



A renaissance in plant development



Since 1959, *Developmental Biology*, the official journal of the Society for Developmental Biology, has reported on developmental insights from a wide variety of model organisms, including mouse, rat, chick, *Xenopus*, zebrafish, sea urchin, *Caenorhabditis elegans*, and *Drosophila*, among many others (Fig. 1). As diverse as the aforementioned models are, spanning vertebrates and invertebrates, protostomes and deuterostomes, all the above animals represent a single evolutionary innovation of multicellularity.

In this special issue we highlight plant development. From the beginning, *Developmental Biology* has published outstanding plant development papers; these include some of the first studies on cell lineage patterns in plants (Jegla and Sussex, 1989; Poethig and Sussex, 1985), some of the first models describing epidermal cell type differentiation (Korn, 1981; Stebbins and Jain, 1960), and a variety of technical approaches over the years that have helped to move the field of plant development into the modern era. Nonetheless, papers on plant developmental mechanisms have tended to be underrepresented in the journal. As of this writing, though, 2016 marks a strong reversal in this trend, in part due to contributions to this special issue on plant development.

Below, we highlight the papers in this special issue and feature the unique perspective plants provide to developmental studies. It is our hope that this issue of *Developmental Biology* marks a renaissance in research in plant development; by combining the unique perspective plant developmental studies provide with the strengths already evident in the animal studies published in *Developmental Biology*, we hope to arrive at a more comprehensive view of the similarities (as well as the amazing diversity of species-specific processes) in developmental mechanisms that operate across all of life.

1. The evolution of plant development

Not only did plants develop multicellularity independently from animals, but they did so multiple times. Plants (Viridiplantae) are divided into two major groups: the green algae (Chlorophyta) and the land plants and their fresh water relatives (Streptophyta). Within the green algae, the order Volvocales presents a gradation of body plans, from single-celled *Chlamydomonas* to the truly multicellular *Volvox*. Matt and Umen (2016) provide an overview of development in *Volvox*, highlighting the independent evolution of asymmetric cell division and germ-soma differentiation in volvocine algae.

Independently from green algae, land plants evolved a multicellular body plan in which an indeterminate, growing shoot tip, the meristem, gives rise to lateral organs. In early diverging land

plant lineages, like moss, iterative indeterminate growth occurs in the gametophyte (haploid) stage, whereas in the flowering plants it occurs in the sporophyte (diploid) phase. Yip et al. (2016) investigate the role of class III HD-ZIP (C3HDZ) genes in the moss *Physcomitrella patens* showing that, unlike the meristems of flowering plants where C3HDZ activity is necessary, these genes are not expressed in the indeterminate meristems of the moss gametophyte, suggesting that they were not co-opted during the transition to a dominant sporophyte lifecycle.

2. Hormones, leaves, and flowers

Angiosperms, the most successful and speciose group of land plants, possess multicellular meristems that iteratively produce lateral organs, the shoot meristem producing both leaves and flowers, with the root meristem producing an extensive root system. The hormone auxin directs a range of developmental processes in plants, including differentiation, cell division, growth, and patterning. Taylor-Teeples et al. (2016) describe the role of auxin across shoot and root development (“as above, so below”) comparing the role of this hormone in patterning lateral root development to phyllotaxy, the patterning of lateral organs in the shoot. Martinez et al. (2016) continue to explore the role of auxin in tomato leaf development. The auxin efflux carrier *PIN-FORMED1* (*PIN1*) is present as a single copy gene in *Arabidopsis*, but a homolog, *Sister of PIN1* (*SoPIN1*), is present in most flowering plants outside the Brassicaceae. In tomato, a *SoPIN1* mutant called *entire-2* has aberrant phyllotactic patterning and abnormal leaf and reproductive development arising from the mislocalization of auxin. Tomato leaves are particularly suited for developmental studies because of their relatively prolonged indeterminacy, creating a compound leaf composed of multiple leaflets. Shwartz et al. (2016) describe the roles of auxin, gibberellin, cytokinin, and the cross-talk between these hormones in balancing morphogenesis and differentiation to regulate tomato leaf complexity.

