Lawrence Bogorad: President-Elect of the AAAS

Hewson Swift

Lawrence Bogorad, Maria Moors Cabot Professor of Biology at Harvard University, is the new President-Elect of the AAAS. His urbane and gracious manner is well known to many biologists in this country and abroad through his numerous ties to organizations for plant physiology cell biology, and developmental biology. His influence on plant science in general, and on the molecular biology and physiology of chloroplasts in particular, has been significant and far-reaching, and his laboratory has been the training ground for a generation of younger plant biochemists dedicated to many aspects of chloroplast research. The wider scientific community has also benefited from his efforts as chairman of two Gordon Conferences, contributions to half a dozen committees of the National Research Council, and his continuing commitment to the Policy Advisory Group for the U.S. Department of Agriculture Office of Competitive Research Grants.

Bogorad was born in Tashkent, U.S.S.R., in 1921, but grew up in the United States, becoming a naturalized U.S. citizen in 1935. He obtained a B.S. in botany (1942) and a Ph.D. in plant physiology (1949), both from the University of Chicago. His Ph.D. thesis, on chlorophyll synthesis in dark-grown pine seedlings (*1*), set the pattern for a research orientation that has persisted over the past 35 years: a consideration of the effects of light in the induction of the complex greening process, whereby the pale, etiolated leaves of dark-grown plants become green and functional in photosynthesis. After receiving his Ph.D., Bogorad spent 2 years (1951–53) as a fellow at the Rockefeller Institute in the laboratory of Sam Granick, which resulted in a series of collaborative papers on the biosynthesis of porphyrins in algal cells as precursors to chlorophyll (*2*). He returned to the then flourishing Department of Botany at Chicago in 1953, climbing the academic ranks to become professor of botany in 1961. Except for a brief period as Fulbright Research Scholar with the CSIRO in Canberra, Australia, in 1960, and at the Karolinska Institute in Stockholm in 1961 as National Science Foundation Senior Postdoctoral Fellow, Bogorad remained at Chicago until 1967, when he left to become professor of biology at Harvard. At Harvard, he was chairman of the Department of Biological Sciences from 1974 to 1976, director of the Maria Moors Cabot Foundation in 1976, and became the Maria Moors Cabot Professor of Biology in 1980. He is currently a member of the National Academy of Sciences and the American Philosophical Society, a fellow of the American Academy of Arts and Sciences, and a foreign member of the Royal Danish Academy of Sciences and Letters. He has served on the Council and Executive Committee of the American Society for Cell Biology and is past president of the Society for Developmental Biology and of the American Society of Plant Physiologists. He has also served on numerous editorial boards and national committees.

Lawrence Bogorad

Bogorad's early investigations of the enzymes involved in chlorophyll synthesis in the green alga *Chlorella* (*2, 3*) have contributed to the broad understanding of the biosynthesis of hemes and bile pigment. These studies dealt with the enzymatic condensation of four molecules of porphobilinogen to form the tetrapyrrol framework, from which the porphyrins of hemoglobin, cytochromes, and chlorophyll are built. Later studies with *Cyanidium* (usually classified as a red alga) demonstrated the light-induced porphyrin synthesis from δ-aminolevulinic acid, as controlled by a cytochrome-like photoreceptor (*4*). Mutants of *Cyanidium*, some without chlorophyll and others with chlorophyll but lacking the accessory pigment phycocyanin, were isolated by Bogorad and his collaborators. These have proved useful to many other workers in the field of photosynthesis, not only in the investigation of the light induction of chlorophyll, but also with respect to the nature of the accessory pigment. New subtleties in light-induced changes in chloroplast pigments were shown with the cyanobacterium *Fremyella*, where the phenomenon of chromatic adaptation was first described. Levels of the blue and red accessory pigments, phycocyanins and phycoerythrin, were found to be influenced by relative intensities of red or blue light (*5*).

