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Stem-borne roots as a framework to study trans-organogenesis and uncover fundamental insights in developmental biology

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Abstract
Plants have a remarkable ability to generate organs with a different identity to the parent organ, called 'trans-organogenesis'. An example of trans-organogenesis is the formation of roots from stems (a type of adventitious root), which is the first type of root that arose during plant evolution. Despite being ancestral, stem-borne roots are often contextualised through lateral root research, implying that lateral roots precede adventitious roots. In this review we challenge that idea, highlight what is known about stem-borne root development across the plant kingdom, the remarkable diversity in form and function, and the many remaining evolutionary questions. Exploring stem-borne root evolutionary development can enhance our understanding of developmental decision making and the processes by which cells acquire their fates.

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Introduction

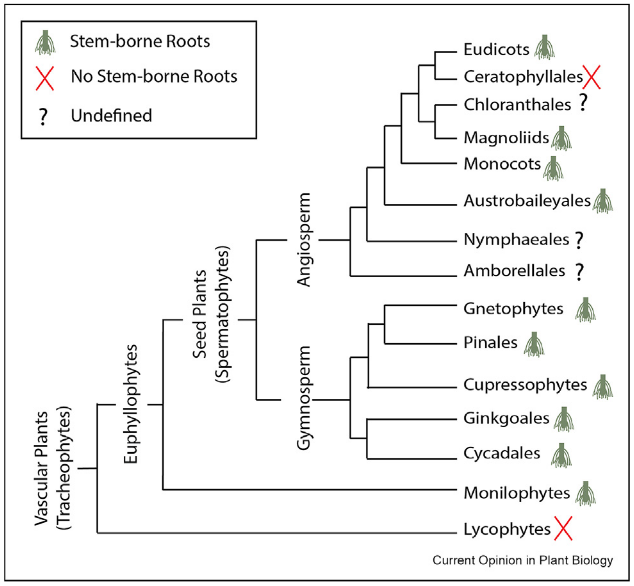
During the evolution of multicellularity, plants and animals converged on common developmental mechanisms — most notably the reliance on multipotent stem/initial cells that give rise to the different tissues within the organism. Despite the core commonality, plants rely heavily on the postembryonic formation of organs *de novo* to establish their body plan, while animals primarily undergo organogenesis during the embryonic phase [1]. In plants, postembryonic development can be broadly divided into two categories: cis-organogenesis and trans-organogenesis. Cis-organogenesis comprises the development of organs of the same type as the originating tissue (e.g. roots branching from other roots or stems branching from other stems), and trans-organogenesis comprises the development of organs that are different from their tissue of origin. In plants, trans-organogenesis can refer to shoots developing from roots or roots developing from shoots.

Roots developing from shoots are called adventitious, and encompass roots arising from stems, leaves and rhizomes (modified belowground stems). The term adventitious root includes roots that develop constitutively and in response to induction. Historically, adventitious roots were thought of as unusual events or only triggered by external factors — hence using the word adventitious. However, adventitious roots are an important and constitutive part of plant development that can be found throughout the plant kingdom. While all adventitious roots can provide insight into the mechanisms of trans-organogenesis, we focus specifically on the constitutive development of roots from stems, as these are well-studied.

Although stem-borne roots are the most well-studied adventitious roots, there is still little known about whether there are subtypes of stem-borne roots, what shared and divergent developmental pathways exist, what are the functional properties of these roots, and what is their evolutionary history. From an evolutionary perspective, we find evidence of stem-borne roots across the plant kingdom (Figure 1), but it is unknown if stem-borne roots are an ancestral trait or an example of convergent evolution.

The earliest roots were arguably adventitious and likely evolved multiple times [2]. However, shared and divergent developmental pathways remain to be defined, for adventitious root types (i.e., stem-, leave- and rhizome-borne) within species and across clades. It

Figure 1



Overview of the vascular plant tree of life indicating where stem-borne roots have been reported - marked by the stem-borne root graphic. Here, we define stem-borne as from true stems (not rhizome-borne roots). In contrast, several clades have been reported to have no stem-borne roots - marked with an ‘X’. In some clades the presence of stem-borne roots has been unreported - marked by ‘?’.

is unknown whether early developmental pathways are reused or rewired, or if increasing tissue complexity has resulted in new or hybrid trans-organogenesis pathways. To address these open questions, we first need to develop a framework that defines how many stem-borne root types exist, and define the anatomical and functional similarities and differences between these stem-borne root types. This review captures what is known across the plant tree of life about these fascinating organs and the current understanding of constitutive stem-borne root development as a framework for studying trans-organogenesis, and emphasising the many open questions that remain.

