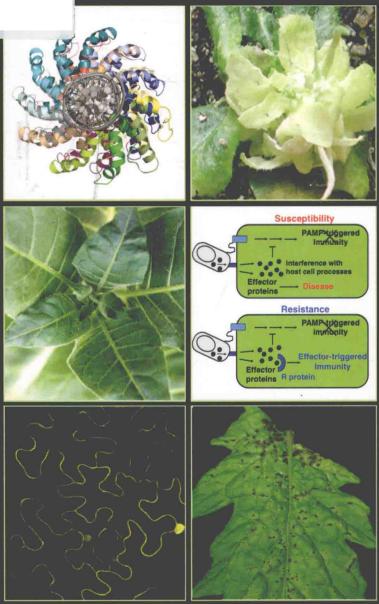
Molecular Plant Immunity



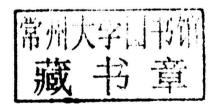
Edited by Guido Sessa

WULEY-BLACKWELL

Molecular Plant Immunity

Editor GUIDO SESSA

Department of Molecular Biology and Ecology of Plants Tel-Aviv University Tel-Aviv, Israel





A John Wiley & Sons, Inc., Publication

This edition first published 2013 © 2013 by John Wiley & Sons, Inc.

Wiley-Blackwell is an imprint of John Wiley & Sons, formed by the merger of Wiley's global Scientific, Technical and Medical business with Blackwell Publishing.

Editorial offices 2121 State Avenue, Ames, Iowa 50014-8300, USA
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
9600 Garsington Road, Oxford, OX4 2DQ, UK

For details of our global editorial offices, for customer services and for information about how to apply for permission to reuse the copyright material in this book please see our website at www.wiley.com/wiley-blackwell.

Authorization to photocopy items for internal or personal use, or the internal or personal use of specific clients, is granted by Blackwell Publishing, provided that the base fee is paid directly to the Copyright Clearance Center, 222 Rosewood Drive, Danvers, MA 01923. For those organizations that have been granted a photocopy license by CCC, a separate system of payments has been arranged. The fee codes for users of the Transactional Reporting Service are ISBN-13: 978-0-4709-5950-3/2013.

Designations used by companies to distinguish their products are often claimed as trademarks. All brand names and product names used in this book are trade names, service marks, trademarks or registered trademarks of their respective owners. The publisher is not associated with any product or vendor mentioned in this book. This publication is designed to provide accurate and authoritative information in regard to the subject matter covered. It is sold on the understanding that the publisher is not engaged in rendering professional services. If professional advice or other expert assistance is required, the services of a competent professional should be sought.

Library of Congress Cataloging-in-Publication Data Molecular plant immunity / editor, Guido Sessa.

p. cm.

Includes bibliographical references and index.

ISBN 978-0-470-95950-3 (hardback)

1. Plant immunology. 2. Molecular immunology. I. Sessa, Guido.

SB750.M665 2013 581.3'5-dc23

2012028578

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

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover design by Nicole Teut

Set in 10.5/12 pt Times by Aptara[®] Inc., New Delhi, India Printed and bound in Malaysia by Vivar Printing Sdn Bhd

1 2013

Molecular Plant Immunity

Contributors

Douglas Baker Department of Plant Pathology

University of California at Davis

Davis, California, USA

Adam J. Bogdanove Department of Plant Pathology and Microbiology

Iowa State University Ames, Iowa, USA

John P. Carr Department of Plant Sciences

University of Cambridge Cambridge, United Kingdom

Yan-Jun Chen Department of Plant Biology and Biotechnology

University of Copenhagen Copenhagen, Denmark

Gitta Coaker Department of Plant Pathology

University of California at Davis

Davis, California, USA

David B. Collinge Department of Plant Biology and Biotechnology

University of Copenhagen Copenhagen, Denmark

Ben J. C. Cornelissen University of Amsterdam

Faculty of Science, SILS Molecular Plant Pathology Amsterdam, The Netherlands

Pierre J. G. M. de Wit Laboratory of Phytopathology

Wageningen University

The Netherlands

Feng Feng State Key Laboratory of Plant Genomics

and National Center for Plant Gene Research Institute of Genetics and Developmental Biology

