (Cryptomeria japonica), and gingko (Gingko biloba) – and the lycophyte spike moss (Selaginella moellendorfii) produce orobanchol-type SLs (Yoneyama et al., 2017) (Table 1). Many angiosperms are orobanchol-type SL producers but cotton (Gossypium hirsutum) (Cook et al., 1969; Sato et al., 2005) and strawberry (Fragaria vesca) plants exude only strigol-type SLs (Xie et al., unpublished). Chinese milk vetch (Astragalus membranaceus) is unique among the Fabaceae plants as it produces strigol-type SLs (Yoneyama et al., 2008). Previously, we reported that Chinese milk vetch produced...
orobanchyl acetate but re-examination with our new liquid chromatography–tandem mass spectrometry (LC–MS/MS) system suggests that the signal assigned to orobanchyl acetate may be background noise. We encountered similar problems in SL detection from Physcomitrella patens (Proust et al., 2011). Although we detected CL in P. patens gametophores as expected, we could not detect any known SLs with the new LC–MS/MS system. The Poaceae family contains both a strigol-type SL producer, sorghum (Sorghum bicolor) (Yoneyama et al., 2007; Xie et al., 2008), and an orobanchol-type SL producer, rice (Oryza sativa) (Umehara et al., 2008). Recently, some Striga-resistant sorghum cultivars were shown to produce orobanchol, which is a weak Striga germination stimulant but a potent branching factor for AM fungi. These cultivars are thus resistant to Striga but still good hosts for AM fungi (Gobena et al., 2017). We also observed that despite the distinctive difference in SL composition, the levels of AM colonization and the community compositions did not differ between the Striga-susceptible and -resistant maize cultivars (Yoneyama et al., 2015). Identities of SLs in these maize cultivars need to be confirmed as these data were obtained with our old MS system.

In addition to these 22 canonical SLs, we characterized at least three novel canonical SLs, 7β-hydroxy-5-deoxystrigol (23) from dokudami (Houttuynia cordata) and two from tall goldenrod (Solidago altissima), indicating that the number of canonical SLs in the plant kingdom may increase as we examine more species. The structures of the two canonical SLs produced by tall goldenrod will be reported elsewhere.

It is intriguing to understand why plants produce orobanchol- and strigol-type SLs. One of rice MORE AXILLARY GROWTH 1 (MAX1) orthologs, Os900 expressed in yeast converts CL to 4DO but not to 5DS (Zhang et al., 2014), presumably via CLA and 18-hydroxy-CLA in vitro (Yoneyama et al., 2017). It is likely that Low Germination Stimulant 1 (LGS1), a sulfotransferase, is involved in formation of strigol-type SLs (Gobena et al., 2017) and therefore orobanchol-type SLs may have evolved due to mutations in the LGS1 gene, as observed for Striga-resistant sorghum cultivars. However, the wide distribution of the orobanchol-type SL, 4DO, in gymnosperms, angiosperms, and a lycophyte may imply that orobanchol-type SLs evolved earlier. The distribution of canonical SLs, orobanchol- and strigol-type SLs, in the root exudates from various plant species is listed in Table 1.
7β-Hydroxy-5-deoxystrigol from dokudami root exudate

Dokudami is a Chinese medicinal plant commonly found in Japan. Strigol (1) and strigone (6) have been identified as a major and a minor SL, respectively, in its root exudate which contained several SL-like compounds as minor germination stimulants (Kisugi et al., 2013). Three had the molecular formula C_{19}H_{22}O_{6} but their retention times in LC–MS/MS analyses differed from those of known SLs, such as strigol. They had quite low contents in root exudate, ca. 1/500 that of strigol, and we isolated a very small amount of one (< 2 µg) with some impurities. The MS spectroscopic data and the proton nuclear magnetic resonance (NMR) spectrum of this stimulant suggested that it was a mono-hydroxy-canonical SL, most likely carrying a hydroxyl group at C_7. Comparing retention times of the natural stimulant and synthetic standards on C_{18}, NAP, and chiral columns using LC–MS/MS, showed that the structure was 7β-hydroxy-5-deoxystrigol (23). Synthesis and spectroscopic data of both natural and synthetic 7β-hydroxy-5-deoxystrigol and its isomers are included in supplementary data.

