Biological Sciences

Botany

Botany – Progress and Prospects

Peter H. Raven^{*}

* Missouri Botanical Garden, St. Louis, Mo., USA

ABSTRACT. Progress in botany has been very rapid over the past half century. Earlier, it was scarcely possible to imagine what would be learned about hormone action, growth, or many other key fields of botany. A few of important new discoveries are mentioned here. The complete sequencing of the genomes of different kinds of plants began in 2000. The information gained from genomic studies soon will make possible a rigorous study in plant evolutionary history. At the same time, the accelerating effects of habitat reduction; the widespread and growing presence of alien invasive species; the gathering of plants in nature for personal use and commercial purposes; and global warming combined threaten to eliminate two-thirds or more of all plant species during the course of this century. As scientists and informed citizens, we must give the global situation our most serious attention. © 2007 Bull. Georg. Natl. Acad. Sci.

Key words: genome, hormone action, plant evolutionary history.

Progress in botany has been very rapid over the past half century, with problems that had been thought to be intractable yielding to modern methods that would earlier have been impossible to conceive, much less to apply. Although Watson and Crick proposed the double helical model for the structure of DNA in 1953, it was not until the unraveling of the genetic code in the early 1960s and the demonstration of how the transcription of proteins actually worked that we began to understand the basic tenets of molecular biology and their central role for the whole field of biology. Earlier, it was scarcely possible to imagine what would be learned about hormone action, growth, or many other key fields of botany, and few people had any premonition of the massive changes that would alter science and the face of the globe over the past 50 years [1,2].

The world population in 1950 was approximately 2.5 billion people; in the ensuing years it has grown to an estimated 6.5 billion! We were probably using about 50% of global productivity then on an ongoing basis, whereas now our rate of use is estimated at 120%. With half of the world's people living on less than \$2 per day and

one out of eight literally starving, the combination of population numbers, consumption levels, and technology is literally reducing the productive capacity of the earth to lower and lower levels with every passing day. Why do we seem to care so little? I first became aware of these problems along with Paul Ehrlich and other colleagues at Stanford about 40 years ago. Gradually it became apparent to us that we were driving species to extinction at an ever-increasing rate, higher by 2-3 orders of magnitude than anything experienced for the past 65 million years, and that the cost of our existence on Earth was rapidly becoming an insupportable burden [3-5].

But what have we learned about botany over these years? There have been so many surprises and important discoveries that I can offer only a few for consideration here.

The complete sequencing of the genomes of different kinds of plants began in 2000, with *Arabidopsis*, which was shown minimally to be of ancient hexaploid derivation, even though it has the smallest genome among the flowering plants. Complete genomic sequences were soon added for rice, poplar, the lycophyte *Selaginella*, with tomatoes, maize, wine grape, and the legume *Medicago* soon to follow. These sequences have made it possible to identify the gene corresponding to a mutation in *Arabidopsis* within a few weeks of the formation of a segregating population between a plant containing a mutant allele and the wild type. The DOE Community Sequencing Program has also supported the ongoing sequencing of genomes or major sections of genomes in manioc, potato, tobacco, a moss, *Mimulus guttatus*, *Sorghum bicolor*, *Capsella bursa-pastoris*, and *Arabidopsis lyrata*, a perennial congener of *A. thaliana* [1,2,6].

The large amount of related activity, evident in the pages of any journal in the field, reminds us that the "\$1,000 genome" is going to become a reality sooner rather than later. As costs decrease rapidly, we will have greatly enhanced ability to assess variation within and among populations, thus making it much easier to learn about adaptation and the process of evolution in plants and to conserve them.

The information gained from genomic studies soon will make possible a rigorous study of the evolutionary history of key innovations in plant evolutionary history such as vascular tissue, leaves, seeds, and flowers. It will also make possible the determination of the genetic basis of significant innovations in the features of mutant individuals and different species and genera of plants. Elegant QTL work in *Mimulus* has documented the genetic basis for species differences. And, genomic studies have also led to a better understanding of the genetics of domestication, particularly in maize, where key genes have been identified and results of selection for a chromosome region documented (selective sweeps) [7,8].

