5- BOURGEONS AXILLAIRES

- A l'aisselle de chaque feuille, du côté adaxial
- Mutation dominante phb:
  - 2 faces adaxiales
  - bourgeons axillaires de part et d'autre de la feuille

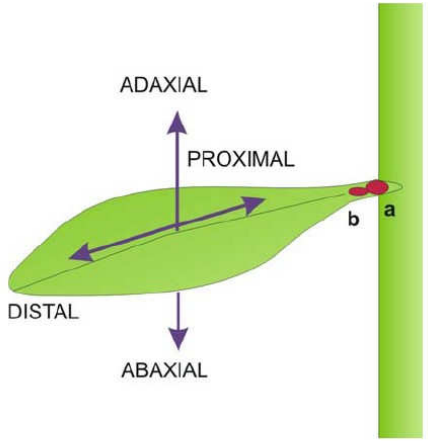


Figure 1. Schematic representation of the axil of a leaf. The axil is the region between leaf and stem, on the adaxial surface. The more proximal red circle (a) represents the site of the axillary meristem. The more distal circle (b) represents the site of the accessory meristem – effectively a secondary axillary meristem. Some species have multiple accessory meristems per axil (e.g., pea (*Pisum sativum*)).

Développement des bourgeons axillaires

1- Formation d'un **méristème axillaire** à partir d'un petit groupe de cellules situées à l'aisselle des feuilles, du côté adaxial, c'est-à-dire à la frontière entre le SAM et le primordium de feuille

2- Fonctionnement **pour une durée limitée** (dominance apicale) du méristème axillaire

→ mise en place d'un certain nombre de feuilles (plus exactement d'ébauches foliaires) pour former un **bourgeon axillaire**.

3- Eventuellement: Reprise de l'activité du bourgeon axillaire (phénomène nommé « **débourrement** ») pour former une tige feuillée sous contrôle de facteurs externes et internes.

Le fonctionnement des bourgeons axillaires détermine l'architecture de toute la plante. L'architecture dépendra de 2 facteurs :

- l'initiation de la formation des méristèmes axillaires
- la régulation de la reprise d'activité des bourgeons axillaires.

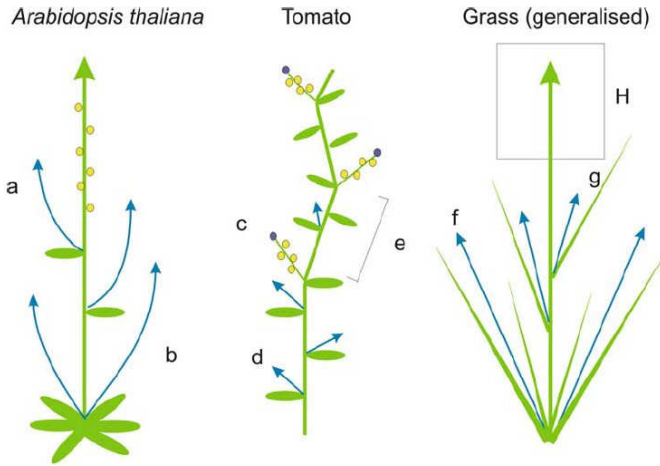


Figure 2. Schematic representations of Arabidopsis thaliana, tomato and a generalised grass; (a) cauline branch, (b) rosette branch, (c) determinate inflorescence, (d) axillary shoot, (e) sympodial shoot, (f) tiller, (g) axillary panicle, (h) primary panicle – see Figure 3. Green lines – primary axes; blue lines – axillary branches; arrows – active indeterminate meristems; purple circles – active determinate meristems; orange circles – dormant meristems; red circles – degenerate/cryptic meristems, yellow circles – flowers.

La mise en place et la reprise d'activité des bourgeons axillaires sont contrôlées par des gènes spécifiques

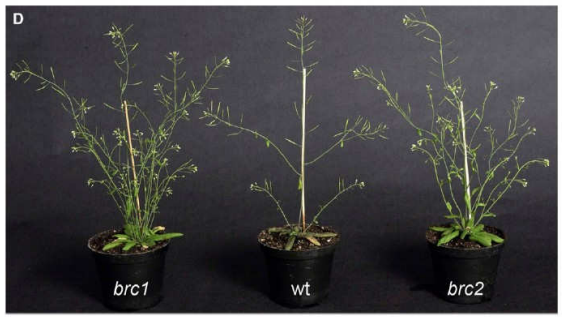
- **Initiation:** les cellules qui formeront le méristème axillaire expriment les gènes *LAS (LAteral Suppressor)* et ***STM:***

  LAS est un activateur de la transcription de *STM*

  mutant las → ↓ STM → ↓ nombre de méristèmes axillaires

- Le produit du gène ***BRC1*** (*Branched1*) est un RT exprimé dans le bourgeon axillaire et qui arrête son développement:

  mutant bcr1 → ↑ nombre de bourgeons reprenant leur activité → ↑ ramifications



- Plusieurs facteurs **hormonaux et externes** contrôlent aussi la dormance/reprise d'activité du bourgeon axillaire:
  - **auxine** (dominance apicale)
  - densité des plantes
  - **SMS** (Shoot Multiplication Signal): les gènes *MAX1-4* (*More Axillary Growth*) contrôlent la synthèse, dans les racines, et la réponse à un signal chimique (**strigolactones** - dérivé de caroténoïdes) qui maintient la dormance du bourgeon
- Le gène *BRC* agit comme intégrateur des différentes informations

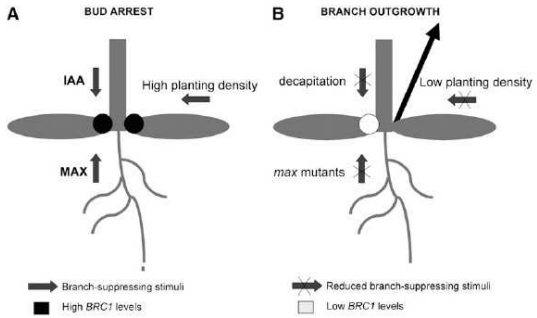


Figure 8. Scheme of *BRC1* Function in the Control of Bud Outgrowth.

Under adverse conditions, branch-suppressing signals are transduced into the bud, resulting in the upregulation of *BRC1* and bud arrest **(A)**. In the absence of these signals, *BRC1* is downregulated and shoots grow out **(B)**. IAA, indole-3-acetic acid.

Résumé: Gènes contrôlant le fonctionnement des bourgeons axillaires

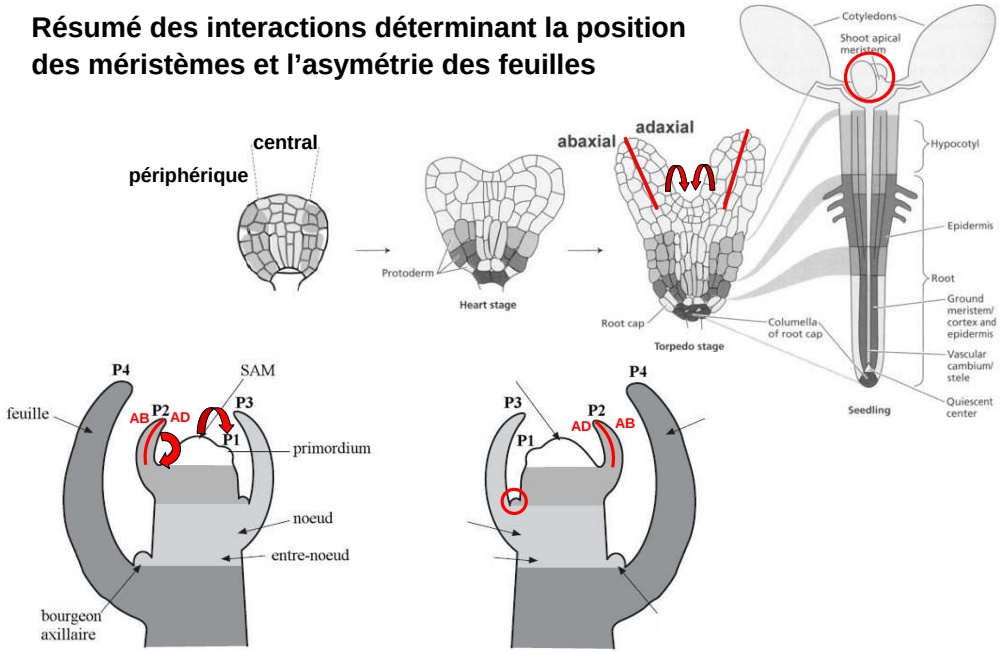
Table 1

Model of the molecular events leading to side-shoot development.

