

---

## Book Reviews

---

*Drosophila Inversion Polymorphism*. Edited by COSTAS B. KRIMBAS and JEFFREY R. POWELL. CRC Press. 1992. 560 pages. Hbk. Price £151. ISBN 0 8493 6547 3.

Sturtevant's 1926 discovery of inversions in *Drosophila*, in which he used purely genetical results to infer their existence, is one of the most wonderful episodes in genetics. His interpretation was only confirmed ten years later by studies of polytene chromosomes. The beautiful cytogenetic studies of Sturtevant and Beadle (published in 1936) established that the suppression of crossing over in *Drosophila* females heterozygous for an inversion is accomplished by a mechanism which eliminates single crossovers without causing a loss in fertility due to the production of unbalanced gametes. Without this mechanism, the natural inversion polymorphisms of *Drosophila*, which form the subject of this book, would not be possible, since new chromosomal arrangements would be eliminated by selection.

Inversion polymorphisms have been the subject for an immense number of studies in a diverse array of *Drosophila* species starting with Sturtevant and Dobzhansky's pioneering work on the inversions of *D. pseudoobscura* in the 1930s. The most important single result of this work has probably been the recognition that inversion polymorphisms are often under the control of natural selection, despite the apparently remote connexion between selectable phenotype and gene order within a chromosomal segment. As pointed out by Costas Krimbas and Jeffrey Powell in their scholarly introductory chapter, Dobzhansky initially believed that the *D. pseudoobscura* polymorphisms were selectively neutral, and he collaborated with Sewall Wright in an attempt to fit data on the geographical distribution of inversions to Wright's models of genetic drift. Observations accumulated by Dobzhansky in the early 1940s indicated that certain inversions in this species experience seasonal cycles of frequency changes. The famous population cage experiments of Wright and Dobzhansky (published in 1946) demonstrated conclusively that stable equilibria of inversion frequencies were rapidly attained in populations kept under constant conditions, and that the speed of approach to equilibrium implied remarkably strong balancing selection. Observations on this and many other species,

which provide further compelling evidence for selection, are reviewed in chapters by Powell (*D. pseudoobscura* and *persimilis*), Krimbas (*D. subobscura*), Max Levitan (*D. robusta*), and Françoise Lemeunier and Sylvie Aulard (*D. melanogaster*).

The evidence is less secure as to how selection acts on inversions. As reviewed by Krimbas and Powell, the favourite theory seems to be the descendant of Dobzhansky's somewhat obscure concept of 'co-adaptation'. If two or more linked polymorphic loci interact in their effects on fitness, and are consequently maintained in linkage disequilibrium, then a crossover suppressor such as an inversion is favoured by selection, and will increase in frequency. Models of this form of selection have shown that inversion polymorphisms can be stably maintained; the associations between the genotypes at the loci under selection and gene arrangement result in detectable selective differences among individuals with different genotypes with respect to gene arrangement. The evidence for this interpretation, which implies widespread balanced polymorphisms with epistatic interactions between them, is less substantial than one would wish, even after nearly fifty years of experimentation. It relies mainly on experiments of Dobzhansky, in which inversions from different geographic populations were placed in the same population cages. Instead of arriving at predictable equilibrium frequencies, the results are unpredictable, often with a complete breakdown in polymorphism, suggesting the existence of interactions in fitness effects involving genes carried within inversions. In addition, patterns of linkage disequilibrium between different inversions have been observed in *D. robusta* and *D. pseudoobscura*, which are difficult to interpret without postulating fitness interactions between loci within each inversion.

Inversions have also been invaluable in tracing the relationships between populations and species in *Drosophila*. As recognized by Sturtevant and Dobzhansky, the occurrence of sets of overlapping inversions on *Drosophila* chromosomes permits the construction of unrooted phylogenetic trees connecting the different gene arrangements. When chromosome rearrangements cross species barriers, this and other methods can provide information about the phylogenetic relations among species. Hampton Carson's chapter describes the use of inversions in the eluci-

dation of relationships between Hawaiian *Drosophila* species, and Marvin Wasserman does the same for the *repleta* species group. John Sourdis and Krimbas describe how the traditional methods of inversion phylogeny can be combined with modern methods of phylogeny reconstruction.

