

deleterious mutation now investigated by Kondrashov, Charlesworth, and others; Kimura (1965) introduced the concept of quasi-linkage equilibrium central to the evolution of genetic modifiers in the current work of Barton and others; Kimura (1962) and later papers studied the fixation of advantageous alleles, with results that are fundamental to current work by Hill and colleagues on the theory of artificial selection. Reading these papers gives a valuable perspective to current research and reminds one of ideas that have not yet been fully explored.

Kimura's overarching technical contribution was to introduce powerful methods based on the diffusion approximation. This achievement marked the start of a second golden age of theoretical population genetics (Ewens, 1979, p. 140), an age that continues to the present. Kimura used this approach most extensively and most famously in studies of drift. The figures from his landmark 1955 paper, showing the probability density for the frequency of a neutral allele through time, may be the most widely reproduced figures in theoretical population genetics. (In fact, they have risen to the status of a scientific totem: I once saw the figures presented to a large undergraduate class with only the explanation that they 'show how genetic drift works'!) The coalescent approach developed over the last 10 years has largely displaced diffusion methods as the preferred way to calculate many quantities important to the neutral theory. Kimura realized, however, that the diffusion machinery has many other applications. He used it to study such problems as evolution under randomly-varying selection. The method is still the only tractable approach available in these areas; it will be interesting to see if alternative methods will eventually be developed there as well.

Reading through these papers, three things struck me time and again. The first was how strongly Kimura was motivated by data. Many experimentalists must think the Gegenbauer polynomials featured in Kimura's early papers to be the apotheosis of inscrutable (and probably useless) theory. But many papers, particularly those on molecular evolution, are motivated by empirical observations. Indeed, several develop new statistical methods to study evolutionary patterns emerging from recently collected data. The second was that there seemed to be no limits to Kimura's ingenuity and creativity. Most of us stop when existing scientific methods prove inadequate. Kimura time and again invented clever new analyses and new concepts. Third was Kimura's tenacity. Important ideas such as the neutral theory do not always carry themselves to wide audiences. This book highlights how critical Kimura's articulate and forceful development of his ideas was to the evolution of modern population genetics.

References

Ewens, W. (1979). *Mathematical Population Genetics*. Springer-Verlag, Berlin.

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Arabidopsis. Edited by ELLIOT M. MEYEROWITZ and CHRIS R. SOMERVILLE. Monograph 27, published by Cold Spring Harbor Laboratory Press 1994. 1300 pages. Cloth cover, price \$175. ISBN 087969 428 9.

This book is a perfect example of Christ's forecast 'The meek shall inherit the earth'. The Meek are not, of course, the editors and authors of the 40 chapters and two appendices, but the small, insignificant weed *Arabidopsis thaliana*, which has captured rapidly increasing attention over the last couple of decades. The argument runs that all angiosperms (flowering plants) share similar life-styles, environmental challenges, modes of reproduction and body plans, and the roughly 250 000 species of angiosperms are thought to have evolved from a common ancestor within the last 150 million years. They will therefore show a good deal of genetic and biochemical homology. Thus a small, rapidly growing flowering plant which can be easily maintained and manipulated in the laboratory should form a good model for intensive study of a variety of aspects of angiosperm biology, whose results can be applied to larger and more cumbersome plants of economic importance.

Friedrich Laibach proposed *Arabidopsis thaliana* as a suitable organism for genetic and developmental study in 1943 and followed with an article on 60 years of *Arabidopsis* research (1905–65), so this little wild mustard was ready to become the role model for research on angiosperms when molecular genetic techniques began to spread to plants. It appears to have all the most suitable characteristics for a laboratory plant: a small genome of 5 chromosome pairs containing roughly 80 Mb of DNA of which only some 10% is highly repetitive or foldback sequences, in one of the smallest of nuclei so far found in a flowering plant; it is very small and fast growing, produces numerous very small seeds (a single plant under optimum conditions can yield over 20 000 seeds within a few weeks), and it reproduces almost entirely by self fertilization, so that pure lines of new mutants are easily obtained. It is amenable to the modern techniques of molecular genetics.

