

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/287234503>

Plant Resistance to Arthropods: Molecular and Conventional Approaches

Book · January 2005

DOI: 10.1007/1-4020-3702-3

CITATIONS

429

READS

1,796

1 author:



[Charles Michael Smith](#)

Kansas State University

200 PUBLICATIONS 3,305 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



molecular breeding for wheat curl mite resistance [View project](#)



distribution of barley yellow dwarf virus vectors [View project](#)



Review in Advance first posted online on September 9, 2011. (Changes may still occur before final publication online and in print.)

Molecular Bases of Plant Resistance to Arthropods

C. Michael Smith^{1,*} and Stephen L. Clement²

¹Department of Entomology, Kansas State University, Manhattan, Kansas 66506; email: cmsmith@ksu.edu

²Retired, USDA ARS Plant Germplasm Introduction and Testing Research Unit, Washington State University, Pullman, Washington 99164-6402

Annu. Rev. Entomol. 2012. 57:309–28

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-120710-100642

Copyright © 2012 by Annual Reviews.
All rights reserved

0066-4170/12/0107-0309\$20.00

*Corresponding author.

Keywords

antixenosis, antibiosis, QTL, marker-assisted selection, tolerance, virulence

Abstract

Arthropod-resistant crops provide significant ecological and economic benefits to global agriculture. Incompatible interactions involving resistant plants and avirulent pest arthropods are mediated by constitutively produced and arthropod-induced plant proteins and defense allelochemicals synthesized by resistance gene products. Cloning and molecular mapping have identified the *Mi-1.2* and *Vat* arthropod resistance genes as CC-NBS-LRR (coiled coil–nucleotide binding site–leucine rich repeat) subfamily NBS-LRR resistance proteins, as well as several resistance gene analogs. Genetic linkage mapping has identified more than 100 plant resistance gene loci and linked molecular markers used in cultivar development. Rice and sorghum arthropod-resistant cultivars and, to a lesser extent, raspberry and wheat cultivars are components of integrated pest management (IPM) programs in Asia, Australia, Europe, and North America. Nevertheless, arthropod resistance in most food and fiber crops has not been integrated due primarily to the application of synthetic insecticides. Plant and arthropod genomics provide many opportunities to more efficiently develop arthropod-resistant plants, but integration of resistant cultivars into IPM programs will succeed only through interdisciplinary collaboration.

Host plant resistance

(HPR): the sum of the genetically inherited qualities that result in a plant of one cultivar or species being less damaged by a pest arthropod than a susceptible plant lacking these qualities

Antibiosis: the adverse effects of a resistant plant on the survival, development, or fecundity of an arthropod

INTRODUCTION

The evolutionary history of terrestrial plants and their arthropod associates is inextricably linked. This coevolutionary relationship, widely accepted by biologists and ecologists, is based on an inherent feature of life on earth in which land plants and herbivores have continually adapted to changing environments and biotic pressures to survive (43, 51). Following the evolution of the earliest land plants from their aquatic ancestors in the Mid-Ordovician (~450 Ma), vascular plants began to evolve (4), followed by large-scale arthropod speciation (38). During arthropod speciation, herbivory began to impose natural selection on vascular plants, leading to plant expression of direct and indirect defensive adaptations (42, 90). In conforming with the reciprocal adaptation of interacting species (coevolutionary hypothesis), phytophagous arthropods then evolved ways to overcome plant defenses (42, 43).

Although the coevolutionary nature of arthropod–host plant associations is not universally accepted by scientists (see 42), vascular plant evolution has yielded vast genetic diversity, enabling plants to surmount biotic pressures (including arthropods) and abiotic stresses over several millennia. *Homo sapiens* inherited this plant biodiversity, recognized it, and began to use portions of it to form agrarian societies about 10,000 years ago. These first efforts at farming involved the cultivation of wild crop relatives in small gardens and fields, a far cry from today's practice of cropping high-yielding, genetically uniform cultivars on large tracks of land (51). As significant as plant genetic diversity was for early agriculture, so it is for the future of world agricultural production. Such diversity is widely recognized and highly sought by plant breeders and entomologists engaged in the development of pest–arthropod-resistant crops through the use of conventional and molecular genetic tools to characterize arthropod–plant relationships (30, 115, 125, 144).

In modern agriculture, host plant resistance (HPR) is an integral component, if not the foundation, of arthropod pest regulation in integrated pest management (IPM) programs (90, 115, 125). The ecological benefits associated with the deployment of resistance are reduced or eliminated insecticide applications and residues, cleaner streams and lakes, and reduced mortality of beneficial arthropod populations. Arthropod-resistant cultivars are economically advantageous for producers because arthropod control is included in the cost of the seed alone (115). The annual value of arthropod resistance genes currently deployed in global agriculture is greater than US\$2 billion (115). A detriment to the use of resistant cultivars is yield drag or other plant fitness costs related to the use of resistance genes from wild relatives of crop species and other unadapted plant germplasm. In a few instances, the level of antibiosis resistance in a cultivar from such relatives may be incompatible with some biological control agents (47). Moreover, antibiosis resistance (see below) controlled by single genes inherited as dominant traits may be transitory, which could promote the development of populations of virulent individuals that are unaffected by plant resistance genes (42, 115, 125, 138).

