Plant biology in the future

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In the beginning of modern plant biology, plant biologists followed a simple model for their science. This model included important branches of plant biology known then. Of course, plants had to be identified and classified first. Thus, there was much work on taxonomy, genetics, and physiology. Ecology and evolution were approached implicitly, rather than explicitly, through paleobotany, taxonomy, morphology, and historical geography. However, the burgeoning explosion of knowledge and great advances in molecular biology, e.g., to the extent that genes for specific traits can be added (or deleted) at will, have created a revolution in the study of plants. Genomics in agriculture has made it possible to address many important issues in crop production by the identification and manipulation of genes in crop plants. The current model of plant study differs from the previous one in that it places greater emphasis on developmental controls and on evolution by differential fitness. In a rapidly changing environment, the current model also explicitly considers the phenotypic variation among individuals on which selection operates. These are calls for the unity of science. In fact, the proponents of "Complexity Theory" think there are common algorithms describing all levels of organization, from atoms all the way to the structure of the universe, and that when these are discovered, the issue of scaling will be greatly simplified! Plant biology must seriously contribute to, among other things, meeting the nutritional needs of the human population. This challenge constitutes a key part of the backdrop against which future evolution will occur. Genetic engineering technologies are and will continue to be an important component of agriculture; however, we must consider the evolutionary implications of these new technologies. Meeting these demands requires drastic changes in the undergraduate curriculum. Students of biology should be trained in molecular, cellular, organismal, and ecosystem biology, including all living organisms.

eeding and sheltering people to protect them from famine and disease will be a major challenge for plant biologists, considering the rapid rate of human population growth. According to estimates, the current 6 billion people on earth may increase to as many as 9-10 billion by the middle of the 21st century. Also, current estimates suggest that nearly 800 million people are hungry, and that to meet expanding demands, we need to produce $\approx 40\%$ more grain by the first quarter of this century. The desire of many countries to develop (and thus use more energy) will put tremendous strain on natural resources and will result in the input of large quantities of greenhouse gases, such as CO₂, N₂O, and CH₄, into the atmosphere. These trends will necessitate a closer association between plant biologists and agricultural scientists concerned with crop production. Thus, because of increasing demands for food and other plant products, research on economically important plants will be intensified in the future. Plant biology has now emerged as a prominent discipline in biology, largely because of progress in understanding the processes of development and gene manipulation at the molecular level (1).

Recent advances in molecular biology of organisms constitute nothing short of a revolution. Our understanding of plant responses and behavior will greatly benefit from the application of molecular biology technologies. The application of molecular techniques has already shown great promise in some important plant products consumed by humans. It is now possible to engineer crops for better yield, make them resistant to diseases and pests, or increase their resistance to drought. For example, genes have been added to rice and maize, two major crops, which allow them to tolerate high levels of aluminum, normally toxic for plants. Furthermore, the development of "Golden Rice" is a major triumph of these new techniques. This rice contains β -carotene, which is converted into vitamin A after the rice is consumed. Thus, people can obtain their required vitamin A by eating rice. Presently there are attempts to use molecular techniques to introduce vaccines into foodstuffs such as bananas, which are consumed in many countries where malnutrition and disease are acute. There is no doubt that various institutions, private and public, will be successful in endeavors such as these in the near future.

Previous Model of Plant Biology

Historically, plant biologists had a simple model for their science. Plant identity (taxonomy), distribution (plant geography), morphology, and physiology were emphasized. With the invention of the microscope, scientists were able to see small processes: internal morphology, development, and the stages in cell division became important subjects for study. Historical plant biology (paleobotany) concerned the evaluation of the progression of vegetation in a given location as the environment changed. It dealt with the relatively slow changes in vegetation in a given region, the evolution of various taxa through geological time, and the evolution of life. Thus, the fields of taxonomy, morphology, and physiology were active. Evolution was approached by assuming the plants were adapted to their environments. With the discoveries of basic principles of inheritance and evolution by natural selection, the science of genetics and evolutionary biology flourished. There was much fascination with convergent evolution, the development of common morphological traits in similar environments across phylogenetically disparate taxa. Many plant biologists sought to accumulate more examples of this interesting phenomenon. Collectively, the investigations of paleobotanists provided a firm foundation for plant biology.