Eventually meristems transition from producing vegetative to reproductive structures—the flowers. The development of a flower is an intricate process, in which a number of genetic pathways are used in different ways to produce diverse organs (sepals, petals, stamens, and carpels) in rapid succession. Wessinger and Hileman (2016) investigate the effects of pleiotropy and genetic correlations in the evolution of flowers. They argue that selection can either act in the direction of a genetic correlation or against it. If selection acts against a set of pleiotropic effects, evolution will be limited by gene duplication allowing for subfunctionalization or neofunctionalization to bypass the constraint. Soza et al. (2016) describe such

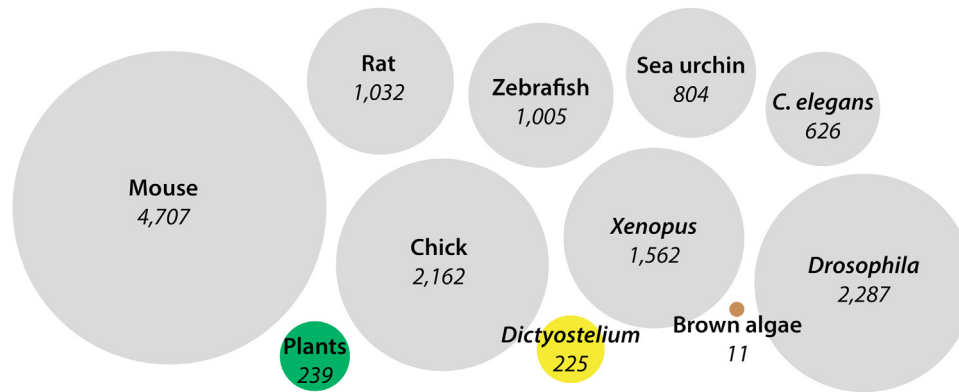


Fig. 1. Plant development papers published in *Developmental Biology*. The number of papers published in *Developmental Biology* since 1959 with the indicated search term. Circle area is proportional to article number. Gray, animals; green, plants; yellow, *Dictyostelium*; brown, brown algae.

a scenario for *SEPALLATA* genes in an early-diverging eudicot without petals, *Thalictrum* (Ranunculaceae). These genes resulted from gene duplication events before the angiosperm diversification and before the origin of Ranunculales. The genes have both conserved functions in floral organ identity and non-conserved functions in floral meristem determinacy compared to *Arabidopsis*.

Ultimately, the specification of roots, leaves, and flowers relies on transcriptional control. [Buendia-Monreal and Gillmor \(2016\)](#) explore the role of Mediator, a large protein complex that regulates transcription via modulating RNA polymerase II assembly, chromatin architecture, RNA processing and epigenetic marks. Mediator is required for a wide variety of developmental events, from hormone action to signaling to developmental timing, with different subunits of Mediator being specific to different processes. While the biochemical function of Mediator is highly conserved across eukaryotes, the extent to which different Mediator subunits have specific roles in particular plant developmental processes, versus a more general role in transcriptional control, is still an open question. The intricacies of transcriptional control are also addressed in [Gonzalez et al. \(2016\)](#) who identify novel transcriptional complexes involved in flavonoid pathway regulation and seed coat differentiation.