This review is an in-depth examination of molecular genetic tools and approaches for HPR to arthropod pests, with specific attention given to advances in using these tools and approaches to develop a wide diversity of resistant germplasm and crop cultivars over the past decade. Thus, we update and complement previous literature on the subject (88, 104, 115, 118, 138, 144). We briefly cover the history, basic concepts (resistance categories and mechanisms), factors affecting the expression of plant resistance, and transgenic plant resistance to arthropods because previous reviews have comprehensively addressed these subjects. We conclude this review by describing the current state of affairs regarding the integration and deployment of arthropod resistance genes into IPM programs, and in so doing, we attempt to determine the extent molecular genetic and genomic innovations have benefited producers and consumers through the delivery of arthropod-resistant crops.

PLANT RESISTANCE TO ARTHROPOD PESTS: VIGNETTES

History

Farmers engaged in the early practice of agriculture in the Fertile Crescent and other regions of the world several thousand years ago likely recognized that the plants they selected for agricultural purposes varied in susceptibility to pests (51, 90). Insect-resistant cultivars were cultivated much later, during the onset of applied entomology in the eighteenth and nineteenth centuries. Such cultivars included *Mayetiola destructor*-resistant wheat (cv. Underhill) in the 1780s in New York and *Eriosoma lanigerum*-resistant apple cultivars (cv. Winter Majetin) in the United Kingdom. Additionally, the grafting of European grapevines onto rootstocks of native American grapes resistant to *Daktulosphaira vitifoliae* restored the profitability of the French wine industry (90, 113).

The breeding of arthropod-resistant plants was formalized after the rediscovery of Mendel's law of heredity in 1900 and blossomed as a field of research in the first half of the twentieth century with the work of Painter (88). Over the past 60 years, breeding crops for pest resistance has accelerated through the efforts of public- and private-sector plant breeders and entomologists in several countries, including active involvement of researchers at Consultative Group for International Agricultural Research (CGIAR) agricultural research centers. These efforts led to spectacular successes in developing arthropod-resistant crops during the Green Revolution in Southeast Asia during the 1960s. A classic example is the development of the rice cultivar IR36, which is resistant to multiple insect pests. This cultivar, developed at the International Rice Research Institute in the 1970s and cropped on 11 million ha by the early 1980s, provided an annual income increase of approximately \$1 billion to Asian rice farmers (90, 115).

By the mid-1970s, over 500 arthropod-resistant cultivars and parent and germplasm lines of food and fiber crops had been developed and registered in the United States (113). Moreover, twentieth-century researchers recorded resistance to several arthropod pest species in crop cultivars not intentionally selected for resistance (58). With the advent and use of molecular tools over the past 30 years, the field of plant resistance to arthropods has been transformed into a new era, offering enormous opportunities for continued development of new crop cultivars with genes for durable arthropod resistance (85, 115, 144).

Resistance Categories

Plant tolerance is a complex set of genetic traits that enable a plant to withstand or recover from arthropod damage. This plant characteristic, which does not adversely affect the growth and survival of attacking arthropods, exists in crop cultivars across a wide taxonomic range (90, 115). Antixenosis describes the nonpreference reaction of arthropods to a resistant plant. Antixenosis occurs when plant morphological or chemical factors adversely affect arthropod behavior, leading to delayed acceptance and possible outright rejection of a plant as a host. By contrast, the antibiosis category of plant resistance occurs when a resistant plant adversely affects the life-history traits (survival, development, fecundity) of an arthropod attempting to use that plant as a host (**Figure 1**). **Table 1** presents the category(s) of resistance identified for more than 40 arthropod resistance genes presently characterized by molecular mapping. Antibiosis resistance alone or in combination with other categories has been identified in more than 90% of the cases in **Table 1**. Conversely, plant tolerance has been identified in less than 10% of the cases. Several excellent reviews on resistance categories in a wide diversity of crop cultivars and germplasm lines have been published (30, 90, 115).

Tolerance:

a polygenic trait enabling a plant to withstand or recover from arthropod damage without adversely affecting the growth or survival of the attacking arthropod

Antixenosis:

the nonpreference reaction of an arthropod to a resistant plant that occurs when biophysical or allelochemical factors adversely affect arthropod behavior, leading to delayed acceptance and possible outright rejection of a plant as a host



Table 1 Crop-plant arthropod resistance genes, number of resistance loci, gene products (where known), inheritance of resistance, and phenotypic resistance categories