Stages of side-shoot development		Genetic regulators in *Arabidopsis*	in other plants	Activities
(1)	Establishment of axil identity	CUC1–3 [7–9] LOB proteins [10] LAS [3]	CUP [12•] Ls, MOC1 [1,5]	Transcript accumulation of *CUC1–CUC3*, *LOB* and *LAS* at the new border region [3,7–10].
(2)	Maintenance of meristem formation competence in leaf axils	LAS [3] MYB[a]	Ls, MOC1 [1,5] Bl[c] [2]	Co-expression of STM and LAS in leaf axils [3,45].
(3)	Organization of lateral meristem	REV, PHB, PHV [16–20] bHLH[a] MYB[a]	LAX, ba1 [4,6•] Bl[c] [2]	Downregulation of LAS in the center of leaf axils [3]. Focused expression of STM in the organizing meristem [3,45,46]. REV expressed in the organizing meristem [3,17].
(4)	Formation of lateral bud	STM[b] WUS[b] [47] CLV1,3[b] [48] CUC[b]		Downregulation of STM at the flanks of the axilary meristem [45,46].
(5)	Lateral bud outgrowth	MAX1–MAX4 [32] TCP[a]	RMS1–RMS6 [30,31] DAD1–DAD3 [49] D3, D10, D14, D17 and D27 [42] tb1 and OsTB1 [43,44]	Elongation of internodes in the bud [32,46].

Schematic drawings represent top views of nodes undergoing progressive steps in lateral-meristem and side-shoot development (red: tissue with leaf-axil identity; green: tissue with leaf identity; dark green: midvein of leaf; blue: lateral meristem and side-shoot). Genes regulating lateral-shoot development that have been identified in *Arabidopsis* are compared to genes identified in other organisms. [a]No homologous function has been identified in *Arabidopsis* (homologs of the *Bl*, *LAX/ba1* and *tb1* genes). [b]The involvement of a gene function in a specific step is only hypothesized (*STM*, *WUSCHEL* [*WUS*], *CLAVATA* [*CLV*] and *CUC*). [c]A gene function cannot be assigned to a specific step (*Bl*).

Résumé des interactions déterminant la position des méristèmes et l'asymétrie des feuilles



Conclusion: le fonctionnement post-embryonnaire du SAM et le développement des feuilles sont déterminés par des événements survenus pendant l'embryogenèse…

6- RACINE

- Système racinaire : très ramifié et caractéristique de chaque espèce
- Principaux types:
  - **Allorhize**:
    racine principale dominante
  - **Homorhize**:
    système racinaire fasciculé

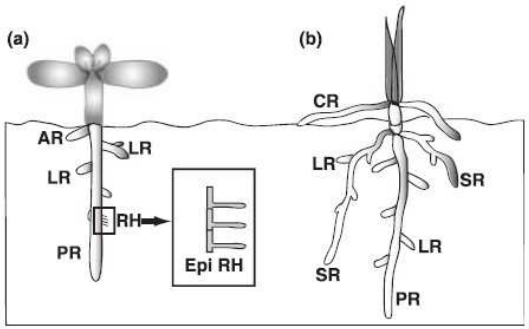
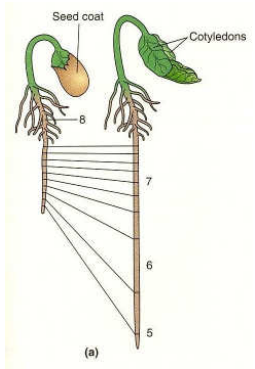
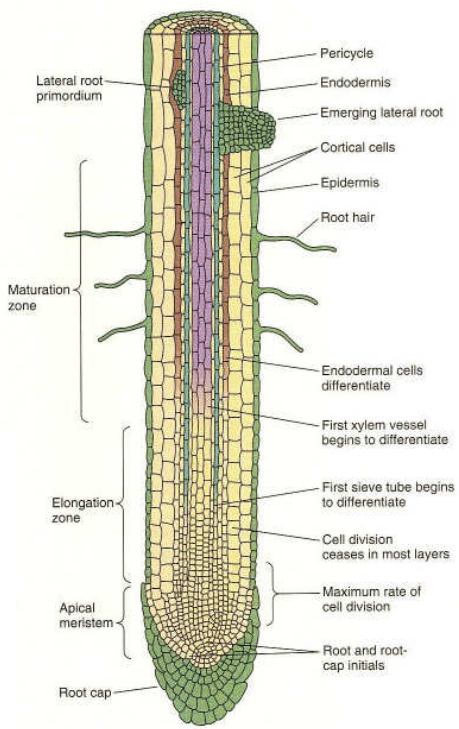


Fig. 1 Components of the root system. (a) A typical dicot (e.g. *Arabidopsis*) seedling root system, consisting of a primary root (PR) originating from the embryo, lateral roots (LR) branching out from the PR during seedling development, and root hairs (RH) that originate from PR epidermal (Epi) cells (shown at higher magnification to the right (inset)). Ultimately, the LRs will undergo higher-order branching to form secondary and tertiary LRs. Adventitious roots (AR) form at the shoot–root junction. (b) A typical cereal (e.g. rice, maize) seedling root system consisting of a primary root (PR) originating from the embryo, seminal roots (SR) that originate postembryonically close to the top of the primary root, and crown roots (CR) that originate from the stem. PR, SR and CR all form LR and undergo higher-order branching.

Organisation de la racine





Croissance : par l'extrémité

2 axes de symétrie:

-axe longitudinal:

zones de division, élongation, différenciation

-symétrie radiale: cylindres concentriques

Zone méristématique de la racine: au microscope

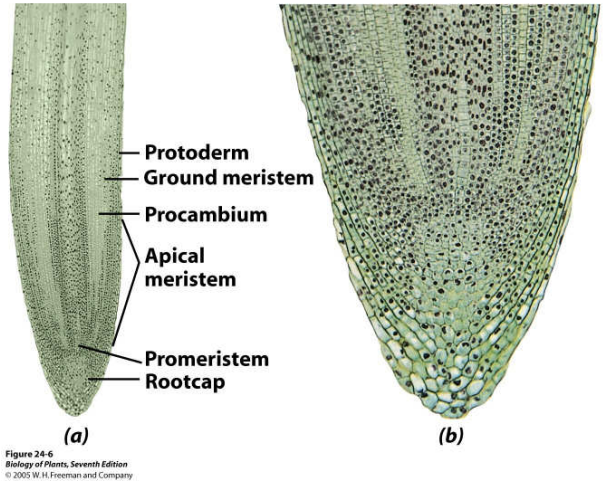


Figure 24-6
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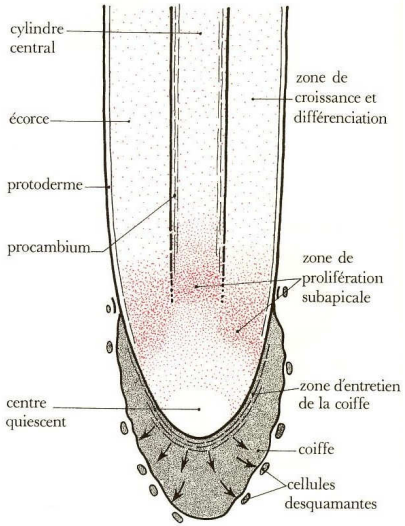
Représentations traditionnelle et « moderne » de la racine