Stem-borne roots across the plant kingdom

The earliest roots in evolution are adventitious roots that develop from rhizomes (e.g., lycophytes). However, the first true constitutive stem-borne roots (as opposed to rhizome-borne) can be found in monilophytes (ferns). These stem-borne roots are best described in the homosporous fern *Ceratopteris richardii* (*C. richardii*), where a single stem-borne root is produced below each leaf in young sporophytes [3]. These roots originate from a defined root apical mother cell arising from hypodermal cell layer in the *C. richardii* stem [3]. The stem-borne roots in young sporophytes are distinct from the leaf-borne roots in older sporophytes and the rhizome-borne roots in mature sporophytes [3]. However, any shared or divergent developmental mechanisms among these adventitious roots have not been determined. Further, while stem-borne roots are prevalent in ferns, this is not true for all monilophyte lineages as some ferns do not have any roots, much less stem-borne roots [4]. While it has been proposed that all ferns which make roots make stem-borne roots [5], a careful dissection of root origin has only been completed in *C. richardii*.

Moving more recently in evolutionary history, stem-borne root formation is also found in gymnosperms [5] (Figure 1). The most common examples reported in the literature are roots that develop from low growing branches or in response to flooding. Low growing branches of *Taxus canadensis*, *Abies balsamica* and species of *Picea*, *Larix* or *Tsuga* are often found to produce roots when buried under leaf litter [6–8]. Other species like *Metasequoia glyptostroboides*, which are often adapted to waterlogged conditions, develop stem-borne roots in response to low oxygen levels [9,10]. These roots appear to develop primarily in response to environmental conditions, and similar to monilophytes there remains to be detailed characterisations of stem-borne root development in gymnosperms.

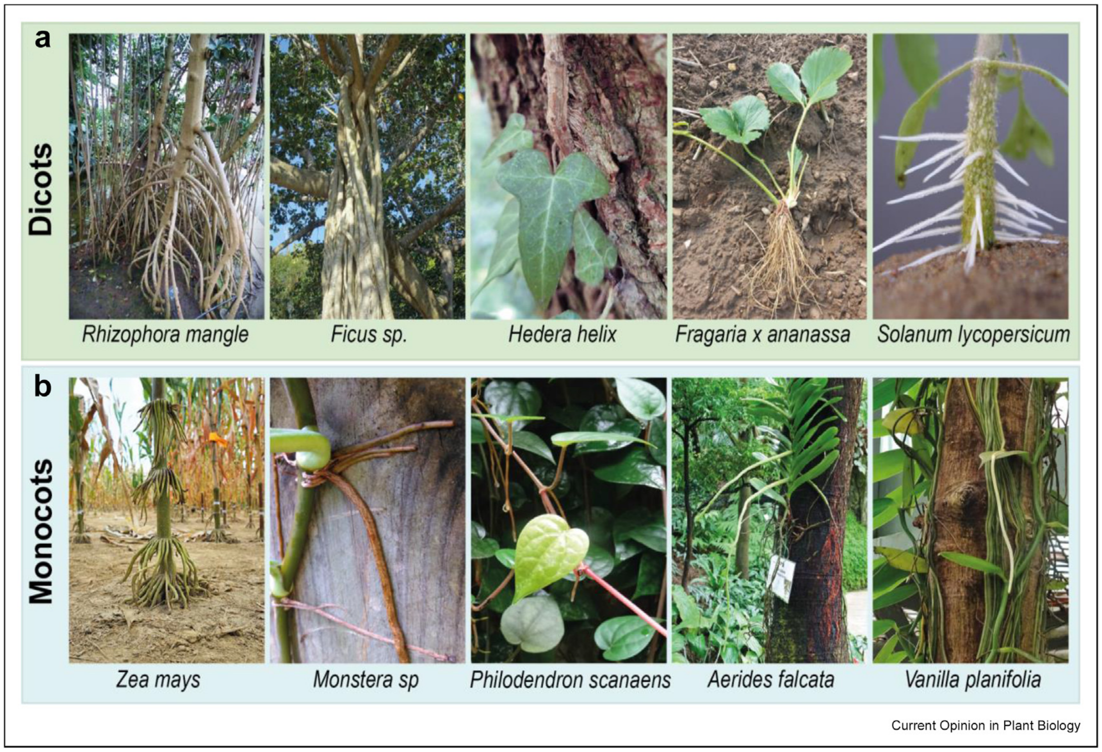
The majority of knowledge on stem-borne roots comes from angiosperms, where constitutive stem-borne roots are found in both monocots and eudicots (Figures 1 and 2). Monocot examples include members of the Poaceae (e.g., maize (*Zea mays*) and rice (*Oryza sativa*)), Orchidaceae (e.g., orchids), and Araceae (e.g., *Epipremnum* sp, *Philodendron* sp, and *Monstera* sp) families. Dicot examples include members of the Araliaceae (e.g., Ivy (*Hedera helix*)), Rosacea (e.g., strawberry (*Fragaria x ananassa*)), Solanacea (e.g., tomato (*Solanum lycopersicum*)), Rhizophoraceae (e.g., mangroves (*Rhizophora mangle*)) and Moraceae (e.g., figs (*Ficus* sp.)) families. Beyond these constitutive stem-borne roots, many plants (especially aquatic or riparian) can induce roots on submerged stems, or on segments broken from the main plant to create new plants downstream [11].

