Plant Stem Cell Research Literatures

Ma Hongbao [1], Margaret Young [2], Yang Yan [1]

[1] Brookdale Hospital, Brooklyn, New York 11212, USA; [2] Cambridge, MA 02138, USA
ma8080@gmail.com

Abstract: The stem cell is the origin of an organism's life that has the potential to develop into many different types of cells in life bodies. In many tissues stem cells serve as a sort of internal repair system, dividing essentially without limit to replenish other cells as long as the person or animal is still alive. When a stem cell divides, each new cell has the potential either to remain a stem cell or become another type of cell with a more specialized function, such as a red blood cell or a brain cell. This article introduces recent research reports as references in the plant stem cell related studies.
[Ma H, Young M, Yang Y. **Plant Stem Cell Research Literatures**. Stem Cell. 2015;6(2):73-79] (ISSN 1545-4570). http://www.sciencepub.net/stem. 9

Key words: stem cell; plant; life; research; literature

1. Introduction

The stem cell is the origin of an organism's life that has the potential to develop into many different types of cells in life bodies. In many tissues stem cells serve as a sort of internal repair system, dividing essentially without limit to replenish other cells as long as the person or animal is still alive. When a stem cell divides, each new cell has the potential either to remain a stem cell or become another type of cell with a more specialized function, such as a red blood cell or a brain cell. This article introduces recent research reports as references in the related studies.

The following introduces recent reports as references in the related studies.

Aichinger, E., N. Kornet, et al. "Plant stem cell niches." Annu Rev Plant Biol. 2012;63:615-36. doi: 10.1146/annurev-arplant-042811-105555. Epub 2012 Feb 9.

Multicellular organisms possess pluripotent stem cells to form new organs, replenish the daily loss of cells, or regenerate organs after injury. Stem cells are maintained in specific environments, the stem cell niches, that provide signals to block differentiation. In plants, stem cell niches are situated in the shoot, root, and vascular meristems-self-perpetuating units of organ formation. Plants' lifelong activity-which, as in the case of trees, can extend over more than a thousand years-requires that a robust regulatory network keep the balance between pluripotent stem cells and differentiating descendants. In this review, we focus on current models in plant stem cell research elaborated during the past two decades, mainly in the model plant Arabidopsis thaliana. We address the roles of mobile signals on transcriptional modules involved in balancing cell fates. In addition, we discuss shared features of and differences between the distinct stem cell niches of Arabidopsis.

Bennett, T., A. van den Toorn, et al. "Precise control of plant stem cell activity through parallel regulatory inputs." Development. 2014 Nov;141(21):4055-64. doi: 10.1242/dev.110148. Epub 2014 Sep 25.

The regulation of columella stem cell activity in the Arabidopsis root cap by a nearby organizing centre, the quiescent centre, has been a key example of the stem cell niche paradigm in plants. Here, we investigate interactions between transcription factors that have been shown to regulate columella stem cells using a simple quantification method for stem cell activity in the root cap. Genetic and expression analyses reveal that the RETINOBLASTOMA-RELATED protein, the FEZ and SOMBRERO NAC-domain transcription factors, the ARF10 and ARF16 auxin response factors and the quiescent centre-expressed WOX5 homeodomain protein each provide independent inputs to regulate the number of columella stem cells. Given the tight control of columella development, we found that these inputs act in a surprisingly parallel manner. Nevertheless, important points of interaction exist; for example, we demonstrate the repression of SMB activity by non-autonomous action of WOX5. Our results suggest that the developmental progression of columella stem cells may be quantitatively regulated by several more broadly acting transcription factors rather than by a single intrinsic stem cell factor, which raises questions about the special nature of the stem cell state in plants.

Busch, W., A. Miotk, et al. "Transcriptional control of a plant stem cell niche." Dev Cell. 2010 May 18;18(5):849-61. doi: 10.1016/j.devcel.2010.03.012.