Chinese Academy of Sciences

Beijing, China

xii CONTRIBUTORS

Amy Wahba Foreman Department of Biological Sciences

University of South Carolina Columbia, South Carolina, USA

Aaron W. Hummel Department of Plant Pathology and Microbiology

Iowa State University Ames, Iowa, USA

Aardra Kachroo Department of Plant Pathology

University of Kentucky Lexington, Kentucky, USA

Pradeep Kachroo Department of Plant Pathology

University of Kentucky Lexington, Kentucky, USA

Michael F. Lyngkjær Department of Plant Biology and Biotechnology

University of Copenhagen Copenhagen, Denmark

Lisong Ma University of Amsterdam

Faculty of Science, SILS Molecular Plant Pathology Amsterdam, The Netherlands

Gregory B. Martin Boyce Thompson Institute for Plant Research

Ithaca, New York, USA

Bilal Ökmen Laboratory of Phytopathology

Wageningen University

The Netherlands

Chang Jin Park Department of Plant Pathology and the Genome Center

University of California at Davis

Davis, California, USA

Gail J. Pruss Department of Biological Sciences

University of South Carolina Columbia, South Carolina, USA

Pamela C. Ronald Department of Plant Pathology and the Genome Center

University of California at Davis

Davis, California, USA

Thierry Rouxel INRA-Bioger

Thiverval-Grignon, France

Frank L. W. Takken University of Amsterdam

Faculty of Science, SILS Molecular Plant Pathology Amsterdam, The Netherlands Brett M. Tyler

Center for Genome Research and Biocomputing

Department of Botany and Plant Pathology

Oregon State University Corvallis, Oregon, USA

Vicki Vance

Department of Biological Sciences

University of South Carolina Columbia, South Carolina, USA

Harrold A. van den Burg University of Amsterdam

Faculty of Science, SILS
Molecular Plant Pathology
Amsterdam, The Netherlands

André C. Velásquez

Department of Plant Pathology and Plant-Microbe Biology

Cornell University Ithaca, New York, USA

Jack H. Westwood

Department of Plant Sciences University of Cambridge Cambridge, United Kingdom

Jian-Min Zhou

State Key Laboratory of Plant Genomics and National Center for Plant Gene Research Institute of Genetics and Developmental Biology

Chinese Academy of Sciences

Beijing, China



Preface

Plants and pathogens are constantly engaged in an "arms race," each party competing to develop molecular weapons for the defeat of its enemy. As a result, plants are equipped with a sophisticated immune system for the recognition of invading pathogens, transmission of alarm signals, and rapid activation of efficient defense responses that limit infection. Concurrently, pathogens have developed strategies to cause disease through sabotaging the plant immune system. In an era of growing food demand for the sustainment of the world's population, understanding the molecular mechanisms of plant immunity and microbial pathogenicity is of cardinal importance for devising strategies that limit the large yield losses owing to plant diseases.

This book provides comprehensive coverage of the molecular basis of plant disease resistance by reviewing fundamental features of the plant immune system as well as the most recent insights into this important field of plant biology. Chapter 1 describes recognition of a novel bacterial quorum sensing factor by the rice Xa21 receptor, representing a paradigm for how a first line of immune responses is activated on recognition of conserved molecular signatures of microbial pathogens by plant transmembrane receptors. Chapters 2 and 3 review molecular mechanisms involving resistance (R) proteins, an additional class of immune receptors responsible for the activation of a second line of immune responses. Topics covered in these chapters include structure, control, and activation of R proteins; molecular mechanisms mediating effector recognition by R proteins; and signaling pathways acting downstream of R proteins and leading to the activation of effective immune responses. Chapter 4 describes the role of the plant hormones salicylic acid and jasmonic acid in signaling pathways downstream of immune receptors. Chapters 5, 6, and 7 discuss molecular features of pathogen effector proteins of bacteria, fungi, and oomycetes that interfere with plant immunity and contribute to bacterial and fungal pathogenicity. Chapter 8 presents molecular mechanisms that modulate the interaction between plants and viruses. Chapters 9, 10, and 11 focus on plant-pathogen interactions representing model systems for the interplay between host plants and bacterial, fungal, or viral pathogens. Chapter 12 describes future prospects for genetically engineering disease-resistant plants.