Nearly all the 40 chapters in this book manage to sing the praises of its subject while presenting us with much interesting new information, and pointing out the many problems that still need solution. Their enthusiasm will doubtless lead to a further increase in what is clearly a very large *Arabidopsis* community (for example, we are told that hundreds of laboratories are selecting new mutations). Following nine chapters on genetics, the chapters on development cover seed

development, pattern formation in the embryo, seed dormancy and germination, development of the root, the vegetative shoot apical meristem, the leaf, the transition to flowering, and flower development leading to the stage from pollination to fertilization. Seven chapters on growth discuss ethylene – a unique plant signalling molecule, gibberellin and abscisic acid biosynthesis and response, auxin and cytokinin, light signal transduction and the control of seedling development, circadian rhythms, the physiology of tropisms, and modulation of root growth by physical stimuli. Five chapters on biotic and abiotic stress examine interaction between *Arabidopsis thaliana* and viruses, microbial pathogenesis of *Arabidopsis*, plant-parasitic nematodes, environmental stress and gene regulation, and *Arabidopsis thaliana* as a model for studying mechanisms of plant cold tolerance.

This leaves us with ten chapters on biochemistry and cell biology, which include articles on amino acid, nucleotide and vitamin biosynthesis, glycerolipids, starch, photosynthesis, the plant cell wall, and secondary metabolism, among other topics. Of the two appendices, (A) describes the Internet and Electronic *Arabidopsis* Information Resources, and includes a useful introduction to the Internet for newcomers, together with details of the two electronic resources: AAtDB Project and AIMS database, how to get at them and what information they contained at the time of writing the article. This information includes physical and genetic maps, seed stocks and clone resources, DNA sequences from GenBank and EMBL, protein sequence similarities between the known *Arabidopsis* DNA sequences and all known protein sequences, etc. and even a list with details of *Arabidopsis* researchers, and ‘much much more’ as the advertisers say.

Appendix (B) gives a list of *Arabidopsis thaliana* genetic variations with gene symbol, name, location when known, origin, alleles, references and phenotype, and is obviously subject to frequent updating using the electronic resources described in Appendix (A). The book ends with 32 pages of index, for which the compilers deserve a vote of thanks.

The authors have certainly made out a very good case for the value of their little cruciferine weed as a model for a broad study of the biology of the flowering plants; and the *Arabidopsis* community are in the fortunate position that no other small weed has a chance of replacing it as a favoured model. This makes a dramatic comparison with the bacterial parallel, as we learn from recent reports in *Science*. Frederick Blattner’s progress in sequencing the 4.7 million kbp (kilobase pairs) of *Escherichia coli* was halted at 40% of its target, i.e. about 1.9 million kbp sequenced, because of loss of his grant (but there is now hope that his funding may be continued, which is devoutly to be desired). Meanwhile, in the next number of *Science* (28th July 1995) 40 scientists, led by J. Craig Venter and Hamilton O. Smith, publish

the complete DNA sequence of the much simpler bacterium *Haemophilus influenzae*, which has only 1.83 million kbp of DNA in total – slightly less than the sequenced fraction of *E. coli*. Venter *et al.* begin their article by claiming that ‘A prerequisite to understanding the complete biology of an organism is the determination of its entire genome sequence’, and Venter is quoted as saying that the success with the *H. Influenzae* sequence has ‘raised the ante world-wide for sequencing the human genome’. Hype of this kind is perhaps necessary to get funding in the United States, but I trust it won’t cause the *Arabidopsis* community to drop all their fiddling with mutations, gene cloning, cell biology and biochemistry of the weed to concentrate on Venter-style sequencing of its 80–100 million kbp of chromosomal DNA. That would have made this book much less readable.

As it is, I look forward to learning how far the narrow evolutionary base of the angiosperms will permit this multi-disciplinary attack on the biology of the model weed to proceed.

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Domestication of Plants in the Old World: The origin and spread of cultivated plants in West Asia, Europe, and the Nile Valley. By DANIEL ZOHARY and MARIA HOPF. Second edition. Clarendon Press, Oxford. 1994. 279 pages. Paperback. Price £15.00. ISBN 0 19 854896 6.

The first edition of this book, which came out in 1988, was based on research published up to 1985. Since then, the authors tell us, ‘archaeobotanical investigations and the study of the Old World’s crops and their wild relatives continued, frequently at an accelerated pace. An impressive body of new evidence was added, both crop-wise and site-wise. Significantly, the new information does not contradict the main conclusions arrived at five or six years ago, but confirms them’. The second edition appeared in hardback in 1993 and led to the paperback edition we are reviewing, which includes a supplementary list of very recent references not available for the 1993 edition. The two versions of the second edition also include a chapter on dye plants (of which more later) and a good deal of new information on vegetables, fruit trees and minor grain crops.

The first definite signs of plant cultivation in the Old World appear in a string of early Neolithic villages that developed in the Near East at least 10000 years ago and showed evidence of domestication of eight or nine local grain species, dominated by emmer wheat, einkorn wheat and barley. These clearly provided the basis for a settled agriculture to replace the previous hunter-gatherer, nomadic form of life, and the farmers soon afterwards domesticated sheep