For the past two decades much of the recent work from Bogorad's laboratory has been concerned with the biogenesis of chloroplasts, the nature of the organelle DNA, and its role in the synthesis of chloroplast proteins. The presence of DNA in chloroplasts of *Chlamydomonas* had been shown by electron microscopy by Ris and Plaut in 1962 (*6*), and small (66s) ribosomes were isolated from spinach chloroplasts by Lyttleton the same year (*7*). Shortly thereafter, work from Bogorad's laboratory with electron microscope cytochemistry directly demonstrated the localization of ribosomes in chloroplasts of maize, which appeared to be slightly smaller than those in the surrounding cytoplasm. These were concentrated in the stromal regions of etiolated chloroplasts, becoming less numerous with the light-induced synthesis of the photosynthetic membrane system (*8*). By the mid-1960's it became increasingly clear that chloroplasts were the

The author is George Wells Beadle Distinguished Service Professor in the Department of Molecular Genetics and Cell Biology and the Department of Pathology, the College, the Committee on Genetics, and the Committee on Developmental Biology at the University of Chicago, 1103 East 57 Street, Chicago, Illinois 60637.

biosynthetic product of two different genomes, one in the nucleus and a much smaller one within the chloroplast itself. Organized cooperation of the two genetic systems in chloroplast biogenesis was clearly demonstrated by Mets and Bogorad in *Chlamydomonas* with their studies of the genetics of resistance to erythromycin, an antibiotic that selectively affects ribosomal proteins of both chloroplasts and mitochondria. Some erythromycin-resistant mutants showed typical biparental (nuclear) inheritance, and one of these was found to include the structural gene for protein 6 of the large ribosomal subunit. Another gene, affecting large subunit protein 4, showed uniparental inheritance and thus was considered to be a product of the chloroplast genome (*9*).

The chloroplast genome was isolated and characterized in the early 1970's by a number of investigators. Although some species variation was described, the chloroplast chromosome was shown to be remarkably conserved, a circular DNA molecule 90 to 100 million daltons in size. Single chloroplasts were found to contain multiple circles, but restriction analysis (*10*) clearly demonstrated that all such circular molecules were genetically identical. Chloroplasts of the green alga *Acetabularia*, however, were found to be strikingly different, with a genome some ten times larger; but up to three-fourths of its chloroplasts lacked DNA altogether and presumably were derived from a population of DNA-bearing organelles by budding (*11*).

Studies of the molecular biology of chloroplast genomes have been accumulating at an accelerating pace, which included, in the mid-1970's, a detailed restriction map of the maize chloroplast genome (*10*) with a description of a large reverse repeat in maize bearing the cistrons for 16 and 23*S* ribosomal RNA (*11, 12*) and the positions of two dozen cistrons for transfer RNA's (*13*). The first structural gene to be localized was for the large subunit of ribulose bisphosphate carboxylase. As shown in tobacco hybrids in the classical studies of Kawashima and Wildman (*14*), this enzyme—easily the most abundant plant protein—is, like the ribosome, the product of nuclear-chloroplast collaboration. The large macromolecular enzyme complex contains eight molecules of the nuclear-encoded small subunit, and eight molecules of the large subunit encoded on the chloroplast genome. During the greening of etiolated maize leaves, Bogorad's laboratory showed that messenger RNA's (mRNA's) for the large subunit reached a maximum after 20 hours of illumination and then declined at a time when mRNA's for the small subunit continued to increase, declining many hours later. This suggests that transcriptional control of the nuclear gene lags behind that of the chloroplast and is perhaps influenced by it (*15*). Interestingly, transcription of the chloroplast gene for ribulose bisphosphate carboxylase produces mRNA's of two different sizes, 1.6 and 1.8 kilobases, differing only in length of the untranslated 5′ leader. During light adaptation there was a consistent shift in ratio of these two mRNA's (*16*). Transcription of the large subunit has also been shown to be under tissue-specific control, as its mRNA's are abundant in the chloroplasts of the bundle sheath of mature leaves but are few or absent in chloroplasts of the mesophyll (*17*). Also cloned and partially sequenced are two polypeptides of the complex formed by P700 chlorophyll and a protein of photosystem I, which display a partial homology to one another and occupy a position adjacent to the large subunit locus (*18*) and the beta and epsilon subunits of coupling factor CF1, proteins of the calcium-activated ADPase system, early shown by Racker and his colleagues (*19*) to be structural components of the chloroplast membrane (*20*). These structural loci are classed as "photogenes," that is, genes whose transcription is markedly increased on illumination in plastids of dark-grown plants. Transcripts from stages in the greening process have been analyzed in detail. Their positions of origin have been mapped on the maize chloroplast genome and comprise some 19 percent of the total DNA. It is concluded that these RNA's are under transcriptional control, some messages probably being polycistronic; but the fact that their patterns of accumulation and decline differ clearly indicates the presence of heterogeneity either in transcriptional control, message stability, or both (*15*).

