

Cambridge University Press

978-0-521-14247-2 - Tropical Trees as Living Systems

Edited by P. B. Tomlinson and Martin H. Zimmerman

Frontmatter

[More information](#)

TROPICAL TREES AS LIVING SYSTEMS

Cambridge University Press
978-0-521-14247-2 - Tropical Trees as Living Systems
Edited by P. B. Tomlinson and Martin H. Zimmerman
Frontmatter
[More information](#)

Tropical trees as living systems

*The proceedings of the Fourth Cabot Symposium
held at Harvard Forest, Petersham
Massachusetts on
April 26–30, 1976*

Edited by

P. B. TOMLINSON and
MARTIN H. ZIMMERMANN

*Harvard University, Harvard Forest
Petersham, Massachusetts*

with a foreword by

LAWRENCE BOGORAD
*Director, Maria Moors Cabot Foundation for
Botanical Research of Harvard University*

CAMBRIDGE UNIVERSITY PRESS
Cambridge
London - New York - Melbourne

Cambridge University Press
978-0-521-14247-2 - Tropical Trees as Living Systems
Edited by P. B. Tomlinson and Martin H. Zimmerman
Frontmatter
[More information](#)

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore,
São Paulo, Delhi, Dubai, Tokyo

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521142472

© Cambridge University Press 1978

This publication 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 1978
This digitally printed version 2010

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

Library of Congress Cataloguing in Publication data

Main entry under title:

Tropical trees as living systems.

Sponsored by the Maria Moors Cabot Foundation for Botanical Research.

Includes index.

1. Trees – Tropics – Congresses. 2. Trees – Physiology – Congresses.
3. Forest ecology – Tropics – Congresses. 4. Rain forests – Congresses.
I. Tomlinson, Philip Barry, 1932- II. Zimmermann, Martin Huldrych, 1926-
III. Harvard University. Maria Moors Cabot Foundation for Botanical Research.
QK493.5.T76 582'.1609'093 77-8579

ISBN 978-0-521-21686-9 Hardback
ISBN 978-0-521-14247-2 Paperback

Cambridge University Press has no responsibility for the persistence or
accuracy of URLs for external or third-party internet websites referred to in
this publication, and does not guarantee that any content on such websites is,
or will remain, accurate or appropriate.

Contents

<i>List of contributors</i>	ix
<i>List of chairmen of sessions and discussants</i>	xi
<i>Foreword by Professor Lawrence Bogorad</i>	xiii
<i>Editorial Preface</i>	xv

I Origins and Variation

1 Fossil evidence on the evolutionary origin of tropical trees and forests <i>James A. Doyle</i>	3
2 Geographic variation in tropical tree species <i>Trevor Whiffin</i>	31

II Reproduction and Demography

3 Chemical aspects of the pollination biology of woody plants in the tropics <i>Herbert G. Baker</i>	57
4 Seeding patterns of tropical trees <i>Daniel H. Janzen</i>	83
5 Strategies of establishment in Malayan forest trees <i>F. S. P. Ng</i>	129
6 Studies on the demography of tropical trees <i>José Sarukhán</i>	163

III Architecture and Construction

7 Branching and axis differentiation in tropical trees <i>P. B. Tomlinson</i>	187
8 Architectural variation at the specific level in tropical trees <i>Francis Hallé</i>	209

vi	<i>Contents</i>	
9	Modular construction and its distribution in tropical woody plants <i>Marie-Françoise Prévost</i>	223
10	Architecture of the New Caledonian species of <i>Araucaria</i> <i>Jean-Marie Veillon</i>	233
11	Growth forms of rain forest palms <i>John Dransfield</i>	247
12	Araliaceae: growth forms and shoot morphology <i>W. R. Philipson</i>	269
13	A quantitative study of <i>Terminalia</i> branching <i>Jack B. Fisher</i>	285
IV Roots, Leaves, and Abscission		
14	Roots and root systems in tropical trees: morphologic and ecologic aspects <i>Jan Jeník</i>	323
15	On the adaptive significance of compound leaves, with particular reference to tropical trees <i>Thomas J. Givnish</i>	351
16	Abscission strategies in the behavior of tropical trees <i>Fredrick T. Addicott</i>	381
V Organizational Control		
17	Formation of the trunk in woody plants <i>P. Champagnat</i>	401
18	Multiple growth correlations in phanerogams <i>R. Nozeran</i>	423
19	Relation of climate to growth periodicity in tropical trees <i>Paulo de T. Alvim and Ronald Alvim</i>	445
20	Control of shoot extension and dormancy: external and internal factors <i>K. A. Longman</i>	465
21	Feedback control and age-related changes of shoot growth in seasonal and nonseasonal climates <i>Rolf Borchert</i>	497
22	Structural requirements for optimal water conduction in tree stems <i>Martin H. Zimmermann</i>	517
VI Community Interactions		
23	Architecture and energy exchange of dicotyledonous trees in the forest <i>Roelof A. A. Oldeman</i>	535

