

The Ecology of Trees in the Tropical Rain Forest

Current knowledge of the ecology of tropical rain-forest trees is limited, with detailed information available for perhaps only a few hundred of the many thousands of species that occur. Yet a good understanding of the trees is essential to unravelling the workings of the forest itself. This book aims to summarise contemporary understanding of the ecology of tropical rain-forest trees. The emphasis is on comparative ecology, an approach that can help to identify possible adaptive trends and evolutionary constraints and which may also lead to a workable ecological classification for tree species, conceptually simplifying the rain-forest community and making it more amenable to analysis.

The organisation of the book follows the life cycle of a tree, starting with the mature tree, moving on to reproduction and then considering seed germination and growth to maturity. Topics covered therefore include structure and physiology, population biology, reproductive biology and regeneration. The book concludes with a critical analysis of ecological classification systems for tree species in the tropical rain forest.

IAN TURNER has considerable first-hand experience of the tropical rain forests of South-East Asia, having lived and worked in the region for more than a decade. After graduating from Oxford University, he took up a lecturing post at the National University of Singapore and is currently Assistant Director of the Singapore Botanic Gardens. He has also spent time at Harvard University as Bullard Fellow, and at Kyoto University as Guest Professor in the Center for Ecological Research.

Cambridge University Press
0521801834 - The Ecology of Trees in the Tropical Rain Forest
I. M. Turner
Frontmatter
[More information](#)

CAMBRIDGE TROPICAL BIOLOGY SERIES

EDITORS:

Peter S. Ashton *Arnold Arboretum, Harvard University*

Stephen P. Hubbell *Princeton University*

Daniel H. Janzen *University of Pennsylvania*

Peter H. Raven *Missouri Botanical Garden*

P. B. Tomlinson *Harvard Forest, Harvard University*

Also in the series

Tomlinson, P. B. *The botany of mangroves*

Lowe-McConnell, R. H. *Ecological studies in tropical fish communities*

Roubik, D. W. *Ecology and natural history of tropical bees*

Benzing, D. H. *Vascular epiphytes*

Endress, P. K. *Diversity and evolutionary biology of tropical flowers*

Cambridge University Press
0521801834 - The Ecology of Trees in the Tropical Rain Forest
I. M. Turner
Frontmatter
[More information](#)

The Ecology of Trees in the Tropical Rain Forest

I. M. TURNER
Singapore Botanic Gardens



CAMBRIDGE
UNIVERSITY PRESS

Cambridge University Press
 0521801834 - The Ecology of Trees in the Tropical Rain Forest
 I. M. Turner
 Frontmatter
[More information](#)

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
 The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
 The Edinburgh Building, Cambridge CB2 2RU, UK
 40 West 20th Street, New York NY 10011-4211, USA
 10 Stamford Road, Oakleigh, VIC 3166, Australia
 Ruiz de Alarcón 13, 28014 Madrid, Spain
 Dock House, The Waterfront, Cape Town 8001, South Africa
<http://www.cambridge.org>

© I. M. Turner 2001

This book is in copyright. Subject to statutory exception
 and to the provisions of relevant collective licensing agreements,
 no reproduction of any part may take place without
 the written permission of Cambridge University Press.

First published 2001

Printed in the United Kingdom at the University Press, Cambridge

Typeface Times 10/12.5pt *System* Poltype® [vN]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

Turner, I. M. (Ian Mark), 1963–
 The ecology of trees in the tropical rain forest / I. M. Turner.
 p. cm. – (Cambridge tropical biology series)
 Includes bibliographical references.
 ISBN 0 521 80183 4
 1. Rain forest plants – Ecophysiology. 2. Trees – Ecophysiology – Tropics.
 3. Rain forest ecology. 4. Forests and forestry – Tropics. I. Title. II. Series.
 QK938.R34T87 2001
 577.34–dc21 00-045508