Plant	Arthropod pest(s)	Order	Gene(s) ^a	Category(ies)	Reference(s) ^b
Apple	<i>Dysaphis devectora</i>	Hemiptera	<i>Sd- (3)</i> ; QTLs	Ab	25, 123
	<i>Dysaphis plantaginea</i>	Hemiptera	<i>Sm-b</i> ; QTLs	Ab	2, 123
	<i>Eriosoma lanigerum</i>	Hemiptera	<i>Er (3)</i>	Ab, Ax	18, 106
Barley	<i>Diuraphis noxia</i> ,	Hemiptera	<i>Rdn (2)</i> ; QTLs unnamed; QTLs	Ab, Tol	27, 82, 83
	<i>Rhopalosiphum padi</i>	Hemiptera			
	<i>Schizaphis graminum</i>	Hemiptera	<i>Rsg (2)</i>	Ab, Tol	94
Barrel medic	<i>Acyrtosiphon kondoi</i> ,	Hemiptera	<i>AKR, AIN RAPI TTR</i>	Ab, Ax, Tol	63, 122
	<i>Acyrtosiphon pisum</i> ,	Hemiptera		Ab, Ax, Tol	
	<i>Therioaphis maculata</i>	Hemiptera		Ab, Ax, Tol	
Common bean	<i>Apion godmani</i> ,	Coleoptera	<i>Arc1 (2)</i> (arcelin) <i>Agm, Agr</i>	Ab	8, 9, 87
	<i>Zabrotes subfasciatus</i>	Coleoptera		Ab	
	<i>Thrips palmi</i>	Thysanoptera	Unnamed; QTLs	Tol	41
Cowpea	<i>Aphis craccivora</i>	Hemiptera	<i>Rac (2)</i>	Ab	84
Lettuce	<i>Nasonovia ribisnigri</i>	Hemiptera	<i>Nr</i>	Ab	76
	<i>Pemphigus bursarius</i>	Hemiptera	<i>Ra</i> or <i>Lra</i>	Ab	141
Maize	<i>Ostrinia nubilalis</i>	Lepidoptera	<i>bx (7)</i> DIMBOA, leaf cell wall factors; QTLs	Ab	19, 20
	<i>Diatraea grandiosella</i> ,	Lepidoptera	<i>Glossy15 (1)</i> (leaf structure); QTLs	Ab	12, 17
	<i>Diatraea saccharalis</i>	Lepidoptera			
	<i>Spodoptera frugiperda</i>	Lepidoptera	<i>Mir (4)</i> (cysteine proteinase)	Ab	92
	<i>Helicoverpa zea</i>	Lepidoptera	<i>p1 (1)</i> (maysin); QTLs	Ab	48, 148
	<i>Rhopalosiphum maidis</i>	Hemiptera	<i>aph (2)</i>	Ab	21
Melon	<i>Aphis gossypii</i>	Hemiptera	<i>Vat (1)</i> (CC-NBS-LRR); QTLs	Ab, Ax	13, 33
Mungbean	<i>Callosobruchus</i> spp.,	Coleoptera	<i>Br (1)</i>	Ab	70
	<i>Zabrotes subfasciatus</i> ,	Coleoptera			
	<i>Riptortus clavatus</i>	Coleoptera			
Pea	<i>Bruchus pisorum</i>	Coleoptera	<i>Np</i>	Ab	34
Peach	<i>Myzus persicae</i>	Hemiptera	<i>Rm1</i>	Ab, Ax	91
Peanut	<i>Aphis craccivora</i>	Hemiptera	Unnamed	Ab	49
Pear	<i>Dysaphis pyri</i>	Hemiptera	<i>Dp-1</i>	Ab	39
Perennial ryegrass	<i>Listronotus bonariensis</i>	Coleoptera	<i>perA</i> (peramine-endophyte alkaloid)	Ax	129
Potato	<i>Leptinotarsa decemlineata</i>	Coleoptera	<i>Lep, AL (2)</i> (leptine alkaloids); QTLs	Ab, Ax	105
Raspberry	<i>Amphorophora idaei</i>	Hemiptera	<i>A (12), dw</i>	Ab, Ax	7, 107
Rice	<i>Nilaparvata lugens</i>	Hemiptera	<i>Bpb (≥23)</i> ; <i>Qbp (2)</i> ; QTLs	Ab, Ax, Tol	98, 99, 102
	<i>Sogatella furcifera</i>	Hemiptera	<i>Wbpb (6), wbpb (1)</i>	Unknown	128
	<i>Laodelphax striatellus</i>	Hemiptera	Unnamed; QTLs	Ab, Ax, Tol	35
Sorghum	<i>Schizaphis graminum</i>	Hemiptera	<i>Ssg (9)</i> ; QTLs	Ab, Tol	143
	<i>Stenodiplosis sorghicola</i>	Diptera	Unnamed; >1; QTLs	Ab, Ax	130, 131
	<i>Atherigona soccata</i>	Diptera	<i>Trit</i> ; QTLs	Ax	108
Soybean	<i>Aphis glycines</i>	Hemiptera	<i>Rag (3), rag (2)</i> ; QTLs	Ab, Ax	50, 78, 147
	<i>Helicoverpa zea</i>	Lepidoptera	Unnamed; QTLs	Ab, Ax	101

(Continued)

Table 1 (Continued)

Plant	Arthropod pest(s)	Order	Gene(s) ^a	Category(ies)	Reference(s) ^b
Tall fescue	<i>Rhopalosiphum padi</i> ,	Hemiptera	<i>LOL</i> (2); (loline-endophyte alkaloid)	Ab, Ax	89, 109, 121
	<i>Spodoptera frugiperda</i> ,	Lepidoptera			
	<i>Schizaphis graminum</i>	Hemiptera			
Tomato	<i>Macrosiphum euphorbiae</i> ,	Hemiptera	<i>Mi-1.2</i> (CC-NBS-LRR)	Ab, Ax	22, 86, 103
	<i>Bemisia argentifolii</i> ,	Hemiptera			
	<i>Bemisia tabaci</i> ,	Hemiptera			
	<i>Bactericerca cockerelli</i>	Hemiptera			
Wheat	<i>Mayetiola destructor</i>	Diptera	<i>H</i> (>33)	Ab	6
	<i>Diuraphis noxia</i>	Hemiptera	<i>Dn</i> (10); QTLs	Ab, Ax, Tol	68, 72
	<i>Schizaphis graminum</i>	Hemiptera	<i>Gb</i> (>10); QTLs	Ab, Ax, Tol	150
	<i>Sitodiplosis mosellana</i>	Diptera	<i>Sm</i> (1); QTL	Ab, Ax	46, 134
	<i>Cephus cinctus</i>	Hymenoptera	<i>Qssmsub</i> (2); QTLs	Ab, Ax, Tol	66, 112
	<i>Aceria tosichella</i>	Acari	<i>Cmc</i> (4)	Ab	74