Cambridge University Press

978-0-521-14247-2 - Tropical Trees as Living Systems

Edited by P. B. Tomlinson and Martin H. Zimmerman

Frontmatter

[More information](#)

	<i>Contents</i>	vii
24	Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia <i>Tatuo Kira</i>	561
25	Crown characteristics of tropical trees <i>P. S. Ashton</i>	591
26	Tree falls and tropical forest dynamics <i>Gary S. Hartshorn</i>	617
27	Gaps in the forest canopy <i>T. C. Whitmore</i>	639
	Index to subjects and plant genera	657

Contributors

Fredrick T. Addicott
Department of Botany
University of California
Davis, CA 95616 U.S.A.

Paulo de T. Alvim
Centro de Pesquisas do Cacau
Caixa Postal 7
Ilhéus/Itabuna
Itabuna Bahia, Brazil

P. S. Ashton
Botany Department and Institute
of Southeast Asian Biology
University of Aberdeen
St. Machar Drive
Aberdeen AB9 24D
Scotland

Herbert G. Baker
Botany Department
University of California
Berkeley, CA 94720 U.S.A.

Rolf Borchert
Department of Botany, Physiol-
ogy, and Cell Biology
University of Kansas
Lawrence, KA 66045 U.S.A.

P. Champagnat*
Centre National de la Recherche
Scientifique
91 Gif-sur-Yvette, Essone
France

James A. Doyle
Department of Ecology and Evolu-
tionary Biology
Museum of Paleontology
University of Michigan
Ann Arbor, MI 48109 U.S.A.

John Dransfield
The Herbarium
Royal Botanic Gardens
Kew, Richmond, Surrey
England

Jack B. Fisher
Fairchild Tropical Garden
10901 Old Cutler Road
Miami, FL 33156 U.S.A.

Thomas J. Givnish
Department of Biology
Harvard University
16 Divinity Avenue
Cambridge, MA 02138 U.S.A.

Francis Hallé
Université du Languedoc
Institut de Botanique
5 rue de A. Broussonet
34000 Montpellier
France

Gary S. Hartshorn
Organization for Tropical Studies
Universidad de Costa Rica
San José, Costa Rica

x *Contributors*

- | | |
|---|---|
| Daniel H. Janzen
<i>Department of Biology
University of Pennsylvania
Philadelphia, PA 19174 U.S.A.</i> | <i>University of Canterbury
Christchurch 1, New Zealand</i> |
| Jan Jeník
<i>Institute of Botany
Czechoslovak Academy of
Sciences
25243 Pruhonice
Czechoslovakia</i> | Marie-Françoise Prévost
O.R.S.T.O.M.
B.P. 165
97301 Cayenne Cedex
French Guiana |
| Tatuo Kira
<i>Department of Biology
Faculty of Science
Osaka City University
Sugimoto-Cho, Sumiyoshi-Ku
Osaka 558, Japan</i> | José Sarukhán
<i>Departamento de Botánica
Instituto de Biología
Universidad Nacional Autónoma
de México
México 20 D. F.
Mexico</i> |
| K. A. Longman
<i>Institute of Terrestrial Biology
Unit of Tree Biology
Bush Estate, Penicuik
Midlothian, Scotland EH26 OQB</i> | P. B. Tomlinson
<i>Harvard University
Harvard Forest
Petersham, MA 01366 U.S.A.</i> |
| F. S. P. Ng
<i>Forest Research Institute
Kepong, Selangor
Malaysia</i> | Jean-Marie Veillon
O.R.S.T.O.M.
B.P. A5
Nouméa, New Caledonia |
| R. Nozeran
<i>Université de Paris-Sud
Laboratoire de Botanique II
Bâtiment 360
91405 Orsay
France</i> | Trevor Whiffin
<i>Department of Botany
La Trobe University
Bundoora, Victoria
Australia 3083</i> |
| Roelof A. A. Oldeman
<i>Agr. University
"Hinkeloord"
Box 342
Wageningen, Netherlands</i> | T. C. Whitmore
<i>c/o British Museum (Natural
History)
Cromwell Road
London SW 7
England</i> |
| W. R. Philipson
<i>Botany Department</i> | Martin H. Zimmermann
<i>Harvard University
Harvard Forest
Petersham, MA 01366 U.S.A.</i> |
| *Not attending | |

