

Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)
 Current Opinion in  
**Genetics  
& Development**

# Evolution of developmental mechanisms in plants

Jane A Langdale

As our understanding of developmental mechanisms in flowering plant species has become more advanced, an appreciation of the need to understand how distinct plant morphologies are generated has grown. This has led to an awareness of the key morphological differences in distinct land plant groups and to an assessment of the major innovations that occurred during land plant evolution. Recent advances demonstrate how developmental toolkits have been recruited for related purposes in different land plant groups, but the limited number of examples highlights both the infancy of the field and the difficulty of working with non-flowering plants.

## Address

Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, United Kingdom

Corresponding author: Langdale, Jane A  
[jane.langdale@plants.ox.ac.uk](mailto:jane.langdale@plants.ox.ac.uk)

**Current Opinion in Genetics & Development** 2008, **18**:368–373

This review comes from a themed issue on  
 Pattern formation and developmental mechanisms  
 Edited by Ottoline Leyser and Olivier Pourquié

Available online 23rd June 2008

0959-437X/\$ – see front matter

© 2008 Elsevier Ltd. All rights reserved.

DOI [10.1016/j.gde.2008.05.003](https://doi.org/10.1016/j.gde.2008.05.003)

## Introduction

Land plants evolved from green algae in the mid-Ordovician, over 450 million years ago [1]. Phylogenetic analyses based on both morphological and molecular data suggest that within the green algae, charophytes in the order Charales are the sister group to the land plants [2]. The cellular innovations that facilitated the transition from growth in water to growth on land include the formation of waxy cuticles on vegetative tissue and the re-localization of sporopollenin deposition from the zygote in charophytes to the spores in land plants. Both of these features are synapomorphies of land plants that enabled reproductive success in a non-aqueous environment by conferring desiccation resistance. Subsequent innovations within different land plant lineages led to the diverse morphologies seen in extant (living) land plant groups. This review outlines our current understanding of the developmental mechanisms underlying those innovations.

## Land plant phylogeny

Since the colonization of land, plant form and function have diversified significantly. The extent and nature of

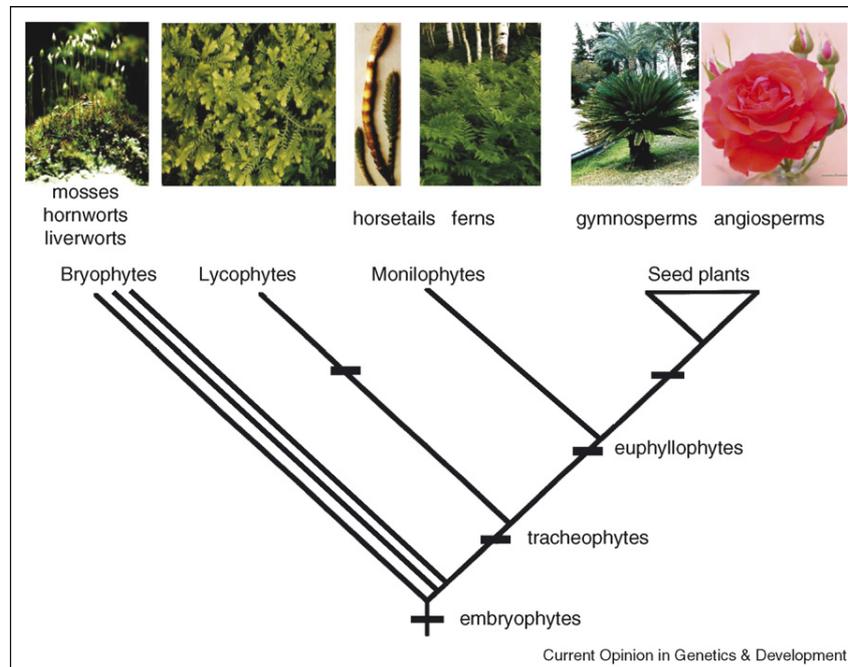
the innovations that led to this diversification is most easily seen by comparing extant land plant groups, and by considering the phylogenetic relationships between them. The least controversial phylogenetic distinction is between the bryophytes (liverworts, mosses and hornworts) and the tracheophytes (vascular plants) (Fig. 1). The vascular plants are monophyletic, with seed plants (gymnosperms and angiosperms), monilophytes (ferns and horsetails) and lycophytes each forming monophyletic groups within that clade. By contrast, the more basal bryophytes comprise a paraphyletic grade in which the relationships between each lineage have been difficult to resolve [3,4]. The most recent and most comprehensive analysis of bryophyte relationships resolves the liverworts as the most basal group (and thus sister group to all other land plants), and the hornworts as most likely sister group to the vascular plants [5\*\*].