Notion de : cylindres, secteurs et files de cellules

(échanges privilégiés par les plasmodesmes)



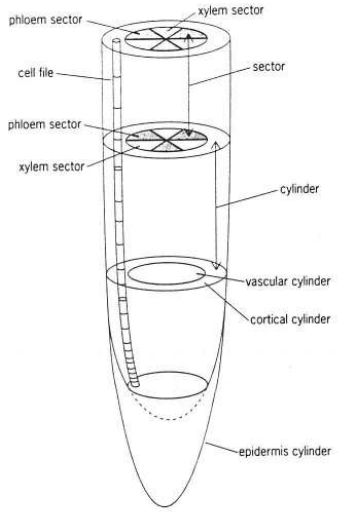


Fig. 1. *Arabidopsis thaliana* root apical meristem of a two-week-old root. The three initial tiers and the tissues which. they derive are clearly shown.

Racine d'Arabidopsis

- 1 seule couche de cellules/ cylindre
- Nombre défini de cellules/ couche

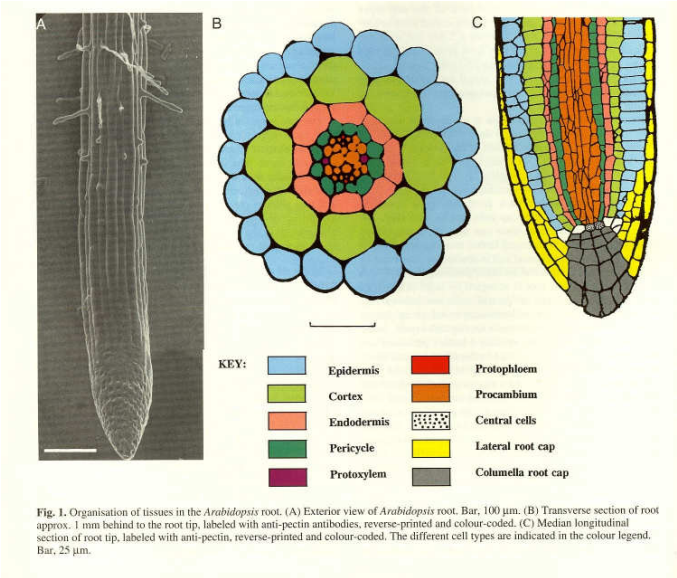


Fig. 1. Organisation of tissues in the *Arabidopsis* root. (A) Exterior view of *Arabidopsis* root. Bar, 100 µm. (B) Transverse section of root approx. 1 mm behind to the root tip, labeled with anti-pectin antibodies, reverse-printed and colour-coded. (C) Median longitudinal section of root tip, labeled with anti-pectin, reverse-printed and colour-coded. The different cell types are indicated in the colour legend. Bar, 25 µm.

Origine embryonnaire de la racine

Origine double:

- embryon (partie inférieure)
- hypophyse (sommet du suspenseur)

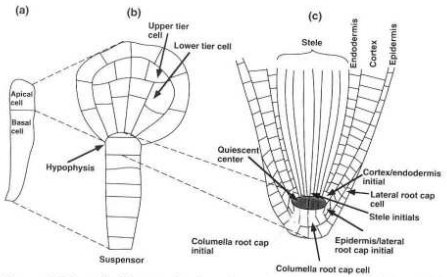


Figure 4 Schematic diagram of embryonic root development in *Arabidopsis*. (*a*) The zygote undergoes an asymmetric division that results in a smaller apical cell and a larger basal cell. The basal cell forms the suspensor and hypophysis, and the apical cell forms most of the embryo proper. (*b*) The mid-globular stage in which lower-tier cells begin to elongate and no longer resemble upper-tier cells. The uppermost derivative of the basal cell, the hypophysis, divides to form the quiescent center and columellar root cap. (*c*) The embryonic root. To simplify the diagram, the individual cells of the stele cell files have not been depicted. The shading of the quiescent center and the cell walls of the columella root cap are to indicate that these cells are derived from the hypophysis. (Reprinted, with permission, from Benfey and Schiefelbein 1994 [copyright Elsevier Trends Journals].)

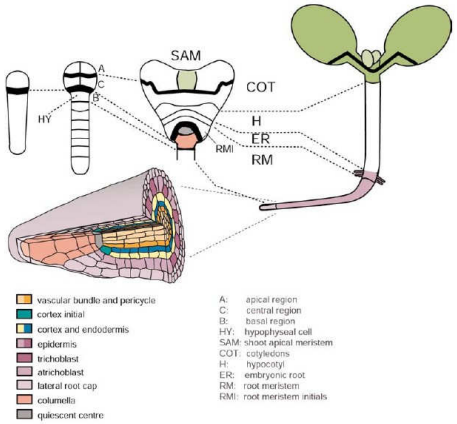


Figure 2. Embryonic origin of the *Arabidopsis* root. From left to right: first zygotic division; octant stage embryo; heart stage embryo; seedling with enlarged root meristem region.

Rappel: le transport polarisé de l'auxine est responsable de la formation du RAM: mise en place du centre quiescent puis des cellules initiales

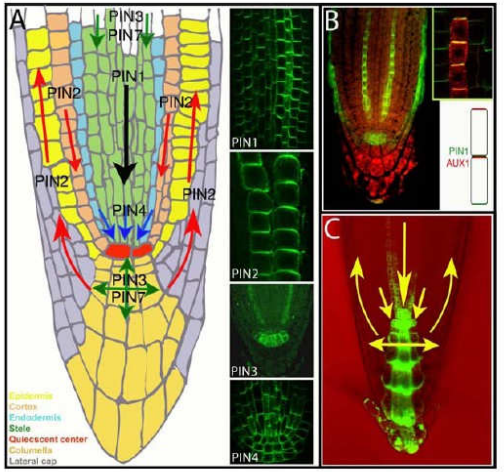


Figure 4. Polar localization of auxin efflux and influx carriers, and the direction of auxin flow in the Arabidopsis root. **(A)** A diagram representing the Arabidopsis root tip with arrows indicating the direction of auxin transport as mediated by PIN1, PIN2, PIN3, PIN4 and PIN7. Inset images show the subcellular polar localization of PIN1, PIN2, PIN3 and PIN4 (by immunolocalization). **(B)** AUX1 subcellular localization (by immunolocalization); inset: a close-up and scheme illustrating opposing PIN1 and AUX1 polar localization in protophloem cells. **(C)** A diagram showing the predominant directions of auxin flow and auxin accumulation in the root tip as visualized by DR5rev::GFP. **B** reprinted from Swarup et al (2001) Localization of the auxin permease AUX1 suggests two functionally distinct hormone transport pathways operate in the Arabidopsis root apex. Genes Dev. 15, 2648-2653 - Figure 1B.

Toutes les cellules de la racine ont pour origine un des quatre types de cellules initiales:

chaque cellule initiale ⟶ 1 ou 2 files de cellules

Les 4 types de cellules initiales forment respectivement:

1- columelles (coiffe)

2- coiffe latérale et épiderme

3- cortex et endoderme

4- péricycle et système vasculaire

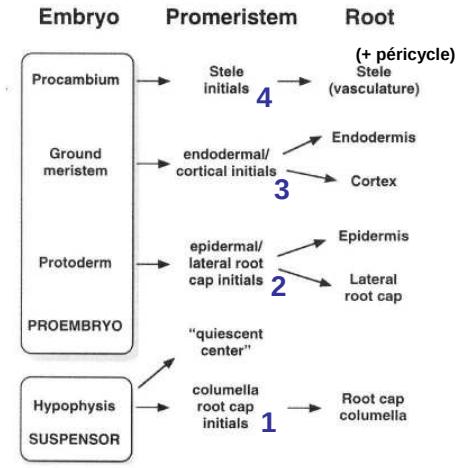


FIGURE 12.7

Origin of cells in various cell layers of the root. Cell lines are traced back through the promeristem to the embryo. Cells are derived in the embryo from both the proembryo and the suspensor.