Chairmen of sessions and discussants

Kamaljit Bawa, *Department of Biology, University of Massachusetts – Boston, Boston, Massachusetts 02125 U.S.A.*

Brian Bowes, *Harvard University, Harvard Forest, Petersham, Massachusetts 01366 U.S.A. Now at University of Glasgow, Glasgow G12 8QQ, Scotland*

Gordon Browning, *John Innes Institute, Norwich NOR 7OF, England*

Robert C. Cook, *Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138 U.S.A.*

Peter Del Tredici, *Harvard University, Harvard Forest, Petersham, Massachusetts 01366, U.S.A.*

Ernest M. Gould, *Harvard University, Harvard Forest, Petersham, Massachusetts 01366 U.S.A.*

D. Roger Lee, *Harvard University, Harvard Forest, Petersham, Massachusetts 01366 U.S.A. Now at Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1C 5S7*

Walter H. Lyford, *Harvard University, Harvard Forest, Petersham, Massachusetts, 01366, U.S.A.*

Thomas A. McMahon, *Division of Engineering and Applied Physics, Harvard University, Cambridge, Massachusetts 02138 U.S.A.*

David Policansky, *Department of Biology, University of Massachusetts – Boston, Boston, Massachusetts 02125 U.S.A.*

Hugh M. Raup, *Harvard University, Harvard Forest, Petersham, Massachusetts 01366 U.S.A.*

Otto Stein, *Department of Botany, University of Massachusetts, Amherst, Massachusetts 01002 U.S.A.*

Peter Stevens, *Arnold Arboretum, Harvard University, Cambridge, Massachusetts 02138 U.S.A.*

John G. Torrey, *Harvard University, Harvard Forest, Petersham, Massachusetts 01366 U.S.A.*

Cambridge University Press

978-0-521-14247-2 - Tropical Trees as Living Systems

Edited by P. B. Tomlinson and Martin H. Zimmerman

Frontmatter

[More information](#)

Foreword

Most of our knowledge of the growth of trees is based upon a study of their temperate representatives, particularly those in Europe and North America, where foresters and botanists are concentrated. In contrast, tropical trees, especially those of the wet lowlands with nonseasonal climates, are relatively little studied, and the task of cataloguing their floristic richness is far from complete. The diversity of tree species in the lowland tropics is insufficiently appreciated by biologists, but may be indicated by a recent assessment of an area 23 ha in extent in the Jengka Forest Reserve, Malay Peninsula, where only trees with a basal circumference greater than 91 cm were measured (M. D. Poore, *J. Ecol.*, 56, 143–96, 1968): 375 species in 139 genera representing 52 families were recorded. To achieve about the same figures in North America, one would have to survey a large part of the continental United States (including tropical Florida).

It seems appropriate that the woody plants of the tropics be given attention at a time when the world has been made acutely aware that fossil fuel resources are dwindling rapidly, and, in contrast, the appreciation of trees as a renewable source of energy is greatly heightened. It was Godfrey Lowell Cabot's early appreciation of this situation that led to his endowment of the foundation under whose auspices we meet. One of his concerns was the genetic improvement of forest trees, and appropriately we give emphasis here to tropical trees because they represent the largest genetic resource of woody plant material available to foresters.

Clearly, we cannot deal in detail with all topics deserving the attention of biologists; indeed, the gaps in our coverage are as numerous and obvious as the gaps in the forest canopy itself. However, in trying to emphasize to the organization and growth of the individual tree, as the unit of which the forest is made, we hope to establish

Cambridge University Press

978-0-521-14247-2 - Tropical Trees as Living Systems

Edited by P. B. Tomlinson and Martin H. Zimmerman

Frontmatter

[More information](#)

xiv *Foreword*

principles that will guide the future advancement of research on tropical woody plants.