## Developmental innovations during land plant evolution

As land plants evolved, developmental mechanisms were either generated *de novo* or were recruited from existing toolkits and adapted to facilitate changes in form. Some of these changes occurred once, others on multiple occasions, and others were gained and then subsequently lost in a subset of lineages. The changes that had most influence on the elaboration of form in the diploid sporophyte growth phase are summarized below and depicted in Fig. 2:

- **Development of a multi-cellular embryo**  
 In charophytes, the majority of the life cycle is represented by the haploid gametophyte and only the unicellular zygote is diploid, undergoing meiosis rather than mitosis after formation. Embryo development represents a major growth transition in that meiotic division of the zygote is delayed and cells divide by mitosis giving rise to a multi-cellular sporophyte.
- **Sporophyte growth from a defined apical cell(s)**  
 Bryophyte sporophytes all have a single axis of growth that terminates in sporangium formation, but distinct growth patterns are seen in each of the main lineages. Liverworts grow from cell divisions throughout the structure, mosses grow from both an apical cell and a basal intercalary meristem and hornworts grow from a basal meristem [6]. By contrast, growth in all vascular plants occurs from an apical cell or cells.
- **Branching in the sporophyte**  
 Whereas bryophytes have unbranched sporophytes that subtend a sporangium, protracheophyte fossil sporophytes from the Silurian have multiple branches that terminate in sporangia, and are therefore named polysporangiates [7]. Unlike extant polysporangiates,

Figure 1



Phylogeny illustrating the monophyly of land plants (embryophytes), the paraphyletic bryophyte grade (mosses plus hornworts plus liverworts), the monophyly of vascular plants (tracheophytes), lycophytes, euphyllophytes (monilophytes plus seed plants), monilophytes (horsetails plus ferns) and seed plants (spermatophytes) (gymnosperms plus angiosperms).

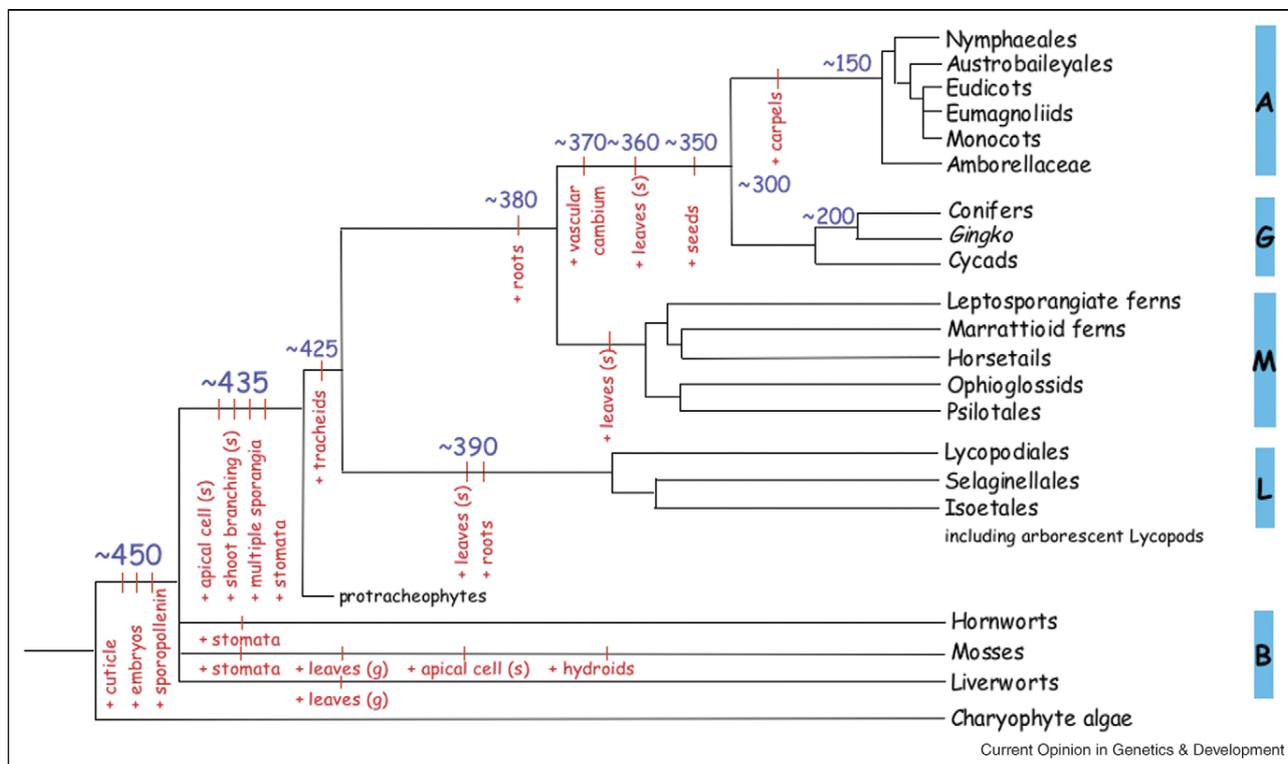
the protracheophyte fossils *Aglaophyton major* and *Horneophyton lignieri* are non-vascular. Therefore, sporophyte branching mechanisms evolved after the divergence of bryophytes and protracheophytes but before the appearance of tracheophytes. From a developmental perspective, this observation is important because it implies that branching evolved before vascularization.

