Strigolactones - Biology and Applications

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Editors

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# Acknowledgements

We strongly believe that this supplementary textbook, both printed book and e-book, may be attractive for graduate and postgraduate students and may help teachers and lecturers to better present and summarize strigolactone-related science and the new emerging concepts.

Finally, we would like to thank all the authors and reviewers for accepting our invitation to contribute to this textbook, the first published so far and entirely dedicated to SLs. Special thanks go to all those scientists who are not formally authors of this book but with their research and their outstanding publications contributed and are still contributing to dissect the still unveiled aspects of this challenging class of molecules and paved the way to possible exploitation in many different fields.

We had the opportunity and pleasure to personally meet most of these scientists in the framework of the COST Action FA1206 "Strigolactones: biological roles and applications". The numerous meetings, workshops and Short-Term Scientific Missions organized thanks to the COST tool allowed us to create synergies among scientists of different expertise and cultural background, enabled new collaborations and established a community of people working on common and shared aims in the name of science.

# Introduction

## Strigolactones: New Plant Hormones and Much More…

Plants produce and release various chemicals into the environment, as well as primary and secondary metabolites. Abiotic and biotic stresses affect the composition and the amount of these compounds by promoting or suppressing their biosynthesis and/or efflux.

*Strigolactones* (SLs) are typical examples of such signalling molecules. Plants release only very small amounts of SLs into the soil, and these molecules decompose rapidly in the rhizosphere. SLs can only be analysed and quantified using recently developed highly sensitive mass spectrometry methods and were originally isolated as germination stimulants for seeds of parasitic weeds of the family *Orobanchaceae*. Therefore, these compounds were regarded as harmful secondary metabolites since they were detrimental to the producing plant. It has been subsequently shown that SLs act as indispensable chemical signals for root colonization by symbiotic arbuscular mycorrhizal (AM) fungi and then became recognized as beneficial plant metabolites.

However, only recently they were recognized as plant hormones that regulate different aspects of plant development, among others as mediators of plant response to abiotic conditions. This recognition led to a dramatic increase in the interest in these new plant hormones, and to thriving research on different biological aspects of these hormones, from different disciplinary fields including their signal transduction, reception and biosynthesis, evolution and genetic regulation. This blooming research unveiled both already existing and new biological concepts, such as redefinition of plant hormones and their crosstalk, new functional diversity of receptors, evolvement of plants to parasitic life habit, smoke and hormone mirrors, core signalling pathways and even phloem transport of receptor protein. Another important aspect of SLs is their developed synthetic chemistry and the opening of a variety of potential applications in agriculture and medicine.

Yet, despite the thriving scientific activity on SLs, our and other scientists' experience suggested that many university and college students and lecturers of plant sciences are not fully aware of SL-related sciences. As a result, these subjects are not being properly conveyed to the next-generation scientists in many different countries.

The above considerations led to the idea of composing a supplementary graduate textbook that addresses teachers, lecturers and biology and agronomy students. The challenge in undertaking the project of writing a textbook on SLs was to write a book whose structure develops around ideas from very different disciplinary fields, rather than presenting a sequence of facts.

We decided to organize the book into six chapters, from SL biosynthesis and perception, to the role of SLs as plant hormones, as parasitic weed germination and hyphal branching inducers respectively, to the chemistry and the stereochemical aspects of natural and synthetic SLs. A full chapter has been dedicated to the involvement of SLs in evolution aspects. Each chapter has been conceived to stand by itself with its general introduction, which enables the reader to look deeply into the specific aspects addressed by every single chapter. Each chapter conveys a certain topic to allow a broad view on each of the presented subjects. Authors and co-authors are the leading scientists in these subjects from around the world and were able to give an accurate, deep and comprehensive view of the subjects. Glossary and synopses that may ease comprehension of the related terms and concepts are also included in each chapter. Given that SLs are a cutting-edge topic nowadays and the literature updates every day, the most relevant literature references embedded in the text enable even non-expert readers to go directly to the focus of their interest. Illustration and figures are provided to better demonstrate the presented topics.

