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Chapter 1 : Holdings : Root development / | York University Libraries

Comparison of legume lateral roots and nitrogen-fixing nodules Recent advances in genetics and genomics of nitrogen-fixing nodule development in legumes Evidences for a crosstalk between symbiotic nodule and LR developmental pathways.

Mysore Find articles by Kirankumar S. Conceived and designed the experiments: Assisted with writing the manuscript: Received Jun 5; Accepted Nov This article has been cited by other articles in PMC. Abstract In plants, root system architecture is determined by the activity of root apical meristems, which control the root growth rate, and by the formation of lateral roots. In legumes, an additional root lateral organ can develop: We identified in *Medicago truncatula* ten allelic mutants showing a compact root architecture phenotype *cra2* independent of any major shoot phenotype, and that consisted of shorter roots, an increased number of lateral roots, and a reduced number of nodules. Grafting experiments revealed that *CRA2* acts through different pathways to regulate these lateral organs originating from the roots, locally controlling the lateral root development and nodule formation systemically from the shoots. The compact root architecture *cra2* mutant form an increased number of lateral roots and a reduced number of symbiotic nitrogen-fixing nodules. Grafting experiments showed that *CRA2* negatively controls lateral root formation and positively controls nodule development through local and systemic pathways, respectively. Introduction Plant growth requires the continuous development of the root system and its adaptation to changing environmental soil conditions. Mechanisms controlling root system architecture at the whole-plant level, including the systemic coordination of shoot and root development, are key breeding targets for maintaining crop productivity under adverse stress conditions but remain poorly understood [1]. Root system architecture is a consequence of the sustained activity of root apical meristems, leading to indeterminate root growth as well as the *de novo* formation of lateral organs. In legume *Fabaceae* plants, the root system can form two types of lateral organs depending on the environmental conditions: Lateral root initiation, emergence and growth depend on water and nutrient availability and are regulated by a combination of local and systemic pathways [5]. Symbiotic nodules are formed under nitrogen-deprived conditions when the specific *Rhizobium* spp. In both types of lateral organogenesis, cell divisions are activated in specific tissues pericycle, endodermis and cortex above the growing root tip [2] – [4], [8]. Root tissues contributing to primordium formation are, however, different depending on the plants and organs: Both types of primordia will then subsequently emerge from the parental root and establish a meristematic stem cell niche ensuring their indeterminate growth. To control meristematic activity, cell differentiation, and lateral organ initiation, non-cell autonomous cues are essential to carry positional information, which can be informed either by mobile phytohormones, small RNAs or peptides [9] – [11]. Interestingly, an increased number of emerged lateral roots was reported in the *Lotus har1* mutant under both symbiotic and non-symbiotic conditions [29]. Allelism tests S1B Fig. Detailed quantitative *in vitro* analyses revealed that the *cra2* phenotype consists, compared to the WT, of shorter roots with an increased number of emerged lateral roots Fig. Accordingly, lateral roots were observed three days post germination dpG; Fig. This root phenotype was observed independently of the growth and nutrient conditions that were used greenhouse versus *in vitro*, Fig. In addition to the faster emergence of lateral roots, we observed a reduction in the primary root growth, which prompted us to analyze the structure of the RAM Fig. In contrast to the A. In addition, cells from diverse files elongate at a slightly different distance from the root apex, leading to a cone-shaped transition zone Fig. When *cra2* RAMs were observed three dpG, both the cell proliferation and elongation zones were reduced, and a lower number of cells was observed in the two zones Fig. Root patterning, however, evaluated based on both longitudinal and transversal sections, seemed unaffected Fig. Among several hypotheses that could explain the *cra2* root system architecture phenotype, we tested whether a RAM activity defect could indirectly lead to increased branching as compensation or if the reduced meristematic activity could be a consequence of the enhanced formation of lateral roots. An analysis

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of root apices at one dpg, i. Compared to previous observations of roots at three dpg Fig. As an independent approach, we experimentally removed the RAM at one or three dpg and followed the kinetics of lateral root formation Fig. The *cra2* mutant showed an increased ability to form lateral roots whether RAM excision occurred before or after lateral root initiation. Collectively, these results suggest that the *cra2* RAM phenotype can be disconnected from its enhanced ability to form lateral roots.