Despite the independent evolution of multicellularity in plants and animals, the basic

organization of their stem cell niches is remarkably similar. Here, we report the genome-wide regulatory potential of WUSCHEL, the key transcription factor for stem cell maintenance in the shoot apical meristem of the reference plant Arabidopsis thaliana. WUSCHEL acts by directly binding to at least two distinct DNA motifs in more than 100 target promoters and preferentially affects the expression of genes with roles in hormone signaling, metabolism, and development. Striking examples are the direct transcriptional repression of CLAVATA1, which is part of a negative feedback regulation of WUSCHEL, and the immediate regulation of transcriptional repressors of the TOPLESS family, which are involved in auxin signaling. Our results shed light on the complex transcriptional programs required for the maintenance of a dynamic and essential stem cell niche.

Chakraborty, A., R. K. Yadav, et al. "Computational tools for quantitative analysis of cell growth patterns and morphogenesis in actively developing plant stem cell niches." Methods Mol Biol. 2012;876:217-27. doi: 10.1007/978-1-61779-809-2_18.

Pattern formation in developmental fields involves precise spatial arrangement of different cell types in a dynamic landscape wherein cells exhibit a variety of behaviors, such as cell division, cell expansion, and cell migration [Reddy (Curr Opin Plant Biol 11:88-931, 2008) and Meyerowitz (Cell 88:299-3082, 2007)]. The information is exchanged between multiple cell layers through cell-cell communication processes to regulate gene expression and cell behaviors in specifying distinct cell types. Therefore, a quantitative and dynamic understanding of the spatial and temporal organization of gene expression and cell behavioral patterns within multilayered and actively growing developmental fields is crucial to model the process of development. The quantification of spatiotemporal dynamics of cell behaviors requires computational tools in image analysis, statistical modeling, pattern recognition, machine learning, and dynamical system identification. Here, we give a brief account of recently developed methods in analyzing both local and global growth patterns in Arabidopsis shoot apical meristems. The computational toolkit can be used to gain new insights into causal relationships among cell growth, cell division, changes in gene expression patterns, and organ development by analyzing various mutants that affect these processes. This may allow us to develop function space models that capture variations in several growth parameters both at local/single-cell level and at global/organ level. In the long run, this may enable clustering of molecular pathways that mediate distinct cell behaviors.

Dinneny, J. R. and P. N. Benfey "Plant stem cell niches: standing the test of time." Cell. 2008 Feb 22;132(4):553-7. doi: 10.1016/j.cell.2008.02.001.

Similar to animal stem cells, plant stem cells require special niche microenvironments to continuously generate the tissues that constitute the plant body. Recent work using computer modeling and live imaging is helping to elucidate some of the mechanisms responsible for the specification and maintenance of stem cells in the root and shoot.

Fulcher, N. and R. Sablowski "Hypersensitivity to DNA damage in plant stem cell niches." Proc Natl Acad Sci U S A. 2009 Dec 8;106(49):20984-8. doi: 10.1073/pnas.0909218106. Epub 2009 Nov 20.

The growing apices of plants contain stem cells that continually produce tissues, which, in the shoot, include the germline. These stem cell populations remain active throughout the plant's life, which can last for centuries, and are particularly exposed to environmental hazards that cause DNA damage and mutations. It is not known whether plants have mechanisms to safeguard the genome specifically in these crucial cell populations. Here, we show that root and shoot stem cells and their early descendants are selectively killed by mild treatment with radiomimetic drugs, x-rays, or mutations that disrupt DNA repair by nonhomologous end-joining. Stem cell death required transduction of DNA damage signals by the ATAXIA-TELANGIECTASIA MUTATED (ATM) kinase and, specifically in the root, also the ATM/RAD3-RELATED (ATR) kinase. Consistent with the absence of p53 and the core apoptotic machinery in plants, death of the stem cells did not show apoptotic but autolytic features as seen in other cases of plant developmentally programmed cell death. We propose that plants have independently evolved selective death as a stringent mechanism to safeguard genome integrity in their stem cell populations.

Geier, F., J. U. Lohmann, et al. "A quantitative and dynamic model for plant stem cell regulation." PLoS One. 2008;3(10):e3553. doi: 10.1371/journal.pone.0003553. Epub 2008 Oct 29.

