

Tree Physiology

Guillermo Goldstein
Louis S. Santiago *Editors*

Tropical Tree Physiology

Adaptations and Responses in a
Changing Environment

 Springer

Tree Physiology

Volume 6

Series editors

Frederick C. Meinzer, Corvallis, USA

Ülo Niinemets, Tartu, Estonia

More information about this series at <http://www.springer.com/series/6644>

Guillermo Goldstein · Louis S. Santiago
Editors

Tropical Tree Physiology

Adaptations and Responses in a Changing
Environment

 Springer

Editors

Guillermo Goldstein
Laboratorio de Ecología Funcional,
Departamento de Ecología Genética y
Evolución, Instituto IEGEBA
(CONICET-UBA), Facultad de Ciencias
Exactas y naturales
Universidad de Buenos Aires
Buenos Aires
Argentina

and

Department of Biology
University of Miami
Coral Gables, FL
USA

Louis S. Santiago
Department of Botany & Plant Sciences
University of California
Riverside, CA
USA

and

Smithsonian Tropical Research Institute
Balboa, Ancon, Panama
Republic of Panama

ISSN 1568-2544

Tree Physiology

ISBN 978-3-319-27420-1

ISBN 978-3-319-27422-5 (eBook)

DOI 10.1007/978-3-319-27422-5

Library of Congress Control Number: 2015957228

© Springer International Publishing Switzerland 2016

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, express or implied, with respect to the material contained herein or for any errors or omissions that may have been made.

Printed on acid-free paper

This Springer imprint is published by SpringerNature
The registered company is Springer International Publishing AG Switzerland

Preface

Our World is changing rapidly, yet, how tropical forests will respond to this change and in turn dampen or accelerate its ripple effects is essentially a physiological question. Addressing important questions regarding the impacts of changes in land utilization, such as deforestation, and effects of global climate change will require specific information on tropical tree physiology. Earth system modeling scientists are clamoring for more physiological data from tropical trees. It seems that the scarcity of information on the physiological responses of trees is the greatest source of uncertainty in predicting how the tropical rain forests will respond to increasing greenhouse gases and in particular increasing atmospheric CO₂. For example, tree species can adjust their physiological behavior to increasing global temperatures or decreases in precipitation, or they can be replaced by other species better adapted to the new environmental conditions. It is also true that the physiology of tropical trees has not been as well-studied as the physiology of trees from temperate regions, leading to major gaps in our understanding of how tropical trees interact with the Earth system over a range of scales.

It is known that the physiological behavior of both tropical and temperate trees is regulated by similar mechanisms. The differences, however, are related to the unique selective pressures to which tropical trees have been subjected during the evolutionary process and its adaptive consequences. The idea put forward by Theodosius Dobzhansky in the 1950s that tropics and temperate zones are areas where selection operates differently, generated fruitful lines of thinking and research. His contention was that in temperate areas mortality was essentially climatically determined, with little or no competition pressure, while in the tropics, where the environment is relatively more constant, at least in terms of seasonal changes in temperature, mortality is the result of the effects of population size and competition. This paradigm of evolutionary pressures has changed substantially but some aspects of it still remain as a guide for understanding differences in patterns of adaptation between temperate and tropical plants. Negative density dependence prevents any single tree species from dominating most tropical forest ecosystems. The reasons for this must be sought not only in ecological and demographic

processes but also among the highly diverse physiological characteristics of tropical trees. In the tropics, seasonal temperature variations are relatively small compared to diurnal temperature changes and if soil water is available, growth and metabolic activities can be maintained throughout the entire year. Heavy herbivore pressure is continuous and the adaptive responses of tropical plants to herbivory are impressive. The physiological implications of various types of mutualisms found among tropical trees are also important. Many trees have a relatively short life span of less than 200 years in the wet tropics compared to more than a 1000 years in some temperate-zone trees.

There has been a substantial increase in the number of studies of tropical tree physiology during the last few decades. The reason for this is not only that trees are the dominant growth form in most tropical ecosystems, but also because of increasing availability and refinement of equipment such as portable photosynthesis systems and instruments for studying water relations of plants. Furthermore, a substantially larger number of tropical biologists are now involved in more mechanistic studies. The use of tower cranes during the last 25 years has allowed scientists to reach the canopy of tropical forests, one of the ultimate frontiers for unveiling not only new organisms but also new processes that were unthinkable just a few years ago.

A distinct feature of tropical trees is not only their high species diversity but also the large variety of life history traits and growth forms that are mostly unique to the tropics such as hemiepiphytic trees, stem succulent trees such as baobab trees, mangroves, palms and other arborescent monocots, and unusual arborescent plants near tree line that are not traditional trees. The wide range of shade tolerance from rapidly growing pioneer trees during gap-phase regeneration to species that can survive by growing slowly in deep shade contribute to this diversity.