I would like to thank all the authors for their excellent contributions that integrate well-established and emerging concepts to provide an up-to-date review of the state of the art in the challenging field of molecular plant immunity.

Guido Sessa

Molecular Plant Immunity

Contents

Contributor Preface	'S	xi xv
Chapter 1	The Rice Xa21 Immune Receptor Recognizes a Novel Bacterial Quorum Sensing Factor Chang Jin Park and Pamela C. Ronald	1
	Introduction Plants and Animal Immune Systems A Plethora of Immune Receptors Recognize Conserved Microbial Signatures Ax21 Conserved Molecular Signature Non-RD Receptor Kinase Xa21 XA21-Mediated Signaling Components Cleavage and Nuclear Localization of the Rice XA21 Immune Receptor Regulation in the Endoplasmic Reticulum: Quality Control of XA21 Systems Biology of the Innate Immune Response Acknowledgments References	1 2 3 8 11 13 14 15 16
Chapter 2	Molecular Basis of Effector Recognition by Plant NB-LRR Proteins Lisong Ma, Harrold A. van den Burg, Ben J. C. Cornelissen, and Frank L. W. Takken	23
	Introduction Building Blocks of NB-LRRs; Classification and Structural Features of	23
	Subdomains Putting the Parts Together: Combining the Domains to Build a Signaling Competent NB-LRR Protein Stabilization and Accumulation of NB-LRR Proteins: Their Maturation and	24 29
	Stabilization	30
	When the Pathogen Attacks: Perception and Signaling by NB-LRR Proteins	33
	Conclusion	35
	Acknowledgments	35
	References	36

vi CONTENTS

Chapter 3	Gitta Coaker and Douglas Baker	41
	Introduction	41
	R Protein Stability	42
	Genetic Separation of CC and TIR-NB-LRR Signaling	42
	NB-LRRs Exhibit Modular Structure and Function	44
	Subcellular Localization of NB-LRRs	45
	NB-LRRs Can Function in Pairs	47
	Common Immune Signaling Events Downstream of R Protein Activation Conclusion	48
	Acknowledgments	50 50
	References	50
Chapter 4	The Roles of Salicylic Acid and Jasmonic Acid in Plant Immunity	55
	Pradeep Kachroo and Aardra Kachroo	
	Introduction	55
	Biosynthesis of SA	55
	Derivatives of SA	57
	SA Signaling Pothywyy	58
	SA Signaling Pathway Jasmonates Mediate Plant Immunity	60 62
	JA Biosynthetic Mutants Are Altered in Microbial Defense	63
	Receptor Protein Complex Perceives JA	65
	Transcription Factors Regulate JA-Derived Signaling	66
	JA Regulates Defense Gene Expression	68
	Conclusion	68
	Acknowledgments	68
	References	69
Chapter 5	Effectors of Bacterial Pathogens: Modes of Action and Plant Targets Feng Feng and Jian-Min Zhou	81
	Introduction	81
	Overview of Plant Innate Immunity	81
	Overview of Type III Effectors	83
	Host Targets and Biochemical Functions	86
	Conclusion	99
	Acknowledgments	99
	References	99
Chapter 6	The Roles of Transcription Activator-Like (TAL) Effectors in Virulence and	
	Avirulence of <i>Xanthomonas</i> Aaron W. Hummel and Adam J. Bogdanove	107
	Introduction	107
	TAL Effectors Are Delivered into and May Dimerize in the Host Cell	107