ISBN 0 521 80183 4 hardback

CONTENTS

<i>Preface</i>	<i>page xi</i>
<i>Acknowledgements</i>	<i>xiii</i>
1 Introduction	1
The tropical rain forest	1
Tropical trees	2
Species	2
Tropical rain-forest diversity	6
Adaptation	9
The importance of phylogeny	10
The ecological classification of tropical rain-forest trees	13
2 The growing tree	15
Trees: form, mechanics and hydraulics	15
Tree stature	15
Wood	18
Tropical timber	21
The mechanical design of trees	24
Buttresses	28
Leaning trees	34
Tree fall	35
Sap ascent	35
Tree hydraulics	37
Tree architecture	40
Allometry	41
Bark	46
Roots	46
Root hemi-parasites	48

viii	Contents	
	Mineral nutrition	50
	Mycorrhizas	52
	Nitrogen fixation	56
	Other methods of obtaining extra nutrients	57
	Comparative use of nutrients	58
	Element accumulation	60
	Leaf form and physiology	60
	Size, shape and other structural characteristics	62
	Leaf protection	67
	The defences of tropical forest trees	69
	Classification of plant defences	81
	Foliar bacterial nodules	82
	Leaf development: coloured young leaves	83
	Leaf longevity	86
	The influence of shade	90
	High light conditions	94
	Other factors influencing leaf performance	95
	Species groups based on leaf characteristics	96
3	Tree performance	103
	Age, size and growth in tropical rain-forest trees	103
	The dynamics of tree populations in the rain forest	105
	Mortality in trees	105
	Tree growth in the forest	108
	Tree performance in relation to light climate	111
	Mortality, growth and adult size	114
	The use of growth and mortality data to recognise species groups	116
	Relative performance of species of similar life history	118
	What limits tree growth?	119
	Herbivory	121
4	Reproductive biology	122
	Reproduction	122
	Vegetative reproduction	122
	Sexual systems	123
	Genetic diversity	125
	When to flower?	127
	Pollination	130
	Pollination syndromes	131
	Tropical flowers	144

Contents	ix
Relative importance of different pollinators	145
Figs	146
Dispersal mechanisms	147
Autochory	147
Anemochory	148
Hydrochory	149
Zoochory	150
Dispersal syndromes	155
Secondary dispersal	162
Efficacy of seed dispersal	163
Clumped or scattered seed distributions	168
Seed survival	168
Tests of the escape hypothesis	171
Other advantages of dispersal	176
The search for the Janzen–Connell effect	177
Co-evolution	178
5 Seeds and seedlings	180
Seeds	180
Seed size	180
Seed rain and the soil seed bank	186
Seed germination	188
Other influences on seedling establishment	194
Germination safe sites	194
Seedlings	194
Seedling and sapling form	195
Seedling dependence on seed reserves	197
Seedling mortality	199
Growth and survival with respect to light	204
Seedling responses to shade	208
Seedling shade tolerance	211
The traits of shade tolerance	213
On being light-demanding	216
The relevance of shade tolerance	216
Sudden changes in light availability	218
Water	220
Mineral nutrients	221
Defence in juveniles	224
6 Classificatory systems for tropical trees	227
Height at maturity	227

The pioneer–climax dichotomy	233
Diagnostic characters	234
Reproduction	236
Demography	237
Growth and form	238
Physiology	241
General	242
Conclusion	243
Combining the two axes	244
Long-lived pioneers or late-secondary species	245
Parallels between pioneers and shade-tolerant understorey species	246
Where does this leave us?	247
<i>References</i>	248
<i>Index of scientific names of plants</i>	281
<i>Index of scientific names of animals</i>	288
<i>General index</i>	290

PREFACE

It is the detail of the . . . tropical forest, in its limitless diversity, that attracts.

F. Kingdon Ward (1921) *In Farthest Burma*, Seeley, Service & Co. Ltd., London.

Trees make a forest: they are both the constructors and the construction. To understand the forest we must know about the trees. This book is about the trees of the tropical rain forest. It was written with the aim of summarising contemporary understanding of the ecology of tropical rain-forest trees, with particular reference to comparative ecology. The analysis of patterns of variation among species is a valuable technique for identifying possibly adaptive trends and evolutionary constraints. It may also provide a means of classifying species in ecological terms. A workable ecological classification might mean that the rain-forest community could be conceptually simplified and made more amenable to analysis.

The organisation of the book follows the life cycle of a tree. The living, growing mature tree is introduced with reference to form and process. Reproduction, including pollination and seed dispersal, follows. Then come consideration of seed germination, seedling establishment and growth, and the completion of the life cycle. At each stage a range of different characteristics and phenomena relevant to tree species growing wild in the tropical rain forest are considered. I have tried to give some idea of what is typical, and what is rare, the range and central tendency exhibited among species, and whether discrete groupings, or a continuous variation, are observed within the forest, and also whether one character tends to be correlated with another. Finally, I have tried to bring all the observations together in a critical analysis of ecological classification systems for tree species in the tropical rain forest. I have deliberately avoided the 'historical approach' to reviewing the scientific literature. There are points in favour of following the chronological development of ideas in a particular field, but in this case I felt it was not absolutely necessary. Firstly, there are several excellent texts that summarise much of the older work on tropical rain forests, notably P.W. Richards' *The tropical rain forest* (Richards 1952, 1996) and T.C. Whitmore's *Tropical rain forests of the Far East* (Whitmore 1975, 1984). Secondly, I wanted to avoid the problems of

interpreting history with the benefit of hindsight. Glimmerings of ideas that later became important can often be found by careful sifting through earlier writing, but at the time such works were published those ideas had little if any impact. Thirdly, I believe many readers are more interested in the contemporary state of knowledge and understanding than how we arrived at that position.