Tropical trees tend to grow in habitats where soil water availability is high all year round or at least in habitats where it is seasonally available. They grow in arid environments where they access deep soil water such as in the case of phreatophytic trees. They also occur along altitudinal gradients within the tropics up to the upper tree line and in some cases, such as the caulescent giant rosette plants, they can grow above the continuous forest line. They extend to the subtropics, and in many cases they share close phylogenetic relationships with subtropical tree species, and the structure and function of subtropical forests are in many cases similar to tropical forests, in regards to gap-phase regeneration and the high abundance of lianas.

Through 20 chapters authored by 55 people, this book captures the current state of knowledge of the main physiological characteristics of tropical trees. The book was as a way to not only to provide information gathered during the last few years across the world, but also for laying the foundation for discussing controversial paradigms and new hypothesis of physiological process and mechanisms of trees. Thus this book will surely capture the attention not only of tropical biologists but also of biologists working in many different types of environments around the globe. Physiological consequences of global environmental change will permeate most book chapters, as it provides a dynamic arena for tropical trees to respond. The book is organized in six main parts. The first one is on the physiology of unique

tropical growth forms. This group of conspicuous plants is extremely important for understanding the structure, function, and dynamics of tropical forests, as well as understanding why certain species live where they do and not elsewhere. Hemiepiphytic trees with an unusual progression of life stages and obligate epiphytes with a unique photosynthetic pathway, are plants that capture the environmental and demographic wonder of forest ecosystems: Do they start their life cycle (as in the case of hemiepiphytic trees) or spend their entire life cycle (as in the case of obligate epiphytes) in the upper canopy to utilize higher levels of incoming solar radiation or to escape the shady understory with high chances of damage by falling debris and exclusion by competition with other plants? Stem succulent trees, such as the fat-stemmed baobabs, which have captured the imagination and attention of writers, such as in the case of “the little prince” by Antoine de Saint-Exupéry, are fascinating trees occurring mostly in seasonally dry forests. The enlarged stem with photosynthetic surfaces, leaves that drop during the dry season and with little biomass allocation to root systems, appear to have a combination of physiological and anatomical traits that at first sight is difficult to understand. Do their low wood density trunks represent conspicuous water storage? Is stored stem water used for new leaf growth near the end of the dry season or to maintain stem conductance during the rainy season? Does the large size of the stem serve a biomechanical role for providing stability to tall mature trees? Palms are another unique growth form, nearly always associated with tropical environments. The hydraulic architectures of these monocots have long intrigued physiologists working on plant water relations and hydraulic architecture. How can trees that do not have secondary growth, and thus cannot produce new xylem tissue after the plants start growing in height, cope with intensive droughts and the dysfunction of cavitated xylem vessels? Finally lianas, which have solved the problem of reaching the upper canopy without investment in a large diameter stem, can move large amounts of water to transpiring leaves. How did these plants solve this important water economy constraint imposed by a relatively narrow stem?

The second part of the book deals with adaptive responses of trees growing in habitats that are unique to the tropics. Mangrove trees occur in coasts across all tropical regions with roots tapping seawater. Floodplain trees tolerate freshwater inundation for several months in inland tropical regions and in some cases are completely covered by water. At high elevation, tropical giant rosette plants represent one of the most fascinating cases of evolutionary convergence among tropical alpine climates that are characterized as “summer during the day and winter at night.”

The third part of the book discusses emergent paradigms on hydraulic architecture and water relations. The high diversity of tropical tree species allows the use of a wide array of physiological and morphological traits. This provides fertile ground for testing new hypothesis on the adaptive significance of physiological mechanisms for how trees cope with drought, and how they may avoid or repair cavitated xylem vessels, or how close they are to their physiological limits of water availability in the face of extreme climatic events.

The fourth part of the book deals with important responses of trees to a limitation common in tropical soils: low amounts of available nutrients. How valid is the paradigm of widespread phosphorous limitation? What can be inferred from litter manipulation and fertilization experiments in tropical forests? What are the dynamics and the roles of litter accumulation and decomposition? What is the main distinctive characteristic of nutrient cycling in tropical ecosystems dominated by trees? Do nutrients limit the ability of tropical trees to respond to climate change, or can trees adjust and adapt to nutrient limitations to carry on the process of photosynthetic carbon assimilation? Do N and P equally limit the photosynthetic process in tropical trees?

Carbon economy and biomass allocation patterns in tropical trees and forests are the focus of the fifth part of the book. Important issues related to carbon cycling and the strength of carbon sinks across terrestrial ecosystems worldwide are analyzed. In particular, the continuum of physiological traits from high light requiring pioneer trees to slow growing shade-tolerant trees is discussed in terms of primary and secondary succession in tropical forests and gap-phase regeneration. These two groups of trees are considered as the extremes of a gradient of species requiring high light levels for photosynthesis and rapid growth and in species tolerant to diffuse light and the use of light flecks for carbon assimilation. Are there trade-offs in carbon allocation between defense against herbivores and growth? Compared to tropical and temperate forests, subtropical forests have received little attention until now, and the contribution of this region to the global carbon cycle has not been fully assessed. In this part the carbon balance of subtropical forests at different spatial and temporal scales will be analyzed. The reader will be surprised to know that many subtropical forests are strong carbon sinks, and perhaps the strongest when compared to other terrestrial ecosystem.