Molecular Biology Revolutionized the Study of Plants

In the second half of the 20th century the discovery of the structure of DNA and RNA, the steps in protein synthesis, and other great discoveries of molecular biology revolutionized the study of plants at all levels, from cells to ecosystems. Taxonomists, evolutionists, ecologists, physiologists, and developmental biologists are now using molecular techniques and are discovering many responses and mechanisms that were not accessible

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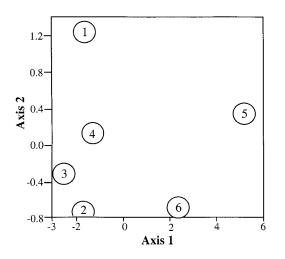


Fig. 1. The influence of spring weather conditions on the development of different communities from a common seed bank in an annual community from the Midwestern United States. Conditions 1–5 represent different weather in the spring.

in the past. It is now possible to identify, with much precision, the particular genes responsible for traits. And, with the techniques of molecular biology, scientists can introduce or eliminate genes for specific traits. Using these advanced techniques we may also alter the present taxonomy and phylogeny and, as the differences and similarities among taxa are modified by human action, we can create new species.

Remarkably, and despite this great revolution, there will be no significant change in the general structure of plant biology and the relationship between the various branches of the field. These approaches will simply lead to a deeper understanding of the mechanisms and a better control of their direction (i.e., soon we will be able to direct the process, to a certain extent, at will).

Risks of Molecular Biology of Plants

These techniques, however, are not without risks. The resistance to consuming foodstuffs produced by such techniques is a strong indication that, right or wrong, the public at large (particularly in Europe) is not yet ready to totally accept these methods. These techniques, coupled with global change, may create unforeseen problems. For example, the spread of pollen from herbicide-resistant plants to natural populations could be a potential problem. The fear of the spread of resistant varieties to natural populations is warranted, especially for invading plants whose populations are kept low in their native habitats because of diseases and pests. Changes in crop production patterns alone may create unforeseen problems. Under the pressure of increased human demand, planting more corn, as has recently occurred in Ethiopia, may lead to higher population sizes and densities of the larvae of Aedes *aegypti*, which is the vector for transmission of the malaria causal agent Plasmodium falciparum. These larvae eat corn pollen that floats on the surface of water bodies. In the meantime, plant populations of native species are being replaced by maize.

The Nature/Nurture Debate in Changing Environments

Because the environment of the future may be quite different from that of today, the nature/nurture argument will become more prominent. All indications suggest that the environment is likely to be more variable than at present. According to many models, temperature and CO_2 levels will rise. Furthermore, it

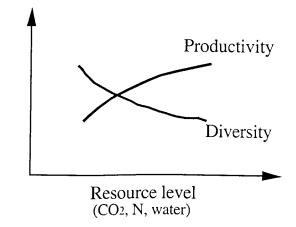


Fig. 2. The anticipated relationship between productivity and species richness in a future climate where variation in weather and resources, e.g., CO₂ and nitrogen, are expected to increase.

is assumed that night temperature will increase disproportionately (2). Although presently very complicated, the genotype \times environment interaction will not simply be $(G \times E)$; it will be much more complicated. Instead, $G \times E$ may well be $G \times E_1$, $E_2 E_3 \dots E_N$ —depending on the changing environments that the plant experiences through its life cycle and on the speed with which traits travel through the environment. We must remember that E, the environment, has a direct influence on G, the genotype, in turning on and off genes (3). Also, we do not know which subset of G or E will impact the most strategies of variation and fitness. All expectations suggest that the role of environmental variation may be increased. Broad-niched species apparently respond well to global change, and it has been suggested that they will be impacted less than narrowniched species (4). Thus it is expected that as increased environmental variation tends to eliminate narrow-niched (specialized) species, broad-niched species or species that are inherently genetically variable and/or plastic in their response to environmental change will be favored (5). The elimination of these species may also lead to a reduction in biological diversity, presently a major concern for humanity (6). By their nature, broad-niched species (which are usually early successional) can tolerate a wider range of environmental variability than narrow-niched, more stable, late successional communities (see ref. 4). In this case, there may be strong selection for plasticity in plants (7) or for broad-niched genotypes and early successional species (as discussed earlier). Because it is fast growing, the potential increased abundance of early successional species may have significant implications for global carbon sequestration. On the other hand, environmental variation can lead to the divergence of communities with different dominant species, thus increasing between patch diversity (B diversity). An illustration of this situation is the development of different communities from similar seed banks when they are exposed to a range of spring conditions e.g., wet, dry, cold, warm, etc. (Fig. 1). These results seem to support the "Initial Condition" hypothesis of the proponents of complexity theory. Furthermore, in a future environment with additional resources, such as nitrogen due to deposition, there is the possibility of an increase in productivity and a decrease in diversity (Fig. 2). This result may occur for two reasons: (i) species in the same ecosystem do not respond in the same manner to elevated atmospheric CO₂, thus CO₂-responsive species may become dominant and exclude other lessresponsive species, and (ii) they do not respond similarly to nitrogen deposition.