- Development of a vascular system  
Increasingly complex body plans and competition for light led to the evolution of taller plants. As such, the need for mechanical support and for transport of water intensified. Coupled with the origin of lignin in vascular plants, these drivers led to the evolution of lignified conducting cells (tracheids). Whereas moss and some liverwort gametophytes transport water through conducting hydroids comprised of elongated cells with just primary cell walls, and protracheophyte fossils show evidence of a similar system [8], true tracheophytes transport water through xylem cells that have lignified secondary cell walls. Tracheophyte fossils indicate that tracheids first evolved in the mid-Silurian (~420 mya) [9].
- Development of roots.  
Charophyte algae and free-living gametophytes develop root-like structures, but 'true' roots are only found in sporophytes of vascular plants. Gametophyte 'roots' are

of three types: single celled rhizoid-like structures that are analogous to root hairs; multi-cellular rhizoid-like projections from a subterranean rhizome or mycorrhizas formed following a fungal association [10]. Whereas rhizoids provide conduits for water and nutrient transport, only the subterranean rhizomes enhance mechanical support. By contrast, true roots provide both transport capability and mechanical support. By definition they are multi-cellular, have a defined endodermis (with the exception of extant *Lycopodium* roots), produce lateral organs endogenously and have a root cap. Fossil data support the suggestion that lycophyte and euphyllophyte (monilophyte and seed plant) lineages diverged before roots evolved [10].

- Development of leaves  
The evolution of leaves followed a very similar trajectory to that of roots in that small 'leaf-like' structures are present on some extant free-living gametophytes but 'true' leaves comprising lignified vasculature and multiple cell layers are only found on sporophytes of vascular plants. Fossil evidence suggests that like roots, sporophyte leaves evolved on at least two separate occasions, once in the lycophytes and once in the euphyllophytes [11].
- Formation of seeds  
Before the evolution of seeds, plants reproduced via spores and fertilization required water because sperm

Figure 2



Land plant phylogeny showing predicted developmental trait acquisition at each node (red; s, sporophyte; g, gametophyte). Approximate timing of divergence at each node is in blue. Protracheophytes refers to non-vascular polysporangiates including *Aglaothyton major*, *Horneophyton lignieri* and some non-vascular *Cooksonia*-like fossils. On the bar at the right, A, angiosperms; G, gymnosperms; M, monilophytes; L, lycophytes; B, bryophytes.

had to swim. In seed plants, the female gametophyte develops inside a modified and protected megasporangium and the male gametophyte (the pollen grain) develops within the microsporangium. Female and male reproductive organs are borne on condensed and modified branching systems (cones in gymnosperms, and flowers in angiosperms). The evolution of these modifications permitted radiation of the seed plants by allowing dispersal of seed into previously uncolonized dryer habitats.

- Development of flowers  
The evolution of angiosperm flowers involved the modification of organ fate to produce ovules enclosed in carpels, and pollen enclosed in two pairs of sacs in the stamen. Sepals and petals evolved within the angiosperm lineage and allowed for specialization to attract animal pollinators.

