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The Importance of Emerging Model Systems in Plant Biology

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Model systems in plant biology include a range of species spanning from "well-established" to "emerging" models, depending on the degree to which they have been developed. There are two phases to building a model system: initiation and maintenance. Model species are initiated usually with a novel and often classic contribution to science (that is, they have provided insight into a process that was previously poorly understood). Mendel's insights into genetics that came from analysis of the phenotype of pea seed coats is a good example. To be sustained, model systems must be experimentally tractable in general and also have a unique area in which their contributions are outstanding. They must be tractable in enough arenas—genetics, development, culture, transformation, and so on—so roadblocks do not prevent progress. For example, *Xenopus* oocytes are outstanding for localization of determinants, and the dearth of genetics can be circumvented with microinjection. Model species must be recognized by the scientific community (in print by peer review, by representation in symposia, and with funding) to emerge as a new model and then to grow into well-established systems.

Emerging Model Systems in Plant Biology, a special issue of *Journal of Plant Growth Regulation,* helps to inaugurate a new format for Springer-Verlag centered on bringing together reviews on a timely topic.

Why are emergent model systems for plant biology a timely topic? Indeed, why should we have more than one model plant system? We will know the complete sequence of *Arabidopsis thaliana* soon. This system has good genetics and excellent molecular tools (cDNA and genomic libraries, bacterial artificial chromosomes, microarrays, ESTs, and so on). Prominent scientists have voiced the opinion that progress in plant biology was slowed to a snail's pace for years by working on too many species at one time. Clearly, having focused on *A. thaliana* has pushed plant biology forward by leaps and bounds in a short time. In the age of modern molecular genetics when we can clone a gene from one plant and use molecular and biochemical techniques (that is, polymerase chain reaction and antibodies) to study that same gene in another species, why bother with more than one plant model system?

It is not an overstatement to say that plants—from green algae to angiosperms—represent the most diverse biochemistry, architecture, life history (including alternation of generations), reproductive biology (sexual and asexual), and body plans on Earth. Flowering plants have an estimated 300,000 species compared with only 4,500 for our closest relatives, the mammals, a group of approximately the same age. No one plant, not even *Arabidopsis thaliana,* can encompass this enormous diversity at the whole plant, physiologic, chemical, genetic, or molecular level.

It behooves us to understand this biodiversity so that we can better use it and protect it as the population and environmental impact of our own species explodes into the next century. Mankind uses plants for fuel, building materials, clothes, medicine, decoration (including beauty products and holiday talismans), recreation, food, and drink. It is hard to imagine life without plants—indeed, plants make

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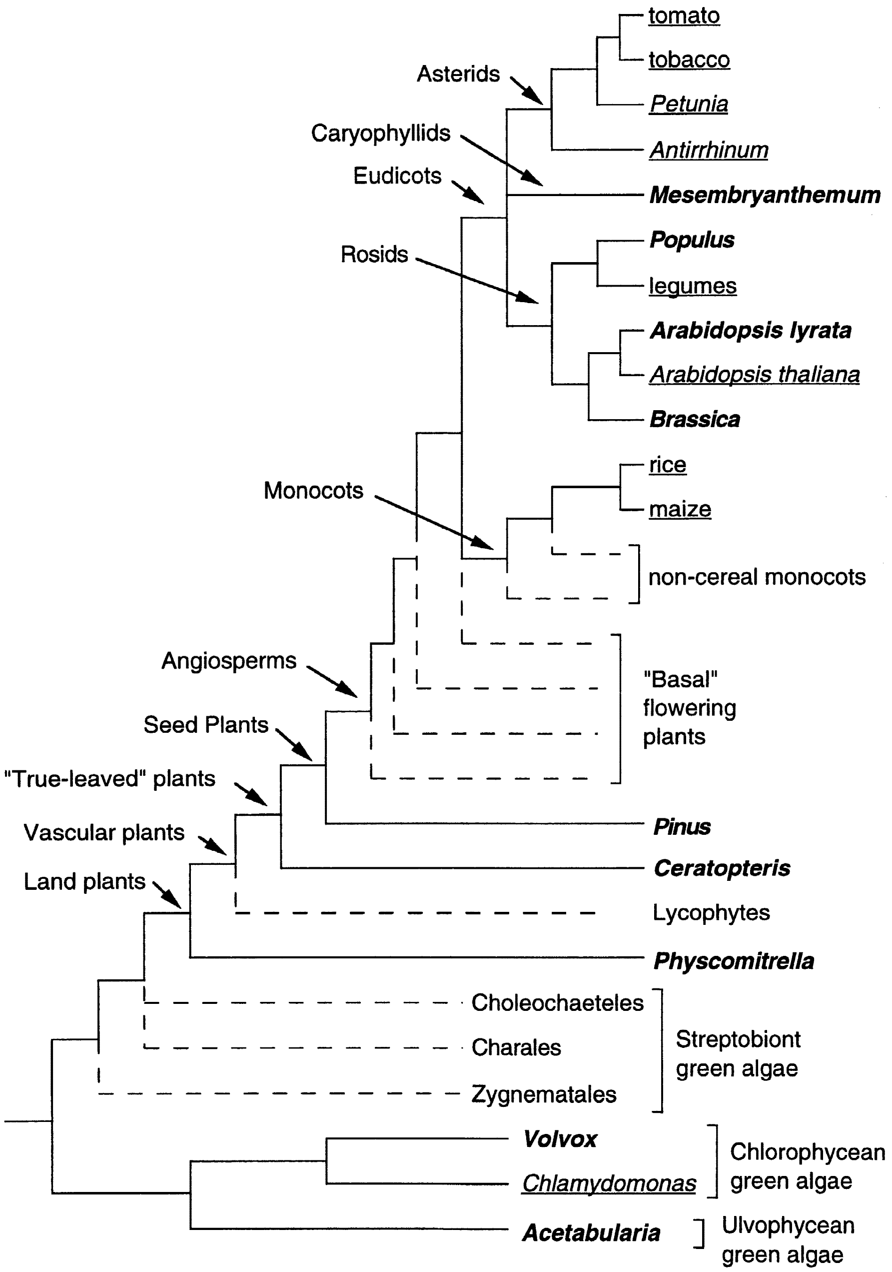

