Bryophyte Biology

Second Edition

Bryophyte Biology provides a comprehensive yet succinct overview of the hornworts, liverworts, and mosses: diverse groups of land plants that occupy a great variety of habitats throughout the world. This new edition covers essential aspects of bryophyte biology, from morphology, physiological ecology and conservation, to speciation and genomics. Revised classifications incorporate contributions from recent phylogenetic studies. Six new chapters complement fully updated chapters from the original book to provide a completely up-to-date resource. New chapters focus on the contributions of *Physcomitrella* to plant genomic research, population ecology of bryophytes, mechanisms of drought tolerance, a phylogenomic perspective on land plant evolution, and problems and progress of bryophyte speciation and conservation. Written by leaders in the field, this book offers an authoritative treatment of bryophyte biology, with rich citation of the current literature, suitable for advanced students and researchers.

BERNARD GOFFINET is an Associate Professor in Ecology and Evolutionary Biology at the University of Connecticut and has contributed to nearly 80 publications. His current research spans from chloroplast genome evolution in liverworts and the phylogeny of mosses, to the systematics of lichen-forming fungi.

A. JONATHAN SHAW is a Professor at the Biology Department at Duke University, an Associate Editor for several scientific journals, and Chairman for the Board of Directors, Highlands Biological Station. He has published over 130 scientific papers and book chapters. His research interests include the systematics and phylogenetics of mosses and liverworts and population genetics of peat mosses.

Bryophyte Biology

Second Edition

BERNARD GOFFINET
University of Connecticut, USA
AND
A. JONATHAN SHAW
Duke University, USA

CAMBRIDGE
UNIVERSITY PRESS

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

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/9780521872256

First published 2000
Second edition 2009

Printed in the United Kingdom at the University Press, Cambridge

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

Library of Congress Cataloging in Publication data
Bryophyte biology / [edited by] Bernard Goffinet & A. Jonathan Shaw. – 2nd ed.
p. cm.
ISBN 978-0-521-87225-6
1. Bryophytes. I. Goffinet, Bernard. II. Shaw, A. Jonathan (Arthur Jonathan)
III. Title.
QK533.B715 2008
588–dc22

2008021975

ISBN 978-0-521-87225-6 hardback
ISBN 978-0-521-69322-6 paperback

To Lewis Anderson

Cambridge University Press
978-0-521-69322-6 - Bryophyte Biology, Second Edition
Edited by Bernard Goffinet and A. Jonathan Shaw
Frontmatter
More information

Contents

List of contributors *page* ix
Preface xi

1 Morphology and classification of the Marchantiophyta
BARBARA CRANDALL-STOTLER, RAYMOND E. STOTLER AND DAVID G. LONG 1

2 Morphology, anatomy, and classification of the Bryophyta
BERNARD GOFFINET, WILLIAM R. BUCK AND A. JONATHAN SHAW 55

3 New insights into morphology, anatomy, and systematics of hornworts
KAREN S. RENZAGLIA, JUAN C. VILLARREAL AND R. JOEL DUFF 139

4 Phylogenomics and early land plant evolution
BRENT D. MISHLER AND DEAN G. KELCH 173

5 Mosses as model organisms for developmental, cellular, and molecular biology
ANDREW C. CUMING 199

6 Physiological ecology
MICHAEL C. F. PROCTOR 237

7 Biochemical and molecular mechanisms of desiccation tolerance in bryophytes
MELVIN J. OLIVER 269

8 Mineral nutrition and substratum ecology
JEFF W. BATES 299

9 The structure and function of bryophyte-dominated peatlands
DALE H. VITT AND R. KELMAN WIEDER 357

10 Population and community ecology of bryophytes
HAKAN RYDIN 393

11 Bryophyte species and speciation
A. JONATHAN SHAW 445

12 Conservation biology of bryophytes
ALAIN VANDERPOORTEN AND TOMAS HALLINGBÄCK 487

Index 535

Contributors

J.W. Bates
Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK.

W.R. Buck
New York Botanical Garden, Bronx, NY 10458-5126, USA.

B. Crandall-Stotler
Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901-6509, USA.

A.C. Cuming
Centre for Plant Sciences, Faculty of Biological Sciences, Leeds University, Leeds LS2 9JT, UK.

R.J. Duff
Department of Biology, ASEC 185, University of Akron, Akron, OH 44325-3908, USA.

B. Goffinet
Department of Ecology and Evolutionary Biology, 75 North Eagleville Road, University of Connecticut, Storrs, CT 06269-3043, USA.

T. Hallingbäck
Swedish Species Information Centre, Swedish University of Agricultural Sciences, PO Box 7007, SE-750 07 Uppsala, Sweden.

