

Plant Variation and Evolution

FOURTH EDITION

We are in the midst of a biological revolution. Molecular tools are now providing new means of critically testing hypotheses and models of microevolution in populations of wild, cultivated, weedy and feral plants. They are also offering the opportunity for significant progress in the investigation of long-term evolution of flowering plants, as part of molecular phylogenetic studies of the Tree of Life.

This long-awaited fourth edition, fully revised by David Briggs, reflects new insights provided by molecular investigations and advances in computer science. Briggs considers the implications of these for our understanding of the evolution of flowering plants, as well as the potential for future advances. Numerous new sections on important topics such as the evolutionary impact of human activities, taxonomic challenges, gene flow and distribution, hybridisation, speciation and extinction, conservation and the molecular genetic basis of breeding systems will ensure that this remains a classic text for both undergraduate and graduate students in the field.

David Briggs is Emeritus Fellow of Wolfson College at the University of Cambridge. He has a lifelong interest in evolution, genetics, conservation and taxonomy. He is also the author of *Plant Microevolution and Conservation in Human-Influenced Ecosystems* (Cambridge, 2009), which won the British Ecological Society's 2011 Marsh Book of the Year award.

S. Max Walters (1920–2005) was a leading British field botanist, and the author and editor of major works on the classification and identification of both wild and garden plants. He served as Director of Cambridge University Botanic Garden from 1973 until his retirement in 1983.

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FOURTH EDITION

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This edition revised by David Briggs



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PREFACE

In writing the earlier editions of *Plant Variation and Evolution*, with my great friend Max Walters (1920–2005), our approach to this complex subject was clearly set out in the preface to the Third Edition. ‘When it was first proposed to establish laboratories at Cambridge, Todhunter, the mathematician, objected that it was unnecessary for students to see experiments performed, since the results could be vouched for by their teachers, all of them of the highest character, and many of them clergymen of the Church of England’ (Bertrand Russell, 1931). While Russell’s mischievously anti-clerical comments do not entirely reflect the views of Todhunter (Todhunter, 1873; Macfarlane, 1916), they do provoke us to take a critical look at the way scientific advances are made, in every historical period, through questioning the opinions of various ‘authorities’. In many texts on evolution a judicious mixture of concepts, mathematical ideas and the results of laboratory and field experiments are combined in an elaborate pastiche to provide a more or less complete edifice. Perhaps one or two areas of uncertainty may be indicated, but the general impression is of a house well built, but awaiting the placing of the last few roof-tiles. Conversations with research biologists, however, quickly reveal a different picture. While the broad outlines of evolution are supported by an increasing body of evidence, almost nothing is completely settled: current views represent a provisional framework, and even some parts of the subject, long held to be clarified, are suddenly overturned by new discoveries. Teaching experience reinforces our view that students of science should be shown the way in which, slowly and painstakingly, our present partial pictures have been built up, how and to what extent they are testable by experiment and observation, and in what way they remain vague or defective. A healthy scepticism in the face of the complexities of organic evolution is the best guarantee of real progress in understanding its patterns and processes.

The aim of this new edition is to provide, as before, an authoritative introductory university text, while at the same time satisfying the general reader with a real interest in the subject, showing how the study of variation and evolution of flowering plants has developed over the last 400 years. This development has been increasingly scientific, leading to the realisation of the crucial importance of hypothesis and experiment.

Throughout the book, I have tried to provide a critical but concise overview of current excitements and advances, while at the same time paying attention to difficulties and uncertainties. Furthermore, I have intentionally introduced and shown the connection between many complex subjects, and have therefore provided references to important research papers and books, in order that the reader may build on the framework provided.

As in previous editions, I emphasise the logical and historical framework of early observation and experiment, which is almost wholly neglected in some university courses. Sapp (2003) stresses this important point when he writes, ‘many teachers of science have noted, [that] scientific problems are usually much better understood from studying their history rather than their logic alone’. Accordingly this book shows how, building on historical foundations, modern investigative methods are providing new insights into past and present patterns of variation in nature and the processes that give rise to them.

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I am very grateful for the friendly help, advice and encouragement I have received from the staff of Cambridge University Library and the Central Science Library. It is a pleasure to thank the staff of Cambridge University Press for their encouragement and assistance through all the stages of writing this new edition: Dominic Lewis, Megan Waddington, Hamish Adamson, Sarah Starkey, Charlotte Thomas and Ilaria Tassistro. Ken Moxham, my copy-editor, played an invaluable role in the final stages of the preparation of the book.

NOTE ON NAMES OF PLANTS

Scientific names are generally in accordance with the third edition of Stace, C. (2010) *New Flora of the British Isles* for British plants; and, for European plants not in the British flora, Tutin *et al.* (1964–93) *Flora Europaea*. In the cases not covered by either work we have used the name we believe to be correct. Where an author has used a non-current name, this is noted in brackets.

While some botanists continue to use long-standing names for important families, increasingly others use names derived from the type genus (e.g. Compositae/Asteraceae; Cruciferae/Brassicaceae, etc.). We give alternative names in the text.

ABBREVIATIONS

AFLP	amplified fragment length polymorphism	K-T	Cretaceous-Tertiary (K-T) boundary
APG	Angiosperm Phylogeny Group	LGM	Last Glacial Maximum
BGCI	Botanic Gardens Conservation International	mtDNA	mitochondrial DNA
BP	before the present	MVP	Minimum Viable Population
BSC	Biological Species Concept	Mya	million years ago
CMS	cytoplasmic male sterility	OTU	operational taxonomic unit
CNI	cytonuclear incompatibilities	PCA	principal component analysis
cpDNA	chloroplast DNA	PCO	principal coordinates analysis
ENM	ecological niche modelling	PCR	polymerase chain reaction
ESM	Earth System Model	ppb	parts per billion
FAO	Food and Agriculture Organization of the United Nations	ppm	parts per million
FISH	fluorescence <i>in situ</i> hybridisation	PVA	population viability analysis
GISH	genomic <i>in situ</i> hybridisation	QTLs	quantitative trait loci
GM	genetically modified	RAPD	random amplified polymorphic DNA
HGT	horizontal transfer of genetic information	RFLP	restriction fragment length polymorphism
IPCC	Intergovernmental Panel on Climate Change	SNP	single nucleotide polymorphism
ISH	<i>in situ</i> hybridisation	SSRs	simple sequence repeats
ISSRs	inter simple sequence repeats	SSSI	Site of Special Scientific Interest in UK
IUCN	International Union for Conservation of Nature	STR	short tandem repeat
		UNEP	United Nations Environmental Programme
		WGD	whole genome duplication
		WCMC	World Conservation Monitoring Centre