Plants maintain pools of totipotent stem cells throughout their entire life. These stem cells are embedded within specialized tissues called meristems, which form the growing points of the organism. The shoot apical meristem of the reference plant Arabidopsis thaliana is subdivided into several distinct domains, which execute diverse biological functions, such as tissue organization, cell-proliferation and differentiation. The number of cells required for growth and organ formation changes over the course of a plants life, while the structure of the meristem

remains remarkably constant. Thus, regulatory systems must be in place, which allow for an adaptation of cell proliferation within the shoot apical meristem, while maintaining the organization at the tissue level. To advance our understanding of this dynamic tissue behavior, we measured domain sizes as well as cell division rates of the shoot apical meristem under various environmental conditions, which cause adaptations in meristem size. Based on our results we developed a mathematical model to explain the observed changes by a cell pool size dependent regulation of cell proliferation and differentiation, which is able to correctly predict CLV3 and WUS over-expression phenotypes. While the model shows stem cell homeostasis under constant growth conditions, it predicts a variation in stem cell number under changing conditions. Consistent with our experimental data this behavior is correlated with variations in cell proliferation. Therefore, we investigate different signaling mechanisms, which could stabilize stem cell number despite variations in cell proliferation. Our results shed light onto the dynamic constraints of stem cell pool maintenance in the shoot apical meristem of Arabidopsis in different environmental conditions and developmental states.

Ito, Y., I. Nakanomyo, et al. "Dodeca-CLE peptides as suppressors of plant stem cell differentiation." Science. 2006 Aug 11;313(5788):842-5.

In plants and animals, small peptide ligands that signal in cell-cell communication have been suggested to be a crucial component of development. A bioassay of single-cell transdifferentation demonstrates that a dodecapeptide with two hydroxyproline residues is the functional product of genes from the CLE family, which includes CLAVATA3 in Arabidopsis. The dodecapeptide suppresses xylem cell development at a concentration of 10(-11) M and promotes cell division. An application, corresponding to all 26 Arabidopsis CLE protein family members, of synthetic dodecapeptides reveals two counteracting signaling pathways involved in stem cell fate.

Nimchuk, Z. L., P. T. Tarr, et al. "Plant stem cell signaling involves ligand-dependent trafficking of the CLAVATA1 receptor kinase." Curr Biol. 2011 Mar 8;21(5):345-52. doi: 10.1016/j.cub.2011.01.039. Epub 2011 Feb 17.

BACKGROUND: Cell numbers in above-ground meristems of plants are thought to be maintained by a feedback loop driven by perception of the glycopeptide ligand CLAVATA3 (CLV3) by the CLAVATA1 (CLV1) receptor kinase and the CLV2/CORYNE (CRN) receptor-like complex. CLV3 produced in the stem cells at the meristem apex limits the expression level of the stem cell-promoting homeodomain protein WUSCHEL (WUS) in the cells beneath, where CLV1 and WUS RNA are localized. WUS downregulation nonautonomously reduces stem cell proliferation. Overexpression of CLV3 eliminates the stem cells, causing meristem termination, and loss of CLV3 function allows meristem overproliferation. There are many questions regarding the CLV3/CLV1 interaction, including where in the meristem it occurs, how it is regulated, and how it is that a large range of CLV3 concentrations gives no meristem size phenotype. RESULTS: Here we use genetics and live imaging to examine the cell biology of CLV1 in Arabidopsis meristematic tissue. We demonstrate that plasma membrane-localized CLV1 is reduced in concentration by CLV3, which causes trafficking of CLV1 to lytic vacuoles. We find that changes in CLV2 activity have no detectable effects on CLV1 levels. We also find that CLV3 appears to diffuse broadly in meristems, contrary to a recent sequestration model. CONCLUSIONS: This study provides a new model for CLV1 function in plant stem cell maintenance and suggests that downregulation of plasma membrane-localized CLV1 by its CLV3 ligand can account for the buffering of CLV3 signaling in the maintenance of stem cell pools in plants.

Nimchuk, Z. L., Y. Zhou, et al. "Plant stem cell maintenance by transcriptional cross-regulation of related receptor kinases." Development. 2015 Mar 15;142(6):1043-9. doi: 10.1242/dev.119677.