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Legume root architecture is characterized by the development of two de novo meristems, leading to the formation of lateral roots or symbiotic nitrogen-fixing nodules.

Dinneny and Philip N. The reason for plant roots to be and remain an exciting and intriguing field of science is not explicitly clear. When compared to flowers, roots distinctly lack the ornamental attractiveness of flowering structures. Pondering over this seeming contradiction, I think the answer might be found in the secret and hidden nature of roots. Scientists are, by default, attracted by mysteries: Among all growth processes occurring in plants, the development of roots is without discussion, at the summit of secrecy. Roots reside their entire life in the soil sheltered from daylight, proliferate and colonize the rhizosphere through the continuous development of new meristems that arise deep inside tissues invisible from the surface, interact sneakily with various microorganisms that provoke dramatic growth changes and are capable of reacting upon the ever-changing soil conditions in an unfathomable way. Indeed, plant roots grow and develop while continuously monitoring information from the environment. Therefore, it will become essential to understand root development in detail in the next decades, to learn how plants cope with a changing environment, and to translate the fundamental knowledge into applications. No doubt, there is still a long way to go and the question is whether a deeper understanding of fundamental root biology could be implemented on time into applications to ease the essential needs of the future world population. Nevertheless, it is at least hopeful to notice that insight into the subterranean part of plants has seriously made progress in the recent years, especially at the level of its developmental biology. Data have been accumulating exponentially and the entire root development area cannot easily be summarized in the format of one single review paper. Hence, I am glad and proud that representatives of all top laboratories on root development have accepted to contribute to the timely publication of this book and have helped me with this challenge. As, you will see, they all did a great job. In the first four basic chapters, the main root developmental processes are covered. In contrast to previous root development reviews, these chapters are characterized by the enumeration of an increasing number of molecular components that are essential for root development and have been identified recently. This tendency reflects that our discipline has come to maturity. The root of this species has all it needs to guarantee easy laboratory handling and experimentation. On top of this, its genome is sequenced and a myriad of molecular tools have become available. In the first chapter, the origin of the primary root during embryogenesis and the establishment of a typical cellular pattern are discussed as well as the preservation of this pattern after germination, implying the introduction of the concept of a stem cell niche in the root tip. In the third chapter, the focus lies on particular tissue layer of the root, namely the epidermis. It is a border tissue through which roots make contact with the soil. Following a discussion on its development and the specification of the different cell types, an outlook on its nutrient uptake function is provided. Chapter 4 discusses the branching of roots, a process that contributes considerably to their plasticity toward changes in the rhizosphere. It is therefore no surprise that this chapter concludes with a section on the agricultural importance of lateral root formation. In contrast to lateral roots, adventitious roots are part of the root system that are not derived from the primary root; their formation is discussed in Chapter 5. This aspect of root development also incorporates a high economic potential because it represents the essential step in the vegetative propagation of plants. An intensively studied developmental process occurring in roots is root gravitropism that is by far the most obvious adaptive trait of roots. Several recent breakthroughs of gravitropism are summarized in Chapter 6. In the following four chapters, we step out of the Arabidopsis-dominated world and learn more about root development of cereals and ferns and changes in root architecture induced by symbiotic interactions with soil microorganisms. In these chapters, our view on root development is largely expanded by the treatment of issues that are completely lacking in the Arabidopsis model. Nevertheless, on many occasions, the authors can make interesting comparisons with some fundamental insights provided by the Arabidopsis root community,