Fonctionnement des cellules initiales

1- divisions asymétriques :

→ initiale est régénérée

→ production d'une lignée de cellules-filles

2- détermination de l'identité des cellules-filles (différenciation)

3- contrôle par des signaux provenant du centre quiescent:

ablation (laser) d'une cellule du CQ → cellules initiales adjacentes s'engagent sur une voie de différenciation

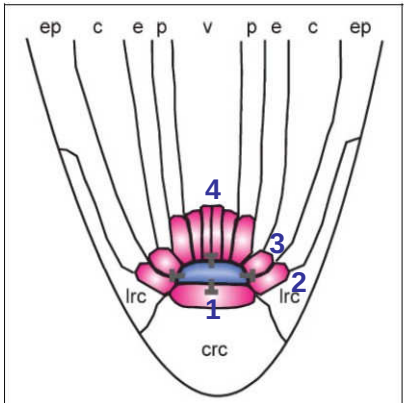
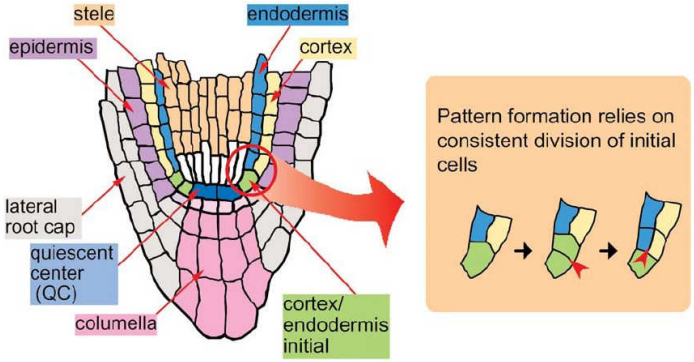


Figure 5. Schematic view of a median longitudinal section through the root tip. The root consists of concentric rings of tissue layers. From the center to the periphery these are: vascular tissue (v), pericycle (p), endodermis (e), cortex (c), epidermis (ep) and lateral root cap (lrc). The central root cap (crc) is located at the very tip of the root and protects the RAM. The QC (blue) inhibits differentiation of the neighboring stem cells (pink). The endodermal and the cortical cell layers as well as the epidermal and the lateral root cap cell layers are each derived from common stem cells.

Exemple: initiales à l'origine de l'endoderme et du cortex

2 types de divisions:

- transversale: régénère initiale + cellule-fille
- division longitudinale de la cellule-fille → 2 lignées (files) de cellules



Cell types in the *Arabidopsis* root meristem

Figure 1. a) Longitudinal section of the Arabidopsis root tip that has been color-coded to show the different cell types. b) Schematic showing the two asymmetric cell divisions that the cortex/endodermis initial and its daughter undergo.

Chaque cellule de la racine fait donc partie d'un **lignée cellulaire** bien précise, originant d'une cellule initiale bien identifiée (files de cellules). Cependant, ces lignées cellulaires n'expliquent pas tout:

- bisection du méristème racinaire → 2 méristèmes fonctionnels (« self-organizing »)
- ablation au laser de certaines cellules initiales → méristème compense…

  → les cellules du méristème peuvent se réorganiser et reformer les parties manquantes (effet de **position** p/r à la lignée)

Lors de l'embryogenèse, les cellules initiales sont mises en place par des divisions très ordonnées

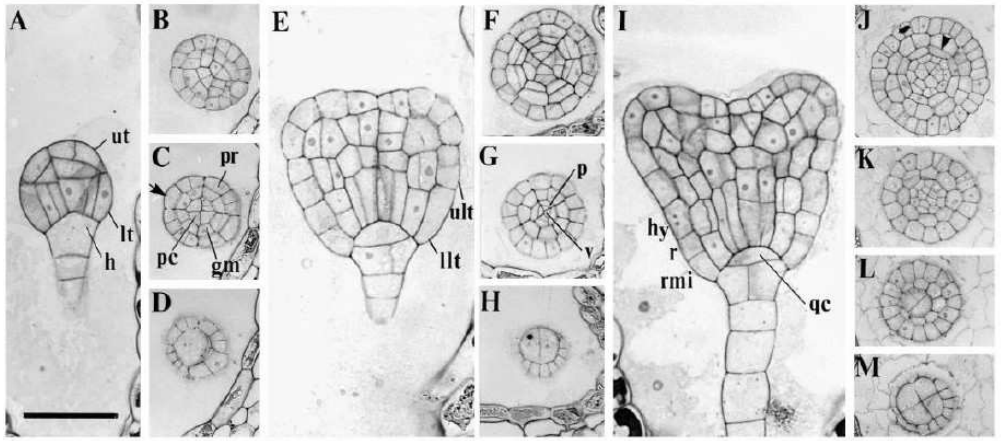
Principe: alternance de divisions périclines et anticlines, qui permettent l'augmentation du nombre de couches de cellules et l'augmentation du nombre de cellules/couche

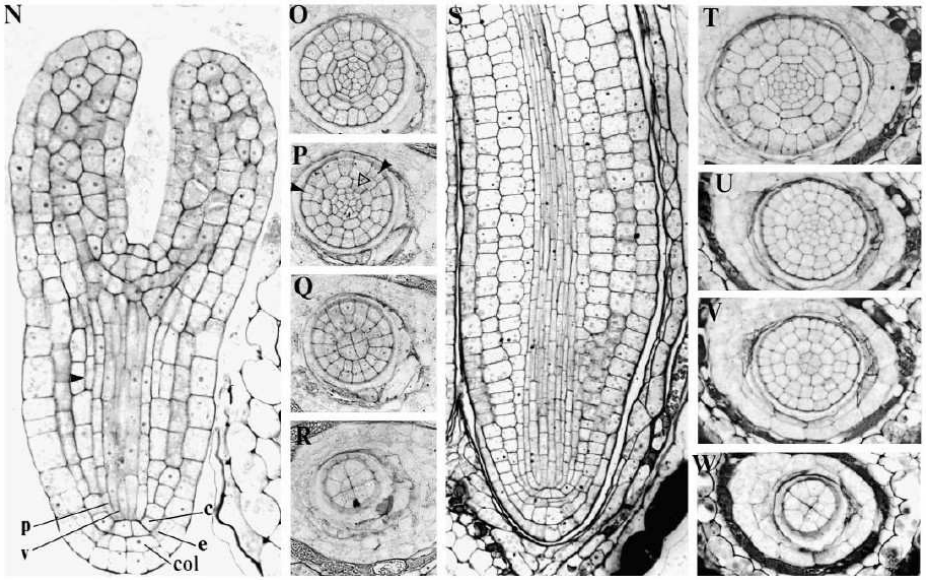
FIGURE 12.6

Schematic representation of alternating anticlinal and periclinal divisions in the embryonic axis that gives rise to the promeristem in the root region of Arabidopsis. Periclinal divisions produce concentric rings of cells, and anticlinal divisions subdivide the rings, increasing the numbers of cells. Thick lines represent most recent divisions. Ordered divisions account for the uniform pattern of cells and the constant number of cells in each tissue layer. (From Scheres, B., et al. 1995. Mutations affecting the radial organisation of the Arabidopsis root display specific defects throughout the embryonic axis. Development 121:56. Reprinted by permission of the Company of Biologists Ltd.)

