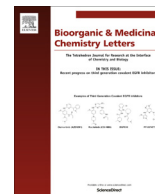




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Digest paper

Strigolactone derivatives for potential crop enhancement applications

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ABSTRACT

New technologies able to mitigate the main abiotic stresses (i.e., drought, salinity, cold and heat) represent a substantial opportunity to contribute to a sustainable increase of agricultural production. In this context, the recently discovered phytohormone strigolactone is an important area of study which can underpin the quest for new anti-stress technologies. The pleiotropic roles played by strigolactones in plant growth/development and in plant adaptation to environmental changes can pave the way for new innovative crop enhancement applications. Although a significant scientific effort has been dedicated to the strigolactone subject, an updated review with emphasis on the crop protection perspective was missing. This paper aims to analyze the advancement in different areas of the strigolactone domain and the implications for agronomical applications.

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High yield agricultural production systems are currently threatened by a wide range of biotic and abiotic stresses.¹ New crop protection solutions have been developed over the years to secure higher and more stable yields. These innovations span across conventional breeding to biotechnology solutions and also encompass new generations of agrochemicals. Chemical solutions to protect crops against biotic stresses (e.g., disease, pests and weeds) are a well-established segment which is reflected in the size of the global crop protection market which attained US\$ 56.7 billion in 2014.² However, there are only limited solutions currently available to mitigate abiotic stresses such as salt, drought and cold at different stages of crop development as well as nutrient deficiency. Crops respond to the above stresses by perception, signal transduction and regulation of genetic and metabolic pathways. Among all molecules involved in the adaptation of their structure and physiology, phytohormones play an essential role. In addition to the well-known phytohormones, very recently a new class has been identified: the strigolactones.³ The present paper aims to provide an overview of this very rapidly evolving domain of plant science and highlight the potential opportunities from a crop protection perspective.

Strigolactones have been first characterized in 1966 for their very potent activity to stimulate the germination of parasitic weed seeds.^{4,5} It has been previously recognized that parasitic weed seeds

as *Striga lutea* (witchweed) remain dormant even for years until germination is stimulated by a chemical signal produced by the host plant. The identification of the germination stimulant was the focus of intensive studies.⁶ In 1966, the first strigolactone has been isolated from the root exudates of cotton, which is not a host for *Striga* and was named (+) strigol.⁴ The isolation of the pure compound was very tedious due to its very low concentration in plant root exudates and to its relative sensitivity to acid and especially to base.⁴ The structure of natural (+) strigol was firmly confirmed by X-ray crystallography⁷ and its absolute stereochemistry was established by total synthesis.⁸ Strigol is the first identified representative of a sizeable class of terpenoids having a tetracyclic structure with three fused rings (A, B, C) containing a γ -lactone connected to a butenolide lactone (D-ring) through an enolether linkage (Fig. 1). Since this pioneering discovery, it has been found that land plants, including higher plants as well as non-vascular plants such as moss, liverworts and stoneworts produce a blend of several strigolactones with different structures and stereoisomers.^{5,9}

Initially, it was assumed that all strigolactones are structurally related with the stereochemistry of (+) strigol. However, as the result of isolation and characterization efforts performed on various plant species, it became apparent that in addition to the strigol prototypic sub-class, there is at least one other preeminent sub-class related to orobanchol (first isolated from red clover), which has the opposite absolute stereochemistry of the A,B,C-rings compared to strigol.⁵ Most representative strigolactones isolated

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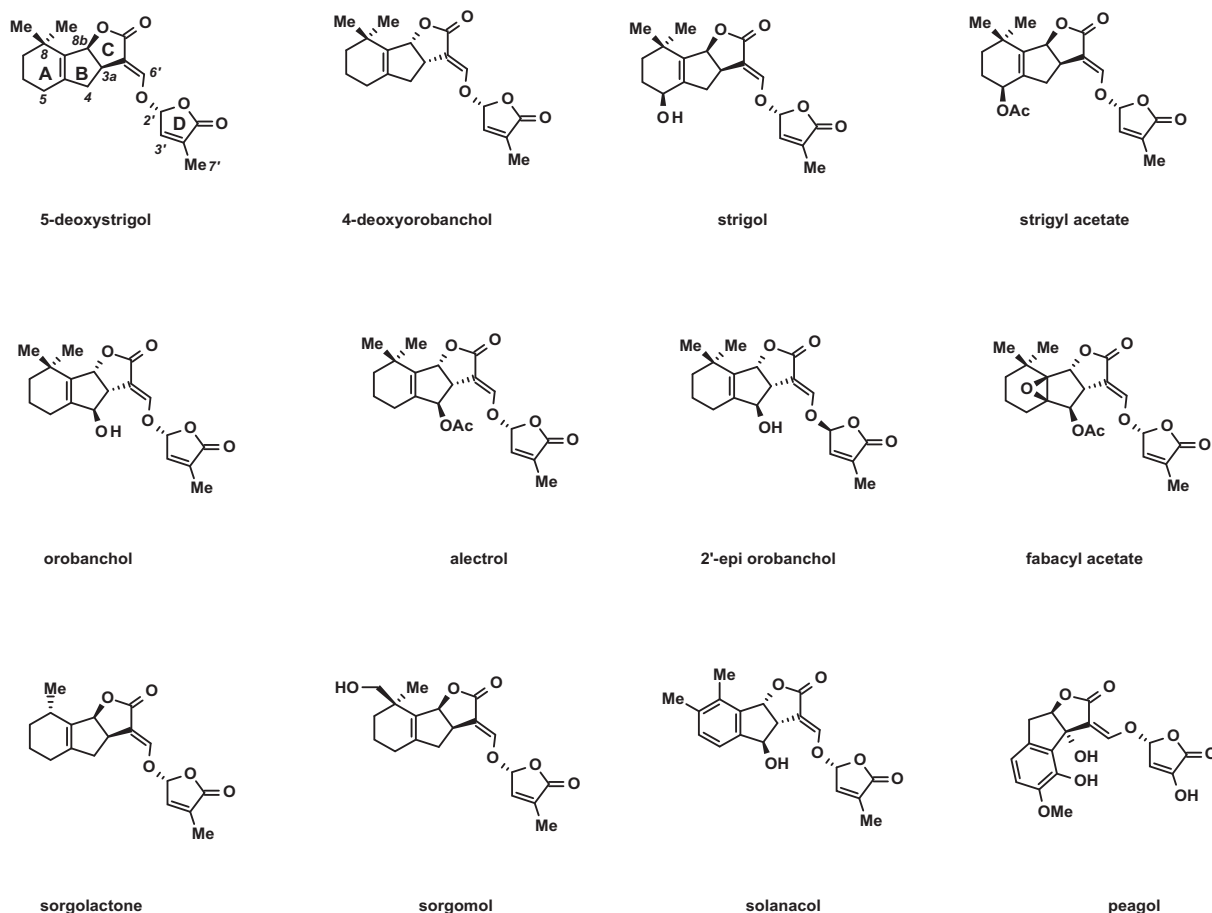