^aGene symbol (lowercase denotes recessive inheritance); number of resistance loci; resistance factor(s) if known; QTLs indicates multiple resistance loci mapped.

^bSee **Supplemental References** for additional references on each plant-arthropod combination. Abbreviations: Ab, antibiosis; Ax, antixenosis; QTL, quantitative trait locus; Tol, tolerance.

Resistance Mechanisms

Here we use the term mechanism “to describe the underlying chemical or morphological plant processes that, where known, are responsible for the negative reactions of arthropods to resistant plants (115). Over time, plants evolved traits for direct and indirect defense mechanisms to counteract arthropod attacks. Direct defenses include structural barriers such as tissue toughness, plant pubescence, and glandular and nonglandular trichomes. Direct defenses also include allelochemicals in plant tissues exhibiting antifeedant, toxic, or repellent effects on attacking arthropods, such as cyanogenic glycosides, digestive enzyme inhibitors, lectins, glucosinolates, alkaloids, and terpenoids (104, 116). Constitutive and induced morphological and chemical plant defenses mediating antixenosis and antibiosis have been extensively reviewed (26, 90, 115, 124) (**Figure 1**). Indirect defenses consist of volatile organic compounds released by pest-arthropod-damaged plants that attract arthropod predators and parasitoids or that repel oviposition of pest arthropods (59). Herbivore-associated molecular patterns (HAMPs) represent specific plant indirect defense responses to specific herbivore-derived elicitors in oral or ovipositor secretions that facilitate indirect defenses against herbivores (81). The most-studied HAMPs are insect fatty acid-plant amino acid conjugates from lepidopterous larvae (59, 110) (**Figure 1**).

Transgenic Resistance

Transgenes from *Bacillus thuringiensis* (*Bt*), which encode insecticidal crystalline proteins and other genes for proteins exhibiting toxicity to or growth inhibition of arthropods (proteinase inhibitors, α -amylase inhibitors, lectins, chitinases), have been expressed effectively in the genomes of many crop plants during the past 30 years. Transgenic *Bt* cotton, maize, and rice cultivars that express resistance to several lepidopteran pests are now major components of agriculture (97). Both *Bt* and non*Bt* transgenic plants are often referred to as insecticidal plants and express, in plant resistance

Resistance mechanisms: directly and indirectly expressed allelochemical or biophysical plant factors responsible for incompatible interactions between an arthropod and a resistant plant