Open questions in stem-borne root evolution

Despite the prevalence of stem-borne roots throughout the vascular plant lineages, there is still very little known about the commonality and divergence of these roots from a developmental perspective. It remains unclear if stem-borne roots arose once during evolution and were lost in specific lineages or have been a repeated adaptation by convergent evolution (i.e., homoplasy) or represent new evolutionary adaptations.

As authors, we can rationalise multiple outcomes which are shaped by our definition of root types. If we consider all adventitious roots, each root type (i.e., stem-borne,

Figure 2



Diversity of species with stem-borne adventitious root types. Examples of a) dicots (mangroves, figs, ivy, strawberry and tomato) and b) monocots (maize, Monstera, Philodendron, and orchids including vanilla). These are just a few examples and the roots can provide support and/or resource supply. (Photo credits: Rasmussen, Vidoz, Sparks, and thanks to Abi Johnson (NIAB EMR) for Strawberry.

leaf-borne, and rhizome-borne) could have unique evolutionary origins that relate to the evolution of stems, leaves, and rhizomes. In contrast, there may be a shared evolutionary origin between stem-borne and rhizome-borne roots since rhizomes are modified stem structures. Despite these generalisations, we argue that classification by tissue-of-origin is still far too broad to successfully link evolutionary outcomes, because even within the stem-borne root classification there are clear subtypes that need to be defined.

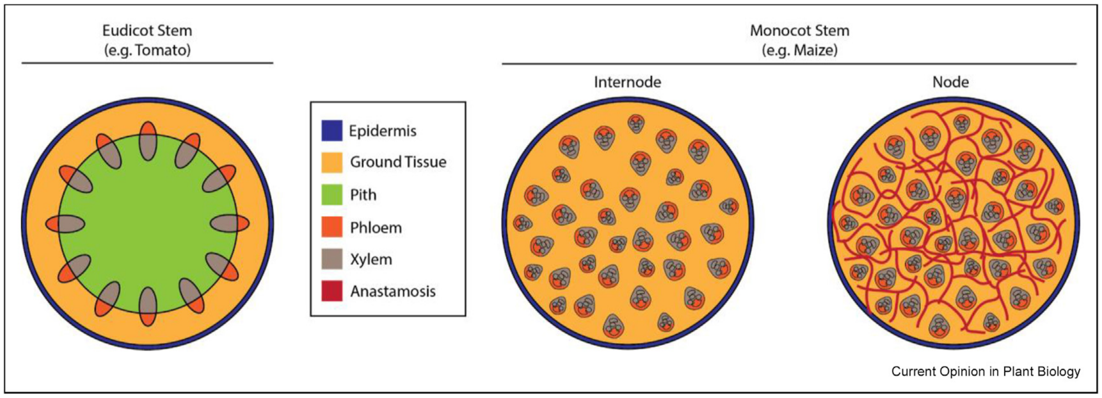
Convergent evolution is the independent evolution of analogous structures similar in form and function. Using this definition, we can already divide stem-borne roots into two broad categories based on their function - roots used for supporting the plant (like holding on to a vertical surface) and those for water and nutrient uptake. The difference between these two root types are easily seen in aroid hemi-epiphytes such as Anthuriums or Monsteras. The climbing roots of these plants are shorter and exude glues to adhere to the underlying surface [12], while along the same branch, long feeder roots grow towards the soil in search of water and nutrients. Thus, each of these root types likely arose from independent evolutionary events. Even within these broad functional categories, we see divergence and convergence of function. For example, stem-borne roots on maize, pandanas palms, mangroves and banyan figs (*Ficus benghalensis)*, provide support for the stem or large branches and also take up water and nutrients [13–15]. Thus, leading us to question how we should categorise adventitious and stem-borne roots for an evolutionary perspective on trans-organogenesis. Whether categorised by anatomy, tissue-origin or function, far more research is needed across the plant kingdom to better define stem-borne roots.