In the last part, ecophysiological processes at different spatial and temporal scales are analyzed. Until recently the trunks of tropical trees in lowland areas were assumed not to have tree rings. Several studies have found that this is not the case, particularly in seasonally dry environments, which opens a window of opportunities for using tree rings to acquire insights into the ecology and climate sensitivity of tropical trees as well as the possibility of obtaining the age of individual trees. This part also addresses biomechanical characteristics of tree, with special references to the constraints of being a tropical tree. Do tropical trees adhere to the same biomechanical laws as temperate trees?

In the past 20 years since we began working together, we have seen tropical ecophysiology evolve from single species studies to large comparative works that embrace the high diversity of tropical forests. We have seen a transition from descriptive and natural history studies, which provided an important foundation, to advanced quantitative and modeling approaches that reveal broader patterns in space and time. Plant ecophysiology in the tropics has also developed strong linkages to disciplines that focus on larger spatial scales, including community ecology, ecosystem ecology, and landscape ecology, as well as smaller spatial scales such as molecular biology, stable isotope ecology, and genomics. This book represents the work of a community of leading tropical ecophysiologicalists, many of

whom are colleagues and collaborators. We hope that it will provide a useful resource for understanding, conserving, and sustainably managing tropical forests, as well as predicting how these ecosystems will respond to future climate change.

Buenos Aires
January 2015

Guillermo Goldstein
Louis S. Santiago

Contents

Part I Physiology and Life History Traits of Unique Tropical Growth Forms

Hemiepiphytic Trees: <i>Ficus</i> as a Model System for Understanding Hemiepiphytism	3
Guang-You Hao, Kun-Fang Cao and Guillermo Goldstein	
Ecophysiology and Crassulacean Acid Metabolism of Tropical Epiphytes	25
Katia Silvera and Eloisa Lasso	
Stem-Succulent Trees from the Old and New World Tropics	45
Eleinis Ávila-Lovera and Exequiel Ezcurra	
Palm Physiology and Distribution in Response to Global Environmental Change	67
Heidi J. Renninger and Nathan G. Phillips	
Carbon Allocation and Water Relations of Lianas Versus Trees	103
Paula I. Campanello, Eric Manzané, Mariana Villagra, Yong-Jiang Zhang, Adela M. Panizza, Débora di Francescantonio, Sabrina A. Rodriguez, Ya-Jun Chen, Louis S. Santiago and Guillermo Goldstein	

Part II Adaptive Responses of Woody Plants to Particular Tropical Habitats

Flood Tolerant Trees in Seasonally Inundated Lowland Tropical Floodplains	127
Pia Parolin, Leandro V. Ferreira, Maria Teresa F. Piedade, Cátia Nunes da Cunha, Florian Wittmann and Mauricio E. Arias	

The Physiology of Mangrove Trees with Changing Climate. 149
 Catherine E. Lovelock, Ken W. Krauss, Michael J. Osland,
 Ruth Reef and Marilyn C. Ball

Functional Diversity in Tropical High Elevation Giant Rosettes. 181
 Fermín Rada

Part III Plant Hydraulics and Water Relations

**Physiological Significance of Hydraulic Segmentation, Nocturnal
 Transpiration and Capacitance in Tropical Trees: Paradigms
 Revisited.** 205
 Sandra J. Bucci, Guillermo Goldstein, Fabian G. Scholz
 and Frederick C. Meinzer

**Maintenance of Root Function in Tropical Woody Species During
 Droughts: Hydraulic Redistribution, Refilling of Embolized Vessels,
 and Facilitation Between Plants** 227
 F.G. Scholz, S.J. Bucci, F.C. Meinzer and G. Goldstein

Drought Survival Strategies of Tropical Trees 243
 Louis S. Santiago, Damien Bonal, Mark E. De Guzman
 and Eleinis Ávila-Lovera

**Part IV Nutrient Limitation of Ecophysiological Processes
 in Tropical Trees**

**Nutrient Availability in Tropical Rain Forests: The Paradigm
 of Phosphorus Limitation** 261
 James W. Dalling, Katherine Heineman, Omar R. Lopez,
 S. Joseph Wright and Benjamin L. Turner

**Tree Nutrient Status and Nutrient Cycling in Tropical
 Forest—Lessons from Fertilization Experiments.** 275
 E.J. Sayer and L.F. Banin

Is Photosynthesis Nutrient Limited in Tropical Trees? 299
 Louis S. Santiago and Guillermo Goldstein