The CLAVATA3 (CLV3)-CLAVATA1 (CLV1) ligand-receptor kinase pair negatively regulates shoot stem cell proliferation in plants. clv1 null mutants are weaker in phenotype than clv3 mutants, but the clv1 null phenotype is enhanced by mutations in the related receptor kinases BARELY ANY MERISTEM 1, 2 and 3 (BAM1, 2 and 3). The basis of this genetic redundancy is unknown. Here, we demonstrate that the apparent redundancy in the CLV1 clade is in fact due to the transcriptional repression of BAM genes by CLV1 signaling. CLV1 signaling in the rib meristem (RM) of the shoot apical meristem is necessary and sufficient for stem cell regulation. CLV3-CLV1 signaling in the RM represses BAM expression in wild-type Arabidopsis plants. In clv1 mutants, ectopic BAM expression in the RM partially complements the loss of CLV1. BAM regulation by CLV1 is distinct from CLV1 regulation of WUSCHEL, a proposed CLV1 target gene. In addition, quadruple receptor mutants are stronger in phenotype than clv3, pointing to the existence of additional CLV1/BAM ligands. These data provide an explanation for the genetic redundancy seen in the CLV1 clade and reveal a novel feedback operating in the control of plant stem cells.

Sablowski, R. "The dynamic plant stem cell niches." Curr Opin Plant Biol. 2007 Dec;10(6):639-44. Epub 2007 Aug 9.

Stem cells exist in specific locations called niches, where extracellular signals maintain stem cell division and prevent differentiation. In plants, the best characterised niches are within the shoot and root meristems. Networks of regulatory genes and intercellular signals maintain meristem structure in spite of constant cell displacement by division. Recent works have improved our understanding of how these networks function at the cellular and molecular levels, particularly in the control of the stem cell population in the shoot meristem. The meristem regulatory genes have been found to function partly through localised control of widely used signals such as cytokinin and auxin. The retinoblastoma protein has also emerged as a key regulator of cell differentiation in the meristems.

Sablowski, R. "Plant stem cell niches: from signalling to execution." Curr Opin Plant Biol. 2011 Feb;14(1):4-9. doi: 10.1016/j.pbi.2010.08.001. Epub 2010 Aug 23.

The shoot and root meristems contain small populations of stem cells that constantly renew themselves while providing precursor cells to build all other plant tissues and organs. Cell renewal, growth and differentiation in the meristems are co-ordinated by networks of transcription factors and intercellular signals. The past two years have revealed how auxin and cytokinin signals are integrated with each other and with regulatory genes in the shoot and root meristems. Small RNAs have also emerged as novel intercellular signals. Downstream of meristem regulatory genes, links have been made to cell division control and chromatin function. Protection of genome integrity, partly through programmed cell death after DNA damage, has recently been revealed as a specialised function in plant stem cells.

Sahlin, P., P. Melke, et al. "Models of sequestration and receptor cross-talk for explaining multiple mutants in plant stem cell regulation." BMC Syst Biol. 2011 Jan 5;5:2. doi: 10.1186/1752-0509-5-2.