Non-canonical SLs

Although maize (Zea mays), a major host of Striga, had been reported to exude strigol (Siame et al., 1993), (Jamil et al., 2012) detected neither strigol nor any other canonical SL in maize root exudates with LC–MS/MS analysis. Instead, they found two novel germination stimulants, SL1 and SL2. Similarly, root exudates from black oat (Avena strigosa), which strongly induced Striga and Orobanche germination, did not contain known canonical SLs. Therefore, germination stimulants produced by maize and black oat have been examined extensively, and two non-canonical SLs, zealactone (24) (Charnikhova et al., 2017; Xie et al., 2017) and avenaol (25) (Kim et al., 2014) were isolated from their root exudates, respectively, and their structures determined. Very recently, the stereochemical structure of avenaol was confirmed by total synthesis (Yasui et al., 2017). These non-canonical SLs lack the A, B, or C ring but retain the enol ether–D ring moiety which is essential for biological activities of SLs. Maize was found to produce several non-canonical SLs, and SL2 was determined to be zealactone (Charnikhova et al., 2017; Xie et al., 2017). SL1 was found to be mixtures of at least two isomers which were difficult to separate. Another non-canonical SL, heliolactone (26), was isolated from root exudates of sunflower (Helianthus annuus), the host of O. cumana.
Sunflower plants do not produce known canonical SLs (Ueno et al., 2014). In addition to these non-canonical SLs, we isolated at least two non-canonical SLs, one (27) from rice and the other (28) from black oat root exudates (Fig. 2). Compound 27 is one of the putative methoxy-5DS isomers produced by rice plants (Jamil et al., 2011). The structures of 27 and 28 in Fig. 2 are only tentative and need to be confirmed, preferably by comparing spectroscopic data with those of synthetic standards. This is because these compounds are present in root exudates in quite low amounts and, in particular, 27 occurs as a mixture of isomers which hampers further purification. Furthermore, these non-canonical SLs are less stable than canonical SLs and gradually decompose during purification and storage.

The first reported non-canonical SL was CL (29), a SL biosynthetic precursor (Alder et al., 2012). The levels of CL in plant tissues appear to be rather high compared to canonical SLs and are not affected by phosphate starvation, indicating that response to phosphate starvation is regulated in the SL biosynthetic steps after CL formation (Seto et al., 2014). Although CL is rather lipophilic, it was detected in the root exudate of tall goldenrod (Xie et al., unpublished). The oxidized metabolite of CL, CLA (30) (Abe et al., 2014), has been detected in root exudates from various plant species. Some plant species such as poplar (Populus spp.) release MeCLA (31) (Yoneyama et al., 2017). These results indicate that CLA and MeCLA are likely involved in chemical communications in the rhizosphere. The model legume plant Lotus japonicus exudes the simplest canonical SL, 5DS (Akiyama et al., 2005), and also a non-canonical SL, tentatively named lotuslactone (methyl lotuslactonoate), whose structure will be reported elsewhere.

So far, less than ten non-canonical SLs have been characterized. It is likely, however, that many more will be identified, since they can be structurally more diverse than canonical SLs. In addition, we have only recently understood how to handle and protect non-canonical SLs from degradation during isolation and purification.

Most canonical SLs are C19 compounds except for acetoxyl derivatives such as orobanchyl acetate which contain additional two carbons, and sorgolactone, a C18 SL. In contrast, non-canonical SLs contain an additional carbon atom, except for CL and CLA, and thus are C20 compounds. It is likely that this additional carbon comes from the ester methyl group and therefore these non-canonical SLs appear to be derived from MeCLA or its isomers and their hydroxyl derivatives. Possible biosynthetic pathways for
non-canonical SLs are shown in Fig. 3. Non-canonical SLs containing a methoxycarbonyl group should be named methyl esters rather than lactones as in the case of MeCLA. In addition, their corresponding free acids may occur in plants and in their root exudates. However, for example, zealactone is much easier to pronounce and remember than methyl zealactonoate. The corresponding free acids for zealactone and heliolactone should be named zealactonoic acid and heliolactonoic acid, respectively.

Although both canonical and non-canonical SLs are chemically unstable, they may persist in the slightly acidic rhizosphere longer than would be expected in bulk soil (Bertin et al., 2003). In general, canonical SLs appear to be slightly more stable than non-canonical SLs. For example, except for 7-hydroxyorobanchols (18, 20), canonical SLs can be stored safely after organic solvents are completely evaporated. In contrast, it is better to store non-canonical SLs as solutions in organic solvents because even CL, the most stable non-canonical SL, decomposes very rapidly when concentrated. However, we detected highly unstable MeCLA in some samples sent from overseas, indicating that non-canonical SLs may be more stable when included in a mixture of various plant primary and secondary metabolites (Bertin et al., 2003). All of the plant species listed in Table 1 have been confirmed to exude CLA (Yoneyama et al., 2017).

