DALE WALTERS

FORTRESS PLANT

How to survive when everything wants to eat you

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OXFORD
UNIVERSITY PRESS

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Great Clarendon Street, Oxford, OX2 6DP,
United Kingdom

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide. Oxford is a registered trade mark of
Oxford University Press in the UK and in certain other countries

First Edition published in 2017

Impression: 1

Published in the United States of America by Oxford University Press
198 Madison Avenue, New York, NY 10016, United States of America

British Library Cataloguing in Publication Data
Data available

Library of Congress Control Number: 2016953029

ISBN 978–0–19–874560–0

Printed in Great Britain by
Clays Ltd, St Ives plc

For Beverley

ACKNOWLEDGEMENTS

I first thought about writing this book nearly twenty years ago when I was walking the dogs. But then my work commitments increased hugely and, reluctantly, I had to put the idea to one side. When I eventually got round to the book again, not only had the field of plant defence moved on, but I began to question whether any publisher would be willing to take on a book on this subject. Here I got lucky, because I sent some material to Latha Menon at OUP and, to my amazement and delight, she was encouraging. That encouragement led to a contract with OUP, culminating in the volume you now hold in your hands. I am grateful to Latha, not just for taking on this project, but for her support and careful editing. Others at OUP have provided support and answers to my numerous questions, and my thanks go especially to Jenny Nugee, who has the patience of a saint, and to Martha Cunneen, Carrie Hickman, Clare Jones, and Phil Henderson. Thanks also to Elizabeth Stone for her meticulous copy-editing, and Nicola Sangster for proofreading. During the writing of this book I have been helped by a number of people who answered queries, provided images and offered to read what I had written. I am grateful to Pietro Spanu, Angela Overmeyer, Richard O'Connell, Danny Kessler, Jonathan Gershenzon, Ian Grettenberger, Gerald Holmes, Martin Heil, Francis Martin, Mark Brundrett, Simon Walker, Allan Downie, John Randles, Stuart MacFarlane, Harry Evans, Neil Havis, and Graham McGrann. Parts of the text deal with historical aspects of research in specific areas. I have tried my best to get things right but I'm sure not everyone will agree with what I've written. Any errors of fact are mine alone.

When I started writing this book, I was still working and I am grateful to two successive Heads of Department (Bill Spoor and Fiona Burnett) for allowing me the freedom to pursue this venture. My special thanks, however, go to my wife Beverley. She has provided unwavering support and encouragement through every step of this journey, as she has for the past 43 years of our life together. How she put up with me while I wrote this book, when she herself was ill, is beyond me. Thanks are simply not enough.

DALE WALTERS
Prestwick
July 2016

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ABBREVIATIONS

ATP	Adenosine triphosphate
DAMP	Damage-associated molecular pattern
ETI	Effector-triggered immunity
GLR genes	GLUTAMATE RECEPTOR-LIKE genes
HAMP	Herbivore-associated molecular pattern
HCD	Hypersensitive cell death
HR	Hypersensitive response
JA-Ile	Jasmonyl-isoleucine
LRR	Leucine rich repeat
PAMP	Pathogen-associated molecular pattern
PGIP	Polygalacuronase-inhibiting protein
PTI	PAMP-triggered immunity
ROS	Reactive oxygen species
RNA	Ribonucleic acid
SAR	Systemic acquired resistance
TIR	Toll interleukin receptor
TMV	*Tobacco mosaic virus*
WASP	Wound-activated surface potential

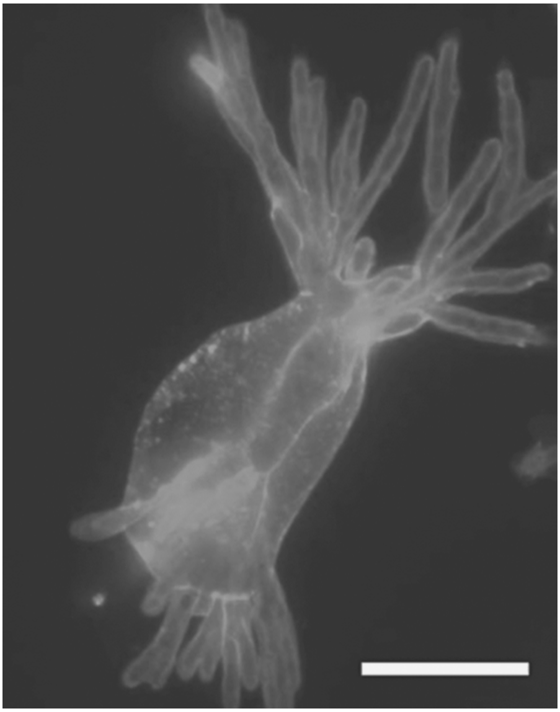

Plate 1 Powdery mildew haustorium. The powdery mildew fungus is a biotroph—it needs to keep host cells alive in order to survive. The haustorium is its feeding structure and the finger-like projections increase the surface area available for nutrient uptake from the host plant.