Also discovered during the last few years is the fact that plant disease-resistant proteins (R proteins) usually detect pathogens indirectly by the damage they do to host cell components, rather than by identifying the pathogen's molecules directly. Recent studies have shown that at least one case of "non-host resistance" (i.e., in which a plant species does not allow growth of a particular pathogen species) is due to active resistance mechanisms encoded by multiple genes. This raises the possibility that it may be possible to engineer stable non-host resistance into crop species.

Of fundamental importance has been the independent discovery by two groups of investigators of the receptor for auxin, which was discovered some 80 years ago — the first plant hormone to be described. This receptor has turned out to be an *Arabidopsis* F-box protein (one of about 700 such proteins in Arabidopsis). Such proteins act in eukaryotic organisms to target regulatory proteins for degradation in a signal-dependent manner. This finding – a beautiful piece of work on a long-standing problem – hints at how plant cells "sense" and respond to this protein, and thus provides a key for 75

investigating the action of plant proteins in general. Recently, the signaling mechanism by which plants sense and respond to gibberellin has also be found to involve an F-box protein, suggesting that the phytohormones may act via similar mechanisms [6,9,10].

Of special significance has been the identification of a molecule, called FT, that has all the hallmarks of the hitherto elusive florigen, and published in three articles in Science in 2005. The FT gene is induced in leaves within hours after plants receive a stimulus that promotes flowering, and its product, the FT protein, acts at the growing tips of the plant to activate the flowering process. The gap between the two sites is bridged through movement of FT RNA from the leaf to the growing tip.

The role of micro RNA, which was poorly understood in 1999, has now been shown to be important in many aspects of plant growth and development.

Transcription factors and other proteins have been shown to move in a regulated way through plasmodesmata, the "plant information superhighway," by Bill Lucas at the University of California – Davis.

Jeff Palmer and his colleagues have demonstrated the massive horizontal transfer of mitochondrial genes from diverse land plant and fungal donors to the basal New Caledonian angiosperm *Amborella*. This has been a startling discovery whose significance for plant evolution in general and mode of origin are receiving further studies in the Palmer laboratory. Certainly the horizontal transfer of genes to plant mitochondria is frequent, but not to the massive degree in which it has occurred in *Amborella* [11].

Another great surprise about angiosperm phylogenetics came in 2007, with the recognition that the tiny grasslike plants of the family Hydatellaceae, endemics of Australia and New Zealand, were the sister group of the Nymphaeaceae, the water lilies. Comparisons with the early angiosperm fossils *Archaefructus* followed, with the promise of exciting advances in understanding for many years to come.

Plant phylogenetic studies have expanded rapidly in precision and in coverage of different groups. Careful developmental studies linked with comparisons of the genetic basis for the patterns observed have much to offer in understanding the relationships of plant groups at all levels, and the basic patterns of relationship that have been emerging over the past 15 years or so – often radically different from what had been suspected earlier – appear durable. Informative studies of fossil plants have begun to teach us much about the nature of the earliest angiosperms. Along the way, numerous discoveries in the fossil record have proved patently false earlier conventional wisdom that held that there simply were not be enough fossil flowers to make any difference in our understanding of angiosperm evolution. Some of the earliest fossil flowers apparently represent entirely extinct major taxa. By the mid and Late Cretaceous, ancient taxa with clear relationships with groups such as Chloranthaceae and other extant angiosperm clades appear. The resolution of such fossils will provide interesting results for years to come.

The Angiosperm Phylogeny Group (APG) has contributed much to the establishment of monophyletic groups in angiosperms, a trend obviously beneficial to the establishment of sound classifications with predictive value. The phylocode, with its cognitive formlessness, has provided a way of organizing information that some students of phylogeny have found useful, but, in principle, since it does not indicate the relationships of taxa nor help us locate information about them it has not been widely accepted.