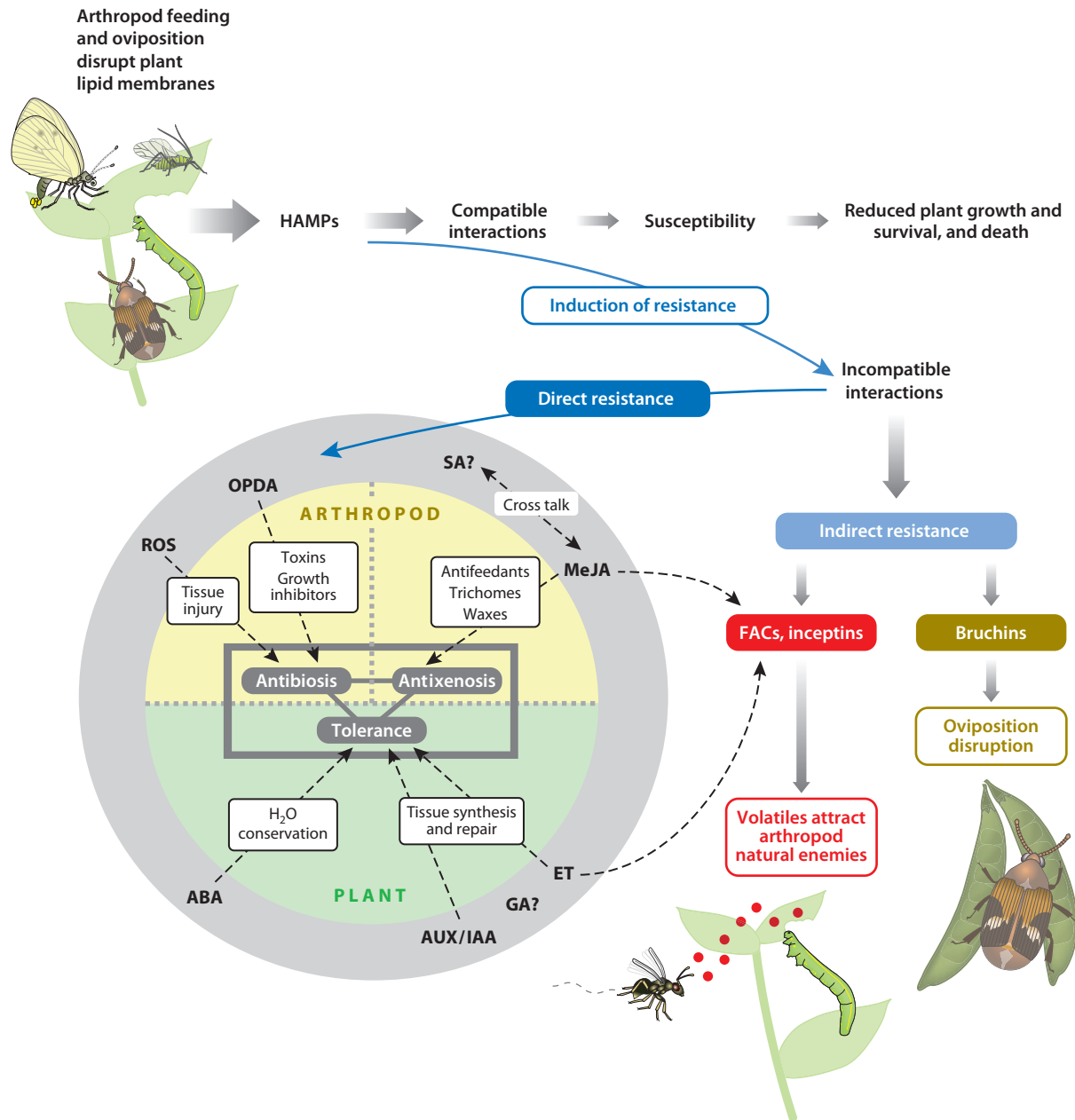


Figure 1

Representative steps in the activation of plant defense responses to HAMPs resulting in compatible plant-arthropod interactions (plant susceptibility) or incompatible interactions (plant resistance) after induction of phytohormone-based signaling pathways that activate direct or indirect resistance responses. Direct resistance may result from induction of MeJA, OPDA, ROS, or SA, which produce anti-arthropod factors expressed as antibiosis or antixenosis, or from induction of ABA, ET, GA, or IAA, which produce plant metabolic components that contribute to expression of tolerance. Arthropod or plant factors contributing to antibiosis, antixenosis, or tolerance may result from either induced or constitutive resistance gene expression. Abbreviations: ABA, abscisic acid; AUX, auxin; ET, ethylene; FAC, fatty acid-plant amino acid conjugate; GA, gibberellic acid; HAMP, herbivore-associated molecular pattern; IAA, indole-3-acetic acid; MeJA, methyl jasmonate; OPDA, 12-oxo-phytodienoic acid; ROS, reactive oxygen species; SA, salicylic acid.

terms, an extreme degree of antibiosis. Insect virulence (the ability to overcome *Bt*) to *Bt* toxins is well documented in the laboratory (127). In the field, the longevity of *Bt* transgenes is successfully extended through the use of insect resistance management programs centered on nontransgene refuge areas that allow survival of individual arthropods homozygous for susceptibility to the *Bt* toxin (44). *Bt* cotton and maize production have substantial economic benefit to producers of non*Bt* crops (54, 142). RNAi technology for insect pest management has also been developed (5) and is becoming available commercially. A thorough discussion of transgenic resistance based on nonplant sources is well beyond the scope of this review, given numerous reviews on the subject (45, 111).

Factors Affecting Expression of Plant Resistance

Numerous examples illustrate how variables such as the age and density of insects and plants, along with environmental variables (light duration and quantity, temperature, and soil micronutrients), influence expression of plant resistance (90, 115). In addition, fungal endophytes and their secondary metabolites affect the expression of HPR to insects (93).

CONSTITUTIVE AND INDUCED RESISTANCE GENES

Selection of a host-plant tissue substrate by an arthropod depends on a suite of well-coordinated interactions between an evolutionarily conserved protein(s) encoded by the attacking arthropod and the responding host plant. Compatible arthropod-plant interactions result in successful manipulations of the host plant by the arthropod, whereas incompatible arthropod-plant interactions prove unsuccessful for the arthropod and ensure that attacked plants survive (56) (**Figure 1**). In both interactions, plant and fungal endophyte genes expressed either constitutively or through an induced defense response following herbivory are involved in arthropod resistance (126, 135). Limited research to date indicates that effects controlled by constitutive genes more fully explain resistance under field conditions than do effects due to induced gene expression (53, 136). Plant- and plant-endophyte-derived constitutive genes controlling production of defense allelochemicals associated with resistance are shown in **Table 1**.

In response to arthropod herbivory plants generate reactive oxygen species and signal cascades involving jasmonic acid (JA), salicylic acid (SA), ethylene, abscisic acid, and gibberellic acid that result in downstream production of direct and indirect defense proteins (32, 61, 69, 71) (**Figure 1**). Defense signals may also be products of aphid bacterial endosymbionts (57).