Développement de la racine d'Arabidopsis au cours de l'embryogenèse

Fig. 1. Radial organisation of the *Arabidopsis* embryo at successive stages. The depicted stages are defined according to Jürgens and Mayer (1994). (A) Median longitudinal (ML) section of globular embryo. (B-D) Transverse (TS) sections of globular embryo at ut, lt and h levels. (E) Triangular embryo, ML. (F-H) Triangular embryo, TS at ult, llt and h levels. (I) Early heart stage embryo, ML. (J-M) Early heart stage embryo, TS at hy, r, rmi, and h levels. (N) Mid-torpedo stage embryo, ML. (O-R) Mid-torpedo stage embryo, TS at hy, r, qc and col levels. (S) Mature embryo, ML. (T-W) Mature embryo, TS at hy, root proximal initials, qc and col regions. Sections were stained with astra blue. ut, upper tier; lt, lower tier; h, hypophysis; ult, upper subtier of lt; llt, lower subtier of lt; pr, protoderm; gm, ground meristem; pc, procambium; p, pericycle; v, vascular primordium; hy, prospective hypocotyl; r, prospective root; rmi, root meristem initials; qc, quiescent centre; e, epidermis; c, cortex; col, columella. Bar, 50 µm.

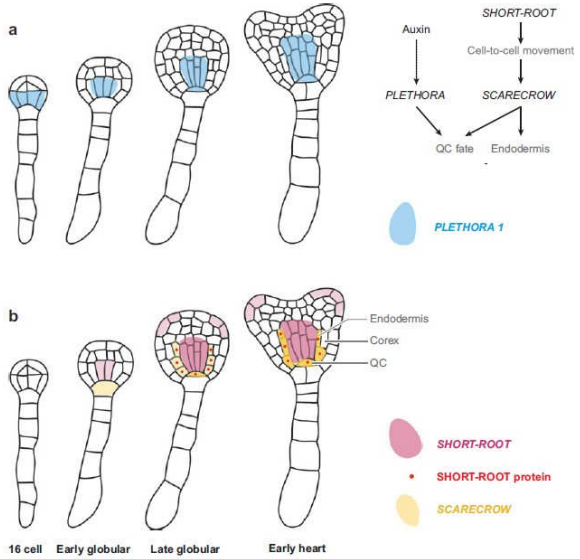




Ben Scheres, Laura Di Laurenzio, Viola Willemsen, Marie-Therès Hauser, Kees Janmaat, Peter Weisbeek and Philip N. Benfey. Mutations affecting the radial organisation of the Arabidopsis root display specific defects throughout the embryonic axis. Development 121, 53-62 (1995)

Plusieurs gènes contrôlent le développement de la racine

p.e. *PLETHORA (PLT), SHORT ROOT (SHR), SCARECROW (SCR)*
(expression débute dans l'embryon)



Sous contrôle de l'auxine, le gène *PLT* contrôle l'établissement de l'axe apical-basal de la racine

- Produit: RT
- Expression: procambium, centre quiescent
- Effet « dose-dependant »; de l'apex vers le haut:
  - expression forte: maintien des cellules souches (centre quiescent)
  - expression moyenne: favorise activité mitotique
  - expression faible: différenciation
- L'expression ectopique de *PLT* (35S-*PLT*) est suffisante pour induire la formation de racines, même à partir du SAM:

L'activité du centre organisateur de la racine (centre quiescent) est maintenue par un gène apparenté à *WUS: WOX5*

- **Gène *WOX5*** *(Wuschel-related homeobox5):* homologue de *WUS*
- **Mutant:** différenciation de cellules méristématiques (initiales)
- **Surexpression:** retard de différenciation des cellules-filles des cellules initiales

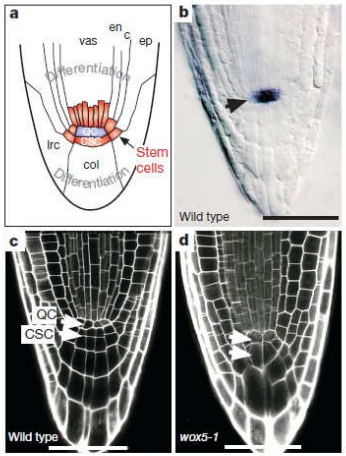


Figure 1 | *WOX5* expression in the quiescent centre is required for root meristem development. **a**, Schematic of *A. thaliana* root meristem with columella (col), columella stem cells (CSC), quiescent centre (QC), lateral root cap (lrc), epidermis (ep), cortex (c), endodermis (en) and vascular bundle (vas), redrawn with permission from ref. 4. **b**, *WOX5* mRNA expression in the quiescent centre. **c–d**, *wox5-1* roots display enlarged cells at the quiescent centre and columella stem cell (CSC) positions. Scale bars, 50 μm.

Les fonctions des gènes *WUS* et *WOX5* sont interchangeables

- *WUS* complémente le phénotype mutant wox5
- *WOX5* complémente le phénotype mutant wus

Conserved factors regulate signalling in Arabidopsis thaliana shoot and root stem cell organizers. Ananda K. Sarkar1, Marijn Luijten, Shunsuke Miyashima, Michael Lenhard, Takashi Hashimoto, Keiji Nakajima, Ben Scheres, Renze Heidstra & Thomas Laux. Nature 446, 811-814 (2007)

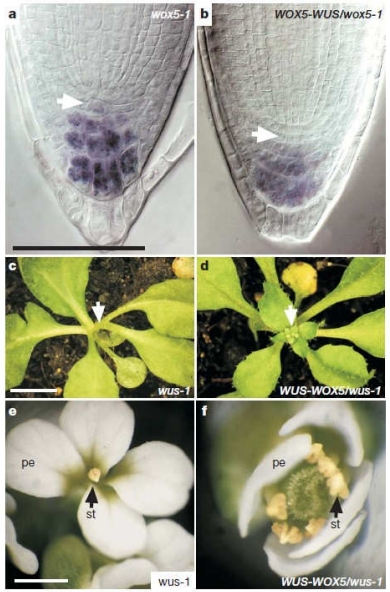
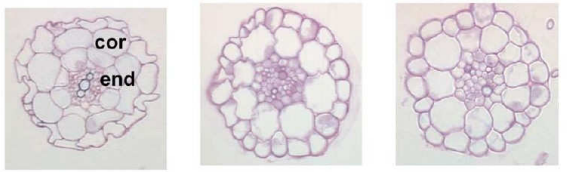
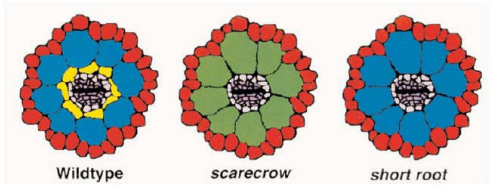


Figure 4 | *WOX5* and *WUS* are interchangeable in stem cell control. **a**, **b**, *WOX5-WUS* expression restores quiescent centre and columella stem cells (white arrows) in *wox5-1*. Violet, starch grains. **c–f**, Rescue of the shoot meristem stem cell niche. *wus-1* shoot (**c**) and floral meristem (**e**) fail to maintain stem cells and terminate prematurely. *WUS-WOX5* expression restores an indeterminate inflorescence meristem (**d**) and complete flowers (**f**). Twenty-six-day-old plants (**c**, **d**) and flowers (**e**, **f**) are shown. White arrows indicate shoot apex (**c**, **d**). pe, petal; st, stamen. Scale bars, 1 cm (**c**, **d**), 1 mm (**e**, **f**) and 50 μm (**a**, **b**).

Des gènes tels que *SCR* et *SHR* déterminent le patron de développement radial de la racine

- mutants shr et scr : pas de 2e division asymétrique de l'initiale
  → une seule file de cellules
  - scr → cellules corticales (différenciation « par défaut »)
  - shr → cellules de nature hybride endoderme/cortex





Bleu: cortex
Jaune: endoderme

Fig. 8. Radial organization of Arabidopsis roots. The *scarecrow* mutant is missing one cell layer, and the resulting mutant layer has differentiated attributes of both cortex and endodermis. The *short root* mutant is also missing a cell layer, but its mutant layer has attributes of only cortex.