BACKGROUND: Stem cells reside in a plant's shoot meristem throughout its life and are main regulators of above-ground plant development. The stem cell maintenance depends on a feedback network between the CLAVATA and WUSCHEL genes. The CLAVATA3 peptide binds to the CLAVATA1 receptor leading to WUSCHEL inhibition. WUSCHEL, on the other hand, activates CLAVATA3 expression. Recent experiments suggest a second pathway where CLAVATA3 inhibits WUSCHEL via the CORYNE receptor pathway. An interesting question, central for understanding the receptor signaling, is why the clavata1-11 null mutant has a weaker phenotype compared with the clavata1-1 non-null mutant. It has been suggested that this relies on interference from the mutated CLAVATA1 acting on the CORYNE pathway. RESULTS: We present two models for the CLAVATA-WUSCHEL feedback network including two receptor pathways for WUSCHEL repression and differing only by the hypothesized mechanisms for the clavata1-1 non-null mutant. The first model is an implementation of the previously suggested interference mechanism. The other model assumes an unaltered binding between CLAVATA3 and the mutated CLAVATA1 but with a loss of propagated signal into the cell. We optimize the models using data from wild type and four single receptor mutant experiments and use data from two receptor double mutant experiments in a validation step. Both models are able to explain all seven phenotypes and in addition qualitatively predict CLAVATA3 perturbations. The two models for the clavata1-1 mutant differ in the direct mechanism of the mutant, but they also predict other differences in the dynamics of the stem cell regulating network. We show that the interference hypothesis leads to an abundance of receptors, while the loss-of-signal hypothesis leads to sequestration of CLAVATA3 and relies on degradation or internalization of the bound CLAVATA1 receptor. CONCLUSIONS: Using computational modeling, we show that an interference hypothesis and a more parsimonious loss-of-signal hypothesis for a clavata1 non-null mutant both lead to behaviors predicting wild type and six receptor mutant experiments. Although the two models have identical implementations of the unperturbed feedback network for stem cell regulation, we can point out model-predicted differences that may be resolved in future experiments.

Scofield, S. and J. A. Murray "KNOX gene function in plant stem cell niches." Plant Mol Biol. 2006 Apr;60(6):929-46.

Homeobox genes encode transcriptional regulators that control development in multicellular eukaryotes. In plants, post-embryonic shoot growth relies on the activity of indeterminate cell populations termed shoot meristems, within which members of the class-1 KNOX sub-family of homeobox genes are expressed. KNOX genes are differentially required for meristem development and function to inhibit cell expansion and differentiation associated with organogenesis. Mechanisms must therefore be employed to prevent KNOX gene expression in developing lateral organs such as leaves. This review focuses on the expression patterns, meristematic functions and regulation of KNOX genes, and how the activities of these genes are integrated within the

framework of pathways that control plant development.

Stahl, Y. and R. Simon "Plant stem cell niches." Int J Dev Biol. 2005;49(5-6):479-89.

Stem cells are required to support the indeterminate growth style of plants. Meristems are a plants stem cell niches that foster stem cell survival and the production of descendants destined for differentiation. In shoot meristems, stem cell fate is decided at the populational level. The size of the stem cell domain at the meristem tip depends on signals that are exchanged with cells of the organizing centre underneath. In root meristems, individual stem cells are controlled by direct interaction with cells of the quiescent centre that lie in the immediate neighbourhood. Analysis of the interactions and signaling processes in the stem cell niches has delivered some insights into the molecules that are involved and revealed that the two major niches for plant stem cells are more similar than anticipated.

Tucker, M. R. and T. Laux "Connecting the paths in plant stem cell regulation." Trends Cell Biol. 2007 Aug;17(8):403-10. Epub 2007 Sep 4.

Stem cell niches are specialized microenvironments where pluripotent cells are maintained to provide undifferentiated cells for the formation of new tissues and organs. The balance between stem cell maintenance within the niche and differentiation of cells that exit it is regulated by local cell-cell communication, together with external cues. Recent findings have shown connections between key developmental pathways and added significant insights into the central principles of stem cell maintenance in plant meristems. These insights include the convergence of important stem cell transcriptional regulators with cytokinin signaling in the shoot meristem, the biochemical dissection of peptide signaling in the shoot niche and the identification of conserved regulators in shoot and root niches.

Vilarrasa-Blasi, J., M. P. Gonzalez-Garcia, et al. "Regulation of plant stem cell quiescence by a brassinosteroid signaling module." Dev Cell. 2014 Jul 14;30(1):36-47. doi: 10.1016/j.devcel.2014.05.020. Epub 2014 Jun 26.

The quiescent center (QC) maintains the activity of the surrounding stem cells within the root stem cell niche, yet specific molecular players sustaining the low rate of QC cell division remain poorly understood. Here, we identified a R2R3-MYB transcription factor, BRAVO (BRASSINOSTEROIDS AT VASCULAR AND ORGANIZING CENTER), acting as a cell-specific repressor of QC divisions in the primary root of Arabidopsis. Ectopic BRAVO expression restricts overall root growth and ceases root regeneration upon damage of the stem cells, demonstrating the role of BRAVO in counteracting Brassinosteroid (BR)-mediated cell division in the QC cells. Interestingly, BR-regulated transcription factor BES1 (BRI1-EMS SUPRESSOR 1) directly represses and physically interacts with BRAVO in vivo, creating a switch that modulates QC divisions at the root stem cell niche. Together, our results define a mechanism for BR-mediated regulation of stem cell quiescence in plants.