In addition to the canonical and non-canonical SLs shown in Figs 1 and 2, Solanaceae plants, tomato, eggplant (Solanum melongena), potato (Solanum tuberosum), sweet pepper (Capsicum annuum), habanero (Capsicum chinense), and tobacco, exude four, four, five, five, and six isomers of putative didehydro-orobanchol, respectively, whose structures remain to be characterized.

SLs as plant hormones regulating shoot branching

In 2008, two research groups independently identified SLs or their further metabolites as a novel class of plant hormones inhibiting shoot branching or axillary bud outgrowth (Gomez-Roldan et al., 2008; Umehara et al., 2008). Since then, despite extensive studies, these true plant hormones have not unequivocally been identified.

This hormone was first suggested by Christine Beveridge through the forward genetic approach using several types of pea mutants impaired in axillary bud outgrowth (Beveridge, 2000). Reciprocal grafting experiments with wild type and mutants of pea and Arabidopsis revealed that this hormone is mainly produced in roots and transported
to shoots (Beveridge, 2006; Dun et al., 2009; Beveridge and Kyozuka, 2010). The most probable route of hormone transportation appeared to be the xylem, and indeed, a canonical SL orobanchol was detected in the xylem sap of tomato and Arabidopsis (Kohlen et al., 2011; Kohlen et al., 2012). However, no other laboratories could confirm this finding. We also collected relatively large volumes of xylem sap from several plant species but could not detect any known SLs in them. Furthermore, SLs fed to roots of rice plants were detected in the shoots harvested 20 h after treatment, but not in the xylem sap (Xie et al., 2015). These results indicate that SLs are transported from roots to shoots relatively slowly, although not through the xylem, but probably through hypodermis passage cells as in petunias where polar and asymmetric localizations of an ABC transporter, Petunia axillaris PLEITROPIC DRUG RESISTANCE 1 (PaPDR1), have been shown to mediate directional SL transport as well as localized exudation into the rhizosphere (Kretzschmar et al., 2012; Sasse et al., 2015).

As mentioned, rice produces only orobanchol-type SLs but tobacco produces both orobanchol- and strigol-types. When roots of these plants were treated with a mixture of four stereoisomers of 5DS (5DS, 4DO, and their enantiomers), only the orobanchol-type SL, 4DO, was detected in shoots of rice plants. However, both orobanchol- and strigol-type SLs, 4DO and 5DS, were detected in shoots of tobacco plants harvested 20 h after treatment, indicating that root to shoot transport of SLs is a structure- and stereo-specific process (Xie et al., 2016). Although root-applied strigol was not transported to shoots in rice plants, it did strongly inhibit rice tillering (Umehara et al., 2008), suggesting that the shoot branching inhibiting hormone is different from known canonical SLs. As mentioned earlier, the limited distribution of canonical SLs in the plant kingdom (Table 1) also supports this hypothesis.

What then, is this true hormone molecule? It should be noted that CL and its oxidized metabolites are widely distributed in the plant kingdom. Therefore, it is likely that these non-canonical SLs or their further metabolites function as plant hormones regulating shoot branching and other biological processes. For example, although root-applied strigol is not transported to shoots in rice plants, it may elicit release of hormone(s) which move shootward from cell to cell or through the xylem. This hypothesis can explain why root-fed GR5 (32), a synthetic SL containing only the C-D ring moiety, was highly active in inhibition of shoot branching but only weakly active
when applied to the axillary buds of *Arabidopsis* (Umehara *et al*., 2015). This implies that root-fed GR5 itself was not transported to the buds but GR5 strongly elicited release of the true hormone or signaling molecule(s) which moved upward to shoots. Unfortunately, in addition to the apparent scarcity, chemical instability makes isolation and structural determination of true hormone molecule(s) difficult. Furthermore, exogenous application of these molecules may not rescue a SL-deficient phenotype due to their instabilities. It is likely however that feeding experiments of candidate compounds or their precursors may provide insight into the identity of the hormone inhibiting the shoot branching.