3. A cellular basis for plant developmental biology

As for animals, plant development relies heavily on positional information to coordinate cellular events. Nonetheless, highly regulated cell divisions underlie plant morphogenesis and organogenesis. [Egger and Walbot \(2016\)](#) provide “a framework for evaluating developmental defects at the cellular level”. In this sweeping survey of 24 pre-meiotic male sterile mutants in maize, confocal microscopy is used to analyze the role of cell proliferation defects and cell morphology in producing defined cell layers of the maize anther lobes. Their work demonstrates that even minor cellular abnormalities can disrupt the developmental context necessary to complete meiosis. Before cellular defects could be directly observed by confocal microscopy, chimeras (a single organism composed of cells from different zygotes) were used to infer the cellular mechanisms by which plant development occurs. [Frank and Chitwood \(2016\)](#) explore the history of classical studies of plant chimeras and how their use, when coupled with modern transgenic and sequencing technologies, is a potentially powerful method to reveal the coordination of plant development at a cellular level.

Asymmetric cell divisions underlie key patterning decisions in plants. A review by [Shao and Dong \(2016\)](#) explores polarity at the cellular level, focusing on mechanisms by which the cytoskeleton

is reoriented to achieve cellular asymmetries and the role of auxin in this process. [Van Norman \(2016\)](#) describes the consequences of cellular asymmetry at the tissue and organ level, focusing on how cell polarity manifests during root development and directs patterning decisions. [Jeong et al. \(2016\)](#) explore the first asymmetric division of all, that of the zygote, and how it is linked to embryonic polarity that establishes the apical-basal axis of plants. Together, these reviews describe how external signals from the environment and internal developmental signals dictate cell divisions to not only pattern the major axes of plants, but have outcomes with emergent consequences, influencing the interaction of plants with the environment through stomatal patterning and nutrient uptake by roots.

Our understanding of the cellular basis of plant development is becoming increasingly dependent on advances in imaging technologies. Two papers detail exciting protocols for live-imaging of plant organs at a cellular level. [Prunet et al. \(2016\)](#) describe a protocol for imaging growing shoot apices to produce stunning time lapses of flower bud growth. [de Luis Balaguer et al. \(2016\)](#) provide a protocol for a 3D-printed growth and imaging chamber (dubbed Multi-sample *Arabidopsis* Growth and Imaging Chamber: MAGIC) to be used with Light Sheet Fluorescence Microscopy (LSFM) and a Fiji-based pipeline to allow semi-automatic processing of images. The set-up allows the tracking of cell division and growth in the root over long time periods. The ability to track cell divisions and growth in real time, in connection with organogenesis, promises to transform our understanding of plant morphogenesis.

4. Plant development and climate change

As sessile organisms rooted in the ground, plants exhibit exceptional developmental plasticity as compared to animals, since they alter their growth in response to changes in the environment rather than fleeing. [Gray and Brady \(2016\)](#) dissect the responses of leaf, root, and reproductive development in plants to rising CO₂ concentrations, temperature fluctuations, and drought. The responses of plants to these variables have been mainly described in only one species, thus the generality of these observations is as yet unknown. Furthermore, the dynamics of how multiple environmental stressors interact to affect developmental responses is also largely unknown. While the developmental processes described in this special issue have generally been characterized in controlled laboratory settings, we still know very little about how these molecular mechanisms are affected by environmental perturbations. With temperatures and CO₂ levels expected to increase dramatically by the end of the century, with concomitant changes

in rainfall (<http://www.ncdc.noaa.gov/sotc/global/201513>), understanding how plant morphology and plant productivity will be affected by these changes is of critical importance as we move into a period of limited natural resources and an uncertain environment.