**Part V Carbon Economy and Allocation of Tropical Trees
 and Forests**

**Facing Shortage or Excessive Light: How Tropical and Subtropical
 Trees Adjust Their Photosynthetic Behavior and Life History
 Traits to a Dynamic Forest Environment** 319
 Guillermo Goldstein, Louis S. Santiago, Paula I. Campanello,
 Gerardo Avalos, Yong-Jiang Zhang and Mariana Villagra

Carbon Economy of Subtropical Forests 337
 Yong-Jiang Zhang, Piedad M. Cristiano, Yong-Fei Zhang,
 Paula I. Campanello, Zheng-Hong Tan, Yi-Ping Zhang,
 Kun-Fang Cao and Guillermo Goldstein

**The Ecophysiology of Leaf Lifespan in Tropical Forests: Adaptive
 and Plastic Responses to Environmental Heterogeneity** 357
 Sabrina E. Russo and Kaoru Kitajima

**The Effects of Rising Temperature on the Ecophysiology
 of Tropical Forest Trees** 385
 Martijn Slot and Klaus Winter

Tree Biomechanics with Special Reference to Tropical Trees. 413
 Karl J. Niklas

Part VI Ecophysiological Processes at Different Temporal Scales

**Tree Rings in the Tropics: Insights into the Ecology and Climate
 Sensitivity of Tropical Trees** 439
 Roel J.W. Brienen, Jochen Schöngart and Pieter A. Zuidema

Index 463

Contributors

Mauricio E. Arias Department of Organismic and Evolutionary Biology, Cambridge, MA, USA

Gerardo Avalos Escuela de Biología, Universidad de Costa Rica, San Pedro, San José, Costa Rica; The School for Field Studies, Center for Sustainable Development Studies, Beverly, MA, USA

Eleinis Ávila-Lovera Department of Botany & Plant Sciences, University of California, Riverside, CA, USA

Marilyn C. Ball Research School of Biology, The Australian National University, Canberra, ACT, Australia

L.F. Banin Centre for Ecology and Hydrology, Bush Estate, Midlothian, Scotland

Damien Bonal INRA, UMR EEF—Université de Lorraine/INRA, Champenoux, France

Roel J.W. Brienen School of Geography, Leeds University, Leeds, UK

Sandra J. Bucci Grupo de Estudios Biofísicos y Ecofisiológicos, Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco, Chubut, Argentina; Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

Paula I. Campanello Laboratorio de Ecología Forestal y Ecofisiología, Instituto de Biología Subtropical, CONICET, FCF, Universidad Nacional de Misiones, Puerto Iguazú, Argentina

Kun-Fang Cao State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources, and College of Forestry, School of Forestry, Guangxi University, Nanning, China

Ya-Jun Chen Key Laboratory of Tropical Forest Ecology, Xishuangbana Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China

Piedad M. Cristiano Laboratorio de Ecología Funcional, Departamento de Ecología Genética y Evolución, Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

Cátia Nunes da Cunha Departamento de Botânica e Ecologia, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil

James W. Dalling Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA; Smithsonian Tropical Research Institute, Panama, Republic of Panama

Mark E. De Guzman Department of Botany & Plant Sciences, University of California, Riverside, CA, USA

Débora di Francescantonio Laboratorio de Ecología Forestal y Ecofisiología, Instituto de Biología Subtropical, CONICET, FCF, Universidad Nacional de Misiones, Puerto Iguazú, Argentina

Exequiel Ezcurra Department of Botany and Plant Sciences, University of California, Riverside, CA, USA

Leandro V. Ferreira Museu Paraense Emílio Goeldi, Belém, Pará, Brazil

Guillermo Goldstein Laboratorio de Ecología Funcional, Departamento de Ecología Genética y Evolución, Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; Department of Biology, University of Miami, Coral Gables, FL, USA

Guang-You Hao State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China

Katherine Heineman Program in Ecology, Evolution and Conservation Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA

Kaoru Kitajima Graduate School of Agriculture, Kyoto University, Kyoto, Japan; Smithsonian Tropical Research Institute, Balboa, Panama

Ken W. Krauss U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA, USA

Eloisa Lasso Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panama; Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

Omar R. Lopez Smithsonian Tropical Research Institute, Panama, Republic of Panama; Instituto de Investigaciones Científicas y Servicios de Alta Tecnología, Ciudad de Saber, Panama, Republic of Panama

Catherine E. Lovelock School of Biological Sciences, The University of Queensland, Brisbane St. Lucia, QLD, Australia

Eric Manzané Smithsonian Tropical Research Institute, Panama, Republic of Panama

Frederick C. Meinzer USDA Forest Service, Forestry Sciences Laboratory, Corvallis, OR, USA

Karl J. Niklas Plant Biology Section, School of Integrative Plant Science Cornell University, Ithaca, NY, USA

Michael J. Osland U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA, USA

Adela M. Panizza Laboratorio de Ecología Forestal y Ecofisiología, Instituto de Biología Subtropical, CONICET, FCF, Universidad Nacional de Misiones, Puerto Iguazú, Argentina

