

Meeting report

Foliage in Madrid

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A report on the 'Leaf Development' workshop hosted by the Instituto Juan March de Estudios e Investigaciones, Madrid, Spain, 11-13 February 2002.

Every day we are surrounded by plants whose leaves vary enormously in shape, size, and even color between species. This variation often extends to leaves on a single plant, which may exhibit differences in an age- or environment-dependent manner. Work presented at a workshop on 'Leaf Development' held in February 2002 provides a foundation for understanding how the enormous diversity of leaf form has evolved in land plants. This article highlights a few of the topics discussed at the meeting, including early formation of leaves, control of leaf shape, and the evolution of compound leaves.

The founding of a leaf

An early step in the formation of leaves is the recruitment of founder cells from the flanks of apical meristems, a group of self-renewing stem cells whose cells contribute either to the leaves or to the stem tissue that separates successive leaves. Michael Scanlon (University of Georgia, Athens, USA) described the role of *narrow sheath (ns)* genes in the recruitment of founder cells to the marginal domains of maize leaf anlage (meristem or primordium). Two genes, *ns1* and *ns2*, are redundantly required to recruit cells in the marginal domains in a non-cell-autonomous manner. Remarkably, the two genes are not homologous at the sequence level, but rather may control different steps in a branched biosynthesis pathway, possibly involved in the synthesis of auxin; this is tantalizingly consistent with the idea that auxin concentration maxima are associated with the establishment of leaf anlage.

Mary Byrne (Cold Spring Harbor Laboratory, New York, USA) and Sarah Hake (Plant Gene Expression Center, Albany, USA) discussed the role of *KNOX* homeobox genes

in the separation of leaf primordia from the adjacent meristem in *Arabidopsis*. Expression of *KNOX* genes is limited to the apical meristem (in species with simple leaves), whereas expression of genes such as *ASYMMETRIC LEAVES1 (AS1)* demarcates leaf anlage. Byrne used an elegant genetic screen to demonstrate that rescue of the apical meristem in *shoot meristemless (stm)* mutants by *as1* mutants is mediated in part by *BREVIPEDICELLUS (BP)*. As *BP* and *STM* encode similar *KNOX* proteins, she hypothesized that this redundancy is due to homology between the proteins. Hake put forward the idea that *BP* acts to form a boundary between leaf anlage and the remainder of the meristem, and thus could act to regulate the allocation of cells to either the anlage or the internode tissues which are derived from cells of the peripheral zone that are not incorporated into leaf primordia. Miltos Tsiantis (Oxford University, UK), in a wine-winning talk, convincingly demonstrated that gibberellins are antagonistic to *KNOX* activity, both when *KNOX* gene expression is ectopically activated in leaves, and also to the *KNOX* gene expression in the apical meristem itself under certain conditions. The expression of *KNOX* and of gibberellic acid biosynthetic enzymes is mutually exclusive, leading Tsiantis to propose that one of the functions of *KNOX* activity may be to suppress gibberellin accumulation. The precise role of gibberellins in patterning leaf and meristem development remains an enigma, however.

The control of leaf shape

One of the remarkable attributes of leaves is their consistency in size, shape and symmetry, which are conspicuous species-specific characters. Little is known about how these attributes are attained at a molecular genetic level, however. Several talks addressed the relative importance of cell division and cell elongation in the development of leaf size and shape. Hirokazu Tsukaya (National Institute for Basic Biology, Okazaki, Japan) presented recent work on the *blade-like petiole* mutant, which exhibits ectopic lamina (leaf blade) formation on the petioles (leaf stalks). An astounding phenotype results, in which each leaf is highly

complex with little resemblance to those of wild-type *Arabidopsis*, demonstrating that single genes can pattern leaf shape complexity.