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highlighting the value of a multidisciplinary thinking while studying roots. I hope that this book will contribute to bring the different root scientists together and will help researchers and students to compare their findings with observations made in other plants. Next, the importance of nutrient availability on root development is treated in Chapter 11 from an evolutionary perspective: Finally, in Chapter 12, we return to the Arabidopsis model, but this time to discuss novel molecular tools that have led to the creation of expression maps of over 22 genes at a cellular resolution. In the coming years, this approach will be extremely valuable to decipher this complex biological process. Furthermore, I am indebted for the daily support and motivation of my scientific work to all present and previous members of the Root Development group at the Department of Plant Systems Biology in Gent and, last but not least, to Martine De Cock, the secret weapon of our department, who has been editing uncountable manuscripts over the years and who, this time again, helped me during the preparation of this book. Tom Beeckman Annual Plant Reviews 37, 1â€™38 doi: In plant development, the basic body plan is laid down during embryogenesis. Development carries on postembryogenically above and below ground with the continuous formation and outgrowth of lateral organs shaping the adult plant. In the past two decades, molecular genetics has been the preferred approach to study Arabidopsis thaliana root development. These efforts have resulted in the identification of numerous genes, involved in as many regulatory processes of root growth and development. Incidentally, conserved mechanisms and genetic factors that act in root and shoot growth have been uncovered, revealing general principles of plant development. Perpetual divisions of the stem cells are tightly regulated, interconnecting epigenetic factors, hormonal control and core cell cycle components. In this chapter, we will focus on recent advances in our understanding of Arabidopsis root development. Taking embryogenesis as a starting point, we will describe the genes and mechanisms involved in root meristem and stem cell patterning and maintenance. With each asymmetric stem cell division, one daughter cell is maintained as a stem cell, while the other will differentiate to form specific tissues. In this way, a limited number of stem cells can generate organs of the size of trees. Because their rigid cell walls make it impossible for plant cells to move, the stereotyped division pattern of the root stem cells organizes the separate tissues in concentric columns or cell files. From outside to inside, these layers are designated as lateral root cap, epidermis, cortex, endodermis and pericycle as the cell files that surround the central vascular tissue. Clonal analysis and ablation studies indicate that cell lineage does not necessarily determine cell fate and pattern formation, but that plant cells are flexible and rather rely on positional information for adapting their final fate Dolan et al. At the basal end, a set of stem cells gives rise to the central portion of the root cap, known as the columella. Internal to and contacting all the stem cells is a small number of mitotically less active cells, the quiescent center QC. Along the apicalâ€™basal axis of the root, stem cell daughters continuously travel through time, crossing the zone of cell division meristematic zone, the zone of cell expansion and elongation elongation zone and, ultimately, meet their destiny in the differentiation zone. In other words, at any time, all developmental stages are present within the root tip. Together with the predictable fate of all individual cells that compose the root, these features make the Arabidopsis root an excellent system to study the genetic control of organ development. First, we will briefly discuss the fundamental principles of auxin transport and action because these processes have become particularly important for our understanding of Arabidopsis root development. Auxin is transported through the plant in a directional cell-to-cell fashion, called polar auxin transport that is mediated by the auxin influx carrier AUX1 Bennett et al. These studies suggest an important link between auxin distribution and early embryo development. We will discuss further evidence in support of this hypothesis. Although the DR5 reporter activity is merely an output of the cellular auxin response, its activity has been shown to correspond well with auxin levels by using immunolocalization with an anti-IAA antibody Friml et al. For reviews on root development of monocots and ferns, see Chapters 7 and 8. While the apical layer of cells gives rise to the shoot meristem and the larger part of the cotyledons, descendants of the basal proembryo layer form the remaining part of the cotyledons, the hypocotyl, the embryonic root and the proximal root stem cells. The larger basal cell of the divided zygote produces a file of seven to nine cells by repetitive horizontal divisions