Pia Parolin Biocentre Klein Flottbek and Botanical Garden, University of Hamburg, Hamburg, Germany; INRA French National Institute for Agricultural Research, Univ. Nice Sophia Antipolis, CNRS, UMR 1355-7254 Institut Sophia Agrobiotech, Sophia Antipolis, France

Nathan G. Phillips Department of Earth and Environment, Boston University, Boston, MA, USA

Maria Teresa F. Piedade INPA, Manaus, Amazônia, Brazil

Fermín Rada Instituto de Ciencias Ambientales y Ecológicas de los Andes Tropicales (ICAE) Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela

Ruth Reef School of Biological Sciences, The University of Queensland, Brisbane St. Lucia, QLD, Australia

Heidi J. Renninger Department of Forestry, Mississippi State University, Mississippi, MS, USA

Sabrina A. Rodriguez Laboratorio de Ecología Forestal y Ecofisiología, Instituto de Biología Subtropical, CONICET, FCF, Universidad Nacional de Misiones, Puerto Iguazú, Argentina

Sabrina E. Russo School of Biological Sciences, University of Nebraska, Lincoln, USA

Louis S. Santiago Department of Botany & Plant Sciences, University of California, Riverside, CA, USA; Smithsonian Tropical Research Institute, Balboa, Ancon, Panama, Republic of Panama

E.J. Sayer Lancaster Environment Centre, Lancaster University, Lancaster, England

Fabian G. Scholz Grupo de Estudios Biofísicos y Ecofisiológicos, Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco, Chubut, Argentina; Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

Jochen Schöngart Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, AM, Brazil

Katia Silvera Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panama; Department of Botany and Plant Sciences, University of California Riverside, Riverside, CA, USA

Martijn Slot Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panama

Zheng-Hong Tan Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China

Benjamin L. Turner Smithsonian Tropical Research Institute, Balboa, Panama, Republic of Panama

Mariana Villagra Laboratorio de Ecología Forestal y Ecofisiología, Instituto de Biología Subtropical, CONICET, FCF, Universidad Nacional de Misiones, Puerto Iguazú, Argentina

Klaus Winter Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panama

Florian Wittmann Department of Biogeochemistry, Max Planck Institute for Limnology, Mainz, Germany

S. Joseph Wright Smithsonian Tropical Research Institute, Balboa, Panama, Republic of Panama

Yi-Ping Zhang Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China

Yong-Fei Zhang Department of Geological Sciences, John A. and Katherine G. Jackson School of Geosciences, University of Texas at Austin, Austin, Texas, USA

Yong-Jiang Zhang Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA; Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China

Pieter A. Zuidema Forest Ecology and Forest Management, Centre for Ecosystems, Wageningen University, Wageningen, The Netherlands

Part I
Physiology and Life History Traits
of Unique Tropical Growth Forms

Hemiepiphytic Trees: *Ficus* as a Model System for Understanding Hemiepiphytism

Guang-You Hao, Kun-Fang Cao and Guillermo Goldstein

Abstract Woody hemiepiphytes that have an epiphytic juvenile growth stage differ crucially in physiology and ecology from common trees. A relatively high degree of ontogenetic plasticity confers these plants stress tolerance during the epiphytic stage and sufficient competitiveness later as independent trees. The genus *Ficus* consists of about 500 hemiepiphytic and about 300 non-hemiepiphytic woody species. Ecophysiological comparative studies between hemiepiphytic (Hs) and non-hemiepiphytic (NHs) *Ficus* tree species reveal that the existence of an epiphytic growth habit even only for a part of their life cycle involves profound changes that persist to a large degree in their terrestrial growth stage. When growing under similar conditions, both as saplings and mature trees, the Hs have physiological traits resulting in conservative water use and drought tolerance contrasting with more prodigal water use and drought sensitivity in NHs. Divergence in water related functional traits between the two groups are centrally associated with a trade-off between xylem water flux capacity and drought tolerance. Two distinct groups of life history traits for Hs and NHs have evolved—epiphytic regeneration with a slow starting growth rate but enhanced ability to tolerate water deficits in the upper canopy environment and regeneration in the forest understory with an initial

G.-Y. Hao (✉)

State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology,
Chinese Academy of Sciences, 110016 Shenyang, China

e-mail: haogy@iae.ac.cn

K.-F. Cao

School of Forestry, Guangxi University, Nanning, Guangxi, China

e-mail: caokf@xtbg.ac.cn

G. Goldstein

Laboratorio de Ecología Funcional, Departamento de Ecología Genética y Evolución,
Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y naturales, Universidad
de Buenos Aires, Buenos Aires, Argentina

e-mail: goldstein@ege.fcen.uba.ar; gold@bio.miami.edu

G. Goldstein

Department of Biology, University of Miami, Coral Gables, FL 33146, USA

burst of growth to rapidly gain a relatively large seedling size that can better survive risks related to terrestrial regeneration. Evidence shows that the underlying physiology distinguishing these two growth forms mostly involves divergences in adapting to contrasting water regimes but not light conditions, contrary to the conventional hypothesis that hemiepiphytism evolved for gaining access to higher irradiance in the canopy than on the forest floor.

