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Auxin: A major regulator of organogenesis

L'auxine : un régulateur majeur de l'organogenèse

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ABSTRACT

Plant development is characterized by the continuous initiation of tissues and organs. The meristems, which are small stem cell populations, are involved in this process. The shoot apical meristem produces lateral organs at its flanks and generates the growing stem. These lateral organs are arranged in a stereotyped pattern called phyllotaxis. Organ initiation in the peripheral zone of the meristem involves accumulation of the plant hormone auxin. Auxin is transported in a polar way by influx and efflux carriers located at cell membranes. Polar localization of the PIN1 efflux carrier in meristematic cells generates auxin concentration gradients and PIN1 localization depends, in turn, on auxin gradients: this feedback loop generates a dynamic auxin distribution which controls phyllotaxis. Furthermore, PIN-dependent local auxin gradients represent a common module for organ initiation, in the shoot and in the root.

RÉSUMÉ

Le développement végétal est caractérisé par la production d'organes tout au long de la vie de la plante. Cette organogenèse continue est permise par des massifs cellulaires organisés, les méristèmes, véritables niches de cellules souches. Le méristème apical caulinaire produit toute la partie aérienne de la plante, organes et tige. Les organes latéraux, feuilles ou fleurs, sont initiés sur les flancs du méristème, dans la zone périphérique, selon une disposition stéréotypée appelée phyllotaxie. L'auxine, hormone végétale transportée de façon polarisée dans les tissus, induit l'initiation d'organes à ses sites d'accumulation dans la zone périphérique du méristème. La distribution de l'auxine dans le méristème suit des gradients de concentration établis par les transporteurs d'efflux de l'auxine PIN1. La localisation cellulaire polarisée de ces transporteurs change au cours de la croissance du méristème, probablement en réponse aux gradients d'auxine ; la distribution de l'auxine évolue ainsi dynamiquement et permet l'initiation des organes aériens selon une phyllotaxie. Les gradients locaux d'auxine établis par transport polarisé sont aussi impliqués dans l'initiation des racines latérales.

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Abbreviations

SAM	shoot apical meristem
IAA	indole-3-acetic-acid
PIN	pin-formed
LFY	LEAFY
ANT	AINTEGUMENTA
CUC	CUP-SHAPED COTYLEDONS
NPA	naphthylpthalamic acid
LAX	Like AUX1
PID	pinoid
PLT	plethora

1. Introduction

In higher plants, post-embryonic development is characterized by the continuous production of tissues and organs during the whole plant life. Histogenesis and organogenesis involve apical zones of cells established during embryogenesis at the opposite poles of the plant embryo which are called meristems. The mitotic activity of pluripotent stem cells located in those meristems permits organ initiation. By comparison with animal stem cells, plant meristems are now considered as stem cell niches, i.e. cellular microenvironments that provide the signals and physical support to maintain stem cells [1]. Consequently, plant development depends on the organization, localization and maintenance of those stem cell niches, which involve several regulatory mechanisms including hormone signaling. The hormone auxin, from the Greek word "*auxo*" to increase (grow), induces various growth responses in plants. It has been identified at the end of the XIX century by the Darwins studying the phototropism of canary grass coleoptiles. Auxin is implied in many developmental processes by inducing cellular and molecular modifications such as cell expansion, cell proliferation or transcription. In this short review, we will focus on the role of auxin in organogenesis at the SAM. Hereby, we will focus on the angiosperms, which have been best characterised.

2. Organogenesis at the SAM

The SAM produces lateral organs, such as leaves, and a growing stem. The SAM is a multilayered structure composed of up to three (sometimes even more) clonally distinct layers of cells, L1 to L3. The descendants of the L1 cells preferentially generate the epidermis, L2 cells produce sub-epidermal tissues and gametes whereas the L3 cell lineage will form inner stem tissues and lateral organs (for a review, see [2]). Organogenesis relies on spatially and temporally coordinated cell proliferation in the SAM. Differences in mitotic activities underline the existence of three cytological zones in the SAM which overlap the layered partitioning [3,4]: the peripheral zone on the sides, the central zone at the apex and the rib zone formed by the internal cells beneath the apex. These zones have different functions. Organ initiation takes place in the peripheral zone and the internal tissues of the stem (pith and vascular system) are formed in the rib zone. Stem cells located in the central zone divide and part of their daughter-cells are displaced into the peripheral and rib zones so as to replenish those regions; the other daughter-cells stay in the central zone and maintain a stem cell pool for future growth. The size of the stem cell pool is controlled by an underlying organizing center, marked by the expression of the transcription factor WUSCHEL, and a regulatory loop involving WUSCHEL and the CLAVATA receptor kinase pathway signaling cascade. ([1,5–7], for detailed reviews on the SAM).

Organ initiation begins with the selection of a group of founder cells in the peripheral zone, followed by the outgrowth of the incipient primordium and then the morphogenesis into a differentiated organ. Studies on living meristems revealed that initial primordium outgrowth is associated with oriented cell divisions; cell proliferation and cell expansion increase once the primordium outgrowth has started [4]. Organ boundaries with the SAM are marked by reduced cell expansion and division [4,8]. These patterns of cellular behavior are correlated with patterns of gene expression. In the organ founder cells, the *KNOX* meristematic genes, in particular SHOOT-MERISTEMLESS (STM), are down-regulated [9,10]; these founder cells then start to express the ANT and the LFY transcription factors respectively associated with organ outgrowth and identity [11,12]. In the same time, the three CUC transcription factors are expressed in the boundary [13–15]. (for reviews, see [16] and [17,18] in this issue).

Lateral organs are arranged in regular patterns around the stem, a phenomenon called phyllotaxis from the Greek words "*phyllo*", leaf and "*taxis*", order. Various phyllotactic patterns are encountered in nature, namely alternate, opposite and spiral. Spiralled phyllotaxis, the most widespread one, follows a mathematical rule: consecutive lateral organs are formed with an angle close to 137.5°, the golden angle defined by the Fibonacci numbers [19]. At the *Arabidopsis* SAM, the first four leaves are formed as opposite pairs and then leaves and flowers follow such a spiraled phyllotaxis (Fig. 1).

What is the mechanism behind this regular spacing between primordia? Historical surgical experiments, consisting in removing an existing primordium, demonstrated that existing primordia determine future sites of organ initiation in adjacent regions of the SAM (for a review, see [20]). These results and others support a lateral inhibition model where developing organs and the centre of the meristem produce an inhibitory signal that acts locally to prevent organ formation. Due to the growth, existing organs move away from the meristem; new primordia can develop, far from the repelling effect (Fig. 1). This inhibitory field theory of phyllotaxis was postulated 80 years ago but the nature of the signal or signals involved remained unknown until recently. In this short review, we focus on the function of a very important signal, the plant hormone auxin (for detailed reviews on phyllotaxis [21–24]).

3. Auxin synthesis and transport

The major form of auxin identified in plants is IAA. Meristems, young primordia, vascular tissues and