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that embody the extraembryonic suspensor that serves as a conduit for nutrients and growth regulators to support the embryo proper development Yeung and Meinke, From this basal cell lineage, the uppermost cell the presumptive hypophysis is sequestered by the embryo to adopt an embryonic fate and participate in development Fig. During heart stage of embryogenesis, the hypophyseal cell divides asymmetrically to generate an upper lens-shaped cell that will form the QC and a basal columella root cap progenitor. When the QC is specified, it induces the surrounding cells to become the root meristem stem cells Dolan et al. Postembryonic development initiates from these stem cells that are laid down in the heart of the root meristem. Over the past two decades, several factors involved in this early patterning event have been identified and linked at the genetic level. The early expression dynamics of several members of the WOX transcription factor family coincides with specific cell fate changes during early embryo development Haecker et al. Before fertilization, WOX2 and WOX8 are expressed in the egg cell and the central cell of the embryo sac and, thereafter, in the elongating zygote. WOX9 expression expands into the central domain of the embryo, crossing the clonal boundary established at the first zygotic division, and weakens in the uppermost suspensor cell Haecker et al. Although this dynamic WOX9 expression pattern is not always observed, these early expressed WOX genes share redundant functions during embryo development Wu et al. Strong *wox9* loss-of-function mutants arrest development of two to three divisions after the zygote stage. Eradicating WOX8 function in the *wox9* background enhances this defect, arresting embryos after the first division. Likewise, *wox8* increases apical embryo defects caused by an insertion mutation in WOX2, resulting in abnormal cotyledon separation Wu et al. In *yoda* loss-of-function mutants, the elongation of the zygote is suppressed and the cells of the basal lineage divide in an unpredictable manner. As a result, these cells fail to form the suspensor and are ultimately incorporated into the developing embryo. The apical cell initially develops normally into a wild-type octant embryo, indicating a specific role for the MAP kinase signaling pathway in the correct specification of the basal cell lineage Lukowitz et al. After division of the zygote, a profound auxin response maximum in the apical daughter cell is quickly established as visualized by fluorescent DR5 reporter expression Friml et al. Expression of PIN1 is restricted to the apical cell and the PIN1 protein is distributed within the cell membrane in a nonpolar fashion. In contrast, PIN7 is polarly localized to the apical membrane of the basal cell facing the apical embryo pole. The asymmetric localization of PIN1 and PIN7 proteins present at the first steps of embryogenesis suggests the auxin transport routes from the maternal tissues to establish the auxin gradient and to initiate polarization Friml et al. In a small, but reproducible, number of early *pin7* mutant embryos, the apical cell divides horizontally rather than vertically, accompanied by misexpression of the DR5 marker in the extraembryonic suspensor. At later stages, these *pin7* embryos display irregular division patterns in the lower embryo regions and, occasionally, fail to establish a proembryo Friml et al. Interestingly, around the globular cell stage, *pin7* embryos start recovering from these defects, eventually resulting in fertile plants with no apparent phenotype. Double, triple and quadruple *pin* mutant embryos show more severe patterning defects and do not recover, indicating functional redundancy among the PIN genes Friml et al. PIN proteins in overlapping expression domains compensate for the loss of one another, even to the extent of ectopic PIN2 expression in *pin3pin4pin7* embryos, whereas PIN2 is normally not expressed at these embryonic stages Blilou et al. Strong loss-of-function *gn* mutants display a nearly symmetric division of the zygote, followed by oblique divisions of the apical cell. Unable to compensate these defects, *gn* mutants fail to specify the hypophysis and, ultimately, develop into seedlings without a functional root meristem. In *gn* embryos, the DR5 reporter activity was detected ectopically in the suspensor, mimicking the DR5 expression upon auxin efflux inhibition Friml et al. Mutants of the vacuolar protein sorting 29 VPS29, a member of the retromer complex, display similar embryonic defects as those reported for *gn* Jaillais et al. Moreover, the PIN1 localization is also affected in these mutants. Although more PIN protein family members have been shown to rapidly cycle between the plasma membrane and endosomal compartments and to internalize upon BFA treatment, the GN action does not seem to mediate all PIN protein trafficking to the same extent Friml et al. As in weak *gn* mutants, growth is impaired in *snx1* roots and the

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normal auxin distribution is perturbed. Double homozygous mutants for *vsp29* and *snx1* could not be obtained, suggesting that the loss of function of these two genes is either gametophytic or embryonically lethal Jaillais et al. Initial abnormalities in *mp* and *bdl* are manifested in the apical region as early as the two-cell stage. In contrast to wild type, the apical cell in *mp* and *bdl* embryos divides horizontally, with twice the number of tiers at the octant stage as a consequence. At later stages, mutant embryos fail to specify the hypophysis correctly see below resulting in the complete absence of a seedling root.