**The evolution of developmental mechanisms**  
**Micro-evolutionary versus macro-evolutionary questions**

The study of how developmental mechanisms evolved in land plants is still in its infancy. To date, most work has

focused on the evolution of flowers, primarily because the genetic basis of floral development is well understood in model organisms and because a number of angiosperm species lend themselves to both forward and reverse genetic manipulations (see [12–14,15\*\*] for examples and recent reviews). Although micro-evolutionary questions within the angiosperms are clearly extremely important, an understanding of how novelties in plant architecture evolved demands answers to macro-evolutionary questions. Unfortunately, these questions are rarely tackled despite the land plant phylogeny being well resolved at deep nodes because of the difficulty with which non-flowering plant species can be grown and experimentally manipulated.

**Experimental organisms**

Within the bryophytes, the most tractable experimental system is the moss *Physcomitrella patens*. Transformation and homologous recombination have been possible for many years with this species, and the genome sequence was completed earlier this year [16\*]. Whilst *P. patens* has been generally accepted as ‘the’ model moss species, there are currently no equivalent liverwort or hornwort

species. *Marchantia polymorpha* has been proposed as a model liverwort partly because transformation of the thalloid gametophyte is possible by particle bombardment [17]. However, *M. polymorpha* is not in the most basal liverwort group, and perhaps more importantly for considerations of morphological novelty, *M. polymorpha* is a complex thalloid liverwort, whereas the majority (85%) of liverwort species are leafy/simple thalloid forms [18]. *Anthoceros formosae* is the hornwort species that has been suggested as a model and the chloroplast genome of this species has been sequenced [19]. To date, however, very little comparative work has been carried out with hornworts.

Lycophyte models are even less well defined than bryophyte models. There are three lycophyte orders—Isoetales, Lycopodiales and Selaginellales. We have advocated *S. kraussiana* as a model, and continue to do so, but the genome of *S. moellendorffii* has been sequenced (<http://selaginella.genomics.purdue.edu>). Unfortunately, *S. moellendorffii* cannot be propagated sexually because megasporangia abort [20], and thus the species cannot be used for genetic studies. Species in other lycophyte orders could potentially be developed as models. *Isoetes* is a particularly interesting group of plants because it is the only extant representative of an order with a long fossil history. Many fossil representatives of the Isoetales show parallel evolution of most of the key innovations that are generally only associated with seed plants; extreme heterospory with an enclosed megaspore, wood and bipolar growth. These features suggest a life history analogous to seed plant trees. Of the Lycopodiales, *Huperzia* provides an ideal system for comparative studies as it has a very large meristem that could easily be manipulated.

The number of fern groups, the morphological variations between groups and the total number of fern species are greater than seen in the lycophytes [21]. This makes the process of choosing model fern species more difficult. However, the leptosporangiate fern *Ceratopteris richardii* has been widely used in the past for both genetic studies and for introducing plant biologists of all ages to the features of non-seed plants (see <http://www.c-fern.org/>). As a consequence it is a viable model species. Transient transformation and subsequent RNAi silencing has also been reported in *C. richardii* gametophytes [22].

#### State of the art

At the time of writing, the following examples represent the majority of published reports that address macro-evolutionary questions by comparing developmental genetics in angiosperms and non-flowering plants:

- GOLDEN2-LIKE (GLK) [23] and HOMEODOMAIN-ZIP (HD-ZIP) [24] transcription factors regulate chloroplast development both in the moss *P. patens* and in angiosperms, suggesting that the regulatory function evolved before the divergence of bryophytes and vascular plants. This function could have evolved within the land plants or in algal ancestors.
- LEAFY/FLORICAULA (LFY/FLO), the transcription factor that regulates the formation of floral meristems in *Arabidopsis thaliana* and *Antirrhinum majus*, regulates the first cell division of the zygote in the bryophyte *P. patens* [25]. Whether the ‘ancestral’ role of LFY in cell division is retained in other non-flowering plants awaits clarification. However, LFY expression patterns in ferns are different from expression patterns of the organ identity genes that are LFY targets in angiosperms and thus the relationship between the two evolved after the divergence of ferns and seed plants [26].
- ROOT HAIR DEFECTIVE 6 (RHD6)-like transcription factors regulate the development of root hairs in *A. thaliana* and rhizoids in the bryophyte *P. patens* [27••]. If rhizoids are not homologous to root hairs, this observation suggests recruitment of an existing ‘gametophyte’ toolkit for sporophyte root hair formation, at least in the euphyllophyte lineage. As roots evolved independently in lycophytes and euphyllophytes, it will be interesting to determine whether there was a parallel recruitment of the RHD6 pathway in lycophyte roots.
- The interaction between KNOTTED1-like homeobox (KNOX) and ARP transcription factors in the vegetative shoot apex regulates leaf development in both the lycophyte *Selaginella kraussiana* [28] and at least three euphyllophytes (*A. thaliana* [29], *Zea mays* and *A. majus* [30,31]). Additionally, ectopic expression of lycophyte (unpublished data) and fern [32] KNOX genes in angiosperm leaves, gives equivalent phenotypes to overexpression of the respective angiosperm genes. As leaves evolved independently in lycophytes and euphyllophytes, these observations suggest that the same pathway was recruited on two separate occasions and that there is a developmental constraint on how leaves can form. However, HD-ZIP proteins have different expression patterns in leaves of lycophytes and euphyllophytes [33•]. These patterns are consistent with a role in regulating the distinct vascularization patterns seen in the two groups and thus once leaf primordia are initiated, different developmental mechanisms may pattern the final form.
- The activity of KNOX proteins in angiosperms has been shown to influence, and/or be influenced by a number of hormones—namely gibberellin, cytokinin and auxin (reviewed in [34]). To date, there have been very few studies on hormone signalling in non-seed plants. However, it is interesting to note that bryophyte (*P. patens*) [35•] and fern [32] KNOX proteins function in the sporophyte but not the gametophyte and that although auxin plays a role in the gametophyte, polar auxin transport has been reported to be

sporophyte-specific in *P. patens* [36]. As auxin plays a pivotal signalling role in regulating the pattern of leaf initiation in angiosperms [37,38], these observations raise the question of whether specific KNOX/auxin interactions co-evolved in the sporophyte.

- Physical interactions between gibberellin (GA), GA receptors (GIDs), and DELLA signalling proteins are conserved in lycophytes and angiosperms, but not in *P. patens* [39,40<sup>\*\*</sup>,41]. However, the role of these interactions in regulating growth is not conserved in either lycophytes or *P. patens*, suggesting a step-wise recruitment of GA-mediated growth patterning during land plant evolution.

## Conclusions

The examples outlined above illustrate how little we know about how land plant form evolved. More significant advances require the development of forward and reverse genetic technologies in non-flowering plants, and the generation of sequence data from diverse plant groups. In this regard, the recent advent of affordable parallel sequencing methods will have a big impact on the field. There are certainly plenty of questions to be answered and for those willing to work with non-model species, there are exciting challenges ahead.

## Acknowledgements

As always, I am grateful to all of the students and post-docs who work with me for keeping me on my toes. Our work is funded by the Gatsby Charitable Foundation, and by the Biological and Biotechnological Sciences Research Council (BBSRC).