Figure 1. A stylized evolutionary tree of green plants. Arrows at the left indicate major clades of land plants. Model species in plant biology are indicated on the branch tips to the right. "Emerging" model species in this issue are highlighted in bold; "established" model species are underlined. ("Legumes" is used as a placeholder for the several species of Fabaceae that have been important in plant biologic research, including pea, soybean, alfalfa, and others, even though none have emerged as a dominant model species within the legumes.) Dashed lines indicate important lineages of green plants for which there are currently no developed model systems. The emerging model species highlighted in this issue fill several important gaps among the land plants and green algae. However, several lineages of green plants that are critical to an understanding of their evolution are not represented. These include the noncereal monocots and basal, or "magnoliid," dicots among the flowering plants, the lycophytes, which are one of the two primary lineages of vascular plants, and the lineages of green algae that gave rise to the land plants (Coleochaetales, Charales, and Zygnematales).

the very air we breathe by maintaining oxygen levels that can sustain animal life. Plants inhabit virtually every environmental niche on Earth from ocean to sky, from tropics to tundra. The biodiversity of plants reflects the genetic and biochemical networks they have evolved over deep time.

The survival of *Homo sapiens* will largely depend on our stewardship and wise use of the resources at hand: plants surely are among the most important of these. In this, nothing can replace fundamental, broad knowledge that enables informed decision making. Our current use of species as model systems (Figure 1) clearly shows that without judicious and purposeful targeting of species that span the enormous biodiversity of plants, we run the risk of sampling only a tiny portion of this abundance. An alternate approach to sampling this biodiversity is being taken by the large pharmaceutical companies who are furiously mining the tropics for new species with traditions of medicinal use by native peoples before the old-growth forests are gone. This approach, however, is one of short-term gain and does not replace the depth of knowledge that judiciously placed model systems can supply. The emerging model systems represented in this issue were chosen with an evolutionary perspective of Earth's biodiversity in mind.

Cloning genes is tremendously powerful, but *in vitro* studies do not always reflect *in vivo* function of genes; one must put genes back in context to see how they work. A similar sequence does not mean that a gene functions in the same way in different species. Localization of mRNA, posttranscriptional control (for example, poly A tail length, mRNA stability), binding to proteins, long-distance movement through the phloem or from cell to cell by means of plasmodesmata are some of the many ways to modulate message expression. Sequestration into different compartments, coupling with different cofactors, or binding partners or regulators (suppressors, enhancers) are all means of changing protein expression and use. If we are going to continue genetic engineering for food and medicine, we must have target species in each major branch of the evolutionary tree so that we can make informed choices about such manipulations. As Figure 1 illustrates, the emerging models in this issue greatly broaden the range covered by more established, crop and noncrop plant model systems. Conversely, the importance of model organisms to systematics was expounded in a Preface to the Symposium on the Phylogenetics of Model Organisms (Kellogg and Shaffer 1993).