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Chapter 3 : Control of root architecture and nodulation by the LATD/NIP transporter

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In legumes, an additional root lateral organ can develop: We identified in *Medicago truncatula* ten allelic mutants showing a compact root architecture phenotype *cra2* independent of any major shoot phenotype, and that consisted of shorter roots, an increased number of lateral roots, and a reduced number of nodules. Grafting experiments revealed that *CRA2* acts through different pathways to regulate these lateral organs originating from the roots, locally controlling the lateral root development and nodule formation systemically from the shoots. *PLoS Genet* 10 This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are within the paper and its Supporting Information files. This work has also benefited from the facilities and expertise of the Imagif Cell Biology Unit of the Gif-sur-Yvette France campus www.cea.fr. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. The authors have declared that no competing interests exist. Mechanisms controlling root system architecture at mainly derive from the inner cortex. Both types of primordia will the whole-plant level, including the systemic coordination of shoot then subsequently emerge from the parental root and establish a and root development, are key breeding targets for maintaining meristematic stem cell niche ensuring their indeterminate growth. Root system architecture is a consequence organ initiation, non-cell autonomous cues are essential to carry of the sustained activity of root apical meristems, leading to positional information, which can be informed either by mobile indeterminate root growth as well as the de novo formation of phytohormones, small RNAs or peptides [9–11]. Among peptides, lateral organs. Lateral root initiation, emergence and growth depend on water involved in local and long-distance systemic pathways controlling and nutrient availability and are regulated by a combination of the development of different plant organs. First, several CLE local and systemic pathways [5]. In both *Arabidopsis thaliana* meristems. The founding example is the types of lateral organogenesis, cell divisions are activated in *CLAVATA3* *CLV3* peptide, which is perceived by the *CLV1* specific tissues pericycle, endodermis and cortex above the receptor to control the shoot apical meristem stem cell niche growing root tip [2–4,8]. Segregation analyses of this root phenotype nodules. The compact root architecture 2 *cra2* mutant revealed a 3: Allelism tests *S1B* number of symbiotic nitrogen-fixing nodules. Grafting experiments showing partially similar phenotypes [32] and were therefore showed that *CRA2* negatively controls lateral root formation named *cra2*. Detailed quantitative in vitro analyses revealed that tion and positively controls nodule development through the *cra2* phenotype consists, compared to the WT, of shorter roots local and systemic pathways, respectively. Overall, our with an increased number of emerged lateral roots Fig. A coordinated with or without nitrogen or carbon sources, Fig. In addition function of the *CRA2* and *SUNN* LRR-RLKs may thereby to the faster emergence of lateral roots, we observed a reduction in permit the dynamic fine tuning of the nodule number the primary root growth, which prompted us to analyze the depending on the environmental conditions. In contrast to the A. In addition, cells from diverse files elongate at a Meristem RAM; [14–16]. A second example is the Tracheary slightly different distance from the root apex, leading to a cone- element Differentiation Inhibitory Factor *TDIF* peptide, which is shaped transition zone Fig. Root organ thickening [17–19]. In controlling root lateral organs number was identified through addition, amyloplast accumulation in differentiated root cap cells grafting experiments as performing a long-distance systemic and the expression of the RAM stem cell niche marker *WOX5* function from the shoots [7]. In enhanced formation of lateral roots. As an independent approach, we experimentally the nodule number depending on these LRR-RLK receptors removed the RAM at one or three dpg and followed the kinetics

