

# PLANT DEFENSE

Warding off Attack by Pathogens,  
Herbivores, and Parasitic Plants

♦ Dale R. Walters

*Crop & Soil Systems Research Group  
Scottish Agricultural College  
Edinburgh, UK*



**WILEY-BLACKWELL**

A John Wiley & Sons, Ltd., Publication

# Contents

<i>Preface</i>	x
<b>Chapter 1 Why Do Plants Need Defenses?</b>	<b>1</b>
1.1 Plants as sources of food	1
1.2 Organisms that use plants as food	2
1.2.1 Microorganisms	2
1.2.2 Parasitic angiosperms	3
1.2.3 Nematodes	5
1.2.4 Insects	5
1.2.5 Vertebrates	6
1.3 Impact of infection and herbivory in natural and agricultural ecosystems	6
1.3.1 Microorganisms	6
1.3.2 Parasitic angiosperms	7
1.3.3 Nematodes	8
1.3.4 Insects	8
1.3.5 Vertebrates	10
1.4 Conclusions	11
Recommended reading	11
References	12
<b>Chapter 2 What Defenses Do Plants Use?</b>	<b>15</b>
2.1 Introduction	15
2.2 Defenses used against pathogens	15
2.2.1 Background	15
2.2.2 Passive or preexisting defenses	17
2.2.2.1 Preexisting structural defenses	17
2.2.2.2 Preexisting chemical defenses	18
2.2.3 Active or inducible defenses	25
2.2.3.1 Inducible structural defenses	25
2.2.3.2 Inducible chemical defenses	29
2.2.4 Defenses used against pathogens—the next step	37
2.3 Defenses used against parasitic plants	37
2.3.1 Background	37
2.3.2 Preattachment defense mechanisms	38

2.3.3	Prehaustorial defense mechanisms	38
2.3.4	Posthaustorial defense mechanisms	40
2.4	Defenses used against nematodes	41
2.4.1	Background	41
2.4.2	Passive or preexisting defenses	42
2.4.3	Active or inducible defenses	43
	2.4.3.1 Phenylpropanoid metabolism	43
	2.4.3.2 Hypersensitive response	43
2.5	Defenses used against herbivorous insects	44
2.5.1	Background	44
◦ 2.5.2	Physical barriers	45
	2.5.2.1 Waxes on the leaf surface	45
	2.5.2.2 Trichomes	45
	2.5.2.3 Secretory canals	46
	2.5.2.4 Leaf toughness and leaf folding	47
2.5.3	Chemical defenses	49
	2.5.3.1 Terpenes	50
	2.5.3.2 Phenolics	52
	2.5.3.3 Nitrogen-containing organic compounds	53
	2.5.3.4 Arthropod-inducible proteins	55
	2.5.3.5 Volatile compounds	56
2.6	Defenses used against vertebrate herbivores	58
2.6.1	Background	58
2.6.2	Physical defenses	58
2.6.3	Chemical defenses	59
	2.6.3.1 Phenolic compounds	59
	2.6.3.2 Terpenoids	62
	2.6.3.3 Nitrogen-containing compounds	63
	2.6.3.4 Other chemicals	64
	2.6.3.5 A final word on chemical defenses against vertebrate herbivory	64
2.7	Defenses used against neighboring plants—allelopathy	64
2.7.1	Background	64
2.7.2	Allelopathy and the black walnut	65
2.7.3	Allelopathy and the Californian chaparral	65
2.7.4	Allelopathy and spotted knapweed	65
2.8	Conclusions	66
	Recommended reading	67
	References	67

### **Chapter 3 Sounding the Alarm: Signaling and Communication in Plant Defense**

3.1	Introduction	77
3.2	Signaling in plant–pathogen interactions	77
	3.2.1 Introduction	77
	3.2.2 Local signaling and basal resistance	78

3.2.2.1	SA signaling	78
3.2.2.2	JA signaling	79
3.2.2.3	ET signaling	80
3.2.2.4	Signaling involving other plant hormones	83
3.2.3	Systemic signaling and induced resistance	84
3.2.3.1	Induced resistance	84
3.2.3.2	Signaling during SAR	84
3.2.3.3	Signaling during ISR	85
3.2.3.4	Priming	86
3.2.4	Volatile signaling	90
3.3	◊ Signaling in plant–nematode interactions	91
3.3.1	Introduction	91
3.3.2	SA signaling	92
3.3.3	JA signaling	92
3.4	Signaling in plant–insect herbivore interactions	93
3.4.1	Introduction	93
3.4.2	Local signaling	95
3.4.2.1	JA signaling	95
3.4.2.2	ET signaling	97
3.4.2.3	SA signaling	97
3.4.2.4	Specificity and regulation of jasmonate-based defenses	97
3.4.3	Systemic signaling	99
3.4.3.1	Systemin	99
3.4.3.2	JA signaling	100
3.4.3.3	Within leaf signaling	101
3.4.4	Volatile signaling	103
3.4.5	Priming	106
3.5	Signaling in interactions between plants and vertebrate herbivores	110
3.6	Signaling in interactions between plants and parasitic plants	110
3.7	Conclusions	111
	Recommended reading	112
	References	112