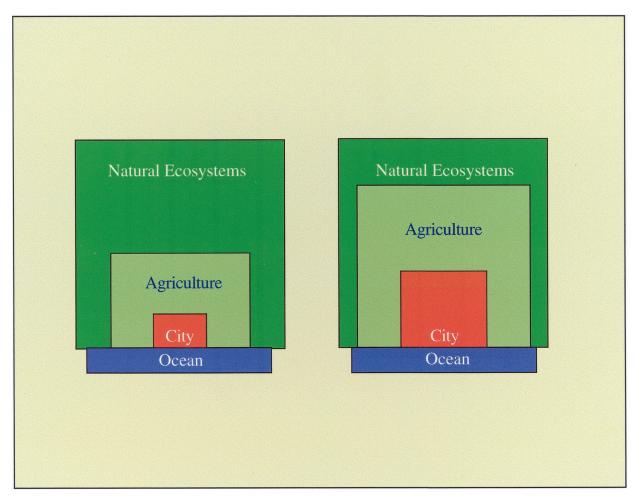


Fig. 3. Diagram showing the change in the area of natural vegetation in the future, where the number of people on earth approaches 10 billion.

Economic Plants and Environmental Variability

In a rapidly changing environment with an ever-increasing human population, work on plants of economic value will have to be intensified. We need to produce varieties with a broader response to the varying environment. The separation between agricultural science and basic plant biology will become less clear as more and more plant biologists work on economically important species and perhaps find (or design) new ones. Thus, the following should be among the aims of plant biologists of the future:

(*i*) To engineer crops that can resist drought and other resource limitations, such as soil nutrients, enabling people to cultivate marginal, presently unproductive, land more successfully;

(*ii*) To increase yield by bioengineering and classical hybridization techniques of major crops; and

(*iii*) To enhance nutritional quality without sacrificing quantity.

Increasing yield usually requires an increase in the application of fertilizer and biocides. This means that we have to manufacture more fertilizers and biocides, and both processes need energy. In fact, the quantities of manufactured nitrogen fertilizer already exceed the amount of nitrogen fixed naturally (8). We do not know the impact of the high-nitrogen production levels on the environment, although we suspect it has negative consequences. Without an increase in the application of fertilizers, something that the developing countries presently cannot manufacture or purchase, it would be difficult to achieve an increase in crop production and maintain quality. Agricultural runoff and pollution by nitrogen and phosphorous fertilizers are major problems, which already are having a detrimental impact on biological drinking water and diversity in parts of the world. Land disturbance may cause large quantities of dust to be added to the atmosphere, compounding the environmental pollution problem (9), but may increase the impact of newly needed nutrients on the soil.

There is no escape from the fact that, with the increase in human populations, the area of natural ecosystems remaining will be reduced, as more land is going to be used to support the billions of people (Fig. 3). However, the area for agriculture relative to population size will likely decrease because of improvements in productivity brought about by molecular biology. A subject of major concern will be the simplification of natural and agricultural systems and a reduction in global biological diversity. These systems can be modified to the point that they cannot supply the necessary services for humanity. It has been suggested (10) that the differences in productivity between developed and developing countries will be magnified as models predict an increase in crop production in the developed countries and a decrease in developing countries (Fig. 4). This situation can have major political and social implications and requires immediate attention.