Xu, Y. Y. and K. Chong "[Progress in research on plant stem cell organizer gene WUSCHEL]." Zhi Wu Sheng Li Yu Fen Zi Sheng Wu Xue Xue Bao. 2005 Oct;31(5):461-8.

The WUS (WUSCHEL) gene encodes a transcription factor that specifies the adjacent cells to be stem cell. The WUS dependent signal systems have been found in different tissues recent years. The feedback loop between the CLV and WUS genes maintains the stem cell self-renewal and apical dominance in shoot apical meristem. In the embryonic meristem, the expression of CLV3 depends on WUS only. During post-embryo development, both WUS and STM are needed for CLV3 expression and the triggering of organogenesis. The expression of AG in floral meristem is activated by co-existence of WUS and LFY, AG acts as a negative regulator of WUS expression to downregulate the WUS level. The signal system established by WUS is also involved in ovule development. The somatic embryogenesis can be promoted efficiently by WUS, especially in the presence of auxin. The results of prevoius works indicated that cell competence to WUS activity is related to microenvironment and the combination of WUS signal with different environmental factors could activate different downstream genes.

Yadav, R. K., M. Perales, et al. "Plant stem cell maintenance involves direct transcriptional repression of differentiation program." Mol Syst Biol. 2013;9:654. doi: 10.1038/msb.2013.8.

In animal systems, master regulatory transcription factors (TFs) mediate stem cell maintenance through a direct transcriptional repression of differentiation promoting TFs. Whether similar mechanisms operate in plants is not known. In plants, shoot apical meristems serve as reservoirs of stem cells that provide cells for all above ground organs. WUSCHEL, a homeodomain TF produced in cells of the niche, migrates into adjacent cells where it specifies stem cells. Through high-resolution genomic analysis, we show that WUSCHEL represses a large number of genes that are expressed in differentiating cells including a group of differentiation promoting

TFs involved in leaf development. We show that WUS directly binds to the regulatory regions of differentiation promoting TFs; KANADI1, KANADI2, ASYMMETRICLEAVES2 and YABBY3 to repress their expression. Predictions from a computational model, supported by live imaging, reveal that WUS-mediated repression prevents premature differentiation of stem cell progenitors, being part of a minimal regulatory network for meristem maintenance. Our work shows that direct transcriptional repression of differentiation promoting TFs is an evolutionarily conserved logic for stem cell regulation.

Zermiani, M., M. Begheldo, et al. "Identification of the arabidopsis RAM/MOR signalling network: adding new regulatory players in plant stem cell maintenance and cell polarization." Ann Bot. 2015 Jun 15. pii: mcv066.

BACKGROUND AND AIMS: The RAM/MOR signalling network of eukaryotes is a conserved regulatory module involved in co-ordination of stem cell maintenance, cell differentiation and polarity establishment. To date, no such signalling network has been identified in plants. METHODS: Genes encoding the bona fide core components of the RAM/MOR pathway were identified in Arabidopsis thaliana (arabidopsis) by sequence similarity searches conducted with the known components from other species. The transcriptional network(s) of the arabidopsis RAM/MOR signalling pathway were identified by running in-depth in silico analyses for genes co-regulated with the core components. In situ hybridization was used to confirm tissue-specific expression of selected RAM/MOR genes. KEY RESULTS: Co-expression data suggested that the arabidopsis RAM/MOR pathway may include genes involved in floral transition, by co-operating with chromatin remodelling and mRNA processing/post-transcriptional gene silencing factors, and genes involved in the regulation of pollen tube polar growth. The RAM/MOR pathway may act upstream of the ROP1 machinery, affecting pollen tube polar growth, based on the co-expression of its components with ROP-GEFs. In silico tissue-specific co-expression data and in situ hybridization experiments suggest that different components of the arabidopsis RAM/MOR are expressed in the shoot apical meristem and inflorescence meristem and may be involved in the fine-tuning of stem cell maintenance and cell differentiation. CONCLUSIONS: The arabidopsis RAM/MOR pathway may be part of the signalling cascade that converges in pollen tube polarized growth and in fine-tuning stem cell maintenance, differentiation and organ polarity.