Seen in this light, our responsibility is a considerable one, and it is one we must accept with a feeling of urgency. The destruction and exploitation of tropical forests proceed at an alarming rate. If we are to appreciate how tropical trees function within forest communities, our research must proceed apace while there is still a tropical forest to analyze.

We hope the exchange of ideas and information that this symposium permits not only will achieve one other of Mr. Cabot's wishes – the dissemination of knowledge about trees – but will rapidly lead to the efficient management of tropical forests in a way useful to mankind, not only presently but for the benefit of later generations.

Lawrence Bogorad
Professor of Biology, Harvard University
Director, Maria Moors Cabot Foundation
for Botanical Research

Cambridge University Press

978-0-521-14247-2 - Tropical Trees as Living Systems

Edited by P. B. Tomlinson and Martin H. Zimmerman

Frontmatter

[More information](#)

Editorial preface

This volume is the outcome of a symposium held at Harvard Forest, Petersham, Massachusetts, in April 1976, the fourth in the series made possible by the Cabot Foundation of Harvard University, but in this instance with additional support from the Atkins Garden Fund of Harvard University. The theme of the symposium was a consideration of the individual tree as an integrated living system and its interaction with similar individuals in tropical vegetation. Participants were selected because of their expert knowledge of tree biology or their extensive field knowledge of tropical woody plants; the goal was to effect interchange across the unnatural and unnecessary barriers that so often exist between the scientists of temperate and tropical countries. Chapters by each of the invited participants are included, together with a summary of the discussion of the majority of the papers. One paper submitted by a participant who was unable to attend is also included.

In choosing so general a theme as tropical trees and in attempting to cover the subject from many different aspects, we were aware of the dangers of omission. One obvious deficiency is in the coverage of periodicity of cambial activity, which relates directly to wood production and the absence of growth rings from the trunks of most tropical trees – a matter of utter frustration to tropical ecologists. However, this aspect had been covered in an earlier Cabot Symposium (*The Formation of Wood in Forest Trees*, ed. M. H. Zimmerman, Academic Press 1964). Despite this omission, we feel attention has been given to most of the important topics.

Contributors were asked not merely to present detailed research data, but to offer a summary of the state of knowledge of the area of their special interest so that a general overview would be presented. It is evident that our speakers responded magnificently to this de-

Cambridge University Press

978-0-521-14247-2 - Tropical Trees as Living Systems

Edited by P. B. Tomlinson and Martin H. Zimmerman

Frontmatter

[More information](#)xvi *Editorial preface*

manding task and have placed our present knowledge of tropical trees within the wider framework of plant biology so that this volume becomes more of a source book than is usual for specialized symposia. The need for such a synthesis is clear to anyone who has attempted to do research on woody plants in the tropics and despaired of assessing information that is currently widely scattered, both geographically and linguistically, in botanic and forestry journals. No one author could fairly cover the field either from a knowledge of the literature or from personal experience. Standard reference books on trees refer overwhelmingly to temperate examples, and this information may not be wholly appropriate to the circumstances of the lowland tropical rain forest. That temperate trees offer only a very limited sampling of the range of morphologic diversity of woody plants becomes evident when a cosmopolitan view is taken – to the extent, for example, that the currently accepted terminology for branch organization can be shown to be inadequate. The present volume, adopting a cosmopolitan viewpoint, provides a corrective influence. It also demonstrates the remarkable impetus to the study of woody plants given by recent work in the tropics that has advanced knowledge of their construction, reproductive biology, productivity, and community interaction. When similar attention is given to adaptive morphology, morphogenesis, translocation physiology, and photosynthetic capability of tropical trees, the discipline will further burgeon. Clearly, we are dealing with an area of rapid future research expansion.