References

- Buendia-Monreal, M., Gillmor, C.S., 2016. Mediator: a key regulator of plant development. *Dev. Biol.* 419 (1), 7–18.
- de Luis Balaguer, M.A., Ramos-Pezzotti, M., Rahhal, M.B., Melvin, C.E., Johannes, E., Horn, T.J., Sozzani, R., 2016. Multi-sample Arabidopsis Growth and Imaging Chamber (MAGIC) for long term imaging in the ZEISS Lightsheet Z.1. *Dev. Biol.* 419 (1), 19–25.
- Egger, R.L., Walbot, V., 2016. A framework for evaluating developmental defects at the cellular level: an example from ten maize anther mutants using morphological and molecular data. *Dev. Biol.* 419 (1), 26–40.
- Frank, M.H., Chitwood, D.H., 2016. Plant chimeras: the good, the bad, and the 'Bizzaria'. *Dev. Biol.* 419 (1), 41–53.
- Gonzalez, A., Brown, M., Hatlestad, G., Akhavan, N., Smith, T., Hembd, A., Moore, J., Montes, D., Mosley, T., Resendez, J., Nguyen, H., Wilson, L., Campbell, A., Sudarshan, D., Lloyd, A., 2016. TTG2 controls the developmental regulation of seed coat tannins in Arabidopsis by regulating vacuolar transport steps in the proanthocyanidin pathway. *Dev. Biol.* 419 (1), 54–63.
- Gray, S.B., Brady, S.M., 2016. Plant developmental responses to climate change. *Dev. Biol.* 419 (1), 64–77.
- Jegla, D.E., Sussex, I.M., 1989. Cell lineage patterns in the shoot meristem of the sunflower embryo in the dry seed. *Dev. Biol.* 131, 215–225.
- Jeong, S., Eilbert, E., Bolbol, A., Lukowitz, W., 2016. Going mainstream: how is the body axis of plants first initiated in the embryo? *Dev. Biol.* 419 (1), 78–84.
- Korn, R.W., 1981. A neighboring-inhibition model for stomate patterning. *Dev. Biol.* 88, 115–120.
- Martinez, C.C., Koenig, D., Chitwood, D.H., Sinha, N.R., 2016. A sister of PIN1 gene in tomato (*Solanum lycopersicum*) defines leaf and flower organ initiation patterns by maintaining epidermal auxin flux. *Dev. Biol.* 419 (1), 85–98.
- Matt, G., Umen, J., 2016. Volvox: a simple algal model for embryogenesis, morphogenesis and cellular differentiation. *Dev. Biol.* 419 (1), 99–113.
- Poethig, R.S., Sussex, I.M., 1985. The cellular parameters of leaf development in tobacco: a clonal analysis. *Planta* 165, 170–184.
- Prunet, N., Jack, T.P., Meyerowitz, E.M., 2016. Live confocal imaging of Arabidopsis flower buds. *Dev. Biol.* 419 (1), 114–120.
- Shao, W., Dong, J., 2016. Polarity in plant asymmetric cell division: division orientation and cell fate differentiation. *Dev. Biol.* 419 (1), 121–131.
- Shwartz, I., Levy, M., Ori, N., Bar, M., 2016. Hormones in tomato leaf development. *Dev. Biol.* 419 (1), 132–142.
- Soza, V.L., Snelson, C.D., Hewett-Hazelton, K.D., Di Stilio, V.S., 2016. Partial redundancy and functional specialization of E-class SEPALLATA genes in an early-diverging eudicot. *Dev. Biol.* 419 (1), 143–155.
- Stebbins, G.L., Jain, S.K., 1960. Developmental studies of cell differentiation in the Epidermis of Monocotyledons .1. Allium, Rhoeo, and Commelina. *Dev. Biol.* 2, 409–426.
- Taylor-Teeples, M., Lanctot, A., Nemhauser, J.L., 2016. As above, so below: Auxin's role in lateral organ development. *Dev. Biol.* 419 (1), 156–164.
- Van Norman, J.M., 2016. Asymmetry and cell polarity in root development. *Dev. Biol.* 419 (1), 165–174.
- Wessinger, C.A., Hileman, L.C., 2016. Accessibility, constraint, and repetition in adaptive floral evolution. *Dev. Biol.* 419 (1), 175–183.
- Yip, H.K., Floyd, S.K., Sakakibara, K., Bowman, J.L., 2016. Class III HD-Zip activity coordinates leaf development in *Physcomitrella patens*. *Dev. Biol.* 419 (1), 184–197.

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