Zhou, Y., X. Liu, et al. "Control of plant stem cell function by conserved interacting transcriptional regulators." Nature. 2015 Jan 15;517(7534):377-80. doi: 10.1038/nature13853. Epub 2014 Oct 26.

Plant stem cells in the shoot apical meristem (SAM) and root apical meristem are necessary for postembryonic development of aboveground tissues and roots, respectively, while secondary vascular stem cells sustain vascular development. WUSCHEL (WUS), a homeodomain transcription factor expressed in the rib meristem of the Arabidopsis SAM, is a key regulatory factor controlling SAM stem cell populations, and is thought to establish the shoot stem cell niche through a feedback circuit involving the CLAVATA3 (CLV3) peptide signalling pathway. WUSCHEL-RELATED HOMEOBOX 5 (WOX5), which is specifically expressed in the root quiescent centre, defines quiescent centre identity and functions interchangeably with WUS in the control of shoot and root stem cell niches. WOX4, expressed in Arabidopsis procambial cells, defines the vascular stem cell niche. WUS/WOX family proteins are evolutionarily and functionally conserved throughout the plant kingdom and emerge as key actors in the specification and maintenance of stem cells within all meristems. However, the nature of the genetic regime in stem cell niches that centre on WOX gene function has been elusive, and molecular links underlying conserved WUS/WOX function in stem cell niches remain unknown. Here we demonstrate that the Arabidopsis HAIRY MERISTEM (HAM) family of transcription regulators act as conserved interacting cofactors with WUS/WOX proteins. HAM and WUS share common targets in vivo and their physical interaction is important in driving downstream transcriptional programs and in promoting shoot stem cell proliferation. Differences in the overlapping expression patterns of WOX and HAM family members underlie the formation of diverse stem cell niche locations, and the HAM family is essential for all of these stem cell niches. These findings establish a new framework for the control of stem cell production during plant development.

The above contents are the collected information from Internet and public resources to offer to the people for the convenient reading and information disseminating and sharing.

References

1. Aichinger, E., N. Kornet, et al. "Plant stem cell niches." Annu Rev Plant Biol. 2012;63:615-36. doi: 10.1146/annurev-arplant-042811-105555. Epub 2012 Feb 9.
2. Bennett, T., A. van den Toorn, et al. "Precise control of plant stem cell activity through parallel