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[25–27]. Collectively, these CLE peptide transport and receptor binding in the shoots, as results suggest that the *cra2* RAM phenotype can be disconnected recently proposed [28]. Interestingly, an increased number of from its enhanced ability to form lateral roots. A and B, Representative examples of wild-type WT and *cra* plants that were grown in the greenhouse for one month on a perlite-sand mixture A or for three months on soil B. C, Quantification of the stems, pods and seeds dry weight of the WT, *cra* and *cra* plants that are shown in B. The *cra2* lateral root and root apical meristem [42]. A Kruskal phenotypes can be disconnected. E, Representative examples of the RAM, stained with Propidium Iodide to visualize cell walls three days WT and *cra* plants that were grown in vitro for three dpg on an N- post germination dpg; A or one dpg E. Bars same zones at three dpg. G, Representative mutant shoot growth was similar with or without *Rhizobium* examples of the WT and *cra* root system architecture seven days post excision dpe of the RAM. The excision was performed either one inoculation Fig. H, Quantification of the lateral roots at two, four low nodulation phenotype could be either linked to a direct CRA2 and seven days post excision dpe of the RAM in WT or *cra* plants. The error bars represent the indirectly hampers nodule formation. The *cra2* mutants have reduced symbiotic nodulation. C, Quantification of the shoot dry weights of the WT, *cra* and *cra* plants that are shown in A. The arrowheads indicate the position of the nodules. E, Quantification of the nodule number 14 days post inoculation with S. The inoculation was performed between one and 14 days post germination dpg. In symbiotic conditions, we surprisingly observed a disconnect addition, an analysis of bacterial nitrogenase activity using an between the lateral root and nodulation phenotypes Fig. Acetylene Reduction Assay ARA showed that despite *cra2* plants Indeed, similar to non-symbiotic conditions, the increased density have a strongly reduced ability to fix atmospheric nitrogen due to of the lateral roots was associated with *cra2* mutant roots, but the their lower number of symbiotic organs S4B Fig. Overall, the detailed analysis of the mutant the root genotype. This result indicates that the systemic activity of phenotypes indicates that, independently of a potential indirect CRA2 in the shoots positively regulates symbiotic nodule effect of the increased lateral root formation on nodule formation, formation in the roots. WT root system architecture but developed more than 10 times fewer nodules Fig. In addition, this included *cra2* mutant roots Fig. CRA2 locally regulates lateral root formation and systemically regulates symbiotic nodule formation from the shoots. A and C, Representative images of different grafting combinations between the wild-type WT and *cra* plants that were grown in greenhouse with a perlite-sand mixture for eight weeks on an N-rich medium A or on an N-deprived medium with *Sinorhizobium meliloti* C. In panel C , detailed pictures showing nodules arrows are included below. D and E, Quantification of the nodule numbers D and the nodule number related to the root dry weight E in the different grafting combinations that are shown in C. Interestingly, to root or symbiotic nodule development this LRR-RLK subfamily contains several other receptors that To identify the gene that is affected in *cra2* mutants, Tnt1 were identified as regulating plant development via local or Flanking Sequence Tags FSTs were generated in the different systemic regulation [10,36]. An Arabidopsis consisting, respectively, in the presence of other M. The bundles; or in the root or stele diameter S7 Fig. These results genomic region that was affected in the 10 available *cra2* alleles suggest that XIP1 and CRA2 are not functional homologs. We then analyzed the CRA2 spatial divergent lateral root phenotypes, whereas no shoot fasciation expression pattern under non-symbiotic and symbiotic conditions phenotype was detected in the *har1* or *sunn* mutant in contrast to using either a transcriptional fusion between an ,2 kb CRA2 *clv1* in Arabidopsis. Both approaches revealed an was identified in *cra2* compared to *xip1*, and no altered root expression that was associated with the root stele and vascular system architecture phenotype was reported in *xip1*. This result bundles Fig. This ability of root systems to form lateral roots depending on species, result agrees with the expression pattern of other LRR-RLKs even inside the legume family. CRA2 was occurred in the different plant genomes, generating functionally additionally expressed in the Cell Proliferation Zone CPZ of divergent or redundant pathways. These scenarios may explain the open RAM Fig. In addition, CRA2 was the apparent phenotypic diversification that is observed. Under symbiotic nodulation conditions, CRA2 the plastic development of the root system depending on the expression was also detected in nodule primordia