## **Chapter 4 Plant Defense in the Real World: Multiple Attackers and Beneficial Interactions**

4.1	Introduction	125
4.2	Dealing with multiple attackers: cross-talk between signaling pathways	126
4.2.1	Trade-offs associated with triggering SA-mediated defenses	126
4.2.1.1	SA suppression of JA-induced defenses	126
4.2.1.2	Molecular basis of SA suppression of JA defenses	128
4.2.1.3	Ecological costs of resistance to biotrophic versus necrotrophic pathogens	130

4.2.1.4	Trade-offs with mutualistic symbioses	131
4.2.1.5	Effects of SA- and JA-mediated defenses on bacterial communities associated with plants	132
4.2.2	Triggering SA-dependent defenses does not always compromise defense against insect herbivores	133
4.2.3	Trade-offs and positive outcomes associated with triggering JA-dependent defenses	134
4.2.4	Putting it all together: orchestrating the appropriate defense response	137
4.3	Can beneficial plant–microbe interactions induce resistance in plants?	143
4.3.1	Introduction	143
4.3.2	Induction of resistance by mycorrhizas	143
4.3.3	Resistance induced by endophytic and other beneficial fungi	145
4.4	Conclusions	146
	Recommended reading	147
	References	147
<b>Chapter 5</b>	<b>The Evolution of Plant Defense</b>	<b>153</b>
5.1	Introduction	153
5.2	Hypotheses of plant defense	153
5.2.1	The growth–differentiation balance hypothesis	155
5.2.2	Optimal defense hypotheses	157
5.2.3	Plant apparency hypothesis	160
5.2.4	The carbon–nutrient balance hypothesis	160
5.2.5	The growth rate hypothesis	161
5.2.6	Hypotheses of plant defense—where next?	163
5.3	Evolution of plant defense strategies	163
5.3.1	The univariate trade-off hypothesis	163
5.3.2	The resistance–regrowth trade-off hypothesis	165
5.3.3	The plant apparency hypothesis	165
5.3.4	The resource availability hypothesis	167
5.3.5	Plant defense syndromes	167
5.4	Patterns of plant defense evolution	169
5.4.1	Adaptive radiation	170
5.4.2	Escalation of defense potency	170
5.4.3	Phylogenetic conservatism	171
5.4.4	Phylogenetic escalation and decline of plant defense strategies	171
5.5	Why do plants have induced defenses?	172
5.5.1	Costs	172
5.5.1.1	Allocation costs associated with induced responses to herbivory	175

5.5.1.2	Allocation costs associated with induced responses to pathogens	178
5.5.2	Targeting of inducible direct defenses	181
5.5.3	Targeting of inducible indirect defenses	182
5.5.4	Dispersal of damage	182
5.5.5	Possible role of pathogenic bacteria in the evolution of SAR	182
5.5.6	Conclusion	183
5.6	The coevolutionary arms race	183
5.7	Conclusions	191
	♦ Recommended reading	191
	References	192
<b>Chapter 6</b>	<b>Exploiting Plant Defense</b>	<b>201</b>
6.1	Introduction	201
6.2	Using plant resistance to protect crops—breeding	201
6.2.1	Introduction	201
6.2.2	Breeding for resistance	202
6.2.2.1	Sources of resistance	202
6.2.2.2	Breeding methods and selection strategies	203
6.2.3	Resistance in practice	205
6.2.4	Types of resistance	205
6.2.4.1	Monogenic resistance	206
6.2.4.2	Polygenic resistance	208
6.2.4.3	Durable resistance	208
6.2.4.4	Gene-for-gene concept	209
6.2.5	Making life more difficult for the attacker	211
6.3	Using plant resistance to protect crops—induced resistance	213
6.3.1	Introduction	213
6.3.2	Induced resistance for pathogen control	213
6.3.3	Induced resistance for control of herbivorous insects	218
6.3.4	Induced resistance for control of nematodes and parasitic plants	219
6.4	Using plant resistance to protect crops—biotechnological approaches	220
6.4.1	Introduction	220
6.4.2	Engineering resistance to pathogens	220
6.4.3	Engineering resistance to insects	223
6.4.4	Prospects for using transgenic resistance	224
6.5	Conclusions	224
	Recommended reading	225
	References	225
<i>Index</i>		231