Le gène *SCR*:

- s'exprime dans la cellule initiale et dans les cellules de l'endoderme (dès l'embryogenèse)
- contrôle la division de la cellule-fille pour former les lignées endoderme et cortex (mutant scr)
- détermine la lignée cellulaire endoderme (mutant scr)

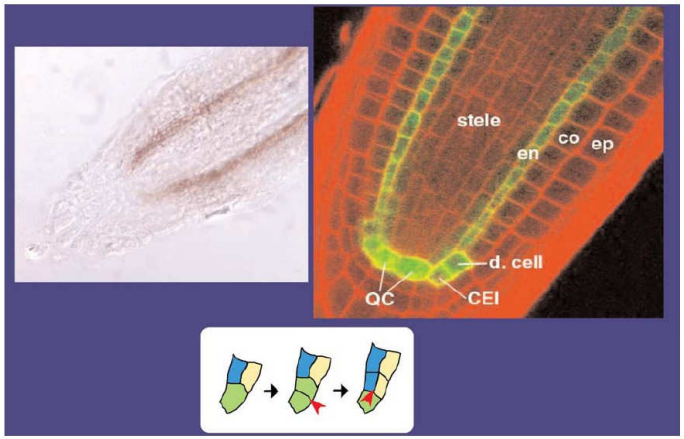


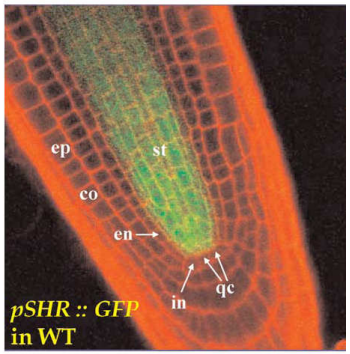
Figure 9. a) RNA expression pattern of *SCARECROW* as determined by in situ hybridization (Di Laurenzio et al., 1996). b)Expression conferred by the *SCR* promoter fused to GFP (Wysocka-Diller et al., 2000).

CEI: Cortex/Endoderm Initial

Le gène *SHR*:

- s'exprime dans la stèle (dès l'embryogenèse)
- la protéine SHR est transportée (plasmodesmes) de façon centrifuge aux cellules du cercle concentrique voisin (endoderme + cellule initiale)
- la protéine SHR active la transcription du gène *SCR* (qui détermine l'identité endoderme)

- Fonction de *SHR* : fournir une **information de position**
  → les cellules qui reçoivent la protéine SHR:
  - sont voisines de la stèle
  - doivent se différencier en endoderme



Vérification : expression du gène *SHR* sous le contrôle du promoteur du gène *SCR* (dans les cellules de l'endoderme) :

- protéine SHR transportée dans la file suivante (cortex, normalement)
- induction de l'expression du gène *SCR:*
  - induction de la division cellulaire
  - détermination de l'identité endoderme pour la file de cellules la plus interne (qui aurait dû devenir cortex)

    → expression du gène *SCR-SHR….*

Résultat : augmentation du nombre de couches de l'endoderme

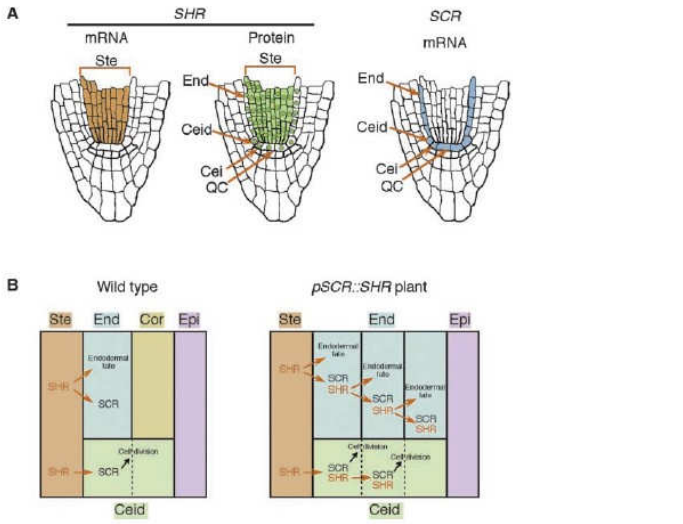


Figure 5. Radial Patterning of the Root Ground Tissue.

(A) Localization of *SHR* mRNA (left), SHR protein (middle), and *SCR* mRNA (right) in the RM (Di Laurenzio et al., 1996; Helariutta et al., 2000; Wysocka-Diller et al., 2000; Nakajima et al., 2001).

(B) Mechanism of intercellular signaling in root radial pattern formation of wild-type (left) and *pSCR::SHR* transgenic plants (right) (Nakajima et al., 2001). In wild-type roots (left), the SHR protein is produced in the stele and appears to move to a single adjacent layer, probably through plasmodesmata (red arrows). In the adjacent layer, SHR activates *SCR* transcription that is essential for the asymmetric cell division of the cortex/endodermis initial daughter (Ceid) cells, resulting in the separation of cortex and endodermis layers. In the mature region, SHR in the adjacent layer confers endodermal cell fate. SHR protein movement is limited to a single cell distance by an as yet unknown mechanism. In *pSCR::SHR* transgenic plants (right), intercellular SHR signaling is considered to be reinforced repeatedly by the production of SHR protein from the *pSCR::SHR* transgene. This results in the production of supernumerary layers because of repeated *SCR*-mediated Ceid divisions and the acquisition of endodermal cell fate in these layers.

Abbreviations for the cell types are given in Figure 4A.

Observation microscopique des racines des plantes exprimant le gène *SHR* sous le contrôle du promoteur *SCR*

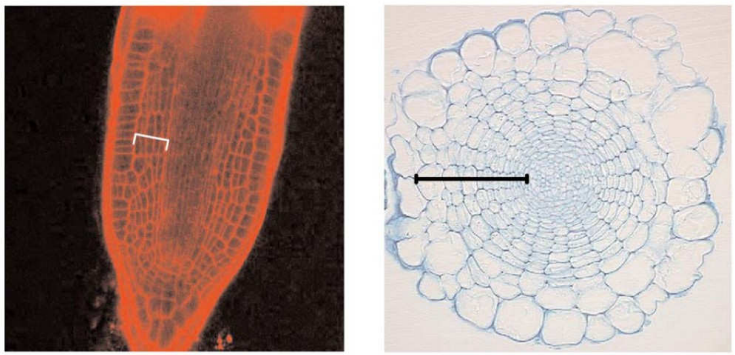


Figure 11. a) Longitudinal optical section of transgenic plants expressing SHR from the SCR promoter. Note the supernumerary ground tissue layers. b) Transverse section from roots of the same plants (Nakajima et al., 2001).

Conclusion

Les cellules du méristème racinaire ne génèrent pas le patron de développement mais perpétuent le patron existant, mis en place pendant l'embryogenèse (sous le contrôle de gènes tels que *SHR*)

→ Comme pour le SAM, le méristème racinaire est maintenant considéré surtout comme une **source de cellules** et non comme une source de signaux (même si le développement est post-embryonnaire, les patrons de développement sont établis pendant l'embryogenèse)

Ramification de la racine

Nombre et position des racines latérales (secondaires) :

- facteurs génétiques
- facteurs environnementaux :
  - abiotiques : eau, gravité, lumière, température, O_2, éléments nutritifs, obstacles
  - biotiques : symbioses (mycorhizes, *Rhizobium*), pathogènes
  - facteurs hormonaux

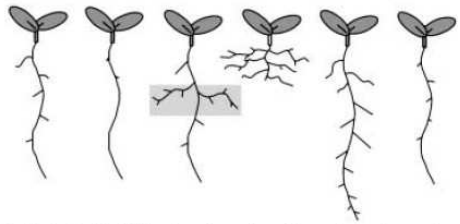


Fig. 5 Lateral root responses to nutrient deprivation. When nitrate (N) levels are high, lateral root (LR) emergence and elongation is represssed compared with normal conditions. Locally high levels of N promote local LR proliferation. In low phosphate (P), primary root growth ceases and LR density increases. In low sulphate (S), primary root growth and lateral root density increase, with LRs originating closer to the root tip. In low potassium (K), LR elongation is inhibited.