Initial reviews indicated that plant tissue damage from arthropods with chewing mouthparts elicits JA-based transcriptomes, whereas JA-SA-based transcriptomes are induced by arthropods with piercing-sucking mouthparts (59). However, JA-SA signaling induced by both types of herbivory, as well as JA-SA cross-talk, has recently been demonstrated (56, 117, 119, 137). JA, 12-oxo-phytodienoic acid, and jasmonoyl-amino acid conjugates (governed by zinc finger protein expressed in inflorescence meristem) repressor proteins control the expression of many plant genes produced in the initial responses to arthropod herbivory (52). Defense response gene up-regulation via JA and other pathways results in the production of many defense allelochemicals (26) (**Figure 1**). Less is known about arthropod-induced expression of plant metabolism genes, but sparse evidence indicates that some of these genes are downregulated in the initial hours after the onset of arthropod herbivory and subsequently upregulated during ensuing days. (117, 149, and **Supplemental References**, follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>).

Only two arthropod resistance genes have been sequenced, *Mi-1.2* from tomato and *Vat* from melon. *Mi-1.2* is a CC-NBS-LRR (coiled coil–nucleotide binding site–leucine rich repeat) gene

Transgenic resistance:

the movement of an arthropod resistance gene from a crop plant, an inaccessible gene pool, or an unrelated organism into a crop plant

Compatible arthropod-plant interactions:

successful manipulations of a host plant by an arthropod that renders the plant susceptible

Incompatible arthropod-plant interactions:

unsuccessful manipulations of a host plant by an arthropod resulting in survival of a resistant plant

Mi-1.2:

a CC-NBS-LRR subfamily gene from tomato conferring resistance to *Meloidogyne incognita* and multiple insect species

Vat: a CC-NBS-LRR subfamily gene from melon conferring resistance to virus transmission by *Aphis gossypii*



Quantitative trait loci (QTL): stretches of DNA containing groups of loci linked to multiple genes affecting arthropod resistance

conferring resistance to multiple species of insects and nematodes (22, 86, 103, and **Supplemental References**). *Vat*, also a CC-NBS-LRR gene, confers resistance to *Aphis gossypii* (33). The LRR region of *Mi-1.2* signals programmed cell death, and one model proposes a gene-for-gene interaction between *Mi-1.2* and aphid elicitors that is similar to plant-pathogen interactions (55). Other studies suggest NBS-LRR involvement in aphid resistance in other crops (14, 16, 119, 141). Arthropod pest elicitors of resistance genes have yet to be identified, but an undefined *Diuraphis noxia* elicitor protein is recognized by wheat plant receptors, and plant-signaling gene products recognize *D. noxia* feeding in incompatible interactions (67).

PLANT RESISTANCE GENES FOR ARTHROPOD PEST MANAGEMENT

The preceding sections in this review and a large body of literature on HPR to arthropods demonstrate the considerable success of plant breeders and entomologists in using conventional plant-breeding methods to develop resistant crop cultivars over the past 50 to 60 years, as well as discovering resistant cultivars not intentionally bred for arthropod resistance. For many of these cultivars, resistance genes have not been named and the mechanistic bases of resistance remain largely unknown, although many are used in cropping systems worldwide to reduce insect and mite damage (90). By contrast, many genes have been identified, named, and correlated with categories of arthropod resistance in cultivars by using classical genetic approaches. Indeed, the vast majority of arthropod resistance genes for cereal, food and forage legumes, fruit, and vegetable cultivars (**Table 1**) have been identified through classical genetic analyses and introgressed into breeding lines and cultivars by using traditional breeding techniques. Many pertinent examples exist for major food crops (6, 7, 18, 29).

MOLECULAR MARKERS FOR ARTHROPOD RESISTANCE GENES IN CROP PEST MANAGEMENT

The emergence and continuing development of molecular tools increase the potential for more rapid breeding of resistant cultivars through the selection of genes directly linked to optimal expression of arthropod resistance (114, 115). Entomologists, breeders, and molecular biologists have used DNA markers to develop genetic linkage maps of resistance genes in apple (to *Eriosoma lanigerum*), barrel medic (to *Acyrtosiphon kondoi*, *Therioaphis maculata*), raspberry (to *Ampborophora idaei*), and wheat (to *Mayetiola destructor*, *Diuraphis noxia*, and *Schizaphis graminum*) (**Table 1**). These approaches have also provided a way to identify new resistance genes to counter damage from virulent populations of *Nilaparvata lugens* on rice (102).

Genetic mapping of quantitative trait loci (QTL) offers a highly efficient molecular approach for working with quantitative traits (115, 144). Several arthropod crop resistance QTL have been identified since Yencho et al. (144) included QTL in six crop genera for resistance to 10 arthropod species from the orders Coleoptera, Hemiptera, and Lepidoptera. **Table 1** summarizes much of the QTL literature since the early 1990s and includes QTL from four additional crop genera mapped for resistance to 11 additional arthropod species, including representatives from Diptera and Thysanoptera.

