

# Regulation of plant form - the role of boundaries

## Department of Plant Sciences

Tel. 972 8 934 2102

Fax. 972 8 934 4181

E-mail: yuval.eshed@weizmann.ac.il

All plants lateral organs such as leaves and floral organs are formed by unique groups of organized cells called meristems. Organ formation is highly regulated in time and space partly through communication between the meristem and the already formed organs. Research in Yuval Eshed's lab focuses on the nature of such communication. Early studies demonstrated that meristem born cues determine the asymmetric development of plant leaves. Ongoing experiments focus on the feedback signaling from the organs to the meristem. Apparently this signaling is mediated by asymmetrically distributed factors. Characterizing this signaling network might uncover basic schemes underlying pattern formation.

The bodies of seed plants are generally composed of two types of distinctly patterned organs. Roots and stems have overall radial symmetry, while lateral organs, such as leaves and floral organs display lateral growth and distinct asymmetric development. The inherent relationship between the lateral organs and the apical meristem from which they are derived is used for axes definition. Primordia have an adaxial-abaxial axis (Fig. 1), with one side forming adjacent to the meristem (ad - close to) and the other side away from the meristem (ab - away from). In most angiosperm leaves, polarity in the adaxial-abaxial axis is evident in differences in morphology and anatomy. These asymmetries are a reflection of the function of the two surfaces. In leaves, the adaxial, or top, surface is specialized for light capture and photosynthesis, whereas the abaxial, or bottom, surface is specialized for gas exchange. Lateral organs of plants are derived from cells recruited from the peripheral zone of the apical meristem. Initially, lateral organ anlage appear to be composed of a small number of cells exhibiting uniform histology and apparently homogeneous gene expression patterns. However, as lateral organ primordia emerge from the flanks of the meristem, polarity is evident both in terms of gene expression patterns and morphological differentiation, suggesting that adaxial-abaxial polarity is established in lateral organs during their transition from anlagen to morphologically distinct primordia. While fully differentiated lateral organs have more than just two cell types, the establishment of polarity only requires the generation of two distinct populations of cells. Subsequent interactions between the two populations could

then lead to the generation of a larger diversity of cellular identities.

### Establishment of adaxial-abaxial polarity

Elegant experiments by Sussex, and others, nearly a half-century ago, in which incipient leaf primordia were physically separated from the shoot apical meristem by incisions, have provided a conceptual framework for the interactions between lateral organ primordia and apical meristems. If separation occurred prior to primordium formation (e.g. at the stage of an anlage), the isolated primordia developed into radially symmetric, apparently abaxialized organs. This developmental pattern suggests that the apical meristem could be the source for a signal required for proper abaxial/adaxial development of the leaf. One interpretation of these data is that a signal(s) emanating from the apical meristem promotes adaxial identity in the cells of the lateral organ primordium closest to the meristem. Several recent studies in *Arabidopsis* and *Antirrhinum* have provided insight into the molecular genetic mechanisms by which polarity is established in lateral organs and these form the base line of our research.

A molecular explanation for the framework of interactions between lateral organs and meristems from which they are derived, established nearly a half-century ago, is beginning to emerge (Fig. 1). Both adaxial and abaxial promoting factors are initially expressed throughout lateral organ anlage. Subsequently, their expression patterns become restricted to their respective complementary domains as lateral organ primordia emerge from the flanks of the apical meristem,

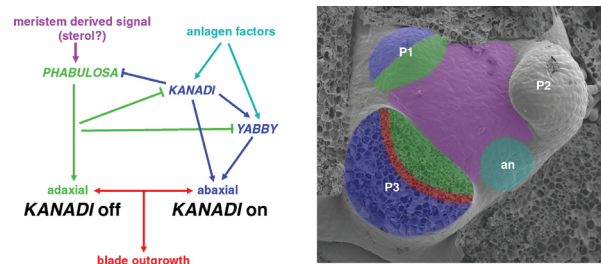
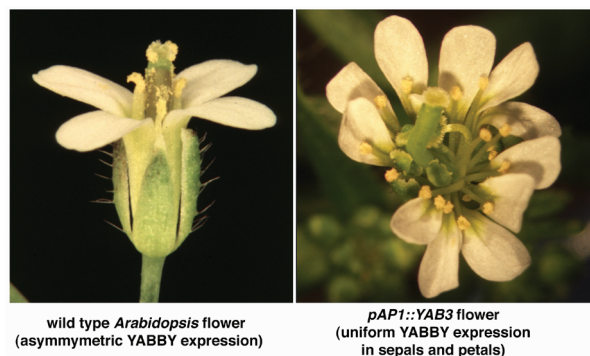


Fig. 1 Molecular frame work of lateral organs polarity establishment.

consistent with the temporal acquisition of polarity as determined by surgical experiments. One attractive hypothesis is that once PHB is “activated” by signals derived from the apical meristem, KANADI and YABBY gene expression is repressed in those cells within the anlage closest to the meristem. These cells, which are destined to give rise to the adaxial portion of the lateral organ, would have a higher level of ‘activated’ PHB/PHV due to their proximity to the source of the signal. FIL expression is nearly undetectable in *phb-1d* homozygotes, concordant with the idea that an ‘activated’ version of PHB is sufficient to repress FIL expression. Thus, the ‘default’ state of abaxial identity would be a consequence of KANADI/YABBY activation throughout lateral organ anlage without subsequent down regulation by factors promoting adaxial identity (e.g. ‘activated’ PHB/PHV). Likewise, constitutive ectopic KANADI activity is sufficient to promote abaxial identity, suggesting it may be able to negatively regulate PHB/PHV. Once established, signaling between them, the nature of which is an unknown lead to lamina outgrowth via localized cell divisions.

Finally, mutations and ectopic expression of genes directing establishment of adaxial-abaxial polarity often result in changes not only in organ symmetry, but also in organ initiation. This implies that these genes, or the generation of asymmetry itself, may have a role influencing the activity of the meristem from which the lateral organs derive (Fig. 2)



**Fig. 2** Changes in organ initiation pattern caused by uniform YABBY distribution.

### **Selected Publications**

- Siegfried, K. R., Eshed, Y., Baum, S. F., Otsuga, D., Drews, G. N., and Bowman, J. L. (1999) Members of the YABBY gene family specify abaxial cell fate in Arabidopsis. *Development* 126, 4117-4128.
- Eshed, Y., Baum, S. F., and Bowman, J. L. (1999) Abaxial cell fate in the carpels is established by two distinct mechanisms. *Cell* 99, 199-209.
- Bowman, J. L. and Eshed, Y. (2000) Formation and maintenance of the shoot apical meristem. *Trends Plant Sci.* 5, 110-115.
- McConnell, J. R., Emery, J. F., Eshed, Y., Bao, N., Bowman, J. L., and Barton, M. K. (2001) Role of PHABULOSA and PHAVOLUTA in determining radial patterning in shoots. *Nature* 411, 709-713.
- Eshed, Y., Baum, S. F., Perea, J. V., and Bowman, J. L. (2001) Establishment of polarity in lateral organs of plants. *Curr. Biol.* 11, 1251-1260.

### **Acknowledgements**

The work in our lab is supported by a research grant from La Foundation Raphael et Regina Levy.