Developmental mechanisms of stem-borne roots

The goal of this article is to highlight the open questions regarding the evolutionary-development of stem-borne roots, which can be used as a framework for understanding trans-organogenesis. However, what we know about the developmental mechanisms is limited to work in a few angiosperm species. A major open question is how these developmental mechanisms can be expanded to other clades within the plant kingdom.

When considering stem-borne root development, the process can be divided into four sequential stages:

Figure 3



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Stem-borne roots arise from diverse stem anatomies. Shown here is an example from a dicot stem (e.g. tomato) and the internode and node anatomy of a monocot stem (e.g. maize). Although there are conserved tissue types, there are also divergent tissue types and changes in the arrangement of these tissues. Thus, although stem-borne roots develop from each of these stem anatomies; there are likely differences due to the diverse originating anatomy.

Induction, Initiation, Emergence, and Growth [16]. For the purpose of this review, we are focusing only on the first stage, Induction, which refers to the establishment of founder cells with the competency to divide. In the context of stem-borne root development, this means that one or more of the cells within the stem either de-differentiates to regain the ability to divide or there is a latent initial cell population that is lying dormant within the stem. Currently, there is little evidence to support either model, although a recent study showed that tomato stem-borne roots initiate from differentiated phloem primary parenchyma cells [17], which would support a de-differentiation model. Overall, the developmental differences between stem induction to make a root (trans-organogenesis) and stem induction to make a branch (cis-organogenesis) are unknown.

In considering the developmental pathways that regulate stem-borne root development, we find pathways that are common to the initiation of all new organs, such as the phytohormone auxin and the WOX (Wuschel-like homeobOX) family transcription factors [18]. However, we hypothesise that there must be signalling pathways that are specific for the generation of roots from stems [19]. Adventitious roots (trans-organogenesis) are often considered a modification of lateral roots (cis-organogenesis). However, the first evolutionary roots were adventitious roots, which suggests that lateral roots arose as a modification of adventitious roots. Thus we argue that using lateral root developmental pathways as a model for adventitious root development is flawed in an evolutionary context.

Taking this evolutionary perspective, it is unclear whether ‘modern’ stem-borne root types have co-opted the ancestral induction pathways or evolved new pathways. One example in stem-borne root development lends insight into this question [17]. LATERAL ORGAN BOUNDARIES DOMAIN (LBD) domain family transcription factors have been implicated in shoot-borne root initiation in maize and rice [20–23], which is perhaps expected as both species are members of the Poaceae family and roots initiate from the same type of stem anatomy (Figure 3). However, a study on tomato stem-borne root development turned up an LBD transcription factor of the same class as maize and rice [17], despite tomato stems having a different anatomy (Figure 3). An evolutionary analysis of the class IB LBD transcription factors divides into 5 subclasses that can provide insight into the evolutionary history of root development [17]. The ancestral state of these LBD transcription factors is subclass I and can be found from bryophytes to angiosperms, but have no known functions. The second subclass (II) is restricted to gymnosperms and angiosperms, but again with no known functions. There is then a divergence into three parallel branches (subclasses IIIG, IIIA and IIIB), with subclass IIIG specific to gymnosperms, IIIA specific to lateral root development and IIIB specific to stem-borne root development [17]. Despite the sequential naming convention, subclass IIIA is not the precursor to subclass IIIB. These data are consistent with the idea that stem-borne roots are the ancestral state and pathways have evolved to differentiate stem-borne roots (trans-organogenesis) from lateral roots (cis-organogenesis). While the evolutionary history of the LBDs highlights the potential to deconvolve trans- and cis-organogenesis mechanisms, there has been little empirical work in this direction.