Keywords Drought tolerance · Hydraulic architecture · Plant water relations · Regeneration · Shade tolerance

Introduction

Hemiepiphytes are plants that grow epiphytically for a portion, but not all, of their life cycle. They are customarily subdivided into primary and secondary hemiepiphytes depending on which part of their life cycle has root connections with the ground. Primary hemiepiphytes normally germinate and grow on other plants but later establish substantial and permanent connections with the ground via aerial roots (Kress 1986; Putz and Holbrook 1986). Secondary hemiepiphytes germinate on the ground, climb up their host plants, and then lose stem connections with the soil (Kress 1986; Putz and Holbrook 1986). Primary hemiepiphytes have a true epiphytic stage, during which their ecophysiological traits are very similar to those of the true epiphytes (Zotz and Winter 1994), while secondary hemiepiphytes differ fundamentally from epiphytes, but are rather functionally similar to vines even after the lower part of their stems die back (Holbrook and Putz 1996b; Moffett 2000). For example, many aroid species that are called secondary hemiepiphytes can establish connections with the soil by producing adventitious roots after severing the stem connections with the ground and regaining access to soil resources. The current use of the term hemiepiphyte thus confounds two radically different life cycle characteristics. Zotz (2013a) suggested to entirely discard the term “secondary hemiepiphyte” and instead use Moffett’s (2000) term “nomadic vine” for climbing plants that germinate on the ground and lose the lower part of their stem later during ontogeny. By doing this, the term “hemiepiphyte” is reserved exclusively for species that were formerly called primary hemiepiphytes. We adhere to this definition hereafter in this chapter.

Hemiepiphytes are an important plant component of tropical vegetation. According to a recent census by Zotz (2013b), there are 19 families and 28 genera that contain more than 800 hemiepiphytic species. Among these taxa, *Ficus* (Moraceae) and *Clusia* (Clusiaceae) are the two most important genera that are composed of more than 600 woody hemiepiphytic species combined. In the tropics many of these species are well known as strangers that germinate on tops of other trees and have the potential to strangle their hosts and become structurally independent trees (Fig. 1a–d). In tropical forests of Panama and Zimbabwe 9.8 and



Fig. 1 **a** The epiphytic growth phase of *Ficus altissima* growing in the canopy of a host palm tree showing multiple dangling aerial roots; **b** *Ficus altissima* during its terrestrial growth stage showing multiple “pseudostems” formed by fused aerial roots; **c** a *Ficus concinna* tree strangling a tree; **d** a free-standing stage *Ficus curtipes* tree showing tangled architecture of aerial roots defining the space occupied by a host tree that has been strangled and decomposed. All plants are growing in the Xishuangbanna Tropical Botanical Garden (XTBG), Yunnan, China *Photo credits: GYH*

12.6 % of trees, respectively, were found bearing hemiepiphytic *Ficus* (Guy 1977; Todzia 1986); in Venezuela 13 % of trees >10 cm DBH carried *Ficus* or *Clusia* (Putz 1983). Hemiepiphytic *Ficus* species are also very commonly found on architectural structures especially in tropical and subtropical regions, such as ancient temples in India and old stone walls in urban Hong Kong (Sitaramam et al. 2009; Jim 2014).

It is commonly considered that there are several potential advantages to start the life cycle as an epiphyte in tropical forests. One of the most important advantages is that the forest canopy offers higher light availability than the forest understory. It has been suggested that hemiepiphytism evolved in plants that colonized rocky areas as an adaptation to access high light environments in the forest canopy (Dobzhansky and Murea-Pires 1954; Ramirez 1977; Putz and Holbrook 1986; Todzia 1986; Laman 1995; Williams-Linera and Lawton 1995). They may also benefit from minimizing risks of fire, flood, terrestrial herbivores and damage or coverage by falling debris. The advantages of spending the initial part of their life cycle as an epiphyte, however, can be offset by the potential limitations of water and nutrient availability (Benzing 1990; Coxson and Nadkarni 1995; Holbrook and Putz 1996a, b, c; Swagel et al. 1997).