## Chapter 1: Strigolactone Biosynthesis and Signal Transduction

Kun-Peng Jia, Changsheng Li, Harro J. Bouwmeester, and Salim Al-Babili

In this chapter, the authors provide an overview on the enormous progress that has been recently made in elucidating SL biosynthesis and signal transduction. They described the tailoring pathway from the carotenoid precursor to the central intermediate carlactone, highlighting the stereo-specificity of the involved enzymes, the all-*trans*/9-*cis*-β-carotene isomerase (D27), the 9-*cis*-specific CAROTENOID CLEAVAGE DIOXYGENASE 7 (CCD7) as well as CCD8 and its unusual catalytic activity. They then outline the oxidation of carlactone by cytochrome P450 enzymes, such as the Arabidopsis MORE AXILLARY GROWTH 1 (MAX1), into different SLs and the role of other enzymes in generating this diversity, and discuss why plants produce many different SLs. This is followed by depicting hormonal and nutritional factors that regulate SL biosynthesis and release and by a description of transport mechanisms. In the second part of the chapter, the authors focus on SL perception and signal transduction, describing the SL receptor DECREASED APICAL DOMINANCE 2 (DAD2)/DWARF14 (D14) and its unique features, the central function of protein degradation mediated by the F-box protein MAX2 and its homologues. They also discuss the latest advances in understanding how SLs regulate the transcription of target genes and the role of SMXL/D53 transcription inhibitors.

## Chapter 2: Strigolactones as Plant Hormones

Catherine Rameau, Sofie Goormachtig, Francesca Cardinale, Tom Bennett, and Pilar Cubas

This chapter presents SL activity as a new class of plant hormones. The authors present evidence to support a role for SLs in regulating aerial and underground plant architecture: they repress shoot branching, promote internode elongation and height, affect gravitropic setpoint angle, control secondary growth in stems and affect leaf shape and leaf serration, reproductive organ size, control of flowering time, leaf morphology and tuberization. SLs also regulate root architecture, adventitious root development and root hair development. SLs are involved in plant response to abiotic stress, including nutrient deprivation and osmotic stress. Also, SL crosstalk with other plant hormones is introduced and discussed. An emphasis is being put on "direct" interactions between SLs and other hormones, and this is rationalized in terms of SL functionality. SLs and interacting hormones are characterized as a systemically acting platform that regulates development and responses to soil conditions. It is stated that the impact of SLs on key developmental processes, such as plant architecture and their involvement in the acclimation of plants to environmental stresses, raises the possibility of using these hormones and signalling pathways as agricultural tools to optimize crop plant architecture and resilience to abiotic stress.

## Chapter 3: Strigolactones and Parasitic Plants

Maurizio Vurro, Angela Boari, Benjamin Thiombiano, and Harro Bouwmeester

A parasitic plant is a flowering plant that attaches itself morphologically and physiologically to a host (another plant) by a modified root (the haustorium). Only about 25 out of the 270 genera of parasitic plants have a negative impact on agriculture and forestry and thus can be considered weeds. Among them, the most damaging root-parasitic weeds belong to the genera *Orobanche* and *Phelipanche* (commonly named broomrapes) and *Striga* (witchweeds) (all belonging to the Orobanchaceae family). Considering the aim of the book, this chapter focuses only on this group of parasitic weeds, as in these plants SLs have a key role both in their life cycle and in management strategies to control them. Distribution, agricultural importance and life cycle of these parasitic weeds are briefly introduced, after which the authors focused on the role of SLs in seed germination, parasite development, host specificity, plant nutrition and microbiome composition. Furthermore, some weed control approaches involving SLs are discussed.

