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A newly discovered Phytohormone: Strigolactones

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ABSTRACT

Plant hormones play a crucial role in controlling the way in which plants grow and develop. While metabolism provides the power and building blocks for plant life, it is the hormones that regulate the speed of growth of the individual parts and integrate them to produce the form that we recognize as a plant. Strigolactones are newly discovered plant hormones that influence diverse aspects of plant growth. Chemically these are sesquetepene lactones. These are host-root produced chemical signals that induce hyphal branching in germinating spores of Arbuscular mycorrhizal (AM Fungi), a process that is probably essential for the host-root colonization association with AM fungi. In addition to these functions, they also inhibit shoot branching. Furthermore, Strigolactones are suggested to have other biological functions in rhizosphere communications and in plant growth and development and recently, they are also found to be potentially positive regulators of light harvesting in plants. Strigolactones are having the physiological role of plant hormones. The well established Plant-hormones are Auxin, Gibberellins, cytokinins, and abscisic acid. Presently these hormones are being used extensively to modify the growth of cultured cell, in a desired way. Hence a possibility exists that in future these Strigolactones will find the same application(s) and may prove to be a turning point in research in Pharmaceutical Plant Biotechnology. Keeping this in mind this review has been compiled.

Keywords: Arbuscular mycorrhizal, Strigolactones, signaling, rhizosphere, host-root colonization, Plant hormone.

INTRODUCTION

The plant hormones are a structurally unrelated collection of small molecules derived from various essential metabolic pathways [1].Plants use hormones to regulate growth, mitigate biotic and a biotic stresses, and to communicate with other organisms. Many plant hormones function pleiotropically in vivo, and often work in tandem with other hormones that are chemically distinct [2]. During the last 15 years the number of known plant hormones has grown from five to at least ten [3]. Strigolactones are considered as a novel class of plant hormones [4]. Strigolactone production has been demonstrated in many plant species and has now been shown

to constitute the long-sought hormone that suppresses lateral branch formation [5].Synthesized mainly in the roots and lower part of the stem and then moving towards the shoot apex. Strigolactones have been shown to play a role in inhibition of shoot branching and thus to affect shoot architecture; they have also been shown to affect root growth and root system architecture [6]. The control of auxiliary bud outgrowth involves a network of hormonal signals and feedback regulation. Strigolactones moves upward in plant stems and can act as a long-distance messenger for auxin [7]. Besides this the majority of so far identified germination stimulants are Strigolactones [8]. These are as apocarotenoids [9] and have been suggested to be derived from the carotenoid pathway via the activity of various oxygenases [6].Strigolactones contain a labile ether bond that is easily hydrolyzed in the rhizosphere meaning that there is a large concentration gradient between areas near the root and those further away [10]. So having biological functions in rhizophore communication [11].Not only this, Seeds of some species that did not respond to GR24 were induced to germinate in the presence of fabacyl acetate or strigol, confirming the role of strigolactones in host specificity [12]. The natural Strigolactones 5-deoxy-strigol, sorgolactone and strigol, and a synthetic analogue, GR24, induced extensive hyphal branching in germinating spores of the AM fungus Gigaspora margarita at very low concentrations [13].

Search strategies:
We identified all English language phytochemical and pharmacognosy papers published, by the means of Pub med electronic database, Google by using the following search terms: Strigolactones, biosynthesis of strigolactones, shoot-branch inhibition, Seed germination by strigolactones, derivatives of sesquiterpenoid, strigolactones, symbiosis, hyphal branching, plant growth regulator, light harvesting genes. Study material from the year 2003 to 2010, has been collected. Only one reference from the year 1992 has been taken. Cross-references picked up during the review search were also selected if they were not included initially. Both studies present at meetings or congresses, with only abstract were not included.