regulatory inputs." Development. 2014 Nov;141(21):4055-64. doi: 10.1242/dev.110148. Epub 2014 Sep 25.
3. Busch, W., A. Miotk, et al. "Transcriptional control of a plant stem cell niche." Dev Cell. 2010 May 18;18(5):849-61. doi: 10.1016/j.devcel.2010.03.012.
4. Chakraborty, A., R. K. Yadav, et al. "Computational tools for quantitative analysis of cell growth patterns and morphogenesis in actively developing plant stem cell niches." Methods Mol Biol. 2012;876:217-27. doi: 10.1007/978-1-61779-809-2_18.
5. Dinneny, J. R. and P. N. Benfey "Plant stem cell niches: standing the test of time." Cell. 2008 Feb 22;132(4):553-7. doi: 10.1016/j.cell.2008.02.001.
6. Fulcher, N. and R. Sablowski "Hypersensitivity to DNA damage in plant stem cell niches." Proc Natl Acad Sci U S A. 2009 Dec 8;106(49):20984-8. doi: 10.1073/pnas.0909218106. Epub 2009 Nov 20.
7. Geier, F., J. U. Lohmann, et al. "A quantitative and dynamic model for plant stem cell regulation." PLoS One. 2008;3(10):e3553. doi: 10.1371/journal.pone.0003553. Epub 2008 Oct 29.
8. Ito, Y., I. Nakanomyo, et al. "Dodeca-CLE peptides as suppressors of plant stem cell differentiation." Science. 2006 Aug 11;313(5788):842-5.
9. Ma H, Chen G. Stem cell. The Journal of American Science 2005;1(2):90-92.
10. Ma H, Cherng S. Eternal Life and Stem Cell. Nature and Science. 2007;5(1):81-96.
11. Ma H, Cherng S. Nature of Life. Life Science Journal 2005;2(1):7 - 15.
12. Ma H, Yang Y. Turritopsis nutricula. Nature and Science 2010;8(2):15-20. http://www.sciencepub.net/nature/ns0802/03_1279_hongbao_turritopsis_ns0802_15_20.pdf.
13. Ma H. The Nature of Time and Space. Nature and science 2003;1(1):1-11.Nature and science 2007;5(1):81-96.
14. National Center for Biotechnology Information, U.S. National Library of Medicine**.** http://www.ncbi.nlm.nih.gov/pubmed. 2015.
15. Nimchuk, Z. L., P. T. Tarr, et al. "Plant stem cell signaling involves ligand-dependent trafficking of the CLAVATA1 receptor kinase." Curr Biol. 2011 Mar 8;21(5):345-52. doi: 10.1016/j.cub.2011.01.039. Epub 2011 Feb 17.
16. Nimchuk, Z. L., Y. Zhou, et al. "Plant stem cell maintenance by transcriptional cross-regulation of related receptor kinases." Development. 2015 Mar 15;142(6):1043-9. doi: 10.1242/dev.119677.
17. Sablowski, R. "Plant stem cell niches: from signalling to execution." Curr Opin Plant Biol. 2011 Feb;14(1):4-9. doi: 10.1016/j.pbi.2010.08.001. Epub 2010 Aug 23.
18. Sablowski, R. "The dynamic plant stem cell niches." Curr Opin Plant Biol. 2007 Dec;10(6):639-44. Epub 2007 Aug 9.
19. Sahlin, P., P. Melke, et al. "Models of sequestration and receptor cross-talk for explaining multiple mutants in plant stem cell regulation." BMC Syst Biol. 2011 Jan 5;5:2. doi: 10.1186/1752-0509-5-2.
20. Scofield, S. and J. A. Murray "KNOX gene function in plant stem cell niches." Plant Mol Biol. 2006 Apr;60(6):929-46.
21. Stahl, Y. and R. Simon "Plant stem cell niches." Int J Dev Biol. 2005;49(5-6):479-89.
22. Tucker, M. R. and T. Laux "Connecting the paths in plant stem cell regulation." Trends Cell Biol. 2007 Aug;17(8):403-10. Epub 2007 Sep 4.
23. Vilarrasa-Blasi, J., M. P. Gonzalez-Garcia, et al. "Regulation of plant stem cell quiescence by a brassinosteroid signaling module." Dev Cell. 2014 Jul 14;30(1):36-47. doi: 10.1016/j.devcel.2014.05.020. Epub 2014 Jun 26.
24. Wikipedia. The free encyclopedia. http://en.wikipedia.org. 2015.
25. Xu, Y. Y. and K. Chong "[Progress in research on plant stem cell organizer gene WUSCHEL]." Zhi Wu Sheng Li Yu Fen Zi Sheng Wu Xue Xue Bao. 2005 Oct;31(5):461-8.
26. Yadav, R. K., M. Perales, et al. "Plant stem cell maintenance involves direct transcriptional repression of differentiation program." Mol Syst Biol. 2013;9:654. doi: 10.1038/msb.2013.8.
27. Zermiani, M., M. Begheldo, et al. "Identification of the arabidopsis RAM/MOR signalling network: adding new regulatory players in plant stem cell maintenance and cell polarization." Ann Bot. 2015 Jun 15. pii: mcv066.
28. Zhou, Y., X. Liu, et al. "Control of plant stem cell function by conserved interacting transcriptional regulators." Nature. 2015 Jan 15;517(7534):377-80. doi: 10.1038/nature13853. Epub 2014 Oct 26.