Conclusions

In animal systems, lineage is often the determining factor for cell fate, but in plants the positional cues drive cell identity. Much of the knowledge about plant development comes from the model system Arabidopsis.

For example in Arabidopsis, ablation of a cell lineage results in the neighbouring cells dividing and taking on a new fate to recover that lineage [24]. This developmental robustness is likely due to the unrelenting nature of plants surviving in different environments. However, the amazing diversity of plant life and developmental plasticity provide the perfect platform for understanding cell fate decisions at an even deeper level. The example we highlight in this review is the process by which roots form from stems, an example of trans-organogenesis. This term has been used almost exclusively in *Ceratopteris elegans* to describe the process of a differentiated cell adopting a new cell fate [25], but also perfectly encompasses the process by which a stem produces roots.

Despite the pervasiveness of stem-borne roots and their importance for everything from food security and urban greenspace diversity, to improving conservation efforts and carbon sequestration, there is limited research in this area. Instead, research on organogenesis in plants has primarily focused on the initiation of organs of the same type as the tissue of origin (cis-organogenesis). For example, the mechanisms of lateral root initiation from a parent root are extremely well-studied. Although there is often the proposition that mechanisms of lateral root development can extend to stem-borne root development as well, there is limited evidence to support this proposition [26]. We further propose that stem-borne roots be discussed within the context of both a) the tissue/organ from which the roots form, b) the environmental conditions that triggered formation/emergence and c) the functional purpose of those roots. For example, stem-borne roots in tomatoes could be post-embryonic, internodal, flood-induced roots. This distinction is needed because the results from these studies may or may not be applicable to other stem-borne roots, such as maize postembryonic, nodal, and aerial brace roots. Thus, we end this opinion article with as many questions as we started - Does *de novo* trans-organogenesis initiate from mechanisms specific to the organ of origin, the organ of fate, or neither? How do the mechanisms of initiation differ between cis- and trans-organogenesis that allows a different organ fate to emerge? Do different environmental cues affect the developmental mechanisms? How does root function relate to developmental mechanisms? There is so much unexplored diversity across the tree of life that can help us to answer these important questions.

Author contributions

EES - Conceptualisation; EES, AR, MLV - Writing - original draft, Writing - reviewing and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

Data availability

No data were used for the research described in the article.

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References

Papers of particular interest, published within the period of review, have been highlighted as:

* of special interest
* * of outstanding interest

1. * Liu L, Qiu L, Zhu Y, Luo L, Han X, Man M, Li F, Ren M, Xing Y: **Comparisons between plant and animal stem cells regarding regeneration potential and application**. *Int J Mol Sci* 2023, **24**.
This paper compares the convergent evolution of plant and animal development in a broader context.

2. Mhimdi M, Pérez-Pérez JM: **Understanding of adventitious root formation: what can we learn from comparative genetics?** *Front Plant Sci* 2020, **11**, 582020.

3. Hou G, Hill JP: **Heteroblastic root development in Ceratopteris richardii (parkeriaceae)**. *Int J Plant Sci* 2002, **163**:341–351.

4. Pryer KM, Schuettpelz E, Wolf PG, Schneider H, Smith AR, Cranfill R: **Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences**. *Am J Bot* 2004, **91**:1582–1598.

5. * * Groff PA, Kaplan DR: **The relation of root systems to shoot systems in vascular plants**. *Bot Rev* 1988, **54**:387–422.
Comprehensive characterization of the different types of shoot-borne roots and root-borne shoots across the vascular plant tree of life.

6. Bannan MW: **Notes on the origin of adventitious roots in the native Ontario conifers**. *Am J Bot* 1942, **29**:593–598.

7. Holtmeier F-K, Broll G: **Layering in the Rocky Mountain treeline ecotone: clonal conifer groups' distribution, structure, and functional role**. *Trees (Berl)* 2017, **31**:953–965.

8. Hitsuma G, Morisawa T, Yagihashi T: **Orthotropic lateral branches contribute to shade tolerance and survival ofThujopsis dolabratavar.hondaisaplings by altering crown architecture and promoting layering**. *Botany* 2015, **93**:353–360.