The hemiepiphytic *Ficus* (Moraceae) is the most conspicuous group of species with such life history in terms of habitat breadth, species richness, abundance and dominance in forest ecosystems (Dobzhansky and Murca-Pires 1954; Putz and Holbrook 1986; Holbrook and Putz 1996b). Species in the genus *Ficus* are among the most important components of tropical lowland rainforests throughout the world (Harrison 2005) and are ecologically important due to their interactions with many frugivorous animals and other plant species (Shanahan et al. 2001). This genus consists of about 500 hemiepiphytic species, including stranglers and banyans, and about 300 non-hemiepiphytic woody species (Putz and Holbrook 1986; Harrison 2005). In *Ficus*, the hemiepiphytic habit most likely evolved four times in the subgenera *Urostigma*, *Sycidium*, *Pharmacosycea* and in a closely related group comprised of the subgenera *Conosycea*, *Galoglychia*, *Americana* and *Malvanthera* (Harrison 2005). From the point of view of evolution, it is important to consider the main environmental factors that selected for this specialized growing habit. Comparative studies in ecophysiology between hemiepiphytic and non-hemiepiphytic *Ficus* species provide valuable information about the main differences between these two groups in environmental adaptation of the seedling/sapling and adult stages, which allow us to infer major selective pressures for the evolution of hemiepiphytism.

Because of the radical changes in rooting environment between the two growth phases, developmental and physiological plasticity is important for hemiepiphytes and enables them first to survive the harshness of the epiphytic habitat and then to compete successfully with other trees when they are later rooted in the ground (Holbrook and Putz 1996b). The change from functional epiphyte to tree is accompanied by a shift in rooting volume and characteristics of the rooting zone. Previous studies have found that nutrient availability does not exert a major limitation to the epiphytic phase of hemiepiphytic *Ficus* (Putz and Holbrook 1989),

whereas measurement of stomatal conductance and leaf phenology indicate that water availability is frequently a major constraint as compared to terrestrially rooted trees of the same species (Holbrook and Putz 1996a, b, c). Epiphytes face frequent and severe water deficits even in areas with very humid climate (Benzing 1990). In seasonally dry climates, hemiepiphytes in the epiphytic stage can experience even more severe drought during the dry season.

In hemiepiphytes, the two different growth phases with contrasting environmental conditions make it interesting and convenient for physiological comparative studies. Some hemiepiphytes, such as species of the genus *Clusia*, switch to the more water efficient facultative CAM metabolism when stressed by drought, but all of the species of *Ficus* studied thus far exhibit only C_3 photosynthesis regardless of the life stage (Ting et al. 1987). Strangler *Ficus* in the epiphytic stage avoids water deficit mainly through strong stomatal control to maintain relatively high leaf water potentials (Holbrook and Putz 1996c). During both the rainy season and the dry season, stomatal conductance of epiphytic stage strangler figs is lower than conspecific trees. Throughout the dry season, epiphytic stage strangler figs only open their stomata in the early morning (Holbrook and Putz 1996c). Furthermore, epiphytic phase *Ficus* can better control water loss from leaf surfaces than conspecific tree-phase plants after stomata are closed (Holbrook and Putz 1996a). The smaller guard cell surface area due to lower stomata density enables the epiphytic stage *Ficus* to lose water more slowly compared to tree phase plants of the same species. Due to these water conservation traits, leaf water potentials of epiphytic stage *Ficus* plants are found to be similar or even less negative than conspecific tree-phase individuals (Holbrook and Putz 1996b). Even when both epiphytic phase and tree phase *Ficus* are well supplied with water during manipulative experiments, the leaves of epiphytic plants still exhibit significantly lower stomatal conductance and much lower epidermal conductance, indicating strong developmental changes from the epiphytic to the terrestrial phase (Holbrook and Putz 1996a).

Physiology related to epiphytic-terrestrial phase transition in *Ficus* has been well studied and reviewed by Holbrook and Putz (1996b). This chapter focuses on ecophysiological comparisons between hemiepiphytic (Hs) and non-hemiepiphytic (NHs) *Ficus* tree species grown under similar environmental conditions to better understand intrinsic differences between these two functional groups.

Comparison of Hydraulics and Water Balance

Stem Hydraulic Conductivity

Only few studies have compared hydraulic architecture between woody hemiepiphytic and free-standing tree species (Patiño et al. 1995; Zotz et al. 1997; Hao et al. 2011). These studies demonstrate that hemiepiphytic plants have stems that are less conductive as shown by relatively low leaf-specific hydraulic conductivity (K_1). According to the studies by Patiño et al. (1995) and Zotz et al. (1997), the lower K_1

found in hemiepiphytic *Ficus* and *Clusia* shoots are largely due to their low investment in water conducting tissue, implying a lower wood cross-sectional area per unit leaf area (Huber value; H_v), rather than less conductive sapwood tissues. Their stem hydraulic conductivity values expressed per wood cross-sectional area are even larger than in tropical and temperate angiosperm trees (Zotz et al. 1997). The more recent study by Hao et al. (2011) comparing mature trees of Hs and NHs grown in a common garden, however, found no significant difference in leaf to sapwood area ratio between the two functional groups but substantially lower specific hydraulic conductivity (K_s , i.e. an intrinsic measure of water transport efficiency of the xylem) in Hs than in NHs.