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Fig. To elucidate the opposite well as in mature nodules in relation to peripheral vascular bundles effects of the CRA2 pathway on lateral root and nodule formation, and the apical meristem Fig. Among other candidate pathways, cytokinins were previously reported to antagonistically control lateral root and symbiotic nodule formation [42]. Data on crosstalk between signaling peptides and CRA2 functions in the regulation of legume root system hormones is just emerging, mainly with auxin and cytokinins [10]. The SUNN pathway therefore limits the formation of extra nodules Plant and bacteria material depending on environmental cues. When initiated, however, a The *Medicago truncatula* Gaertn. The Tnt1 insertional mutants were negative regulation and further permit new symbiotic infection generated and screened at the Noble Foundation USA; lines events. The seeds were scarified on sandpaper, together or independently. The seeds were then [36] or even other RLKs e. The seedlings were grown in The Lotus HAR1-dependent AON pathway was additionally vitro in a growth chamber at 25uC with a 16 h light period and a shown to control negatively lateral root formation [20â€™29]. The nodula- indicating their related function in a single AON pathway [40]. The transposon display, genotyping PCRs, and the process. A, Structure of the CRA2 protein indicating the 10 mutant alleles arrowheads that were identified by forward and reverse genetic screens the indicated position is related to the predicted ATG and functional domains. The vertical black bars indicate the predicted transmembrane domains; in grey are the Leucine-Rich Repeats; and the hatched region represents the kinase domain. The black arrowheads represent alleles that are linked to a Tnt1 retro-element insertion; the grey arrowheads represent another insertional element; and the white arrowhead represents a nucleotide deletion causing a translational frameshift. The sequences were aligned using Muscle, and the regions that were conserved between all of the sequences were defined with Gblocks. The phylogenetic relationships were determined using a maximum likelihood analysis PhyML , and statistical support for each node was estimated by approximate likelihood ratio tests. The *Chlamydomonas reinhardtii* XP protein was used to root the tree. This region fusion downstream of the cloning recombination site. CRA2 expression in the shoot, root and symbiotic nodules. A, A root apex observed in bright field with dichroic illumination Nomarski. C, Detail of the root meristem transition zone using a z-stack projection in confocal sections. The cell walls are visualized with a Propidium Iodide counterstaining, and GUS staining appears in reflectance as blue dots. F Detail of the purple signal associated with vasculature strands. Gâ€™H, In situ hybridization of the CRA2 transcripts in stem transversal sections G, purple signal or with a sense probe used as a negative control H. Brackets indicate vascular bundles. Iâ€™J, Detail of the stele in the root differentiated region in bright field I to visualize the GUS staining in dark blue and phloem vascular bundles poles Phl, in turquoise blue or under UV illumination J, same section as I to visualize the blue autofluorescence of the xylem vascular bundle poles Xy and endodermis End. Kâ€™L, Lateral root primordium initiation K, arrow and emergence L observed in bright field.

Chapter 4 : Root Development (Annual Plant Reviews, Volume 37) - PDF Free Download

The soil environmental conditions and symbiotic interactions are the major determinants of legume root architecture. Investigating cues that affect root developmental adaptations to the environment as well as understanding the mechanisms underlying the control of the root architecture are crucial to improve agronomical traits, notably in the legume family.

Chapter 5 : Annual Plant Reviews, Root Development (ebook) by Tom Beeckman |

What makes the legume root system so peculiar? The aim of this chapter is to give an overview of the current knowledge of the development of secondary root organs in legumes.

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Chapter 7 : Legume root architecture: a peculiar root system.

10 Legume Root Architecture: A Peculiar Root System (Silvina Gonzalez-Rizzo, Philippe Laporte, Martin Crespi and Florian Frugier). Comparison of legume lateral roots and nitrogen-fixing nodules. Recent advances in genetics and genomics of nitrogen-fixing nodule development in legumes.