## References and recommended reading

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

- of special interest
- of outstanding interest

- Sanderson MJ: **Molecular data from 27 proteins do not support a precambrian origin of land plants.** *Am J Bot* 2003, **90**:954-956.
- Lewis IA, McCourt RM: **Green algae and the origin of land plants.** *Am J Bot* 2004, **91**:1535-1556.
- Palmer JD, Soltis DE, Chase MW: **The plant tree of life: an overview and some points of view.** *Am J Bot* 2004, **91**:1437-1445.
- Shaw J, Renzaglia K: **Phylogeny and diversification of bryophytes.** *Am J Bot* 2004, **91**:1557-1581.
- Qiu YL, Li L, Wang B, Chen Z, Knoop V, Groth-Malonek M, Dombrowska O, Lee J, Kent L, Rest J *et al.*: **The deepest divergences in land plants inferred from phylogenomic evidence.** *Proc Natl Acad Sci U S A* 2006, **103**:15511-15516.  
Uses large scale datasets to resolve relationships between bryophytes and vascular plants.
- Kato M, Akiyama H: **Interpolation hypothesis for origin of the vegetative sporophyte of land plants.** *Taxon* 2005, **54**:443-450.
- Crane PR, Herendeen P, Friis EM: **Fossils and plant phylogeny.** *Am J Bot* 2004, **91**:1683-1699.
- Boyce CK, Cody GD, Fogel ML, Hazen RM, Alexander CM, Knoll AH: **Chemical evidence for cell wall lignification and the evolution of tracheids in early devonian plants.** *Int J Plant Sci* 2003, **164**:691-702.
- Edwards D, Feehan J, Smith DG: **A late Wenlock flora from County Tipperrary, Ireland.** *Bot J Linn Soc* 1983, **86**:19-36.
- Raven JA, Edwards D: **Roots: evolutionary origins and biogeochemical significance.** *J Exp Bot* 2001, **52**:381-401.
- Kenrick P, Crane PR: *The Origin and Early Diversification of Land Plants: A Cladistic Study.* London: Smithsonian Institution Press; 1997.
- Hanzawa Y, Money T, Bradley D: **A single amino acid converts a repressor to an activator of flowering.** *Proc Natl Acad Sci U S A* 2005, **102**:7748-7753.
- Irish VF, Litt A: **Flower development and evolution: gene duplication, diversification and redeployment.** *Curr Opin Genet Dev* 2005, **15**:454-460.
- Kramer EM, Hall JC: **Evolutionary dynamics of genes controlling floral development.** *Curr Opin Plant Biol* 2005, **8**:13-18.
- Prusinkiewicz P, Erasmus Y, Lane B, Harder LD, Coen E: **Evolution and development of inflorescence architectures.** *Science* 2007, **316**:1452-1456.  
Shows how a combination of developmental genetics and mathematical modelling can be used to predict particular morphologies and to illustrate why certain developmental transitions may be constrained.
- Rensing SA, Lang D, Zimmer AD, Terry A, Salamov A, Shapiro H, Nishiyama T, Perroud PF, Lindquist EA, Kamisugi Y *et al.*: **The Physcomitrella genome reveals evolutionary insights into the conquest of land by plants.** *Science* 2008, **319**:64-69.  
Report of the first complete bryophyte genome sequence. Uses bioinformatics to infer how particular genomic changes may have contributed to the movement of plants to land.
- Takenaka M, Yamaoka S, Hanajiri T, Shimizu-Ueda Y, Yamato KT, Fukuzawa H, Ohyama K: **Direct transformation and plant regeneration of the haploid liverwort *Marchantia polymorpha* L.** *Transgenic Res* 2000, **9**:179-185.
- Crandall-Stotler B, Stotler R: **Morphology and classification of the Marchantiophyta.** In *Bryophyte Biology.* Edited by Shaw A, Goffinet B. Cambridge University Press; 2000:21.
- Kugita M, Kaneko A, Yamamoto Y, Takeya Y, Matsumoto T, Yoshinaga K: **The complete nucleotide sequence of the hornwort (*Anthoceros formosae*) chloroplast genome: insight into the earliest land plants.** *Nucl Acids Res* 2003, **31**:716-721.
- Little DP, Moran RC, Brenner ED, Stevenson DW: **Nuclear genome size in Selaginella.** *Genome* 2007, **50**:351-356.
- 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.
- Rutherford G, Tanurdzic M, Hasebe M, Banks JA: **A systemic gene silencing method suitable for high throughput, reverse genetic analyses of gene function in fern gametophytes.** *BMC Plant Biol* 2004, **4**:6.
- Yasumura Y, Moylan EC, Langdale JA: **A conserved transcription factor mediates nuclear control of organelle biogenesis in anciently diverged land plants.** *Plant Cell* 2005, **17**:1894-1907.
- Sakakibara K, Nishiyama T, Sumikawa N, Kofuji R, Murata T, Hasebe M: **Involvement of auxin and a homeodomain-leucine zipper I gene in rhizoid development of the moss *Physcomitrella patens*.** *Development* 2003, **130**:4835-4846.
- Tanahashi T, Sumikawa N, Kato M, Hasebe M: **Diversification of gene function: homologs of the floral regulator FLO/LFY control the first zygotic cell division in the moss *Physcomitrella patens*.** *Development* 2005, **132**:1727-1736.
- Himi S, Sano R, Nishiyama T, Tanahashi T, Kato M, Ueda K, Hasebe M: **Evolution of MADS-box gene induction by FLO/LFY genes.** *J Mol Evol* 2001, **53**:387-393.
- Menand B, Yi K, Jouannic S, Hoffmann L, Ryan E, Linstead P, Schaefer DG, Dolan L: **An ancient mechanism controls the development of cells with a rooting function in land plants.** *Science* 2007, **316**:1477-1480.  
Shows that components of the pathway that regulate root hair formation in Arabidopsis also regulate rhizoid formation in *Physcomitrella*. As