D.G. Kelch
California Department of Food and Agriculture, Plant Pest Diagnostics Laboratory, CDA Herbarium, 3294 Meadowview Road, Sacramento, CA 95832-1448, USA.

D. G. Long
Bryology Section, Royal Botanic Garden, Edinburgh EH3 5LR, UK.

B. D. Mishler
University Herbarium, Jepson Herbarium, and Department of Integrative Biology, University of California, Berkeley, 1001 Valley Life Sciences Building #2465, Berkeley, CA 94720-2465, USA.

M. J. Oliver
USDA-ARS-MWA-PGRU, 205 Curtis Hall, University of Missouri, Columbia, MO 65211, USA.

M. C. F. Proctor
School of Biosciences, University of Exeter, The Geoffrey Pope Building, Stocker Road, Exeter EX4 4QD, UK.

K. S. Renzaglia
Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901-6509, USA.

H. Rydin
Department of Plant Ecology, Evolutionary Biology Centre, Uppsala University, Villavagen 14, SE-752 36 Uppsala, Sweden.

A. J. Shaw
Department of Biology, Duke University, Durham, NC 27708, USA.

R. E. Stotler
Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901-6509, USA.

A. Vanderpoorten
Département des Sciences de la Vie Université de Liége, Sart Tilman B22, B-4000 Liége, Belgium.

J. C. Villarreal
Department of Ecology and Evolutionary Biology, 75 North Eagleville Road, University of Connecticut, Storrs, CT 06269-3043, USA.

D. H. Vitt
Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901-6509, USA.

R. K. Wieder
Room 105, St. Augustine Center, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085, USA.

Preface

Bryophytes have gained a lot of publicity in the past 10–15 years, at least among scientists. While there have always been those who for inexplicable reasons have had a particular fondness for bryophytes, in academic circles these organisms were generally viewed as just "poor relatives" of the more flashy and exciting angiosperms. The bryophytes include fewer species, of smaller stature, with more subdued colors, of less obvious ecological significance, and with apparently simpler and less exciting evolutionary stories to tell. That view has changed.

The three major groups of bryophytes – mosses, liverworts, and hornworts – comprise the earliest lineages of land plants derived from green algal ancestors. Although we still do not know with certainty which of the three lineages is the sister group to all other land plants, we do know that the earliest history of plants in terrestrial environments is inextricably bound to the history of bryophytes. If we wish to understand fundamental aspects of land plant structure and function, we should turn to the bryophytes for insights. These aspects include the origin and nature of three-dimensional plant growth from apical cells and meristems, the evolution of cellular mitotic mechanisms and machinery, the development of thick, water- and decomposition-resistant spore (and later pollen) walls, the molecular and biochemical mechanisms underlying desiccation tolerance, and plant genome structure, function, and evolution. Even if our ultimate goal is to understand the structure and function of angiosperms because it is indeed those plants that feed the human world as agricultural crops, we are nevertheless wise to look more deeply into plant history for a thorough understanding of plant unity and diversity. We cannot fully understand how evolution has tinkered with structure and function in angiosperms without a sense of history. Although the angiosperms are impressively diverse in numbers and structure, they are, we now know from phylogenetic insights into plant evolution, just glorified bryophytes!

Although it is well established that the bryophytes do not constitute a single monophyletic lineage, these organisms share a fundamentally similar life cycle with a perennial and free-living, photosynthetic gametophyte alternating with a short-lived sporophyte that completes its entire development attached to the maternal gametophyte. There are a number of bryophytes that have variously reduced gametophytes and/or sporophytes, and at least one liverwort that is parasitic and non-photosynthetic, but however much the morphological details vary from species to species, the basic bryophyte life cycle is shared among mosses, liverworts, and hornworts. The gametophytes of many species have the ability to replicate clonally either through specialized asexual propagules or by fragmentation, and at sexual maturity they form multicellular female and male gametangia, archegonia and antheridia, respectively. Water is required for fertilization, as bryophyte sperm are flagellated and must swim to reach an egg. Because of their life cycles, bryophytes are ideally and uniquely suited to address some questions of fundamental significance in biology.

Sporophytes and gametophytes differ greatly in morphology, yet under some circumstances (e.g. bryophytes with bisexual gametophytes that self-fertilize) they differ only in ploidy: the sporophyte has the exact but duplicated genome of the gametophyte. This alternation of haploid gametophytes and diploid sporophytes that differ in morphology and function is one of the most basic aspects of plant (and indeed organismal) life cycles, and control of morphological and functional differences between gametophyte and sporophyte generations has intrigued scientists since these alternating life cycles were discovered in the nineteenth century. Given the identity in genome sequence between isogenic sporophytes and gametophytes, differences between the generations obviously derive from differences in gene expression rather than genetic composition. Technological advances during the past 20 years have for the first time allowed us to begin to understand molecular processes that underlie the alternation of generations in plants, and bryophytes have proven to be invaluable organisms for this sort of research. Yet we are only now scratching the surface in this area of inquiry: bryophytes will continue to play a central role in new developments.