Notable in recent years has been the sturdy growth of the Tree of Life Project, which will provide a sound basis for understanding the relationships of major taxa within the next few years. Numerous surprises, such as the rooting of the Equisetales within the ferns, and, controversially, the Gnetales within the conifers, will clearly be encountered along the way. With respect to the latter hypothesis, in which Gnetales are seen as sister to Pinaceae, there has been much doubt, but further critical evaluation is clearly necessary in view of the material presented.

In terms of the material available for systematic botany and its availability, the total number of plant specimens in the world's roughly 3,000 herbaria is growing at the rate of about 10 million specimens per year, with approximately 345 million specimens in the world's herbaria today. The total number of distinct vascular plant species validly described has not been reliably estimated, but there are clearly at least 325,000 of them, with what I would estimate as 100,000 more still to be named and defined. Over 100,000 species are cultivated in botanical gardens already, and the gardens themselves have grown by about a third over the past decade, with about 2,700 operating today.

Major increases in the availability of information about plants on the World Wide Web foretell even greater increases in such useful information in the future. For example, the African Plants Index now includes high-resolution images of about 80% of the types of African plant species, and will go on line later this year; and a similar project for the types of Latin American plants, again backed by the A. W. Mellon Foundation of New York, was started in 2005.

The literature of systematic botany is likewise becoming available on line: the Missouri Botanical Garden's *Botanicus* project, funded by the Keck Foundation and the Institute of Museum and Library Services, has already recorded over 400,000 pages of pre-1923 systematic literature in a searchable format, with 2,500 additional pages being added each week. In this way, the complete literature of systematic botany will become universally available relatively soon. All of the *Botanicus* information is linked to the Missouri Botanical Garden's *Tropicos* 2 database, the most comprehensive and widely consulted database on plants.

At the same time, the accelerating effects of habitat reduction; the widespread and growing presence of alien invasive species; the gathering of plants in nature for personal use and commercial purposes; and global warming combined threaten to eliminate two-thirds or more of all plant species during the course of this century. Following a call for increased efforts to conserve the world's plants at the 1999 International Botanical Congress in St. Louis, a Global Strategy for Plant Conservation was approved within the Convention for Biological Diversity in 2002. The Global Strategy then established specific, ambitious goals for the preservation of plant diversity that are intended to be met by 2010. The efforts made to realize these goals are clearly having an important impact on plant conservation throughout the world, starting with our knowledge about the amount of diversity that exists.

Transgenic crops have now been grown on more than 1 billion acres (in aggregate) throughout the world, amounting to approximately an eighth of the total cultivated land globally. More than a decade of experience has demonstrated no damage related to the cultivation of these crops, which have offered proven economic and environmental benefits. Even more impressive gains are in sight for the decades to come. Plants that exhibit improved levels of cold, freezing, salt, and drought tolerance have been developed and are expected to improve crop productivity in regions where it is limited by these factors. Although investigations continue, there seems little doubt that the intensive production of adequate supplies of food on the least amount of land possible will contribute a great deal to the preservation of biodiversity at a time of maximum threat to its continued existence.

The appearance of the Millennium Ecosystem Assessment in 2005 demonstrated that human beings over the past 50 years have degraded ecosystems more rapidly than any earlier time. These changes have allowed major increases in human well-being but at the same time rapidly diminished the benefits that future generations will be able to obtain from ecosystems. Achieving the Millennium Development Goals will require significant changes in policies, institutions, and practices, but few nations seem ready to embrace these changes fully and certainly they have not been accepted as a basis for action here in the United States.

As scientists and informed citizens, we must give the global situation our most serious attention. We live in a more diverse world today than will ever exist again, but our efforts will play a major role in shaping the contours of that future world and the opportunities that its citizens will enjoy. As botanists, we have a great deal to contribute, and exciting future discoveries await us in all of the subfields of our discipline.