Figure 1. Representative strigolactones isolated from root exudates of plant.

from plants are shown in Figure 1. The list of natural strigolactones isolated from plants is still growing and they are all biosynthetically derived from 5-deoxystrigol for the strigol sub-class and from 4-deoxyorobanchol for the orobanchol sub-class.⁵

The main steps in the biosynthesis of strigolactones have been elucidated, although several transformations have not yet been fully characterized at the molecular level. Nevertheless, the existing data allow an understanding of the key features and key enzymes involved in the production of strigolactones in plants as well as uncovering the role of strigolactones in plant physiology, thanks to the analysis of the corresponding mutant plants.^{10,5}

Strigolactones are derived from all-trans- β -carotene through an isomerization into 9-cis- β -carotene mediated by the enzyme D27 (Fig. 2).¹⁰ 9-Cis- β -carotene is the substrate recognized by the carotenoid cleavage dioxygenase enzyme CCD7, which cleaves it into 9-cis- β -apo-10'-carotenal and β -ionone. A second carotenoid cleavage dioxygenase enzyme CCD8 is required for the transformation of 9-cis- β -apo-10'-carotenal into carlactone, a key intermediate in the strigolactones biosynthesis. In addition, carlactone is also a potential representative of an additional sub-class of natural strigolactones which are not transformed via cyclization into the tetracyclic framework but could play several physiological roles.^{10b} The transformation of carlactone into 5-deoxystrigol and/or 4-deoxyorobanchol is mediated by a CYP450 enzyme (MAX1 in *Arabidopsis thaliana*).^{10b} Further enzymatic oxidation/dehydration of the A- and B-rings lead to the various strigolactones isolated from plants (Fig. 1).

Strigolactones are mainly biosynthesized in roots, although other plant tissues are also able to produce them, and have been initially reported to be transported through the xylem.¹¹ Active

transport of strigolactones by the PDR1 protein, a member of the ABC transporter family, has been reported recently.¹² PDR1 is involved in strigolactone secretion into the rhizosphere and is also expressed near axillary buds suggesting that it could play a role in strigolactones loading from the xylem in the shoot.^{12a} However, a very recent study reveals that strigolactones are not detected in xylem saps of rice, tomato, cucumber, tobacco, sorghum and *Arabidopsis thaliana* suggesting that endogenous and exogenous strigolactones are transported from roots to shoots, but not through the xylem.^{12b}

Strigolactones are very potent germination stimulants of parasitic weed seeds.^{4,13} Parasitic weeds such as *Striga*, *Phelipanche*, *Alectra* and *Orobanche* genera infest many fields not only in Asia and Africa but also in the Mediterranean and black sea regions.¹³ The contamination of additional fields is due to the huge number of seeds produced during each weed plant cycle and the resistance of the parasitic seeds to a broad range of environmental conditions allowing them to remain dormant for many years until a strigolactone signal arising from a host plant root exudate stimulates their germination.¹³ After germination the parasitic weed will anchor itself on the host plant roots through haustorial penetration and after connection to the vascular system extract all nutrients required for its survival and development. This parasitic behavior causes severe damages to the crop and significant losses in economically important crops as maize, sorghum, millet and sunflower.¹³ For example, the *Orobanche cumana* (broomrape) infestation of sunflower has become one of the most significant challenges for growing this key crop in the whole black sea area, as well as in some parts of Spain, causing significant losses in yield.¹⁴ Several approaches have been explored to control parasitic

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