

## TEACHING TOOLS IN PLANT BIOLOGY™: LECTURE NOTES

# Evolutionary and Developmental Origins of Leaves

In our poetic and artistic imagination, flowers rule. Leaves, from which flowers are derived, rarely take center stage. Even our diet largely ignores leaves, much to the detriment of our health. Yet without leaves, we would not exist, at least not in our present form. When they first appeared more than 300 million years ago, they contributed to the oxygenation of our atmosphere, paving the way for diversifications of animals and eventually mammals. In the modern era, they maintain a hospitable climate through acting as heat sinks, carbon sinks, and contributing to the return of water into the atmosphere. For centuries scientists and naturalists have wondered about the evolutionary and developmental origins of leaves. The recent work of paleobotanists, geneticists, and computational biologists provides us with insights into how leaves have been and continue to be formed.

### EVOLUTIONARY ORIGINS OF LEAVES

All land plants have a single evolutionary origin. We know that these early ancestors were small and did not have vascular tissues and probably resembled modern mosses. Over time, some plants developed vascular tissues and greatly increased in size. Only vascular plants produce leaves. We now know that leaves have evolved multiple times independently, although they share many of the same genetic components.

Nonseed vascular plants, such as *Lycopodium* and *Selaginella*, make small leaves with a single vascular strand; these leaves are sometimes called microphylls. Microphylls are hypothesized to have evolved during the Silurian/Early Devonian period (approximately 400 million years ago). The larger leaves in ferns and seed plants are often called megaphylls. Megaphylls are thought to have derived from sterile, determinate branches sometime in the Late Devonian/Carboniferous period, approximately 360 million years ago. A model in which leaves are derived from planar tissues forming between and fusing together adjacent branches is called the telome theory after the telome, the terminal branch segment of a primitive plant. Fossil evidence is scarce though, and some have argued that the known genetic mechanisms do not support such a webbing origin for the leaf blade.

Exploration into the early origins of leaves also raises questions about the selective advantages conferred by leaves. An important study focuses on the global decrease in CO<sub>2</sub> levels that occurred around the time that megaphylls originated. Fossil evidence points to a coincident increase in the density of stomatal pores, probably to compensate for lower CO<sub>2</sub> levels. It has been proposed that with increased stomatal density, the leaf's capacity for evaporative cooling by transpiration increased, allowing leaves to become much larger without overheating. To

support the increased rate of transpiration, the root system also developed in size and complexity at this time.

Many questions about leaf origins remain. Our increasing understanding of developmental genetics and plant evolution is enabling us to revisit these important questions and has generated the exciting new field of evolutionary development (also known as evo-devo). Many of the experimental studies of leaf development have been performed on angiosperms, but we now have excellent resources for experimental and genomic investigations in nonangiosperms, including moss (*Physcomitrella patens*) and lycophytes (*Selaginella* species). Through comparative studies, it is becoming clear that many of the genes required to produce a leaf are widely conserved and that many have identical or closely related functions. This lecture focuses on the processes that occur at the shoot apex to determine the site of leaf placement, whereas the ensuing genetic programs to initiate and form a leaf are discussed in *Teaching Tools in Plant Biology 3: Genetic Control of Leaf Development*.

### DEVELOPMENTAL ORIGINS OF LEAVES

Developmental biologists study the processes through which organisms grow and change. Multicellular organisms usually start as single-celled zygotes that grow by cell division and expansion. To become anything more interesting than a ball of cells, the developing organism has to acquire spatial variation and patterning. This can involve a gradient of information from one end to another (e.g., apical-basal polarity) or the acquisition of a different developmental fate by a small group of cells. Patterning leads to differential growth, differential gene expression, and cellular differentiation. The importance of gradients and transcriptional controls in the establishment of pattern was beautifully worked out in *Drosophila melanogaster* in the 1980s, but we now know that similar processes occur in plants (see NobelPrize.org for an introduction to developmental patterning in fruit flies).