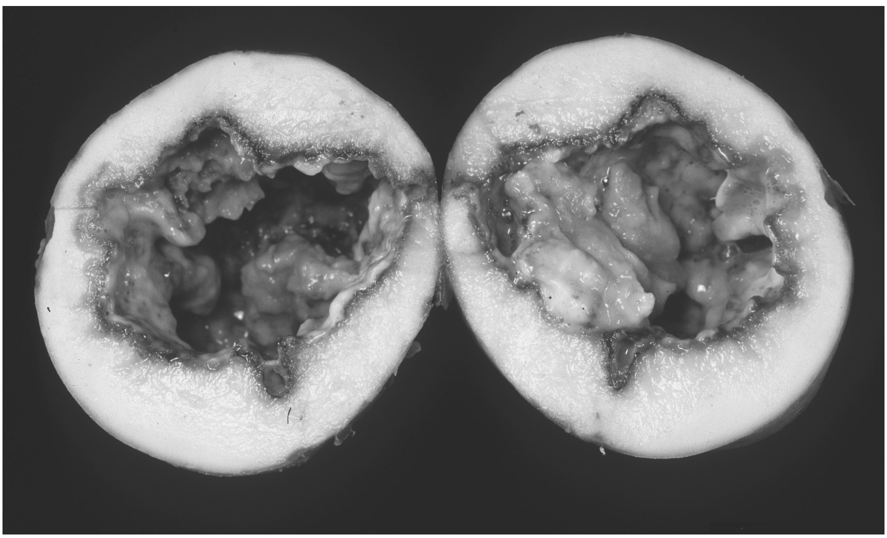

Plate 2 Soft rot of potato. Soft rot is caused by *Pectobacterium carotovorum*. It uses enzymes to break down plant cell walls, resulting in a soft mass of rotting and smelly plant tissue.

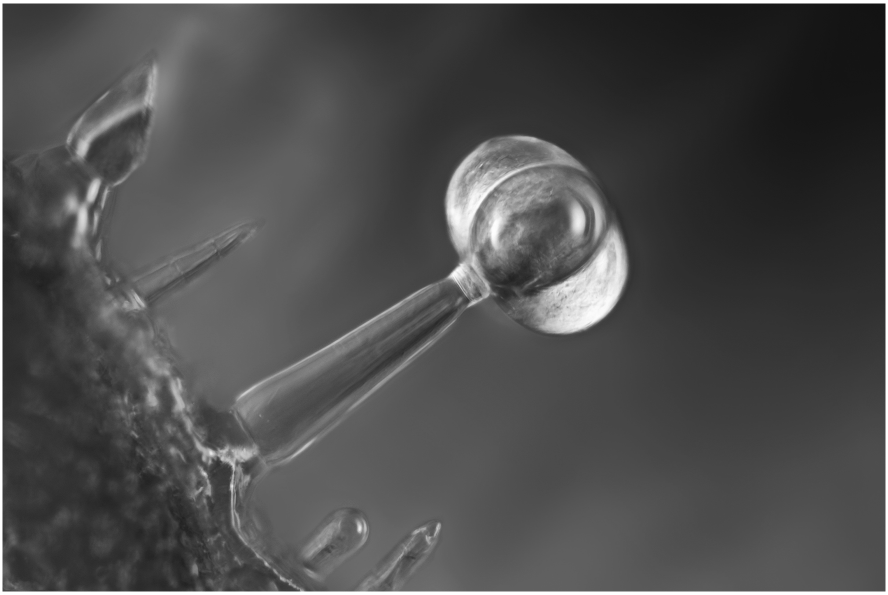

Plate 3 Light micrograph of a glandular hair (trichome) on a tomato leaf. The four secretory cells at the tip of the trichome contain essential oils important in defence against pests. The typical smell of tomato plants depends on these oils.

Plate 4 Goldenrod gall fly (*Eurosta solidaginis*). This insect lays its eggs in buds of the goldenrod plant, *Solidago altissima,* leading to the formation of galls.

Plate 5 Gall on a goldenrod plant (*Solidago altissima*) caused by the goldenrod gall fly *Eurosta solidaginis*.