For many years, bryophytes had a reputation of being “unmoving, unchanging sphinxes of the past” with little going on in terms of current evolutionary activity. In other words, evolutionarily boring! This view has proven inaccurate. Bryophyte species show local adaptation to heterogeneous environments, demonstrating their responsiveness to natural selection, and have engaged in complex speciation processes that include hybridization, polyploidization, and morphologically cryptic genetic differentiation. Indeed, the homosporous life cycle of bryophytes provides an opportunity for these organisms to exhibit more – not fewer – variations in reproductive biology than is possible in heterosporous seed plants, including angiosperms. Bryophyte species with bisexual gametophytes, those that produce both archegonia and antheridia, can undergo true or intragametophytic self-fertilization, which results in a completely homozygous sporophyte in a single generation. This is not possible in heterosporous plants because, unlike bryophytes, they form male and female gametes meiotically rather than mitotically. "Self-fertilization" in a seed plant describes the situation in which two genetically different (albeit related) gametophytes produced from the same sporophyte mate to form the next sporophyte generation. Bryophytes can engage in such sexual behavior as well, in addition to true self-fertilization. This reproductive mode, mating between different but related gametophytes, is commonly referred to as "selfing" in the seed plant literature because of a bias in the way we view plant life cycles. Coming from an angiosperm point of view, gametophytes (e.g. pollen, embryo sacs) are seen as part of the reproductive apparatus of the "individual" or "self", which is the sporophyte. There is nothing objectively accurate about viewing sexual crosses between genetically different gametophytes as "selfing", even if those gametophytes came from the same sporophyte. The common perception of sporophytes as individuals or "selfs" and gametophytes as simply parts of those "selfs" is an example of *ploidy-ism*, which can cloud our ability for insight akin to the way racism clouds our perceptions in humanistic issues. It is just as correct to think of a chicken as an egg's way of reproducing itself, as the reverse! Bryophytes offer a fresh perspective in plant reproductive biology that can loosen the intellectual shackles of an angiosperm-centered worldview.

The second edition of *Bryophyte Biology* is thoroughly revised and should be viewed as complementary to, rather than as a substitute for, the first edition. Our goal when the first edition of *Bryophyte Biology* was being developed was to produce a volume that could serve simultaneously as an intermediate to advanced text for a bryology course, and as a reference for scientists dealing with bryophytes in physiological, biochemical, molecular, or ecological research. In retrospect we felt that we only partly fulfilled our goal in making a hybrid book that serves both of these sometimes conflicting purposes. The second edition of *Bryophyte Biology* is also designed to serve both functions, and we feel that we have come closer to our goal by including new and revised chapters that cover the breadth of subjects that should be included in a bryology course, and that are also relevant to researchers working in other fields. As in the first edition, every chapter provides extensive bibliographic citations to primary literature. We consider this resource important, both for the developing student of bryology and for established scientists in some more specialized field who want to learn more about bryophytes. The first three chapters dealing with the morphology and classification of liverworts (Chapter 1), mosses (Chapter 2), and hornworts (Chapter 3) have expanded coverage of morphology as appropriate for a textbook, and also have revised classifications that reflect developments since the first edition was published. We include a new chapter (Chapter 4) on phylogenomics, reviewing relatively recent developments from using whole-genome characters to resolve phylogenetic relationships among early land plants. With the growing importance of *Physcomitrella patens* for molecular genetic research, Chapter 5 provides a timely overview of mosses as model organisms. Chapters 6–12 deal with the physiology, biochemistry, ecology, evolution, and conservation of bryophytes. A new chapter (Chapter 7) focused on desiccation tolerance in bryophytes reflects the importance of these organisms for modern molecular and biochemical research in this area. Desiccation tolerance is arguably the most thoroughly studied physiological adaptation in plants, and mosses have proven to be an invaluable group of organisms for such research. This value derives both from the relative structural simplicity of mosses and their phylogenetic position in the land plant tree of life. All chapters in the second edition of *Bryophyte Biology* are either completely new or completely revised relative to those included in the first edition.

We hope that *Bryophyte Biology*, edition 2, will provide an entry for established scientists into the literature dealing with bryophytes, and will stimulate enthusiasm among young bryology students for careers focusing on these humble but fantastic organisms.