One last point: the quality of agricultural products may become a big problem in the future and may require extensive work in agricultural molecular biology. Elevated CO_2 may influence the C/N ratio and possibly protein content, reducing

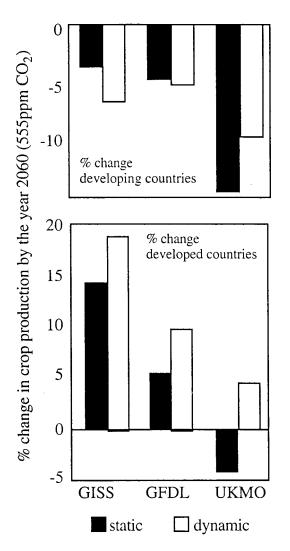


Fig. 4. Three model predictions of changes in grain yield in developed (increase) and developing (decrease) countries (from ref. 9).

the nutritional quality of crops. For example, when we grew wheat in ambient and high CO_2 , the resulting grain from the elevated CO_2 yield was not suitable for bread-making according to U.S. Department of Agriculture mixogram analysis. [A mixogram tests the protein strength in the grain and estimates mixing tolerance and ability to produce quality bread (Fig. 5).]

A Curriculum to Train Plant Biologists for the Future

Advances in plant biology through the use of the techniques of molecular biology and other approaches and the expected integration of various levels of inquiry in the field dictate that a new curriculum of study be espoused. Of course, there are many possibilities. Plant biologists should be aware of these advances regardless of the level of organization at which they work. For example, in addition to a course in integrative biology presenting the principles of biology to all college biology students, these students should have good grounding in molecular, cell, organismic, and ecosystem biology. The first two fields, molecular and cell biology, should not be presented, as they are now in many universities, with the exclusion of plants, bacteria, protists, fungi, and archaea. Molecular biology courses of the future should address animals, plants, bacteria, and all other taxa, and the similarities and differences among these organisms should be

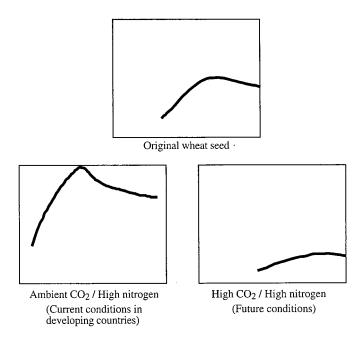


Fig. 5. Mixogram (produced by the U.S. Department of Agriculture) of wheat grown from the original seed at ambient and high CO_2 and fertilized with nitrogen. (Based on L. T. Meyer and F.A.B., unpublished data.)

made clear. Then students can take from a variety of courses those that are related to their area of study and specialization. For example, cell-wall structure and biosynthesis and the details of the biophysics and biochemistry of photosynthesis (plant characters) should not be ignored in courses on cell biology. In fact, we may wish to examine the usefulness of a 4-year college or a 5- to 6-year Ph.D. program to fulfill these requirements, to see whether these periods are long enough to accommodate the new biology. Another option is to drop some subjects that appear unnecessary or have already been covered in high school. Enacting changes in the curriculum will require clear thinking and a daring attitude.

Conclusions

(*i*) The techniques of molecular biology are revolutionizing the study of plants and will be used more and more by all plant biologists to discover the mechanisms of development and the control of developmental processes.

(*ii*) Disease- and herbivore-resistant plant varieties will be developed by agricultural scientists and applied botanists. This may lead to the development of new taxa and phylogenies.

(*iii*) To feed the burgeoning human population, the gap between applied and theoretical plant biology should narrow. More work will be done by plant biologists on economically important plants.

(*iv*) The science of ecology will become more important as the issues that face humanity become more ecological in nature.

(v) The basic structure of plant biology may not change. Great interest will remain in phylogeny, genetics, development, physiology, morphology, and ecology.

(*vi*) A new curriculum is needed in biology that emphasizes the unity of biology. Plant biology students should have a basic understanding of molecular, cell, and organismic biology and ecosystem ecology.

Attempts to correctly predict the future will depend on good data and good models. We should not shy away from the approaches of molecular biology. We should be prepared to accept mistakes, as these will undoubtedly occur.

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