Acknowledgments: This review is based on a talk presented at the XVII International Congress in Vienna, Austria, in July 2005, revised for the annual meeting of the Botanical Society of America in August 2006, and published in the Bulletin of the Botanical Society of America subsequently.

ბოტანიკა

ბოტანიკა – პროგრესი და პერსპექტივა

პ. რეივენი*

* მისურის ბოტანიკური ბაღი, სანტ ლუისი, მონტანა, აშშ

უკანასკნელი ნახევარი საუკუნის განმავლობაში ბოტანიკა სწრაფად განვითარდა. უწინ ძნელად წარმოსაღგენი იყო ის, რაც ახლა ვიცით ჰორმონების მოქმედების, ზრდის და ბოტანიკის ბევრი სხვა მნიშვნელოვანი საკითხის შესახებ. აქ საუბარია რამდენიმე ღირსშესანიშნავ ახალ აღმოჩენაზე. სხვადასხვა მცენარის გენომების სრული გაშიფრვა 2000 წ. დაიწყო. გენომების გამოკვლევის შედეგად მიღებული ცოდნა მალე შესაძლებელს გახდის მცენარეთა ევოლუციის ინტენსიურ შესწავლას. ამავე დროს, ჰაბიტატთა მზარდი შემცირება, უცხო ინვაზიური სახეობების ფართო გავრცელება, მცენარეთა შეგროვება ველურ ბუნებაში პირადი და კომერციული საჭიროებისათვის და გლობალური დათბობა საფრთხეს უქმნის მცენარეთა ყველა სახეობის ორი მესამედის ან მეტის არსებობას ამ საუკუნეში. როგორც მეცნიერები და გათვითცნობიერებული მოქალაქეები, ვალღებულები გართ გლობალურ ვითარებას უღიღესი ყურაღღებით მოვეკიღოთ.

REFERENCES

- 1. P. H. Raven (Editor) (1997), Nature and Human Society. National Academy Press, Washington DC.
- 2. P. H. Raven & L. R. Berg (2001), Environment. Harcourt College Publishers, Philadelphia, Pennsylvania.
- 3. P. Ehrlich & P. H. Raven (1965), Butterflies and plants: a study in Coevolution. Evolution 18: 586-603.
- 4. A. O. Richardson & J. D. Palmer (2007), Horizontal gene transfer in plants. J. Exp. Bot. 58 (1): 1-9.
- 5. G. B. Johnson & P. H. Raven (2004), Biology. Holt, Rinehart & Winston Publishers, Austin, Texas.
- 6. J.-Y. Lee, K. Taoka, B.-C. Yoo, G. Ben-Nissan, D.-J. Kim, & W.J. Lucas (2005), Plasmodesmal-associated protein kinase in tobacco and Arabidopsis recognizes a subset of non-cell-autonomous proteins. Plant Cell 17: 2817-2831.
- 7. A. L. Angert (2006), Demography of central and marginal populations of monkeyflowers (Mimulus cardinalis and M. lewisii). Ecology 87(8): 2014-2025.
- 8. R. L. Gilbertson, M. R. Rojas, & W. J. Lucas (2005), Plasmodesmata and phloem: conduits for local and long-distance signaling. Annual Plant Reviews 18: 162-187.
- 9. P. Ehrlich & P. H. Raven (1969), Differentiation of populations. Science 165: 1228-1232.
- 10. A. L. Angert (2006), Growth and leaf physiology of monkeyflowers with different altitude ranges. Oecologia 148:183-194.
- 11.U. Bergthorsson, A. O. Richardson, G. J. Young, L. R. Goertzen, & J. D. Palmer (2004), Massive horizontal transfer of mitochondrial genes from diverse land plant donors to basal angiosperm Amborella. PNAS, 101, no 51:17747-17752.

Received June, 2007

77