**SLs as germination stimulants for root parasitic plants**

It is well known that SLs were originally identified as germination stimulants for root parasitic plants: witchweeds (*Striga* spp.) and broomrapes (*Orobanche* and *Phelipanche* spp.). Canonical and non-canonical SLs elicit *Striga* and *Orobanche* seed germination at as low as pM to µM concentrations. The seeds of various *Striga* and *Orobanche* species show different sensitivities to each SL (Kim *et al*., 2010; Kisugi *et al*., 2013) and plants in general do not release a single SL but a mixture of at least two SLs. For example, 11 different canonical SLs were detected in root exudate of tobacco (Xie *et al*., 2013; Xie, 2016). In addition to these canonical SLs, tobacco exudes the non-canonical SL, CLA. Therefore, it is likely that not a single SL but a SL mixture profile in the root exudate contributes to host-specific germination of root parasitic plant seeds. So far, effects of SL mixtures on seed germination stimulation have not been reported. There may be additive, synergistic, and antagonistic effects in mixtures of SLs on their germination stimulation activities. For example, root exudates of legumes that are good SL producers did not induce seed germination of *O. cumana*, indicating that an antagonistic effect occurs among SLs produced by leguminous plants on *O. cumana* seed germination (Fernández-Aparicio *et al*., 2011). This suggests that seed germination of a particular root parasite may be reduced or inhibited through modifications of the SL profile of a crop as in *Striga*-resistant sorghum cultivars (Gobena *et al*., 2017). In contrast, fractions from reverse phase high-performance LC separation of root exudates from English ivy (*Hederae helix*) that were active for *O. hederae* germination were not active for *O. minor* germination and vice versa (Kim *et al*., unpublished), indicating the presence of host-specific germination stimulants.
SLs as host recognition signals for AM fungi

Structural requirements for hyphal branching activity of canonical (Akiyama et al., 2010) and some non-canonical SLs (Mori et al., 2016) have been reported. In general, canonical SLs are more active than non-canonical SLs in inducing hyphal branching in Gigaspora margarita. Although CL is a weakly active branching factor, oxidation at C19 greatly enhanced its potency and CLA was as active as the typical canonical SL strigol (Mori et al., 2016). Since CLA has been detected in root exudates from various plant species, CLA can be considered the most common branching factor released from plant roots (Yoneyama et al., 2017). Then the question arises – why did plants develop canonical SLs? The chemical instability of CLA could be one reason, as it may decompose too rapidly to be sensed by AM fungi. In addition, CLA as a free acid may move and leach in soil more easily than do canonical SLs. These would have hampered precise host recognition by AM fungi and thus resulted in the evolution of canonical SLs. Characterization of SL receptor(s) in AM fungi and also in root nodule bacteria will shed light on why plants produce various canonical and non-canonical SLs.

Conclusion

The wider distribution of non-canonical SLs, in particular CLA, in plant root exudates than that of canonical SLs suggests that CLA and some non-canonical SLs may be more common than canonical SLs as rhizosphere signals. Although we reported detection of orobanchol in Arabidopsis root exudates (Goldwasser et al., 2008), we could not confirm this with our new MS system. Germination stimulants released from Arabidopsis roots (Goldwasser et al., 2000) may be CLA and its derivatives rather than canonical SLs. This in turn implies that soil microorganisms which have been exposed to these signaling molecules for 400 million years would utilize them as an energy source and modify them metabolically, in some cases, into more stable and active compounds like canonical SLs. Germination stimulation by rhizosphere soils would be due in part to these metabolites (Zhang et al., 2013). In addition, both canonical and non-canonical SLs and other short-lived rhizosphere signals would also be involved in plant–plant communications including self/non-self and kin-recognitions (Falik et al., 2003; Biedrzycki et al., 2014).
Acknowledgements

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Figure legends

Fig. 1. Structures of canonical strigolactones. Strigol-type (1–8, 23) and orobanchol-type strigolactones (9–22).

Fig. 2. Structures of non-canonical strigolactones and GR5 (32)

Fig. 3. Possible synthetic pathways for non-canonical strigolactones
Table 1. Distribution of canonical strigolactones (SLs) in the plant kingdom. SLs in italics need to be confirmed.

<table>
<thead>
<tr>
<th>Lycophyte</th>
<th>Spike moss (Selaginella moellendorfii)</th>
<th>Oroboran-type SLs</th>
<th>Strigol-type SLs</th>
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<tr>
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<td>4-deoxyorobanchol</td>
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<td>Gymnosperm</td>
<td>Japanese black pine</td>
<td>orobanchol, orobanchyl acetate</td>
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<td>Gingko</td>
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<td>Cedar</td>
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<td>Angiosperm</td>
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<td>Cucumber</td>
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