## Chapter 4: The Role of Strigolactones in Plant–Microbe Interactions

Soizic Rochange, Sofie Goormachtig, Juan Antonio Lopez-Raez, and Caroline Gutjahr

Plants associate with an infinite number of microorganisms that interact with their hosts in a mutualistic or parasitic manner. Evidence is accumulating that SLs play a role in shaping these associations. The best described function of SLs in plant–microbe interactions is in the rhizosphere, where, after being exuded from the root, they activate hyphal branching, enhanced growth and energy metabolism of symbiotic arbuscular mycorrhizal fungi (AMF). Furthermore, an impact of SLs on the quantitative development of root nodule symbiosis with symbiotic nitrogen-fixing bacteria and on the success of fungal and bacterial leaf pathogens is beginning to be revealed. Thus far, the role of SLs has predominantly been studied in binary plant–microbe interactions. It can be predicted that their impact on the bacterial, fungal and oomycetal communities (microbiomes), which thrive on roots, in the rhizosphere and on aerial tissues, will be addressed in the near future.

## Chapter 5: Evolution of Strigolactone Biosynthesis and Signalling

Sandrine Bonhomme and Mark Waters

In this chapter, the authors present the current knowledge on when and how SLs originated and what functions they have in non-seed plants. Although this field is still much in its infancy, rapid advances are being made in the acquisition and interpretation of data and information. These advances lead to several emerging concepts that are conveyed in this chapter. The evolution of land plants is suggested to be associated with increases in developmental complexity, brought about by diversification of gene families and hormone signalling pathways. Good model species for the study of early diverging land plants are the moss *Physcomitrella patens* and the liverwort *Marchantia polymorpha*. Also, with minor exceptions, the core enzymes for SL biosynthesis via carlactone are present in all land plants. This suggests that SLs, or SL-like compounds, are common to all land plants. However, while SLs have a clear developmental/hormonal role in angiosperms, the function of SLs in early land plants is equivocal. Some receptor enzymes that perceive SLs and/or SL-like compounds predate land plants and have undergone substantial duplication throughout land plant evolution, whereas others essential for SL perception in angiosperms are not required in moss. It is also presented and discussed that parasitic weeds demonstrate evolution in action.

## Chapter 6: The Chemistry of Strigolactones

Cristina Prandi and Christopher S. P. McErlean

SLs are a group of small molecules which were first reported after isolation from the root exudates of cotton in 1966. These compounds were potent germination stimulants of the parasitic witchweed (*Striga lutea* Lour.), which has an economically devastating effect on many important crops. As such, SLs captured the attention of chemists who sought to (1) determine the structures of these molecules, (2) synthesize the molecules and (3) synthesize molecules that mimic the biological actions of natural SLs. This chapter highlights the progress that has been made in each of these areas, which can collectively be categorized as "the chemistry of SLs".

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# About the Editors

**Prof. Hinanit Koltai**, PhD, is a Senior Research Scientist at the Agricultural Research Organization, Volcani Center, Israel. She is the Editor of books and a member of Editorial boards in international scientific journals. She is a leading Author of more than 80 peer reviewed publications and more than 30 book chapters and invited reviews and she holds more than 10 patents. Research in Koltai lab is focused on plant hormones and medicinal plants, specifying their medical influence at the molecular level on human cells and tissue. She teaches plant development and medical cannabis courses in Bar Ilan University, Israel.

**Cristina Prandi** is a Full Professor of Organic Chemistry at the University of Torino, where she also serves as Deputy Director for Research. Her main interests are in organometallic chemistry, gold catalysis and target-oriented synthesis. She has conducted research on the synthesis of bioactive phytohormone analogues, focusing on SAR (structure–activity relationship) studies and the design of active derivatives. Recently, she has also investigated the use of plant metabolite analogues for their potential anticancer benefits. She is the author of more than 100 scientific publications and holds three patents.

Prof. C. Prandi and Prof. H. Koltai chaired a COST ACTION exclusively dedicated to strigolactones (FA1206 2012–2017, Strigolactones, biological roles and applications).