9. Yang C, Zhang X, Wang T, Hu S, Zhou C, Zhang J, Wang Q: **Phenotypic plasticity in the structure of fine adventitious Metasequoia glyptostroboides roots allows adaptation to aquatic and terrestrial environments**. *Plants* 2019, **8**.

10. Krause C, Lemay A: **Root adaptations of black spruce growing in water-saturated soil**. *Can J Res* 2022, **52**:653–661.

11. Jackson MB, Drew MC: **Chapter 3 - effects of flooding on Growth and metabolism of herbaceous plants**. In *Flooding and plant Growth*. Edited by Kozlowski TT, Academic Press; 1984: 47–128.

12. Tay JYL, Kovalev A, Zotz G, Einzmann HJR, Gorb SN: **Holding on or falling off: the attachment mechanism of epiphytic Anthurium obtusum changes with substrate roughness**. *Am J Bot* 2022, **109**:874–886.

13. Méndez-Alonzo R, Moctezuma C, Ordoñez VR, Angeles G, Martínez AJ, López-Portillo J: **Root biomechanics in Rhizophora mangle: anatomy, morphology and ecology of mangrove's flying buttresses**. *Ann Bot* 2015, **115**:833–840.

14. Rollon RN, Villamayor BMR, Oropesa LJB, Samson MS: **Prop root production response of planted Rhizophora to abrupt**

subsidence-induced sea level rise. *Ocean Coast Manag* 2017, **142**:198–208.

15. Rasmussen A, Dobrijevic DP, Ola A, Ishaya FD, Lovelock CE: **Aerial root physiology: reaching for the sky or down to earth?** *Annual Plant Reviews online* 2018, **36**:753–784.

16. Hostetler AN, Khangura RS, Dilkes BP, Sparks EE: **Bracing for sustainable agriculture: the development and function of brace roots in members of Poaceae**. *Curr Opin Plant Biol* 2021, **59**, 101985.

17. ** Omary M, Gil-Yarom N, Yahav C, Steiner E, Hendelman A, Efroni I: **A conserved superlocus regulates above- and belowground root initiation**. *Science* 2022, **375**, eabf4368.

Foundational work identifying the LOB domain transcription factors as conserved regulators of stem-borne root development.

18. Liu W, Xu L: **Recruitment of IC-WOX genes in root evolution**. *Trends Plant Sci* 2018, https://doi.org/10.1016/j.tplants.2018.03.011.

19. Birnbaum KD: **How many ways are there to make a root?** *Curr Opin Plant Biol* 2016, **34**:61–67.

20. Inukai Y, Sakamoto T, Ueguchi-Tanaka M, Shibata Y, Gomi K, Umemura I, Hasegawa Y, Ashikari M, Kitano H, Matsuoka M: **Crown rootless1, which is essential for crown root formation in rice, is a target of an AUXIN RESPONSE FACTOR in auxin signaling**. *Plant Cell* 2005, **17**:1387–1396.

21. Liu H, Wang S, Yu X, Yu J, He X, Zhang S, Shou H, Wu P: **ARL1, a LOB-domain protein required for adventitious root formation in rice**. *Plant J* 2005, **43**:47–56.

22. Hetz W, Hochholdinger F, Schwall M, Feix G: **Isolation and characterization of rtcs, a maize mutant deficient in the formation of nodal roots**. *Plant J* 1996, **10**:845–857.

23. Taramino G, Sauer M, Stauffer Jr JL, Multani D, Niu X, Sakai H, Hochholdinger F: **The maize (Zea mays L.) RTCS gene encodes a LOB domain protein that is a key regulator of embryonic seminal and post-embryonic shoot-borne root initiation**. *Plant J* 2007, **50**:649–659.

24. van den Berg C, Willemsen V, Hage W, Weisbeek P, Scheres B: **Cell fate in the Arabidopsis root meristem determined by directional signalling**. *Nature* 1995, **378**:62–65.

25. Riddle MR, Spickard EA, Jevince A, Nguyen KCQ, Hall DH, Joshi PM, Rothman JH: **Transorganogenesis and transdifferentiation in C. elegans are dependent on differentiated cell identity**. *Dev Biol* 2016, **420**:136–147.

26. Bellini C, Pacurar DI, Perrone I: **Adventitious roots and lateral roots: similarities and differences**. *Annu Rev Plant Biol* 2014, **65**:639–666.