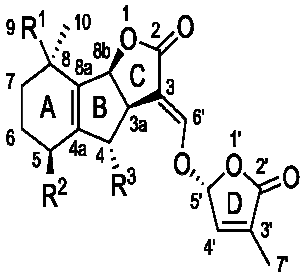
Isolation of Strigolactones:
The Strigolactones are produced by plants in extensively low quantity and may be unstable during the purification process. Therefore, the isolation, purification and structure elucidation are very difficult. So far nine Strigolactones are characterized. Strigol(1), Strigyl acetate(2), 5-deoxystrigol(3),Orobanchol(4), Orobanchyl acetae(5) Sorgolactone(6),2-epiorobanchol(7), Solanocol(8), Sorgomol(9).Strigolactones have been isolated from root exudates of variety of plants, including the monocots sorghum, maize and pros millet, and the dicots cotton, cowpea, red clover, Menispermum dauricum and Lotus japonicus. The Strigol, the first Strigolactone, was isolated from the root exudates of a false host, Cotton (Gossypium hirsutum L.), and also from an aseptic root organ culture of Menispermum dauricum DC. A Chinese medicinal, non host plant, Strigol is therefore produced by both host and non host plants. In contrast to Stigol, all of other natural Strigolactones, to date have only been isolated from host plants. Sorgolactone from Sorghum, alectrol from cowpea and orobanchol from red clover. It is likely that these strigolactones whole also be produced by non host plants [14]. Among the known Strigolactone, Sorgolactone was first isolated from root exudates of Sorghum Sorghum bicolor Linn. identified Strigol in the root exudates of host plants of striga, Sorghum, maize (Zea mays L.) and prosomilet (Pennisetum glaucum L.) [15]. In preliminary example however, a sorghum cultivar M 800 was found to produce an isomer of strigol but not strigol [16].

Biogenesis /Biosynthesis of Strigolactones:
The biogenesis of these unusual terpenoid lactones originally identified in minute quantities in the root exudates of a small number of host plants and two or three "false hosts" also remains obscure [17].little is known about the biosynthesis of strigolactones in plants, Inhibition of shoot

branching by new terpenoid plant hormones [18]. However it was known that the hormone was derived from the 2-CCDS-max3 and max4[19].During the study it was found that the branching phenotype of mutants in the Arabidopsis P450 family member, MAX1, can be fully rescued by strigolactone addition, suggesting that MAX1 acts in SL synthesis [20]. The plastid-localized carotenoid biosynthetic pathway is now known to play a key role in strigolactone biosynthesis [21]. MAX1, MAX3/RMS5/D17, and MAX4/RMS1/D10 are essential components for the biosynthesis of strigolactones, whereas MAX2/RMS4/D3 is involved in the perception of the signal. D27 is a new component of the MAX/RMS/D pathway and plays an essential role in biosynthesizing strigolactones. Based on the findings that the D27 protein is localized in chloroplasts and contains iron and the fact that the complex structure of strigolactones should undergo a number of enzymatic reactions, including hydroxylation, epoxydation, oxidation, etc., to achieve its biosynthesis so that D27 may participate in a redox reaction involved in the biosynthesis of strigolactones [22].Further it was to be suggested that Dioxygenase7 (CCD7) and Dioxygenase8 (CCD8) enzymes are believed to be the key steps at the beginning of the pathway [23].And this establishing an essential role for CCD7 and CCD8 in there synthesis [24]. Still it is known that limited-Pi conditions improve the production and/or exudation of strigolactones, there is no information concerning the effect of these conditions on the enzymes involved in strigolactone production. However, the SL biosynthesis pathway still needs to be uncovered [25].

Structure of Strigolactones:

Strigolactones are as sesquiterpene lactones. The structural core of the molecule is a tricyclic lactones (A, B and C rings) connected via an enol ether bridge to an α, β- un- saturated Furanone moiety (the D- ring) [26].Extensive studies on the structure–activity relationships of Strigolactones in germination stimulation of parasitic plant seeds have revealed that the C–D ring moiety is thought to be the essential structure for exhibiting biological activity. The introduction of substitutions on the A-B ring moiety of 5-deoxystrigol, the basic strigolactone, affords various strigolactones, e.g. hydroxylation on C-4, C-5 and C-9 leads to orobanchol, strigol and sorgomol respectively. Then, acetylation and probably other dramatizations of these hydroxy-strigolactones would occur. Although the C-2'-(R) stereochemistry was thought to be an important structural feature for potent germination stimulation activity [27].