Over the past decade, QTL mapping has been used to characterize antixenotic, antibiotic resistance, and, to a lesser extent, plant tolerance, thereby increasing the possibility to develop arthropod-resistant germplasm with which to examine the individual effects of specific QTL. Such knowledge about specific QTL provides the potential to broaden the genetic bases of arthropod plant defense and to develop more durable resistance. Examples and references in **Table 1** reveal

the extent to which this information has been generated for specific crop–arthropod pest associations. For example, QTL are related to both antixenotic and antibiotic resistance to at least six insects, including *D. noxia*, *Schizaphis graminum* (23, 24), *Stenodiplosis sorghicola* (130), *Laodelphax striatella* (35), *Helicoverpa zea* (101), and *Aphis gossypii* (13). QTL also exist for antixenosis in wheat resistance to *Cephus cinctus* and *Sitodiplosis mosellana* (10, 112) and for antibiosis in apple resistance to *Dysaphis plantaginea* (123). Two antibiotic allelochemicals in maize have long been linked to insect resistance: DIMBOA [2, 4-dihydroxy-7-methoxy-2H-1, 4-benzoxazin-3 (4H)-one], the main hydroxamic acid in maize, is linked to *Ostrinia nubilalis* resistance (3), and the C-glycosyl flavone maysin in corn silks inhibits *H. zea* larval growth (139). Molecular genetic approaches have successfully elucidated QTL linked with the majority of the DIMBOA metabolic pathway *bx* genes (19), and QTL mapping has identified the *p1* locus as a key to maysin biosynthesis (148) (**Table 1**).

Molecular approaches have also significantly advanced the development and use of insect resistance in perennial ryegrass and tall fescue. Endowing cultivars of these forage grasses with strong anti-insect properties involves infecting host grasses with *Epichloë* and *Neotyphodium* fungal endophyte strains that produce minimal or no amounts of alkaloids [ergot alkaloids (including ergovaline) and indole-diterpenes (including lolitrems)] toxic to grazing livestock yet produce the necessary metabolites (peramine, pyrrolizidine lolines) for insect resistance (36, 93). Endophyte strains producing only peramine or loline alkaloids are called novel strains. In New Zealand, peramine-producing strains, when coupled with perennial ryegrass cultivars, protect plants from attack by *Listronotus bonariensis*. Infecting tall fescue cultivars with strains producing lolines provides strong plant resistance against many pest species of Coleoptera, Hemiptera, and Lepidoptera (**Table 1**) that significantly affect productivity and persistence of Australian tall fescue pastures (93). Given the biological and commercial importance of endophyte secondary metabolites (15), characterizing genes encoding endophyte alkaloid biosynthesis will expedite the development of endophyte-infected cultivars with the required bioprotective features to resist insect herbivory (93). In this regard, there has been progress in indentifying the loline biosynthesis gene clusters (*LOL-1*, *LOL-2*) (65, 121, 146), a peramine gene (*perA*) (129) (**Table 1**), the locus required for the biosynthesis of lolitrem (10 *ltm* genes) (145), and ergot biosynthesis genes (*dmaW*, *IpsA*) (89). Cloning these metabolite genes and inactivating them by gene knockout generate direct genetic evidence of the contribution of specific endophyte metabolites to insect resistance, as recently revealed by the elimination of ergot alkaloids in perennial ryegrass by endophyte gene knockout with *Agrotis ipsilon* resistance retained in the infected host (96). This molecular approach has the potential to expedite screening of diverse endophyte strains for the presence and distribution of endophyte genes that produce desirable metabolites for agricultural applications in which insect-resistant grass cultivars are required.

To what extent have breeding programs purposefully bred cultivars with named arthropod resistance genes (**Table 1**) for production agriculture? Genes have been introgressed into wheat for resistance to *D. noxia*, *M. destructor*, and *S. mosellana* (6); sorghum resistance to *S. graminum* and *S. sorghicola* (130); rice resistance to *N. lugens* (99); and mungbean resistance to *Callosobruchus chinensis* and *Riptortus clavatus* (**Supplemental References**). In addition, lettuce cultivars containing the *Nr* gene for resistance to *Nasonovia ribis* have been bred in Europe, and similar conventional breeding efforts are underway in the United States (76). For more than 30 years single major genes or polygenic minor genes have successfully protected European red raspberry cultivars from *A. idaei*, the most important vector of four raspberry viruses (7). Although apple cultivars have long been known to exhibit variable susceptibility to different species of pest aphids, resistance genes were not conclusively identified until molecular results provided answers to this question (18, 123). The initial use of maize QTL in molecular marker-assisted selection (MAS) of resistance to multiple species of stem-boring Lepidoptera was problematic due to epistatic gene interactions, with

DIMBOA:

2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3-one

bx: a maize biosynthesis gene controlling production of the hydroxamic acid DIMBOA that inhibits larval feeding of several species of pest Lepidoptera

p1: a gene controlling production of the C-glycosyl flavone maysin in maize silk that inhibits larval growth of *Helicoverpa zea*

LOL: a loline alkaloid biosynthesis gene in fungal endophytes in tall fescue that imparts resistance to pest species of Coleoptera, Hemiptera, and Lepidoptera

perA: a peramine alkaloid gene in fungal endophytes in perennial ryegrass that imparts resistance to *Listronotus bonariensis*

MAS: marker-assisted selection



Np: a gene in pea genotypes that promotes formation of neoplastic callus on pods at the oviposition sites of *Bruchus pisorum*

QTL offering no advantage over phenotypic selection (140). However, utilizing recently identified QTL for maize allelochemicals (see above) to allow accurate and efficient MAS breeding for arthropod resistance looks promising.