This volume begins by placing tropical trees in an evolutionary context: Their likely origins are now being traced with increasing reliability as angiosperm phylogeny is traced via the study of leaf and pollen fossils. Modern methods of chemical analysis are then shown to be useful in measuring geographic variation, which may represent incipient material for evolutionary advance. Four important aspects of reproductive biology are considered, because the sexual process is the medium for evolutionary change. The chemical significance of floral rewards, mainly nectar, is examined from the point of view both of pollinating agents and of the physiology of the tree itself. The resulting seed crop is a major attraction to many predators, and the way in which the periodicity of seed production may provide a mechanism for minimizing losses is considered in detail. But seeds do survive this onslaught to germinate and renew tree populations. The examination of seedlings in a large sample of tropical tree species shows a wider range of morphologic categories than previously recognized, with some indication of their adaptive significance and relation to seed size. As a population of new recruits is admitted to the forest undergrowth, mortality continues, and a

Cambridge University Press

978-0-521-14247-2 - Tropical Trees as Living Systems

Edited by P. B. Tomlinson and Martin H. Zimmerman

Frontmatter

[More information](#)

demographic study of selected examples can be presented, despite the difficulties of estimating tree age indirectly.

A subsequent series of chapters emphasizes morphologic aspects that are appropriate in view of the diversity of tree form, evident to even the most casual observer in the tropics. Recent research has begun to catalog accurately this diversity in terms of recognizable genetic growth plans (architectural models) that often include modular construction and marked differentiation between kind of axis. The classic example of *Terminalia* is analyzed in quantitative detail for the first time. Two distinctive tropical plant families, the Palmae (monocotyledons) and the Araliaceae (dicotyledons) together with the gymnospermous genus *Araucaria* are selected for detailed case studies. It is useful to contrast these accounts with intraspecific variations that result from "mutation," although this is not necessarily genetic. Two opposite parts of the tree are next drawn to our attention. First, the greatly neglected root system, which is seen to be almost as diverse as the shoot system – often conspicuously so, as aerial roots are common in tropical trees. Second, compound leaves are considered from the point of view of their adaptive significance, with the suggestion that they provide a means for rapid adjustment to water stress because they are relatively large, "throwaway" units of construction. This chapter can be linked to the next, which surveys processes of abscission, emphasizing that loss of parts is as important a biologic process as their accretion.

Earlier chapters having emphasized constructional diversity, it is now appropriate to examine the physiologic mechanisms that determine form. A tree develops a trunk because it limits basal branching by a process variously described as apical control or acrotony, and what we know of temperate examples suggests that the controlling mechanism is complex and not explicable solely by "apical dominance." This leads naturally to a discussion of the evidence for multiple correlations that determine branch expression in woody plants. A feature of many tropical climates is the absence of marked seasonality, so that the obvious constraints of cold winters or extended dry periods on shoot extension might appear to be lacking. However, tree growth in the tropics is frequently periodic, and the factors that govern rhythmic behavior are shown to be subtle and dependent on elaborate hormonal interactions. This subject is discussed from several points of view, with experimental analysis strongly emphasized. Evidence for feedback control mechanisms in rhythmic growth is supported by computer simulation models. Because water supply to shoots appears to be a limiting factor, it becomes appropriate to discuss hydraulic conductivity in tropical trees, which in turn depends on a detailed knowledge of their anatomy.

Cambridge University Press
978-0-521-14247-2 - Tropical Trees as Living Systems
Edited by P. B. Tomlinson and Martin H. Zimmermann
Frontmatter
[More information](#)

xviii *Editorial preface*

So far, the tropical tree has been analyzed largely at the level of the individual and its parts, but the final chapters address the problem of how these individuals interact within natural communities. Overviews that indicate how the forest is constructed in qualitative and quantitative terms are presented, and the concept of the forest as a mosaic of successional stages is established by the last three contributors. The smallest segment of the mosaic is obviously the individual tree. The conclusion is that not only the tropical tree, but also the tropical forest itself, is a living system.

As the discussion of tropical trees progresses from parts, to whole, and finally to community, it is evident that a linear sequence is inappropriate and artificial: The topics dwelt upon can be interrelated in a reticulate fashion.

We expect the reader will move backward and forward through this volume along paths of his own choosing, but we hope the ways we have charted are clear and well sign-posted. The tropical forest is an awesome place into which biologists need to venture in increasing numbers. We will be satisfied if our efforts provide helpful guidance in the future.

The success of our meetings at the Harvard Forest was the result of the willing collaboration of its staff, to whom we express our collective thanks. All played a significant part, but perhaps we dare single out Mrs. Sandra K. Weidlich and Mrs. Dorothy R. Smith for individual mention.

P. B. Tomlinson
Martin H. Zimmermann

Harvard Forest
Petersham, Massachusetts
December 1977