

The Botany of Mangroves

Second Edition

Mangroves are distinctive tropical plant communities that occupy the intertidal zone between sea and land. They are of major ecological importance, have economic value as a source of food and raw materials, and serve as a buffer from flooding and climate change-induced sea level rise. Mangroves are under threat from pollution, clearance, and overexploitation, and increasing concern has driven demand for an improved understanding of mangrove species.

This book provides an introduction to mangroves, including their taxonomy, habitat-specific features, reproduction, and socioeconomic value. Fully updated to reflect the last two decades of research, this new edition of a key text includes newly documented taxa, new understandings of vivipary and the evolution of mangrove species, and a rich set of color illustrations. It will appeal to researchers and students across a range of disciplines, including botany, ecology, and zoology.

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Cambridge University Press
978-1-107-08067-6 — The Botany of Mangroves
P. Barry Tomlinson
Frontmatter
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Frontispiece: *Rhizophora x harrisonii*, Tivives, Costa Rica. (*"If I have seen further than you. . . it is by standing on the shoulders of Giants."* Isaac Newton, 1675.)

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P. B. TOMLINSON



CAMBRIDGE
UNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning, and research at the highest international levels of excellence.

www.cambridge.org

Information on this title: www.cambridge.org/9781107080676

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First published 1986

First paperback edition 1994

Reprinted 2004

Second Edition 2016

Printed in the United Kingdom by T.J. International Ltd., Padstow, Cornwall

A catalog record for this publication is available from the British Library

Library of Congress Cataloging-in-Publication Data

Names: Tomlinson, P. B. (Philip Barry), 1932– author.

Title: The botany of mangroves / P.B. Tomlinson.

Description: Second edition. | New York : Cambridge University Press, 2016. |

Includes bibliographical references and index.

Identifiers: LCCN 2016015459 | ISBN 9781107080676 (Hardback : alk. paper)

Subjects: LCSH: Mangrove plants. | Mangrove ecology.

Classification: LCC QK938.M27 T66 2016 | DDC 583/.763–dc23 LC

record available at <https://lccn.loc.gov/2016015459>

ISBN 978-1-107-08067-6 Hardback

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Preface to Second Edition of *The Botany of Mangroves*

Mangroves form the “rain forests of the sea” (Warne, 2011) and impact the lives of millions of people in the tropics and in over 120 nation states, as a source of food, raw material, and even recreation, as they have done for millennia. This book is therefore presented as an updated introduction to the study and identification of plants of the mangal, or such of it that still remains! In an era in which humanity has become aware of the effects of global warming on climate change, it is salutary to realize that one effect – rising sea levels – places mangroves at the front line of such change. Knowledge about them is, more than ever, absolutely vital.

Originally written in 1986, with a paperback reprint including an appendix in 1994, *The Botany of Mangroves* has achieved steady sales for 30 years as a primer for the study of plants in tropical intertidal forests. This success reflects the biological uniqueness of this distinctive tropical community. *Mangal* has become the accepted name for the community; *mangroves* for the constituent plants. Their economic value has always been understood, but increasingly their sustainability has been under threat because of frequent overexploitation and conversion. Clearly, however, the original book has become out-of-date in some respects so that the invitation from Cambridge University Press to produce this second edition was received with enthusiasm. The specialized nature of the mangal is reflected in its exclusion by Peter Ashton from his monumental survey of South-East Asian rain forests (Ashton, 2014) largely because of space limits and the subject being too far outside his personal research experience. He kindly defers to *The Botany of Mangroves* as an alternative source.

However, in the course of the last three decades, exploitation of mangroves has proceeded at such a pace that there is now global concern for their very existence. Destruction and conversion have displaced many of those millions whose livelihood is determined by the existence of mangal, either as an ever-present resource, or even as living space (Warne, 2011). This concern has been expressed in the development of organizations devoted to their study. Expanded interest in establishing detailed knowledge is provided by the *World Atlas of Mangroves* (Spalding et al., 2010). This book is the result of an international collaborative effort, involving many contributors, which produced a socioeconomic overview on a pantropical scale. The book charts, in great detail, the distribution of mangrove communities and a country-by-country listing of mangrove species. The book is based on many individual reports and ground-truthing of mangrove locations, but particularly emphasizes the extent of mangal destruction by agronomic and other practices. This book demonstrates the concern of ecologists and

botanists for the future sustainability of these tidal forests. It mentions the existence of an International Society for the Study of Mangrove Ecosystems, founded in 1990 in Japan, but which, in 2009, included 38 institutions, in 90 countries, with a membership of over 1000 individuals. Spalding et al. (2010) thus reflects the global concern for the continued development of an understanding of the mangal ecosystem and its plant constituents, their association with resident and visitor wild life, and the effects of human and natural disturbances.