- rhizoids are present on the gametophyte and root hairs on the sporophyte, this work demonstrates that the same pathway was recruited independently for the formation of non-homologous structures.
28. Harrison CJ, Corley SB, Moylan EC, Alexander DL, Scotland RW, Langdale JA: **Independent recruitment of a conserved developmental mechanism during leaf evolution.** *Nature* 2005, **434**:509-514.
  29. Byrne ME, Barley R, Curtis M, Arroyo JM, Dunham M, Hudson A, Martienssen RA: **ASYMMETRIC LEAVES1 mediates leaf patterning and stem cell function in Arabidopsis.** *Nature* 2000, **408**:967-971.
  30. Tsiantis M, Schneeberger R, Golz JF, Freeling M, Langdale JA: **The maize rough sheath2 gene and leaf development programs in monocot and dicot plants.** *Science* 1999, **284**:154-156.
  31. Timmermans MCP, Hudson A, Becraft PW, Nelson T: **ROUGH SHEATH2: A myb protein that represses knox homeobox genes in maize lateral organ primordia.** *Science* 1999, **284**:151-153.
  32. Sano R, Juarez CM, Hass B, Sakakibara K, Ito M, Banks JA, Hasebe M: **KNOX homeobox genes potentially have similar function in both diploid unicellular and multicellular meristems, but not in haploid meristems.** *Evol Dev* 2005, **7**:69-78.
  33. Floyd SK, Bowman JL: **Distinct developmental mechanisms reflect the independent origins of leaves in vascular plants.** *Curr Biol* 2006, **16**:1911-1917.  
Shows that the expression patterns of class III HD-ZIP genes that are required for vascularization and polarity in angiosperm leaves differ between gymnosperms and lycophytes. This observation suggests that different mechanisms regulate vascular development in leaves of lycophytes and euphyllophytes, consistent with the independent origin of leaves in the two groups.
  34. Hay A, Craft J, Tsiantis M: **Plant hormones and homeoboxes: bridging the gap?** *Bioessays* 2004, **26**:395-404.
  35. Singer SD, Ashton NW: **Revelation of ancestral roles of KNOX genes by a functional analysis of Physcomitrella homologues.** *Plant Cell Rep* 2007, **26**:2039-2054.  
Demonstrates that loss of KNOX gene function in Physcomitrella has no impact on the development of the gametophyte. This observation infers that KNOX function evolved with/in the multi-cellular sporophyte.
  36. Fujita T, Sakaguchi H, Hiwatashi Y, Wagstaff SJ, Ito M, Deguchi H, Sato T, Hasebe M: **Convergent evolution of shoots in land plants: lack of auxin polar transport in moss shoots.** *Evol Dev* 2008, **10**:176-186.
  37. Reinhardt D, Mandel T, Kuhlemeier C: **Auxin regulates the initiation and radial position of plant lateral organs.** *Plant Cell* 2000, **12**:507-518.
  38. Reinhardt D, Pesce ER, Stieger P, Mandel T, Baltensperger K, Bennett M, Traas J, Friml J, Kuhlemeier C: **Regulation of phyllotaxis by polar auxin transport.** *Nature* 2003, **426**:255-260.
  39. Hirano K, Nakajima M, Asano K, Nishiyama T, Sakakibara H, Kojima M, Katoh E, Xiang H, Tanahashi T, Hasebe M *et al.*: **The GID1-mediated gibberellin perception mechanism is conserved in the lycophyte Selaginella moellendorffii but not in the bryophyte Physcomitrella patens.** *Plant Cell* 2007, **19**:3058-3079.
  40. Yasumura Y, Crumpton-Taylor M, Fuentes S, Harberd NP: **Step-by-step acquisition of the gibberellin-DELLA growth-regulatory mechanism during land-plant evolution.** *Curr Biol* 2007, **17**:1225-1230.  
The two papers above characterize the relationship between gibberellin, the GA receptor GID1, and DELLA proteins, in distinct land plant groups. The results show a gradual acquisition during land plant evolution, of both the physical interactions between the three components and of their role in growth.
  41. Vandenbussche F, Fierro AC, Wiedemann G, Reski R, Van Der Straeten D: **Evolutionary conservation of plant gibberellin signalling pathway components.** *BMC Plant Biol* 2007, **7**:65.