

centers elsewhere in Eastern Europe—Warsaw's Copernicus Center and the cosmology group at Tartu, Estonia, to name but two—whose viability is precarious in the present situation.

This is therefore an opportune moment for the foundation of the European Astronomical Society—explicitly (like the European Physical Society in physics) embracing the former “Eastern” countries—under the presidency of Lodewijk Woltjer, former Director-General of ESO (and, incidentally, one of Oort's many former students). Scientific societies do not have substantial resources at their direct disposal. But pan-European societies can play a role in ensuring that funds from the EEC and other bodies get channeled in the most effective way.

The style of astronomy has evolved toward multi-wavelength studies. In Europe

this has led to international collaboration, not only at the level of big projects where it is forced by economic realism, but at the level of academic groups and individual investigations. There is a growing trend for students graduating with Ph.D.'s in one European country to move to another for their postdoctoral work. In the past, the United States was the most likely meeting place for such people. The integration of Europe has its controversial aspects, but in science the potential of greater Europe is already apparent. Astronomers are well placed to play an effective part in catalyzing a real European community.

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Genes to Greens: Embryonic Pattern Formation in Plants

Gerd Jürgens

Genetic analyses, in combination with molecular studies, have led to remarkable insights into the mechanisms that generate body organization in the embryo of higher animals (1). Plant developmental biology is just on the verge of taking the same direction, as indicated by recent advances in the understanding of flower development (2). In two widely divergent plant species, the common laboratory weed *Arabidopsis* and the snapdragon *Antirrhinum*, a small number of genes coding for transcription factors have been found to be crucial for the formation of floral structures. Although the flowers look very different in the two species, their development follows common principles: similar interactions of homologous genes. Thus, plant developmental biology is undergoing the same transformation that has revolutionized animal developmental biology in the past 10 years. Other aspects of plant development are also now being subjected to genetic analysis (3) and these studies are beginning to elucidate the mechanisms underlying the formation of the body organization in the embryo.

The idea that the body organization of plants is laid down in the embryo, like that of animals, runs counter to traditional views, which have stressed the “open”

mode and “plasticity” of plant development (4). At first glance, the plant body grows by the addition of new structures from so-called primary meristems located at the opposite ends of the body axis. However, recent studies indicate that the primary body pattern is actually generated in the embryo and that the meristems are just terminal elements of the embryonic axis (5). After bisection of the embryo, the upper half can regenerate a full embryo including the root meristem, which thus behaves like other, nonmeristematic pattern elements in this assay. This observation also implies that the primary body pattern is established at an earlier stage of embryogenesis. Although pattern formation itself cannot easily be studied experimentally because of the small size of the early embryo, the genetic approach is not limited in this way. Mutational “dissection” only requires that relevant genes mutate to cause diagnostic phenotypes that deviate from the normal pattern.

The primary body pattern of higher plants as laid down in the embryo is best illustrated in the structurally simple seedling, which is remarkably uniform across species (6). Along the single axis of polarity, which is to become the main axis of the plant, four distinct pattern elements can be recognized. These are, from top to bottom, the epicotyl including the shoot meristem, one or two cotyledons, the hypocotyl, and

the root including the root meristem. Thus, the meristems arise as terminal elements of the apical-basal pattern in the embryo. A second pattern consists of the main types of plant tissue: epidermis, ground tissue, and vascular tissue. These elements are arranged in a radial fashion, with the epidermis at the surface and the vascular tissue in the center.

The mechanisms by which the seedling pattern is generated during embryogenesis are unknown (6). Thus, the genetic approach has to perform two functions: (i) it must dissect the process of pattern formation by identifying mutant phenotypes that define different aspects or steps and (ii) it must characterize molecularly the genes thus identified. These goals can only be achieved in a plant species such as *Arabidopsis* that allows large-scale screening for embryonic pattern mutants as well as pursuit of the phenotype-to-molecule strategy.

Mutations causing embryonic lethality have long been known in both maize and *Arabidopsis* (7). It is not clear, however, whether pattern formation is affected in these mutants. More direct attempts have recently been made in *Arabidopsis* to identify genes involved in embryonic pattern formation on the basis of their mutant seedling phenotypes. This approach has been called the “*Drosophila* approach” because of its similarity to earlier work in the fruit fly (8). The large-scale screens for embryonic pattern mutants in both *Drosophila* and *Arabidopsis* were based on the assumption that genes directing pattern formation are not involved in general cell processes. This assumption implied that in *Arabidopsis* mutations in patterning genes cause diagnostic seedling phenotypes, such as specific changes in the body organization, without interfering with the completion of embryogenesis (9). The strategy has yielded several mutant alleles of a small number of genes with very specific pattern defects (10). What has been learned about pattern formation in the plant embryo from the analysis of such mutants?

First of all, the identified genes act very early in embryogenesis, possibly at a stage when the embryo consists of only eight cells. Thus, early events have a long-lasting effect on pattern formation. Second, formation of the different tissues does not require apical-basal polarity. Thus, pattern formation along the axis of polarity and formation of the radial pattern are two separate processes. Third, some genes appear to act in specific spatial domains. For example, the apical-basal axis may be initially partitioned into only three regions: the apical region includes the primordia of both the shoot meristem and the cotyledons; the central region gives rise to the hypocotyl;

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and the basal region produces the root and the root meristem (10). This is a rather coarse subdivision, and it is obvious that subsequent events are required to refine the pattern. Nonetheless, the early partitioning of the axis bears some superficial resemblance to similar events in the *Drosophila* segmentation process where the gap genes are involved in the initial regionalization of the anterior-posterior axis (1). It will be interesting to see whether similarities between the two systems can be extended to the molecular level. For example, as in *Drosophila*, the early-acting *Arabidopsis* genes may also code for transcription factors that are present only in the regions affected in the mutant embryos. Even if this is the case, it will still be a long way to a mechanistic understanding of pattern formation in the plant embryo.

Plant cells are immobilized by cell walls, which limit their responses to positional cues in the developing embryo. They can only respond by changing their shape or mitotic activity or by orienting their planes

of division (4, 11). Cell walls also prevent cellular interactions that involve the cell membrane, a common form of cell-cell communication in animals. Thus, any subsequent refinement of the initial pattern very likely requires a different kind of cell signaling. For instance, only some of the cells in the apical region will eventually become meristematic, while most of these cells contribute to the formation of the cotyledons. How such a refinement occurs is not at all clear. Studying plant embryogenesis at the cellular level will eventually reveal common principles in the formation of the body pattern in multicellular organisms—if they exist.

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