The need for an updated edition of *The Botany of Mangroves* as a description of the plants of the mangal is justified in this global context. As a primer, it retains much of the morphological descriptions, which intrinsically do not change, but also needs to describe recent advances in many relevant disciplines. Recent applications of molecular systematic methods are now included, but change little the appreciation that the mangrove habitat has been occupied by a diversity of unrelated taxa. A major addition made possible by similar methods allows a discussion of the way in which genetic interchange is possible between populations that are in varying degrees discontinuous, especially those long separated by plate tectonic events. The existence of hybridization among certain taxa, long suspected on morphological grounds, has also been verified by appropriate molecular methods. Other advances include increased knowledge of biological features, especially of vivipary, some of this coming from my own research. However, not all included knowledge is necessarily new because I add a historical introduction of the early development of mangrove naming and description made possible by a translation of the *Herbarium Amboinense* of Rumphius (Beekman, 2011) demonstrating that old knowledge also can be new-found. This work of the seventeenth century originally drew the attention of western eyes to the strange intertidal forests of the tropics.

The recent available literature on mangroves reflects the continuing activity of research workers in many disciplines. An online search relevant to the subject of common mangrove species can produce several hundred citations and hence a realization that this edition cannot survey it all. I have retained much of the early literature as a historical record, but have been very selective of the massive new literature. Selection has therefore been limited to review articles or those seen by me as adding new but basic information to my descriptions. This means I inevitably must apologise to those numerous authors whose work I have not cited. Rollet (1981) produced a bibliography on mangrove research for the period 1600–1975 that included over 6000 citations. This number has been easily doubled in the last 30 years. The members of the International Association mentioned earlier have been very busy and productive!

In conclusion, there is no shortage of water on Earth; the problem is that most of it is salty. We should therefore have as complete an understanding as possible of those few trees that have mastered an existence that allows them to flourish at the intersect of land and sea. This book introduces them.

Acknowledgments

To the First Edition. An introduction to mangrove ecosystems followed almost naturally from my interest in field botany and a position at Fairchild Tropical Garden (1960–1971), which allowed reasonable freedom of research objectives with one of the largest areas of mangroves at hand in South Florida. Dr. A. M. Gill on the staff of Fairchild Garden (1967–1970) did much to stimulate my interest through his own ecologically oriented research. Financial support from 1965 to the present has come from the Maria Moors Cabot Foundation for Botanical Research and subsequently from the Atkins Garden Funds, both of Harvard University. In addition, I have received travel support from the National Geographic Society (Tomlinson, 1982a) and the National Science Foundation, Office of International Programs (United States–Australia Scientific Collaborative Program). These awards facilitated the limited knowledge I had gained in the Caribbean area to be broadened by visits to the richer mangal of the Indo–Pacific region. Several institutions and many individuals have contributed facilities and field assistance. They include the Australian Institute of Marine Science, Townsville, Queensland (AIMS), and the Division of Botany, Department of Forests, Lae, Papua New Guinea (PNG). Individuals who have made fieldwork possible include J. S. Bunt, B. Clough, N. C. Duke (AIMS), J. S. Womersley, E. E. Henty, M. Galore, R. J. Johns (PNG), and Dr. J. Davey (University of Brisbane). Professor Engkik Soepadmo of the University of Malaysia, Kuala Lumpur; Dr. Paul Chai and the staff of the Forestry Department, Sarawak; and Mr. J. M. Maxwell of the Singapore Botanic Garden all were helpful on a visit to Malaysian mangroves. Jorge Jiménez was my host when I visited Costa Rican mangroves. Richard Primack of Boston University was a stimulating field companion and a guide to the theoretical and applied aspects of floral biology. The libraries and collections of the Harvard University Herbaria served as an indispensable source of systematic, geographic, and historical information. Peter Stevens, Curator of the Harvard University Herbaria, was particularly helpful in a critical review of the systematic descriptions. Adrian Juncosa made helpful comments on early drafts and supplied some material for illustration. John Sperry provided discussions of mangrove physiology. The morphological illustrations in Section B are the work of Priscilla Fawcett, Botanical Illustrator at Fairchild Tropical Garden, supplemented in Massachusetts by the drafting skills of Susan White and Elizabeth Bullock. Ms. D. R. Smith worked without complaint to maintain some coherence throughout the many draft versions of the book.