This book provides an invaluable resource for *Drosophila* evolutionists, with extensive bibliographies which cover both the classical and modern literature. With the advent of the *Drosophila* genome project, it should soon be possible to establish the ages of origin of many of the inversions which have been the objects of study for so long by sequencing of genes close to the breakpoints; this will probably mean another burst of activity in this venerable area of research, for which the information summarized here forms an essential background.

BRIAN CHARLESWORTH  
Department of Ecology and Evolution,  
University of Chicago

*Experimental Design and Analysis for Use in Tree Improvement.* By E. R. WILLIAMS and A. C. MATHESON. CSIRO. 1994. 174 pages. Paperback. Price US\$45.00 plus US\$6.00 postage. ISBN 0 643 05555 X.

This book started life as a series of two-week courses given by E. R. Williams in China (along with A. C. Matheson), Thailand and Kenya on behalf of the Australian Centre for International Agricultural Research (ACIAR). Experience gained whilst delivering those courses caused the authors to generate a book aimed particularly at experiments involved in the design and analysis of forestry field trials.

It is a relatively short book divided into eight chapters. Each chapter covers a different aspect of design and analysis so that gradually the experimenter understands what sort of experiment he should be planting, how to organize himself so that he collects data most efficiently, how to analyse the data at a single site and how to bring data together for across sites analysis. There is a complete chapter on calculation of variance components and heritability before finishing up with a further two chapters on the theory and analysis of more complicated incomplete block designs. Mixed model analysis is being used increasingly in connexion with genetic tests in tree improvement circles. The book makes a good attempt at introducing Residual Maximum Likelihood (REML) and illustrating its use in analysis of progeny tests.

The book is concentrated reading. GENSTAT 5 is the recommended statistical package and throughout the book every step of analysis is accompanied by a sample set of data, GENSTAT 5 programme to analyse the data, and likely output from GENSTAT. This means that any experimenter could just follow

the supplied 'recipe' when it comes to data analysis and should be sure of getting results.

It is also nice to see a GENSTAT orientated book whilst so many others prefer SAS. I did, however, get the feeling that too many pages are occupied with GENSTAT programs and output as opposed to a more thorough breakdown of how to calculate variance components and heritabilities from calculated mean squares. And really it is not necessary to supply two or more pages of sample data when space is so scarce. There are often so many tables in each chapter that the text becomes far removed from the table it may be referring to.

Two other software packages are heavily recommended – DATACHAIN to help collect data in a logical manner and in a form readily understood by GENSTAT, and ALPHA+ which provides a convenient means of constructing alpha (incomplete block) designs. If a tree improvement team decides to use any other form of computer software, it really does devalue the relevance of the book.

When it comes to planting a large number of varieties in genetic tests the use of multi-tree plots in incomplete blocks is suggested rather than Single Tree Plots (STPs) with many replications. This book is quite clear that the former is best despite use of the latter by large numbers of organizations across the USA, Europe and New Zealand. It takes advantage of a few opportunities to relate the problems of missing trees and less effective ways of calculating error components in ANOVAs when using STPs.

Despite these minor criticisms it has to be recommended as a good 'how to do it' book. Following the directions of this book will result in properly collected and analysed data (if you use the illustrated software), but it will probably be better to refer to some of the other texts in order to interpret what the numbers mean in terms of genetic gain.

I suggest that if you are in the business of experimental design and analysis of forest trees, or a student of tree improvement, you buy this book. But make sure you keep it next to Falconer (*Introduction to Quantitative Genetics*) or Fins, Friedman and Brotschol (*Handbook of Quantitative Forest Genetics*).

S. J. LEE  
Tree Improvement Branch  
The Forestry Authority,  
Northern Research Station  
Roslin, Midlothian  
EH25 9SY, UK

*Molecular Mechanisms of the Immune Response. Cancer Surveys Volume 22.* Edited by W. F. BODMER and M. J. OWEN. Cold Spring Harbor Laboratory Press. 1994. 117 pages. Price \$75.00. ISBN 0 87969 442 4.

This slim volume represents the proceedings of a symposium held in late 1993 to celebrate the career of