To a first approximation, an animal is fully formed at the end of embryogenesis, and most of its postembryonic development involves growth rather than new organ initiation. By contrast, at the end of embryogenesis, a plant has only a rudimentary body plan and no true leaves. Postembryonic growth occurs through the actions of meristems, including shoot and root apical meristems and lateral meristems. The meristems are the sites of postembryonic growth and organogenesis. Because much of plant development occurs postembryonically, it is environmentally plastic, meaning that information about the environment is integrated with genetic programs to affect the pattern of growth. This effect is easily seen when two identical plants are grown in the presence or absence of light. The light-grown plant remains shorter, greener, and produces leaves, whereas the dark-grown

plant becomes elongated, stays pale, and does not produce leaves. Environmental plasticity ensures that the plant body forms in a way that is appropriate for its environment, even when the environment is continually changing.

Leaf development involves the formation of leaves postembryonically by the action of the shoot apical meristem or apical cell. A concept that unifies the morphology of leaf production across the plant kingdom is that of the phytomer, which is the morphological unit of development caused by the initiation of successive leaves. A phytomer consists of a node, a leaf, an internode, and an axillary meristem that can grow out and create branches. It is the reiteration of phytomers that generates the characteristic architecture of a plant. Unlike the shoot and root systems, leaves are (usually) determinate organs that grow to a predetermined finite size and often only function for a finite period. Deciduous trees produce and discard leaves in annual cycles, as regular and reproducible as the genetic pathways that underlie leaf formation and maturation.

### STRUCTURE AND FUNCTION OF THE ANGIOSPERM SHOOT APICAL MERISTEM

Cell proliferation and leaf initiation occur by the action of a specialized tissue at the shoot apex. In ferns and some other nonseed plants, this is a single, pyramid-shaped apical cell. In angiosperms, gymnosperms, and some nonseed plants, this is a multicellular tissue with a conserved structure, the shoot apical meristem (SAM). Most of our understanding of the developmental origins of leaves comes from studies of the SAM of angiosperms, as discussed here.

The SAM consists of three zones of cells. Cells in the central zone divide infrequently and have a similar broad developmental potential as the stem cells in a developing animal. Just below these are the cells of the rib meristem, which proliferate and differentiate to form the plant stem. Cells in the peripheral zone of the SAM divide and differentiate and are progenitors of lateral organs that form in a regular spatial and temporal progression.

Lateral organ development has been divided conceptually into several stages. At the earliest stage of development, the cells that will ultimately generate an organ are termed founder cells. Founder cells become destined to acquire a particular fate by the process called specification, which involves signals that are virtually unknown for most organs. Following specification, coordinated cell division generates an organ Anlage, or pre-primordium, which becomes a morphologically distinct primordium after further cell divisions.

The minimum number of founder cells required to form a leaf has been estimated for several species using a method called clonal analysis (also known as sector or lineage analysis). The plants created contain a visible marker, such as a reporter gene or lack of chlorophyll synthesis, that can be randomly switched on or off in single cells. A population of plants with visible sectors derived from single cells can be produced. The size of each sector and proportion of the final organ it encompasses can be extrapolated to determine a minimum number of cells that are needed to generate an organ. This method has shown that the number of leaf founder cells varies between species, with the maize leaf being derived from about 200 founder cells, but dicot

leaves usually being derived from considerably fewer, for example, 30 for *Arabidopsis thaliana*.

The tiny immature leaves formed on the flanks of the meristem are called primordia and are numbered from youngest to oldest,  $P_1 \dots P_n$ . The next primordium to form is called the incipient primordium; incipient primordia are numbered  $I_1$  for the next to form,  $I_2$  for the one to form after that, etc. The pattern of placement of these primordia and the resulting leaves around the developing stem is called phyllotaxy.