Les ramifications de la racine proviennent d'un tissu interne, le péricycle:

- dédifférenciation d'un petit groupe de cellules **OU**
- **cellules ayant conservé un caractère méristématique (RAM)**

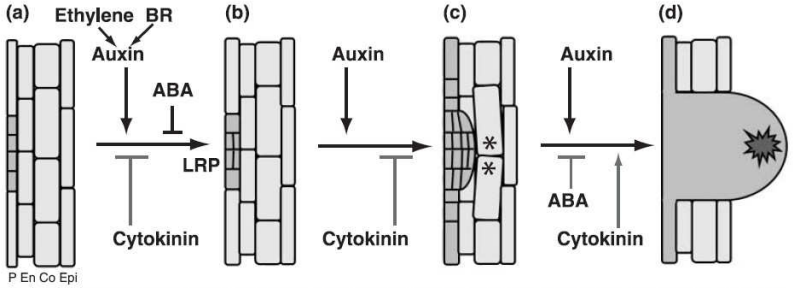


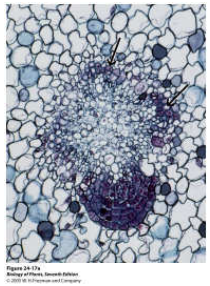
Fig. 4 Lateral root development in *Arabidopsis* shown in longitudinal section. P, pericycle; En, endodermis; Co, cortex; Epi, epidermis. (a) Early initiation – a founder xylem pole pericycle cell (dark grey) undergoes initial anticlinal cell divisions (perpendicular to the surface of the root). (b) Periclinal cell divisions (parallel to the surface of the root) begin and the lateral root primordium (LRP) begins to grow. (c) The LRP undergoes further organized cell divisions and begins to emerge through the outer cell layers of the primary root, resulting in cell separation (asterisks). (d) The new lateral root is fully emerged and its new meristem is activated (dark grey star). It will continue to grow and elongate. At each stage, the effect of various key plant hormones is indicated. ABA, abscisic acid; BR, brassinosteroids.

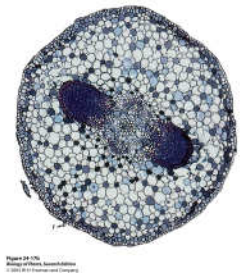
NB. Les cellules du péricycle sont à l'origine:

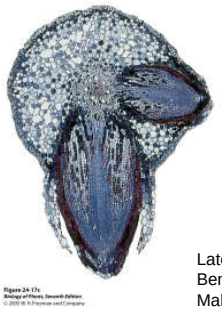
→ des plante régénérées à partir de cellules de racines (*A. rhizogenes*)

→ des nodosités (*Rhizobium*): méristème à partir du péricycle

Au microscope : formation et émergence de racines latérales







Lateral root emergence: a difficult birth. Benjamin Péret, Antoine Larrieu and Malcolm J. Bennett. Journal of Experimental Botany, 60, 3637–3643, 2009

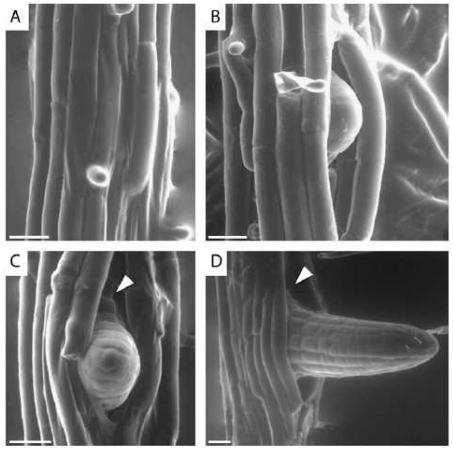


Fig. 1. Formation of a lateral root strongly impacts the primary root structure. Before the production of a new LR the epidermal cells are tightly attached (A). During the emergence process, the outer tissues undergo cell separation as the primordium pushes its way towards the rhizosphere (B, C). Once the LR formation process is over, the primary root still bears the effects of the emergence process (D). Note the formation of large gaps between the epidermal cells at sites of emergence (arrows). Environment scanning electron microscopy (ESEM) of 5–7-d-old *Arabidopsis* seedlings; scale bars are 20 μm.

Au niveau cellulaire…

Cellules à l'origine de la ramification:

- divisions asymétriques anticlines
- généralement « associées » au proto-xylème

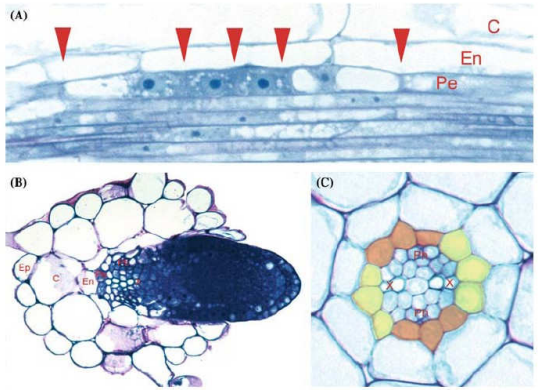


Figure 1. Morphological and anatomical characteristics of the pericycle and LRI in *Arabidopsis*. (A) The first visible manifestation of LRI, i.e. the alignment of two short cells in the midst of two larger cells (cell walls are indicated with arrowheads). (B) Transverse section through an emerging LR opposite the xylem pole. (C) Two distinct pericycle cell populations can be recognized, one opposite the xylem pole (yellow) and one opposite the phloem pole (orange). Symbols: C, cortex; En, endodermis; Ep, epidermis; Pe, pericycle; Ph, phloem; X, xylem.

Lateral root initiation or the birth of a new meristem. Ive De Smet, Steffen Vanneste, Dirk Inzé and Tom Beeckman. Plant Molecular Biology (2006) 60:871–887

Rôle de l'auxine

Comme pour les primordia foliaires, une augmentation locale de la concentration d'auxine (dans le proto-xylème) est responsable de la formation des racines latérales

corrélation [auxine]-nombre de racines latérales, d'après :

-apport externe d'auxine ou d'inhibiteur

-mutants

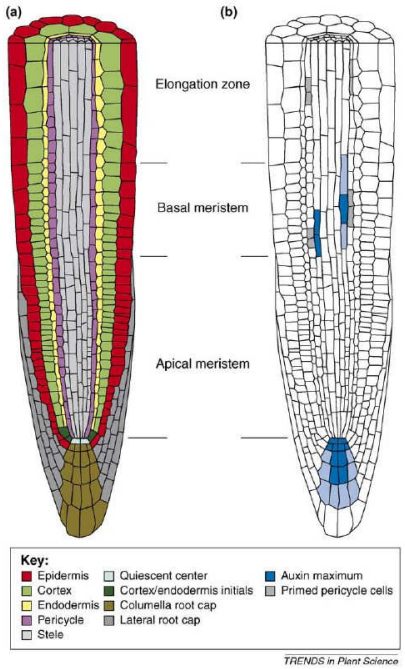
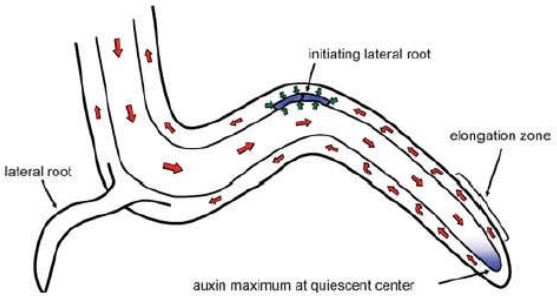


Figure 2. Lateral root priming occurs in the basal meristem. Schematic overview of the different root tissues (**a**) and the auxin signalling maximum present (**b**) as reported by the *DR5::GUS* marker line [21]. The regularly spaced auxin accumulation sites in the protoxylem primes the adjacent pericycle cells to become pericycle founder cells.