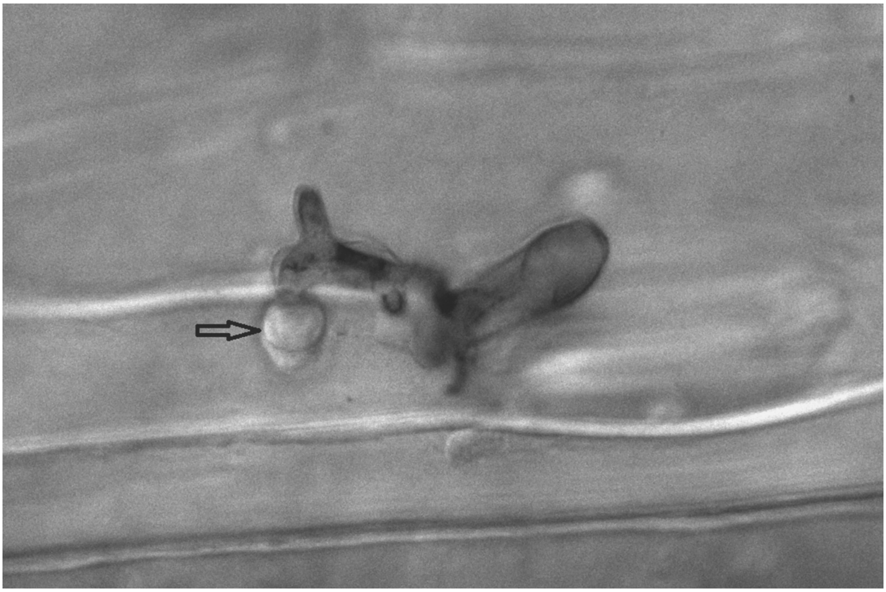

Plate 6 Papilla. This is a structural barrier produced by a plant cell in response to attack by a fungus. Here, the papilla is produced by a barley leaf cell in response to attempted penetration by the powdery mildew fungus, *Blumeria graminis* f.sp. *hordei*. Papillae are composed of the carbohydrate callose and can be impregnated with additional chemicals, such as phenolics and lignin.

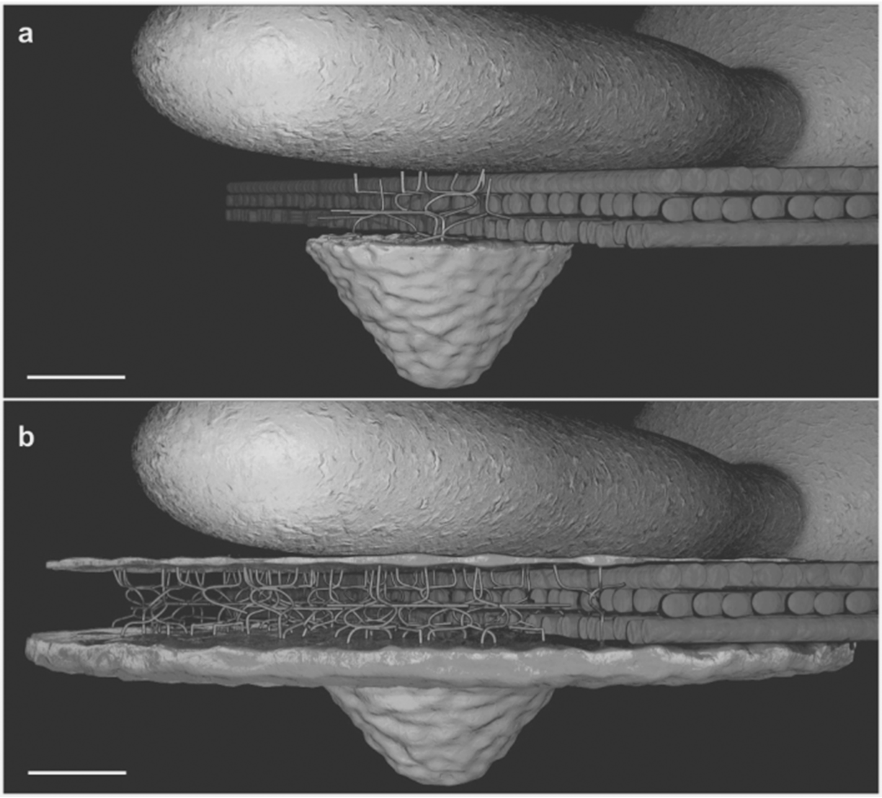

Plate 7 A 3D model of callose deposition at the site of attempted fungal penetration. The model represents the formation of callose deposits, callose/cellulose polymer networks, and superficial callose layers at sites of attempted fungal penetration six hours following attack in (a), *Arabidopsis thaliana* and (b), a mutant of *A. thaliana* expressing penetration-resistance to powdery mildew. Underneath the fungal infection structure the plant cell has responded by depositing a layer of callose and a network of callose and cellulose. The response is considerably greater in the plant exhibiting enhanced penetration resistance (b). Scale bars = 2 μm.