Leaves form at the SAM in regular phyllotactic patterns, often spiral, but sometimes alternating by  $180^\circ$  in opposing pairs or in whorls of three or more leaves per node. The spiral pattern is particularly intriguing because the leaves tend to form  $\sim 137.5^\circ$  apart. This angle dissects the circumference into two segments: the larger one of  $222.5^\circ$  and the smaller  $137.5^\circ$ . The whole ( $360^\circ$ ) divided by the larger segment yields the golden ratio of 1.618, and the larger ( $222.5^\circ$ ) divided by the smaller also yields a ratio of 1.618. The golden ratio recurs in nature and has been used extensively in the arts and architecture; it is considered exceptionally pleasing to the eye. In the plant, the resulting spiral ensures that leaves are placed so as to minimize their shadowing of one another. How this phyllotactic pattern forms has intrigued scholars for hundreds of years and has been a subject of intense study for nearly as long (see Adler et al., 1997).

### EXPERIMENTAL STUDIES OF PHYLLOTAXY

Many models have been proposed to explain the patterns of phyllotaxy. One model proposed that the biophysical forces acting at the meristem determine the placement of leaf primordia. Others proposed that chemical interactions between primordia are involved. Evidence for the latter came from microsurgical experiments performed in the early part of the 20th century. Incisions within the meristem between primordia and incipient primordia altered the placement of the newly forming leaves. These studies revealed that the position at which a new leaf primordium forms is influenced by preexisting primordia and specifically those primordia adjacent to the incipient site. A model was developed in which the central region of the meristem and each primordium produce an inhibitory field that diminishes as the primordium ages. An alternative model consistent with these experimental results suggests that the incipient primordium competes with existing primordia for a limiting resource and that younger primordia compete with the incipient primordium more effectively than older primordia.

Further evidence of communication between primordia and the new initiation site comes from genetic studies of plants with abnormally large or small central zones in their meristems. Meristem size is rigorously controlled and is determined by the rate of cell production and the rate at which cells leave the meristem as leaf primordia. In the *Arabidopsis clavata1* mutant, cell proliferation in the meristem is unrestrained, the meristem grows abnormally large, and phyllotactic patterns are disrupted. CLAVATA1 is a component of the feedback loop that restricts the size of the meristem. Two mutants in monocot species, *abphyl* in maize (*Zea mays*) and *decussate* in rice (*Oryza sativa*), have a change in phyllotaxy so that leaves are produced in pairs rather than alternately. ABPHYL and DECUSSATE affect

cytokinin signaling. Cytokinin regulates cell proliferation in the SAM, and both these mutants have an increased SAM size. Therefore, the altered phyllotactic patterns are probably a secondary consequence of changes in meristem size that affect communication between primordia.

### ROLE OF AUXIN AND AUXIN TRANSPORT

The plant hormone auxin has an important role in determining primordium position. Auxin is synthesized in most plant cells but accumulates in certain cells and tissues due to a highly regulated system of polar transport between cells. Auxin's chemical nature is critical to its patterns of transport and accumulation; at a neutral cytoplasmic pH, auxin (indole-3-acetic acid) is a negatively charged anion that cannot move across the plasma membrane except through a specific auxin efflux carrier protein called PIN1. At the low pH characteristic of plant cell walls, auxin is re-protonated and becomes uncharged and freely able to enter the cell by diffusion across the plasma membrane, although its reentry is also facilitated by the AUX/LAX family of auxin influx carriers. These efflux and influx carriers are able to direct auxin flow according to their positions on the cell membranes.

Studies examining both auxin and PIN1 protein distribution at the SAM have revealed that sites of leaf initiation are determined by a locally elevated region of auxin accumulation. This local auxin maximum is generated by polar auxin transport into this region from surrounding cells, primarily via the epidermal layer. In *Arabidopsis pin1* loss-of-function mutants, defects in auxin transport interfere with organ initiation at the meristem, but a localized application of auxin is sufficient to stimulate primordium outgrowth. Similarly, leaf initiation is arrested in maize apices treated with an inhibitor of polar auxin transport.