Much of the chloroplast genome remains to be studied, and the nature of the genetic information it contains awaits further analysis. With the detailed investigations on the greening process, however, Bogorad's laboratory is approaching fundamental problems concerning the nature of control mechanisms in chloroplast development, differentiation, and the physiological response to environmental change. In terms of a diverse and multifaceted approach to such problems, Bogorad has clearly presented strong scientific leadership. The AAAS will be in good hands during his term as President.

References

1. L. Bogorad, *Bot. Gaz.* **111**, 221 (1950).
2. _____ and S. Granick, *Nature (London)* **170**, 321 (1952); *Proc. Natl. Acad. Sci. U.S.A.* **39**, 1116 (1953).
3. L. Bogorad, *Methods Enzymol.* **5**, 885 (1962).
4. K. E. Nichols and L. Bogorad, *Nature (London)* **188**, 870 (1960); *Bot. Gaz.* **124**, 85 (1962).
5. L. Bogorad, *Ann. Rev. Plant Physiol.* **26**, 369 (1975).
6. H. Ris and W. Plaut, *J. Cell Biol.* **13**, 383 (1962).
7. J. W. Lyttleton, *Exp. Cell Res.* **26**, 311 (1962).
8. A. Jacobson, H. Swift, L. Bogorad, *J. Cell Biol.* **17**, 557 (1963).
9. L. J. Mets and L. Bogorad, *Science* **174**, 707 (1971); *Proc. Natl. Acad. Sci. U.S.A.* **69**, 3779 (1972).
10. J. R. Bedbrook and L. Bogorad, *Proc. Natl. Acad. Sci. U.S.A.* **73**, 4309 (1976).
11. C. L. F. Woodcock and L. Bogorad, *J. Cell Biol.* **44**, 316 (1970).
12. R. Kolodner and K. K. Tewari, *Proc. Natl. Acad. Sci. U.S.A.* **76**, 41 (1979).
13. L. A. Haff and L. Bogorad, *Biochemistry* **15**, 4105 (1976).
14. N. Kawashima and S. Wildman, *Biochim. Biophys. Acta* **262**, 42 (1972).
15. S. R. Rodermel and L. Bogorad, *J. Cell Biol.* **100**, 463 (1985).
16. L. D. Crossland, S. R. Rodermel, L. Bogorad, *Proc. Natl. Acad. Sci. U.S.A.* **81**, 4060 (1984).
17. G. Link *et al.*, *Cell* **15**, 725 (1978).
18. L. Fish, U. Kuck, L. Bogorad, *J. Biol. Chem.* **260**, 1413 (1985).
19. R. E. McCarty and E. Racker, *Brookhaven Symp. Biol.* **19**, 202 (1967).
20. E. T. Krebbers, I. M. Larrinua, L. McIntosh, L. Bogorad, *Nucleic Acids Res.* **10**, 4985 (1982).