C. R. Biologies 333 (2010) 344–349

Contents lists available at ScienceDirect

Comptes Rendus Biologies

www.sciencedirect.com

Plant biology and pathology/Biologie et pathologie végétales

Strigolactones, a novel class of plant hormone controlling shoot branching

Les strigolactones, une nouvelle classe d'hormones végétales contrôlant la ramification

Catherine Rameau

INRA, institut Jean-Pierre Bourgin, UMR1318 INRA-AgroParisTech, INRA Centre de Versailles-Grignon, 78026 Versailles cedex, France

ARTICLE INFO

Article history:
Available online 16 March 2010

Keywords:
Strigolactones
Branching
Plant architecture
Apical dominance

Mots clés :
Strigolactones
Ramification
Architecture de la plante
Dominance apicale

ABSTRACT

For several decades, auxin and cytokinin were the only two hormones known to be involved in the control of shoot branching through apical dominance, a process where the shoot apex producing auxin inhibits the outgrowth of axillary buds located below. Grafting studies with high branching mutants and cloning of the mutated genes demonstrated the existence of a novel long distance carotenoid derived signal which acted as a branching inhibitor. Recently, this branching inhibitor has been shown to belong to the strigolactones, a group of small molecules already known to be produced by roots, exuded in the rhizosphere and as having a role in both parasitic and symbiotic interactions.

RÉSUMÉ

Depuis les années 1930, l'auxine et les cytokinines étaient les deux seules hormones connues pour être impliquées dans le contrôle de la ramification des plantes par le processus de la dominance apicale par lequel l'apex de la tige, producteur d'auxine, inhibe le démarrage des bourgeons axillaires sous-jacents. Des expériences de greffes avec des mutants hyper-ramifiés et le clonage des gènes mutés ont permis de démontrer l'existence d'un nouveau signal dérivé de caroténoides agissant à longue distance et réprimant la ramification. Récemment, il a été démontré que cet inhibiteur de la ramification fait partie des strigolactones, groupe de petites molécules déjà connues pour être produites par les racines des plantes et exsudées dans la rhizosphère où elles jouent un rôle dans des interactions parasitaires et symbiotiques.

1. Introduction

Land plants are fixed organisms which have to integrate multiple endogenous and environmental factors to coordinate the differentiation and development of their different parts according the environmental conditions. This coordination is based on the action of small signaling molecules which act at very low concentrations and provide a means of communication between cells and organs. The 'classical' phytohormones, identified during the first half of the twentieth century, are auxin, abscisic acid, cytokinin, gibberellin and ethylene. More recently, several additional compounds have been recognized as hormones, including brassinosteroids, jasmonate, salicylic acid and nitric oxide [1]. It is very likely that others have to be identified with a more specific role in the different processes of plant development.

In plants, during post-embryonic development, meristems are initiated at the axils of leaves that will develop a few nodes (short internodes and leaves) to give axillary buds. Many factors will influence the fate of each bud, such

---

E-mail address: Catherine.Rameau@versailles.inra.fr.

1631-0691/$ – see front matter © 2010 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crvi.2010.01.012

as nutrition, photoperiod, plant density (quality of light), or position of the axillary bud itself along the main stem. For each axillary bud, integration of these factors will result in its outgrowth to give a branch or to its maintenance in a dormant state. Recently, the study of high-branching mutants in several species has demonstrated the existence of a novel, graft-transmissible signal, which acts as a branching inhibitor. This work has culminated in the recent identification of this branching inhibitor as a strigolactone, or derived compound which suppresses the outgrowth of a bud located at the axil of leaves [2,3].

2. The classical theory of apical dominance

Before the use of developmental mutants, early studies of shoot branching in the 1930s focussed on decapitation-induced bud outgrowth [4]. The pea was one of the first systems used to study apical dominance. During the vegetative phase, most pea cultivars present dormant axillary buds at most nodes and axillary buds separated by long internodes make such studies easy. After decapitation, axillary buds that were dormant enlarge and start to grow. The term 'apical dominance' was used because the removal of the shoot apex leads to the release of dormant axillary buds to form branches. Auxin application studies provided evidence that the hormone auxin, produced in the shoot tip, was involved in the inhibition of axillary bud outgrowth at nodes below [4]. The development of these new stems, also activated by cytokinin produced in roots, allows the plant to survive and to reproduce. The presence of dormant axillary buds at the axil of each leaf and the mechanism of apical dominance have probably evolved in plants as a survival response to herbivory. For several years, auxin and cytokinin were known as the only two hormones controlling branching through apical dominance. Further studies led to the hypothesis that auxin required a second messenger, to inhibit branching [5]. In particular, the two-shoot experiments from Snow [5] suggested that this unknown long-distance signal was moving in the plant with a root-to-shoot direction very likely in the xylem. These "two-shoot" plants were obtained by decapitation of young pea or *Vicia faba* seedlings to get two similar cotyledonary shoots. When only one cotyledonary shoot was decapitated, the axillary buds on this shoot were inhibited by the apex of the second intact shoot.

More than a decade ago, the detailed physiological characterization (grafting, hormone quantifications) of the high-branching *rms* pea mutants, demontrated the existence of a novel signal, in addition to auxin and cytokinin, which represses axillary bud outgrowth.

3. Existence of a novel carotenoid derived branching inhibitor

3.1. The genetic approach

In several species, screening for high branching (tillering in rice) mutants led to the identification of the *more axillary growth* (*max*) mutants in Arabidopsis, the *ramosus* (*rms*) mutants in pea (Fig. 1), the *dwarf* (*d*) mutants in rice and the *decreased apical dominance* (*dad*) mutants in Petunia (*Petunia hybrida)* [6–9]. The mutations are all recessive and relatively non pleiotropic. The other characters affected are the stem width and the height of the plant, particularly in rice where the mutants were called *dwarf (d)* or *high tillering dwarf (htd)* mutants. These other effects were supposed to be linked to the high branching of the plant. In Arabidopsis, 4 *MAX* genes were identified and 5 *RMS* genes in pea.

3.2. Grafting experiments with the ramosus (rms) high branching mutants from the pea

Grafting has long been used to study long-distance transport and signaling between different plant tissues. In the pea, epicotyl wedge grafting using 7-day-old plants is very easy to perform. When the *rms1* (or *rms5*) mutant shoot is grafted on a wild-type rootstock, branching in the scion is repressed (Table 1). This result suggested the existence of a graft-transmissible signal produced in WT rootstock able to repress bud outgrowth in mutant scion. The reciprocal graft demonstrated that the signal is also produced in shoots, because WT shoots did not branch when grafted to mutant rootstocks [10]. Whereas branching is inhibited in shoots of reciprocally grafted mutant and WT plants, it is not inhibited in reciprocal grafts between *rms1* and *rms5* (Table 1). This result suggested that the *RMS1* and *RMS5* genes control the biosynthesis of the same graft-transmissible signal and that they have to act in the same tissue [11]. In contrast, when *rms3* or *rms4* mutant shoot is grafted on a WT rootstock, branching is not inhibited (Table 1). These mutants could be considered as response mutants [6]. More complex two-shoot grafts with WT and *rms1* shoots growing from the same *rms1* rootstock and showing different branching phenotypes provided

Fig. 1. Pea *rms1* high branching mutant plant (right) and wild-type plant (left).