Derivatives of Strigolactones:

Strigolactones have been isolated, and a number of structural analogues have been synthesized.5-Deoxy-strigol is the common precursor of these strigolactones and found both in monocots and dicots [28]. 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) [28]. 2-epiorobanchol was isolated from tobacco [29]. Further oxidation of the hydroxymethyl group of sorgomol and subsequently decarboxylation afford sorgolactone [30].A homoallylic hydroxylation of orobanchol and obrobanchyl acetate (5, R=H), leads to 7α and 7β hydroxyorobanchol (6, R=H) and other acetates [31]. These are oxidized to 7-oxo derivatives or dehydroxylation and migration of methyl group result in the formation of didehydro-orobanchol which leads to solanacol. [32]

Fabacylacetate, the first ent-strigolactone was found in pea root exudates [33]. New analogues derived from 1-indanone, 1-tetralone, cyclopentanone, cyclohexanone and a series of substituted cyclohexanones (including carvone and pulegone) are prepared by formylation of the ketones with ethyl formate followed by coupling with a halo butenolide. Both enantiomers of the analogue derived from 1- tetralone have been prepared by employing a homochiral synthon for the coupling reaction. For three other strigolactone analogues the antipodes have been obtained by chromatography on a chiral column. All analogues have an appreciable germinating activity towards seeds of *Striga hermomonthica* and *Orobanche crenata* and *cernua*. Stereoisomers having the same configuration at the D-ring as in naturally occurring strigol, have a higher stimulatory effect than the corresponding antipodes. The analogues obtained from 1- indanone and 1-tetralone have an activity comparable to that of the well known stimulant GR 24. Analogues derived from 2-phenyl-cylohexanone, carvone and pulegone also have a good germinating response[34].

Shoot branching inhibition by Strigolactones:

Hormones play a central role in shoot branching control [35].Branching pattern are determined by whether dormancy in bud is maintained or whether the bud is active to grow out into branch[36].The regulation of their outgrowth is a complex process that involves crosstalk among multiple hormones and signals moving within and between the root and shoot.[37].Shoot branching is a major determinant of plant architecture and is highly regulated by endogenous and environmental cues. Two classes of hormones, auxin and cytokinin, have long been known to have an important involvement in controlling shoot branching. Previous studies using a series of mutants with enhanced shoot branching suggested the existence of a third class of hormone(s) that is derived from carotenoids [38]. Strigolactones have recently been identified as the long sought-after signal required inhibiting shoot branching [39]. These endogenous strigolactones or related compounds inhibit shoot branching in plants [40]. It can be transported in shoots and act at low concentrations [41]. During the last century, two key hypotheses have been proposed to explain apical dominance in plants: auxin promotes the production of a second messenger that moves up into buds to repress their outgrowth, and auxin saturation in the stem inhibits auxin transport from buds, thereby inhibiting bud outgrowth The recent discovery of strigolactone as the novel shoot-branching inhibited bud outgrowth in pea (Pisum sativum) even when auxin was depleted after decapitation. Strigolactone application reduced branching in Arabidopsis (Arabidopsis thaliana) auxin response mutants, suggesting that auxin may act through strigolactones to facilitate apical dominance. Moreover, strigolactone application to tiny buds of mutant or decapitated pea plants rapidly stopped outgrowth, in contrast to applying N-1-naphthylphthalamic acid (NPA), an auxin transport inhibitor, which significantly slowed growth only after several days. Whereas strigolactone or NPA applied to growing buds reduced bud length, only NPA blocked auxin transport in the bud. Strigolactones do not act primarily by affecting auxin transport from buds. Rather, the primary repressor of bud outgrowth appears to be the auxin-dependent production of strigolactones [42].

Seed germination:

An essential step in parasitic seed germination is sensing a group of structurally related compounds called strigolactones that are released by host plants [43]. The bioactiphore in this strigolactone family of stimulants is deduced from a structure-activity relationship and shown to reside in the CD part of the stimulant molecule [44]. The induction of seed germination in parasitic weeds is thought to proceed via a receptor-mediated mechanism [45].A tentative molecular mechanism proposed for the stimulation of seed germination involves the addition of a nucleophilic species, present at a putative receptor site, to the enol ether carbon double bond in a Michael fashion, followed by elimination of the D ring Labeled strigolactone analogues were

synthesized for isolation and purification of the strigolactone receptor by affinity chromatography, though the receptor has not yet been isolated [46]. There is synthetic germination stimulant GR24 and it's a-ring di-methyl substituent. Further concluded that its dimethyl substituent is slightly less efficient than GR24 itself on Striga hermonthica seeds. [47]