Des courbures de la racine provoquent un transport polarisé de l'auxine localement plus important et la formation de ramifications



doi:10.1371/journal.pbio.0060323.g004

Figure 4. Auxin Transport Model of Lateral Root Initiation

Polarly localized auxin export proteins (red arrows) pump auxin toward the quiescent center at the tip of the root, creating an auxin maximum there (blue). Auxin is then returned upwards by polarly localized auxin exporters in the outer layers of cells in the root. A portion of the auxin returns into the reflux stream due to lateral orientation of some of the exporters. In the model of Laskowski et al., bends in the root caused by anisotropic growth in the elongation zone induce a mini-reflux loop, causing auxin to accumulate preferentially on the outside of the curve. This induces cells to produce additional import carriers (small green arrows), which creates an auxin maximum (blue cells) by skimming auxin out of the transport stream. This auxin maximum then triggers lateral root formation.

Modèle

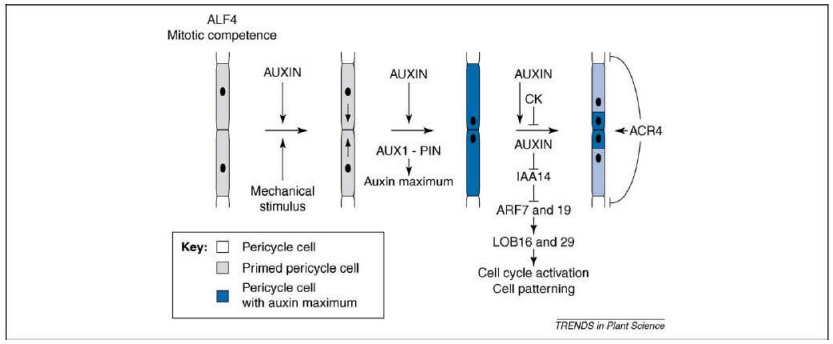


Figure 3. Early events during lateral root initiation. Local auxin accumulation in primed xylem pole pericycle cells activates the auxin signalling cascade. Auxin causes the degradation of IAA14, thereby de-repressing *ARF7* and *19* and activating downstream gene expression. The receptor-like kinase ACR4 promotes formative divisions in the primordium and represses cell divisions in surrounding pericycle cells [54]. Abbreviation: LOB, LATERAL ORGAN BOUNDARIES.

Gènes/mutants:

- signalisation par l'auxine
- contrôle de la mitose
- enzymes modifiant paroi cellulaire: séparation des cellules au site d'émergence
- peu de gènes spécifiques p/r au RAM: structure et fonctionnement identiques

- **1ères étapes**: divisions périclines de cellules du péricycle:

  cause ou conséquence? Utilisation d'inhibiteurs de la division: tout de même formation de racines latérales → expansion cellulaire compense. Donc, les divisions sont plutôt la conséquence)
- **Etapes suivantes**: formation progressive d'un nouveau méristème racinaire, tout à fait identique à celui de la racine principale (à partir d'un groupe de cellules différenciées vs cellules embryonnaires)

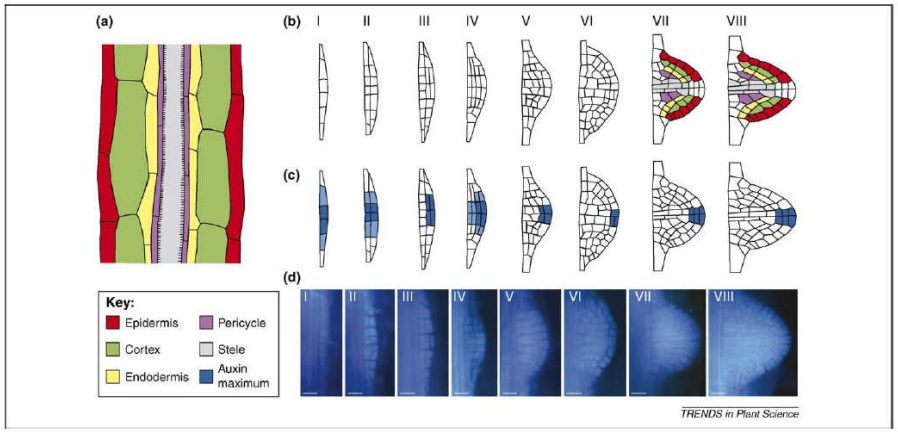


Figure 1. Morphological changes during lateral root development. Lateral roots originate deep within the primary root from the pericycle cells (**a**). The eight stages of primordium development (roman numbers [6]) are shown (**b**) as well as establishment of the auxin signalling maximum as demonstrated with the *DR5:GUS* reporter (blue gradient (**c**) [30]). The cartoons were drawn from aniline-blue-stained roots for each stage of lateral root development (**d**). The scale bars represent 20 μm.

Au site d'initiation d'une racine latérale, une cascade d'événements génétiques:

- induit le prolifération cellulaire et le « patterning »
- inhibe (rétro-contrôle négatif) la formation d'autres racines latérales

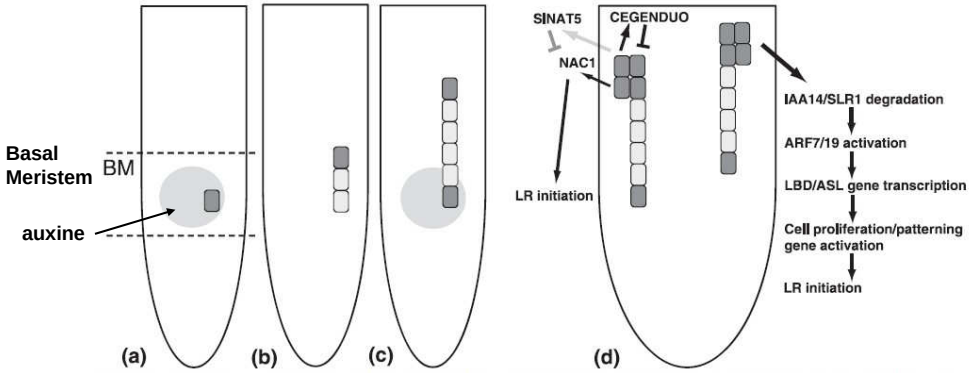


Fig. 3 Aspects of auxin signalling during lateral root (LR) development. (a) A pulse of auxin (light grey) in the basal meristem (BM) primes a pericycle cell (dark grey) to become competent to form a lateral root initial cell. (b) Cells (white) leaving the basal meristem between cyclical auxin maxima are not specified to become LR initials. (c) The first primed pericycle cell arrives at a point where it can initiate LR development; meanwhile another pericycle cell (dark grey) is primed in the basal meristem by the subsequent auxin pulse. (d) Lateral root initiation begins with auxin-induced IAA14 degradation. This allows activation of the ARF7 and ARF19 transcription factors, which activate expression of *LBD/ASL* genes. LBD/ASL proteins in turn activate cell cycle genes and cell patterning genes, enabling formation of a new lateral root primordium (LRP). Auxin also activates transcription of NAC1 to stimulate LR initiation, and at the same time induces expression of two ubiquitin ligases, CEGUENDO and SINAT5, which feed back to attenuate the auxin response.