In addition to the figures prepared especially for this book, a number of sources have been used for illustration. Permission to reproduce these figures has been given by the following authors and/or journal editors: *American Fern Journal* (Figs. B.60, B.61); *American Journal of Botany* and A. M. Juncosa (Fig. 8.5); *Annals of Botany*, London (Figs. 4.4, B.51, B.52); *Biotropica* (Figs. 5.10, 5.11, B.66, B.67, B.71, B.72, B.74, B.76); *Biological Journal of the Linnean Society* and A. G. Marshall (Fig. 7.2); *Botanical Journal of the Linnean Society* (Fig. 4.8); *Bulletin of the Fairchild Tropical Garden* and I. Olmsted (Figs. 1.10, 1.11, 1.12); *Contributions Herbarium Australiense* (Figs. B.66, B.70); *Journal of the Arnold Arboretum* (Fig. B.21); *Vegetatio* and V. Semeniuk (Fig. 1.7); J. Cramer and Helen Correll (Figs. B.6, B.15, B.29, for figures that first appeared in D. S. Correll and H. B. Correll, *Flora of the Bahama Archipelago*); and Figures B.8, B.19, B.24, B.25, B.26, B.28, B.37, B.38 first appeared in P. B. Tomlinson's *Biology of Trees Native to Tropical Florida*, copyright by the author. In addition, previously unpublished diagrams and photographs were supplied by J. S. Bunt and N. C. Duke (Figs. 1.8, 3.5); A. M. Gill (Figs. 5.4, B.41, B.62, B.75); and A. M. Juncosa (Figs. 1.3, 1.4, 4.10, 5.5, 8.6, B.22, B.23, B.55, B.57, B.58, B.80). All other figures are either original or redrawn.

To the Second Edition. Some continuity with the old version is seen in the further support of individuals who appeared in it. These include Norman Duke [NCD], Malcolm Gill [AMG], Adrian Juncosa [AMJ], Ingrid Olmsted [IO], and Jeff Vincent [JRV], who have supplied illustrations in the form of color transparencies that appeared initially as black-and-white images, but for the most part now appear here in color. To this company can now be added individuals who have supplied old and new color images; they include Aaron Ellison (with Elizabeth Farnsworth) [AE], Jack Fisher [JBF], Doug Goldman [DG], Jay Horn [JWH], David Lee [DL], Tracy Magellan [TMM], and Tokushiro Takaso [TT]. Their included initials in the captions acknowledge this help. All other photographic illustrations are my own, often now reproduced in color. Line drawings by the late Priscilla Fawcett [PF] are reproduced as in the first edition, with a few added from other sources. For continued help with the mammoth new literature, I benefitted enormously from the professional assistance of Judy Warne and her staff at the Harvard University Herbarium Library [HUH]. Guidance through the nomenclatural maze was provided by K. Ghandi, at the same location. Help in resolving numerous computer problems was provided by Brett Huggett, Madelaine Bartlett, Benjamin Burnham, and John Stevenson, Sr. The support of the staff of the Montgomery Botanical Center, Coral Gables, Florida, especially Patrick Griffith and Tracy Magellan, has been continually sustaining.

I, a capable mistake-maker, apologise for any deficiencies.

Figures in Section A (General Account) are numbered according to chapter (e.g., Fig. 4.6 is the sixth illustration in Chapter 4); figures in Section B (Detailed Description by Family) are numbered consecutively with the prefix B (i.e., B.1–B.69). Tables in Section A are also numbered according to chapter (e.g., Table 2.2 is the second table in Chapter 2).