It is difficult to make a new model system "emerge." Several factors, combined with the initial involvement of few laboratories, make this true. In the prior centuries, authors were paid by the word or the page, so negative results were often published. Now, however, printing costs are often passed on to the authors so articles are kept as short as possible and negative results are omitted. A consequence of this sea change in publishing has fostered a new kind of elitism in science: one needs "insider's" access to the negative results to successfully navigate the land mines and sand traps that others have found. In addition, funding agencies and the scientists who sit on their advisory panels do not want to fund tool building, the painstaking and often risky construction of essential infrastructure for a system. The result of not sharing negative results can become a disproportionate waste of time and funds for scientists trying to build new model systems with limited funding. Hence, along with describing the advances that have been made in these emerging model systems, each author in this issue has been asked to describe in broad terms areas in which negative results have been obtained or are to be expected so that others do not waste their time and funds.

Several criteria were used to select the systems in this issue: (1) sufficient evidence of progress that the system could truly be considered a viable model, (2) representation of a branch of phylogeny not well covered by better established systems, and (3) the willingness of a key scientist—in most cases someone who has been instrumental in helping that system "emerge"—to write such an unusual review. Each of the senior authors was given the freedom to assemble a team to contribute to their review. The Editor-in-Chief, Judith Croxdale, asked Dina Mandoli to write a review on the green alga, *Acetabularia acetabulum.* Selections of other model systems were solely Mandoli's responsibility. *Volvox carterii,* reviewed in a delightful manner by David Kirk, was included to provide evolutionary depth to the issue, as a second representative of the 72% of the planet that is covered with water, and as a multicellular algal counterpoint to *A. acetabulum.* David Cove writes about *Physcomitrella patens,* the most established model moss, which homologous recombination has made much more powerful. Including these first three systems is an attempt to counterbalance the current tendency to vascular plant myopia. *Ceratopteris richardii,* reviewed with deserved excitement by Ani Chatterjee and Stan Roux, continues the trend to land plant evolution. *Brassica oleraceae,* reviewed broadly by Mary Musgrave, has a strong and important place in being highly useful to both research and education. In the face of the debate on genetically modified organisms, public understanding of research in plant biology has never been more important. Inclusion of two trees, *Populus* (primarily *P. deltoides* and *P. trichocharpa* and their hybrids) and *Pinus taeda,* discussed by teams assembled by Reinhard Stettler and Ron Sederoff, respectively, are timely as 2000 finds us combating possibly the largest loss of acreage caused by fire in our national forests since 1910. These trees—one gymnosperm and one angiosperm—exemplify different human uses of fiber and wood and may well make important contributions as models for carbon metabolism in a time of global warming. *Mesembryanthemum crystallinum,* beautifully reviewed by John Cushman and Hans Bohnert, brings an example of biochemistry unique to plants and the promise of functional genomics to explore its depths. Finally, Mikhail Nasrallah succinctly weaves the promise of the depth of research on *Arabidopsis* into interspecific hybridization and hybrid vigor, aspects of biology in which plants excel. Many more new model systems are out there with people just as passionate and dedicated to their systems as the ones who authored articles here. To these folks, I (DFM) extend my apologies for not having the space to include them all.

Frank appraisal of the strengths and weaknesses of any model system is always a productive exercise. It is especially helpful to scientists, whether young or experienced, who are looking for a new venue for scientific discovery and progress in a less crowded niche. Each author briefly discusses the strengths and weaknesses of the system in which they work. We hope these articles welcome newcomers to these emerging systems and provide them with a roadmap to success on which the hazards are clearly marked.

Finally, each author has been asked to share a wish list for their model system. This is not something that is typically shared in print but is usually reserved for private, late-night sessions with trusted colleagues. Each of us has spent many late nights dreaming of having just the suite of tools in our kit that would let us most quickly and elegantly do the experiments we dreamed up when we committed ourselves to a system. Each of us wants to share the vision of the heights that these model systems can attain given enough funds and willing hands. Each of us is painfully aware that the success of a model system depends on the number of scientists, each with his or her own questions and skills, who take up the study of that organism. In sum, the value of sharing such visions is that they encompass the sum total of the expertise of each of these authors in a way that maps the future potential greatness of the system and most clearly welcomes others to enjoin in that vision.

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Guest Editor

REFERENCES

Kellog EA, Shaffer HB. 1993. Model organisms in evolutionary studies. Syst Biol 42(4):409–414.