I estimate that there are some 50 000–60 000 tree species occurring in the tropical rain forests of the world. We have a detailed knowledge of the ecology of perhaps a few hundred of these at best. This book is therefore written from a perspective of abject ignorance, which I hope readers will bear in mind when consulting these pages.

ACKNOWLEDGEMENTS

I could not have written this book without the opportunity provided by consecutive visiting fellowships in the USA and Japan that allowed me uninterrupted time to complete the first draft. My Bullard Fellowship at Harvard University ran from July to December 1997. I am very grateful for the hospitality of Harvard Forest and Harvard University Herbaria. My special thanks go to Professor David Foster and Professor Peter Ashton. I was a Guest Professor at the Center for Ecological Research of Kyoto University for the period February–June 1998 and was made welcome by all the staff and students. The Director, Professor Eitaro Wada, provided assistance in many ways including funding for drawing of many of the figures in the book. Dr Noboru Okuda skilfully prepared these. My stay in Japan would not have been so enjoyable without the many services and opportunities provided by Professor Tohru Nakashizuka. I took up a post with Singapore Botanic Gardens after my stay in Japan. I am grateful to the Director, Dr Chin See Chung, for encouraging me to complete the book and for supporting me in many different endeavours. Dr Tan Wee Kiat, Chief Executive Officer of the National Parks Board, the parent organisation of the Botanic Gardens, is also thanked for his support.

The research for this book involved raking through a plethora of publications on various aspects of tropical forests. I bothered many different people with requests for copies of articles, leads on references or visits to libraries. Special thanks must go to the various librarians at Harvard University whom I confronted with long lists of things to find, particularly the team, led by Judy Warnement, in the Botany Libraries, who were ever willing to meet the next bibliographic challenge.

I have asked many people to read and comment on all or parts of the book. Nearly all have willingly done so and provided much valuable and constructive criticism. I thank Peter Becker, David Burslem, Richard Corlett, Stuart

Davies, Peter Grubb, Bernard Moyersoén, Tim Whitmore for their help and apologise for not always taking their advice.

Among the figures appearing in the book a large number are reproduced from other publications. I acknowledge the following for granting permission to reproduce material: Academic Press (Fig. 4.2), the editors of *American Journal of Botany* (Figs. 2.15, 4.1), the Association for Tropical Biology (Figs. 2.16, 4.3, 4.9), the editors of *BioScience* (Fig. 3.4), Blackwell Science Publishers (Figs. 2.23, 2.31, 3.9, 5.8, 5.9, 5.14), Botanical Society of Japan (Fig. 5.7), the editors of *Bulletin of the Torrey Botanical Club* (Fig. 2.12), Cambridge University Press (Figs. 2.3, 2.8, 2.13, 2.14, 3.7, 5.6, 6.2), Ecological Society of America (Figs. 3.6, 4.8, 5.4, 5.11, 6.3), Heron Publishing (Fig. 2.10), the editors of *Journal of Tropical Forest Science* (Fig. 3.3), Kluwer Academic Publishers (Figs. 2.24, 4.11), the editors of *The New Phytologist* (Fig. 5.16), NRC Research Press (Fig. 5.5), Oxford University Press (Fig. 2.9), the editors of *Revista Biología Tropical* (Figs. 2.20, 6.4), The Royal Society (Fig. 5.15), Society of American Foresters (Fig. 2.7), Springer Verlag (Figs. 2.2, 2.6, 2.11, 2.22, 2.25, 4.12, 5.13, 5.17, 6.1), the editors of *Tropics* (Fig. 4.10), UNESCO (Fig. 5.10), University of Chicago Press (Fig. 2.26), Urban & Fischer Verlag (Fig. 2.30), Yale University Press (Fig. 3.2). Through the assistance of Professor Tohru Nakashizuka and Dr Shoko Sakai, I was able to use some of the photographs taken by the late Professor Tamiji Inoue.