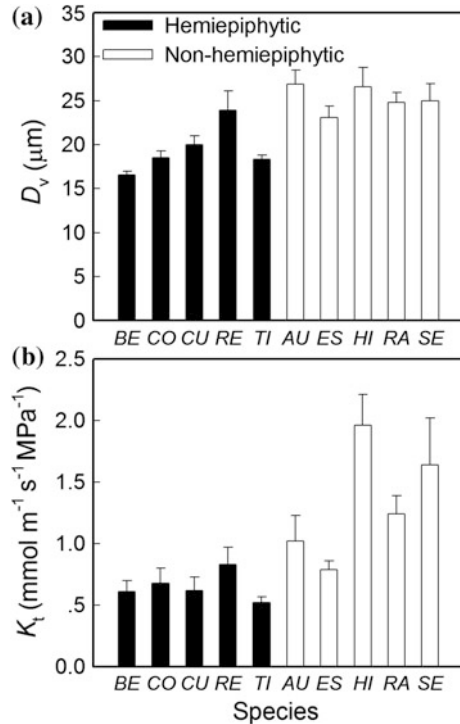
The discrepancies between different studies, however, may largely be due to methodological differences in the way K_s and Huber values are estimated. A close examination of the Patiño et al. (1995) and Zotz et al. (1997) studies reveal that in both studies K_s and H_v were calculated on a whole stem cross sectional area basis rather than the sapwood area basis. This may strongly affect the interpretation of the results of such comparative studies because non-hemiepiphytic *Ficus* species usually have large pith in their stem, but the pith is negligible in the stems of hemiepiphytic species. In the stems of non-hemiepiphytic *Ficus* species, the pith can account for up to 70 % (on average 45 %) of the “wood” cross-sectional area (G.-Y. Hao unpublished). By using only the sapwood area, excluding the pith, for K_s calculation, we find that Hs have sapwoods that are far less efficient in conducting water even when both types of species are growing as independent trees in a common garden (Hao et al. 2011). Consistent with the differences in stem hydraulic conductivity, Hs and NHs show significant differences in leaf properties related to water transport, water conservation and drought tolerance (Hao et al. 2010). These findings can be parsimoniously explained by the hypothesis that Hs are adapted to drought conditions associated with an epiphytic growth stage in the canopy, whereas NHs are selected for strong competitive ability given the higher water availability that they experience during their first growth stages.

Water Flux Through the Leaf

Hemiepiphytic *Ficus* species have low leaf water flux capacity that parallels their relatively low stem-level hydraulic conductivity. Compared with congeneric terrestrial species, Hs have significantly narrower vessels in their leaf petioles and lower theoretical leaf area adjusted hydraulic conductance calculated from petiole xylem vessel dimension measurements (Fig. 2a, b; $P < 0.05$, t-tests). The NHs have vessel lumen diameters that are on average 30 % larger than Hs but the number of vessels per petiole standardized by leaf area does not differ between the two growth forms. The resultant theoretical xylem hydraulic conductance of NHs averages 104 % higher than that of Hs (Hao et al. 2010).

The lower leaf water flux capacity in Hs is consistent with their lower transpirational water requirement per unit leaf area. Compared to NHs grown under similar

Fig. 2 **a** Leaf petiole average vessel diameter (D_v) and; **b** theoretical hydraulic conductance (K_t) of five hemiepiphytic and five non-hemiepiphytic *Ficus* species. Mean values \pm SE for each species are reported ($n = 5-6$). Species name abbreviations: *Ficus benjamina*, BE; *F. concinna*, CO; *F. curtipes*, CU; *F. religiosa*, RE; *F. tinctoria*, TI; *F. auriculata*, AU; *F. esquiroliana*, ES; *F. hispida*, HI; *F. racemosa*, RA; *F. semicordata*, SE (data from Hao et al. 2010)



conditions, Hs have significantly lower stomatal conductance and higher intrinsic water use efficiency measured both on mature trees well rooted in the soil and saplings growing in pots supplied with sufficient water (Hao et al. 2010, 2013). Differences in water use between Hs and NHs are most significant when diurnal courses of leaf gas exchange are compared. Epiphytic stage Hs in their native habitats have been found to open stomata only in the early morning during the dry season (Holbrook and Putz 1996c). When saplings are grown in pots and are well watered, Hs still have lower stomatal conductance and a shorter duration of active CO_2 assimilation on sunny days (Fig. 3a, b). In both groups of species, photosynthetic net assimilation rates reach maximum values around 11:00 h, but rates start to decline in Hs there after until the end of the day, whereas in NHs rates remain at high levels until 14:00 h with an afternoon peak following a slight midday depression (Fig. 3b). The different diurnal patterns of photosynthesis between the two growth forms of *Ficus* are likely associated with the intrinsically low xylem hydraulic conductivity in Hs compared to NHs. Higher water use efficiency in Hs suggests a constitutively conservative water use strategy (Table 1), consistent with adaptations to cope with drought-prone canopy habitats.

In juvenile plants of Hs, more conservative water use may contribute to the protection of their xylem vascular systems from catastrophic cavitation when facing unpredictable drought conditions associated with canopy growth in their natural