CONTENTS	

	TAL Effectors Function in the Plant Cell Nucleus	108
	AvrBs4 Is Recognized in the Plant Cell Cytoplasm	109
	TAL Effectors Activate Host Gene Expression	109
	Central Repeat Region of TAL Effectors Determines DNA Binding Specificity	110
	TAL Effectors Wrap Around DNA in a Right-Handed Superhelix	111
	TAL Effector Targets Include Different Susceptibility and Candidate	111
	Susceptibility Genes	112
	1 2	
	MtN3 Gene Family Is Targeted by Multiple TAL Effectors	114
	Promoter Polymorphisms Prevent S Gene Activation to Provide Disease	
	Resistance	115
	Nature of the Rice Bacterial Blight Resistance Gene xa5 Suggests TAL Effector	
	Interaction With Plant Transcriptional Machinery	115
	Executor R Genes Exploit TAL Effector Activity for Resistance	116
	Diversity of TAL Effectors in Xanthomonas Populations Is Largely Unexplored	117
	TAL Effectors Are Useful Tools for DNA Targeting	118
	Conclusion	118
	References	119
Chapter 7	Effectors of Fungi and Oomycetes: Their Virulence and Avirulence	
	Functions and Translocation From Pathogen to Host Cells	123
	Brett M. Tyler and Thierry Rouxel	
	Introduction	123
	Plant-Associated Fungi and Oomycetes	125
	Identification of Fungal and Oomycete Effectors	126
	Defensive Effectors: Effectors That Interfere With Plant Immunity	137
	Offensive Effectors: Effectors That Debilitate Plant Tissue	146
	Effectors That Contribute to Fitness via Unknown Mechanisms	149
	Entry of Intracellular Effectors	149
	Genome Location and Consequences for Adaptation/Dispensability	152
	Conclusion	153
		154
	Acknowledgments	
	References	154
Chapter 8	Plant-Virus Interaction: Defense and Counter-Defense	169
-	Amy Wahba Foreman, Gail J. Pruss, and Vicki Vance	
	Introduction	169
	RNA Silencing as an Antiviral Defense Pathway - the Beginning of the Story	169
	Small Regulatory RNA Biogenesis and Function	172
	The Silencing Mafia – the Protein Families	174
	Defense: Antiviral RNA Silencing Pathways	177
	Counter-Defense: Viral Suppressors of Silencing and Their Targets	178
	Viral Suppressors of Silencing and Endogenous Small Regulatory RNA Pathways	181
	References	182

viii CONTENTS

Chapter 9	Molecular Mechanisms Involved in the Interaction Between Tomato and Pseudomonas syringae pv. tomato	107
	André C. Velásquez and Gregory B. Martin	187
	Introduction	187
	PAMP-Triggered Immunity in Solanaceae	188
	Pseudomonas syringae pv. tomato Virulence Mechanisms	192
	Effector-Triggered Immunity in Solanaceae	197
	Races of Pseudomonas syringae pv. tomato	200
	ETI Is Involved in Nonhost Resistance to Pseudomonas syringae Pathovars	200
	ETI Signaling Pathways in Solanaceae	201
	Conclusion	203
	Acknowledgments	204
	References	204
Chapter 10	Cladosporium fulvum-Tomato Pathosystem: Fungal Infection Strategy and	
	Plant Responses	211
	Bilal Ökmen and Pierre J. G. M. de Wit	
	Introduction	211
	History of the Interaction Between C. fulvum and Tomato	212
	Compatible and Incompatible Interactions	212
	Cf-Mediated Downstream Signaling	219
	Effectors in Other Fungi with Similar Infection Strategies	220
	Conclusion	221
	References	221
Chapter 11	Cucumber Mosaic Virus-Arabidopsis Interaction: Interplay of Virulence	
	Strategies and Plant Responses	225
	Jack H. Westwood and John P. Carr	
	Introduction	225
	Biology of CMV	226
	Host Resistance Responses to Virus Infection	230
	Targeting of Host Factors by the Virus	236
	Phenomenon of Cross-Protection	237
	Functions of SA in Antiviral Defense	237
	Metabolic Responses to CMV Infection	239
	Vector-Mediated Transmission	240
	Conclusion	242
	Acknowledgments References	242 243
Chapter 12	Future Prospects for Genetically Engineering Disease-Resistant Plants Yan-Jun Chen, Michael F. Lyngkjær, and David B. Collinge	251
	Introduction	251
	Targets for Second-Generation Transgenic Strategies for Resistance	252
	Hormones	253