Plate 8 Hooked trichomes on *Mentzelia pumila* and fly trapped on a trichome-covered leaf.

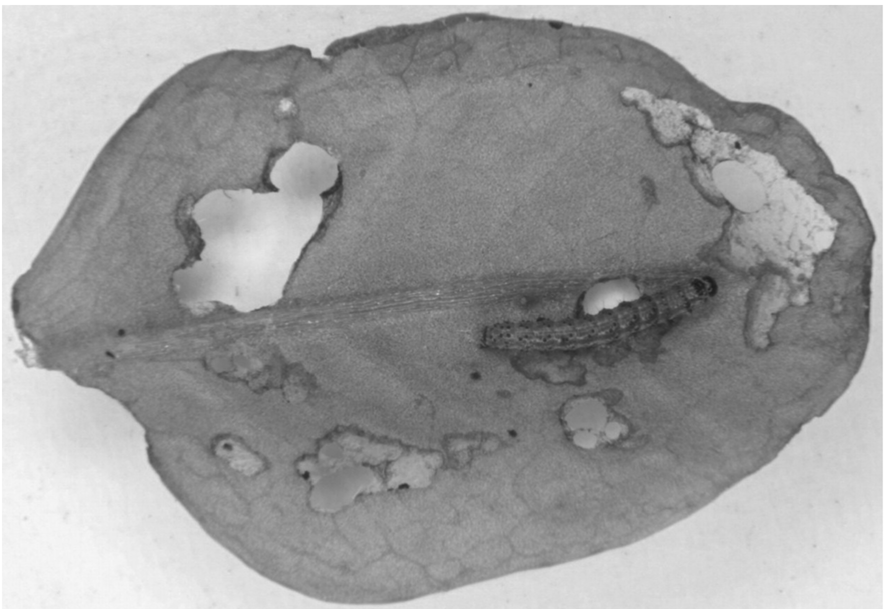

Plate 9 Feeding pattern of larvae of the cotton bollworm, *Helicoverpa armigera* on a leaf of *Arabidopsis thaliana*. Larvae of the cotton bollworm avoid feeding on the midvein and periphery of rosette leaves of *Arabidopsis* and feed instead on the inner lamina of the leaves. This feeding pattern enables the larvae to avoid toxic glucosinolates which are more abundant in the tissues of the midvein and leaf periphery than the inner lamina.

Plate 10 Highly magnified view of an arbuscule of an arbuscular mycorrhizal fungus belonging to the genus *Glomus*. This structure, which resembles a cauliflower floret, has a greatly increased surface area for effective nutrient exchange between the plant and fungal partners.

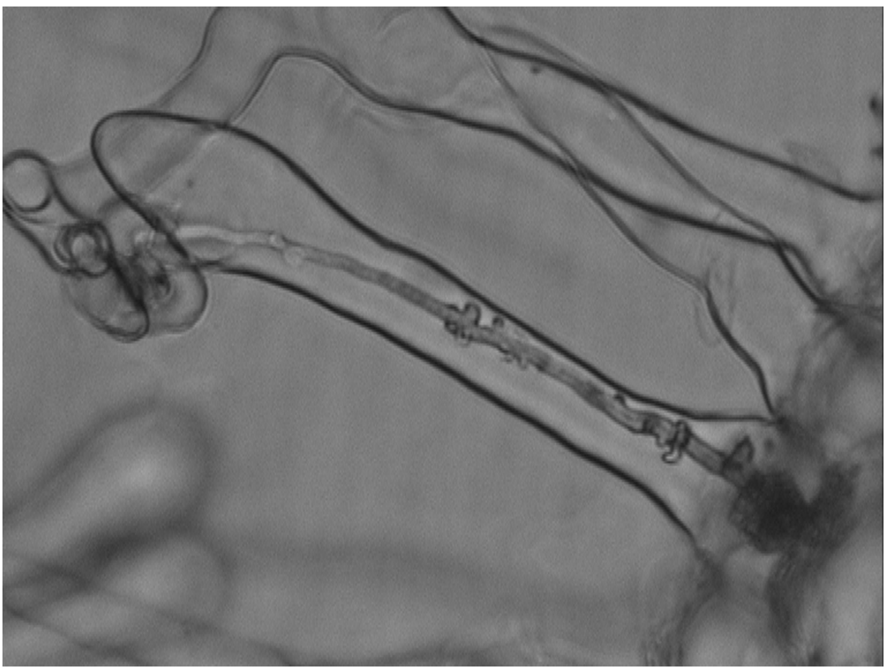

Plate 11 Light microscopy photograph of an infection thread in a root hair of the vetch *Vicia hirsuta* following infection by the nitrogen-fixing bacterium *Rhizobium leguminosarum* biovar *viciae*.