Two speakers, Yukiko Mizukami (University of California, Berkeley, USA) and Gerrit Beemster (University of Gent, Belgium) discussed the relationship between cell division and leaf shape. Remarkably, leaf morphogenesis can compensate for considerable alterations in cell division rates: reduced cell division rates lead to leaves with fewer, larger cells, and conversely, increased cell division rates result in leaves with larger numbers of smaller cells. In both cases overall leaf shape and tissue organization is relatively normal, suggesting that leaf shape is not simply altered by changing the rates of cell division uniformly. The possibility remains, however, that localized cell division could help to determine leaf shape. In contrast, it appears that the extent of cell elongation can dramatically affect leaf shape. Tsukaya reported that mutations in *ANGUSTIFOLIA* (*AN*) and *ROTUNDIFOLIA* alter leaf shape as a result of reductions in the extent of cell elongation in particular dimensions. In *an* mutants, cortical microtubules are altered and cell expansion is reduced such that leaves are narrower than those of wild type. *AN* is likely to act as a transcriptional regulator, and one of its potential targets, identified via microarray experiments, is *MER15*, which encodes an endoxyloglucan transferase, consistent with a role in cell-wall modifications. Two speakers dramatically demonstrated that the cell cycle and cell-type-specific differentiation can be uncoupled. Mizukami reported that ectopic expression of an *Arabidopsis* Frizzy-related gene (Frizzy-related proteins target cyclin B for degradation) in tobacco converted multicellular trichomes (epidermal hairs) into single-celled structures, without altering their differentiation. Conversely, Mizukami and Martin Hülskamp (University of Cologne, Germany) reported that ectopic expression of D-type cyclins, which suppresses endoreduplication (genome doubling without cell division), results in the normally single-celled *Arabidopsis* trichomes differentiating as multicellular structures.

Exploring diversity in leaf morphology

If we are to begin to understand how the variety of leaf morphologies has evolved, we will need to look at plants beyond the typical model species. Leaf morphology is complex, as is most obvious when comparing simple leaves and compound leaves, the latter being made up of two or more leaflets. On the basis of the fossil record and presently accepted phylogenies of flowering plants, compound leaves appear to have evolved multiple times within vascular plants. Two speakers, Neelima Sinha (University of California, Davis, USA) and Julie Hofer (John Innes Centre, Norwich, UK) presented evidence that at least two different molecular mechanisms have led to the evolution of compound leaves. On the basis of gene-expression patterns, Sinha hypothesized that *KNOX* gene expression, which in simple-leaved plants is restricted

to the apical meristems, may in leaf primordia be a factor in the development of compound leaves in most vascular plant taxa, from cycads to tomatoes. The developmental mechanism mediated by *KNOX* expression is not known, but *KNOX* expression in leaf primordia may render the primordia less determinate (that is, more able to change form) and thus able to form complex structures. The one exception noted by Sinha is a clade within the legumes that includes peas, and Hofer demonstrated that two legume genes, *UNIFOLLATA* and *STAMINA PISTILLOIDA*, whose orthologs in *Arabidopsis* (*LEAFY* and *UFO*, respectively) are involved in promoting flower meristem identity, are required for compound leaf development within the legume clade that contains peas. Thus, both different mechanisms and multiple recruitments of one mechanism (*KNOX* gene expression in leaves) might underlie the generation of compound leaf evolution in plants.

To examine more subtle changes in leaf shape and size, Andrew Hudson (University of Edinburgh, UK) described efforts to use closely related *Antirrhinum* (snapdragon) species, which differ substantially in morphology but can be intercrossed, to investigate the genetic and evolutionary origin of such morphological differences. Preliminary analyses suggest the involvement of several genes, and their identification should provide great insight into how shape and size are controlled at the molecular level. Furthermore, such studies promise insight into the processes of the evolution of morphology. While we are presently at a loss to describe leaf development mechanistically in even the model species, emerging genomic tools in a wide variety of plant species promises to facilitate our understanding of the diversity in the foliage that surrounds us.