Fascinating *in vivo* imaging studies have been performed in which the expression patterns of auxin-responsive genes and distribution of PIN1 proteins are examined over time in a living plant. Such studies strongly support the role of PIN1 orientation as the major determinate of an auxin maximum and primordium initiation. If PIN1 orientation establishes the site of primordium initiation, what determines where the PIN1 protein orients? Genes that act upstream of PIN1 to regulate phyllotaxy have recently been characterized: mutation in three redundant members of the *PLETHORA* gene family of transcription factors results in alterations in phyllotaxy that are caused by a misregulation of PIN1. Furthermore, new evidence suggests a role for differential stress perception in specifying PIN1 orientation.

### MECHANICAL SIGNALS AND COMPUTER SIMULATIONS

Mechanical events within the meristem are thought to precede changes in auxin fluxes. The earliest event is thought to be pectin demethylesterification of subepidermal cells, resulting in increased tissue elasticity in these regions. Expansins are a family of extracellular proteins that regulate cell wall extensibility. In a study of tomato (*Solanum lycopersicum*) apices, the local application of expansin directly to the SAM resulted in a bulge in an abnormal phyllotactic position, showing that the relaxation of cell wall extensibility *in vivo* accompanies leaf induction.

Microtubule reorganization is another early event in leaf initiation. Microtubules are protein roadways along which cellular

cargo is moved. They form stable but dynamic patterns depending upon the activity of the cell. During mitosis they are responsible for moving the chromosomes into the new daughter cells. In plant cells, microtubules also provide a blueprint for the deposition of cell wall components.

*In vivo* imaging has revealed that epidermal cells in the shoot meristem respond to mechanical stress by reorganizing their microtubules into an array parallel to the direction of stress. The stress experienced by a cell can be experimentally modified by compressing the cell or using a laser to ablate an adjacent cell. Since plant cells are under pressure, ablation of a cell changes the stress environment of the adjacent cells. Cells also change their polarity of PIN1 distribution in response to stress. These studies have led to a phyllotactic model that involves both auxin transport and responses to cell stress. When a cell perceives an increase in the pressure from an adjacent cell, PIN1 reorients toward that cell, leading to increased auxin flux into that cell, increased auxin-induced growth, and increased stress. This can create a positive feedback loop in which cell expansion causes PIN1 to localize near expanding walls, providing auxin to stimulate additional growth. This auxin transport/cell stress model gives us an exciting glimpse into how a pattern can initiate and be maintained.

Outstanding questions remain, such as how changes in components of mechanical stress, including pectin demethylesterification and microtubule orientation, are locally initiated and coordinated and exactly how the plasma membrane senses mechanical stress to alter the concentration of proteins such as PINs embedded in it. Additionally, how stress patterns change to initiate the next primordium and how environmental signals such as light are integrated into meristem function are important issues to address.

Meristems are truly amazing self-organizing systems. Although the formation of a SAM normally occurs during plant embryogenesis, numerous experimental studies have shown that shoot apical meristems can spontaneously organize from undifferentiated tissues when given the proper set of hormonal signals. This ability to form a SAM *de novo* postembryonically is the basis for plant tissue culture, in which plants are propagated vegetatively. Remarkably, the newly formed meristems acquire normal phyllotactic patterns, demonstrating that pattern initiation is not restricted to embryogenesis. Similarly computer simulations based on the auxin transport model are capable of generating *de novo* a pattern of auxin accumulation and leaf primordium placement that faithfully recapitulates that of a real plant. These simulations faithfully recreate experimental results and can be used to test assumptions about phyllotactic models, bringing a long-awaited predictive element to biology.

### SUMMARY

Leaves are remarkable structures upon which our own evolutionary history and current survival are utterly dependent. Their appearance in the ancient world drastically changed the earth's atmosphere and opened the door for the emergence of larger and more complex animal forms. Through their roles as photosynthetic organs, they feed us, and through their contributions to

evaporation and gas exchange, they maintain our accommodating climate. This century's extraordinary advances in biological imaging, computational modeling, and genomic analysis give us unprecedented insight into the very complex and minute processes that underlie the formation of a leaf primordium at the SAM. The ensuing genetic programs that unfold to control leaf growth, patterning, and cell differentiation are described in *Teaching Tools in Plant Biology 3: Genetic Control of Leaf Development*.

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