Hyphal branching:

Arbuscular mycorrhizal (AM) fungi form mutualistic, symbiotic associations with the roots of more than 80% of land plants. The fungi are incapable of completing their life cycle in the absence of a host root. Their spores can germinate and grow in the absence of a host, but their hyphal growth is very limited. Little is known about the molecular mechanisms that govern signaling and recognition between AM fungi and their host plants [48]. Hyphal branching has long been described as the first morphological event in host recognition by AM fungi during the pre-infection stages. Host roots release signaling molecules called 'branching factors' that induce extensive hyphal branching in AM fungi. Signal exchange during symbiosis an a symbiotic cell constitutively releases root exudates, strigolactones[49] Strigolactones exuded from host roots have recently been identified as an inducer of hyphal branching in AM fungi.Strigolactones as well as non-strigolactone-type chemical signals were tested on the germinating spores of the AM fungus Gigaspora margarita. All tested compounds with tricyclic lactones coupled to a methylbutenolide via an enol ether bond showed activity, but differed in the active concentration and in the branching pattern of hyphae. Truncation of the A- and AB-rings in the tricyclic ABC lactones of strigolactones resulted in a drastic reduction in hyphal branching activity [50].Although the connection of the C-ring in the tricyclic lactones to the methylbutenolide D-ring was shown to be essential for hyphal branching, the bridge structure in the C–D part was found not necessarily to be enol ether, being replaceable. The natural strigolactones 5-deoxy-strigol, sorgolactone and strigol, and a synthetic analogue, GR24, induced extensive hyphal branching in germinating spores of the AM fungus Gigaspora margarita at very low concentrations [51].

Latest role of Strigolactone as positive light harvesting genes:

Light is vital for plant growth and development. To respond to ambient light signals, plants are equipped with an array of photoreceptors, including phytochromes that sense red (R)/far-R (FR) regions and cryptochromes and phototropins that respond to the ultraviolet-A/blue (B) region of the light spectrum, respectively. Several positively and negatively acting components in light-signaling pathways have been identified using genetic approaches [52]. Strigolactones are newly identified plant hormones, shown to participate in the regulation of lateral shoot branching and root development. However, little is known about their effects on biological processes, genes and proteins. GR24 treatment interferes with the root's response to IAA treatment and that strigolactones are potentially positive regulators of light harvesting in plants [53].Chemical genetic screening using Arabidopsis thaliana as a platform identified a collection of related small molecules, cotylimides, which perturb strigolactone accumulation. Suppressor screens against select cotylimides identified light-signaling genes as positive regulators of strigolactone levels. Molecular analysis. Showed strigolactones regulate the nuclear localization of the COP1 ubiquity ligase, which in part determines the levels of light regulators such as HY5. This information uncovers new functions for strigolactones [54].

CONCLUSION

The growth and development of plants is largely controlled by plant hormones. Plants produce these chemicals themselves, thus controlling the growth and development of roots and stems, for example. A number of plant hormones, such as auxins, gibberellins and cytokinins, were

discovered by scientists decades ago. There role in modifying the growth of cultured cell in desired way are well established. Presently, newer discovered Striglactones are best explored class of plant hormones. During the compilation of review it was studied there beneficial role as seed germinating stimulants, in shoot branching inhibition, hyphal branching production or newer role as a positive light harvesting genes. It was also concluded that a specific 'receptor reaction' for the strigolactones occurs in plants, a phenomenon that is characteristic for plant hormones. Not only this, plants are capable of transporting strigolactones internally and that the chemicals work at very low concentrations, two other typical characteristic of plant hormones. Studying these characteristics of this hormone we can assume that as other hormone works in culture techniques to modify plant cell in desired way these also may work in same manner alone or in together.Because they have physiological role of phytohormones, so possibility exists that they may in nearby future play a vital role in Plant tissue culture techniques in modification of cell culture in a desired way and may open new door in pharmaceutical plant biotechnology.

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