In addition, resistance in many cultivars has not been linked to a specific gene(s) (90, 125). This is illustrated by the incorporation of the pubescence trait into commercial soybean cultivars for resistance to *Empoasca fabae*, which has “virtually relegated this insect to nonpest status on soybean in the U.S.” (11). Conversely, there are instances in which the genetic bases of resistance have been characterized in unadapted germplasm and even in advanced breeding lines, but the utility of these resistance genes in agriculture has not been realized. A look at cool-season food legumes (chickpea, faba bean, lentil, pea) reveals little global progress in transferring resistance genes from unadapted germplasm to regionally adapted and agronomically acceptable cultivars for pest management (29, 37).

Given the large increase in global soybean production over the past 40 years, and the large number of pestiferous insects associated with this important crop, it is somewhat surprising that arthropod-resistant cultivars are not yet available to producers. Although breeding programs have developed resistant cultivars, they are not popular among soybean producers, presumably because of yield limitations (11). The arrival of *Aphis glycines* in North America in 2000 resulted in the discovery of multiple sources of aphid resistance and the naming and mapping of resistance genes (**Table 1**) (50, 147). Soybean breeding programs are benefiting from molecular-generated information, but the appearance of new soybean aphid biotypes has complicated the breeding, release, and acceptance of resistant cultivars (62). At the time of this writing, aphid-resistant cultivars were not commercially available in North America (50). Similarly, Latin American bean growers are not growing insect-resistant cultivars, although researchers have discovered dominant genes and tightly linked diagnostic molecular markers for resistance to Mexican bean weevil and bean pod weevil in common bean (**Table 1**) and have developed an improved understanding of the genetic and mechanistic bases of resistance to these pests (79 and **Supplemental References**). Finally, the *Np* gene in pea genotypes that provides resistance to *Bruchus pisorum* has not been deployed in cultivars (29, 34).

INTEGRATION OF ARTHROPOD RESISTANCE GENES INTO IPM PROGRAMS

Although hundreds of insect resistance genes have been deployed in improved cultivars globally (115), the literature offers few examples in which these cultivars have been actually combined with other methods to form IPM programs at the farm level (125, 133). An IPM approach harmoniously combines available pest management methods or tactics (HPR, biological control, cultural control, chemical control, and other methods) to suppress pest densities to below crop-damaging levels (73). Notably, plant resistance is one of multiple management methods, along with biological control and insecticides, comprising highly successful rice IPM programs in Asia (75). Single *N. lugens* resistance genes, gene pyramids, and seasonal rotations have been successfully deployed in Asian rice cultivars (1 and **Supplemental References**).

Australian sorghum production is centered on growing commercial hybrids with antibiosis resistance to *Stenodiplosis sorghicola*, and this resistance has been successfully combined with other management methods such as flexible planting times, synthetic insecticides, and biological control (40). Widespread use of *S. sorghicola*-resistant hybrids by Australian growers has reduced the number of insecticide applications and has allowed significant increases in the survival of parasitoids that reduce *S. sorghicola* populations. North American sorghum growers' use of plant resistance and chemical control to manage *Schizaphis graminum* has reduced insecticide use since 1977, when

S. graminum-resistant commercial hybrids became available (132). Useful multiline resistance also exists in sorghum but has yet to be deployed (131).

In much of the arthropod crop pest management literature shows that HPR is used in conjunction with other management methods. In wheat, examples include the deployment of *H* genes for *M. destructor* resistance in North American production areas where cultural practices such as puparia and volunteer wheat destruction, delayed planting, and crop rotation could be used (100). Several of the same cultural practices and biological control via conservation of parasitoid wasps could be used to augment the value of cultivars resistant to *C. cinctus* (64). A Canadian program for management of *Sitodiplosis mosellana* could potentially incorporate an interspersed refuge of susceptible plants among a resistant wheat crop to help sustain resistance conferred by *Sm1* and biocontrol of the midge by parasitoids (120). In Europe, concerns about *Amphorophora idaei* resistance-breaking biotypes on resistant raspberry cultivars requires additional management tactics to control aphid populations and virus transmission. Biological control and semiochemical technologies are in development, because the few certified insecticides are largely ineffective at controlling aphids in time to prevent virus transmission (77, 80).

Finally, despite repeated justifications in the literature for alternative pest management options such as the cultivation of arthropod-resistant cultivars, early twenty-first century control strategies for most crop pests involve synthetic insecticides. A case in point is sugarcane production in Louisiana, where producers rely heavily on insecticides to control *Diatraea saccharalis* on a widely grown susceptible variety, even though multiple control tactics (plant resistance, chemical control, arthropod predation) effectively reduce infestations (95). The obstacles to increased use of host plant resistance and other economical and environmentally friendly methods in an IPM framework have been reviewed elsewhere (31, 125).

MOLECULAR GENETICS IN ARTHROPOD-RESISTANT CROPS: PROGRESS, BENEFITS, AND CHALLENGES

Steady progress has been made in the past five decades to advance the science of HPR to arthropods and, more importantly, to deploy arthropod-resistant crop plant cultivars as foundations of cropping systems. Major advances have been made in understanding resistance categories and mechanisms mediating resistance, as well as the biotic and abiotic variables affecting resistance. To bridge gaps with plant pathogen resistance research, plant-arthropod relationships are now being described as compatible (susceptible plant) and incompatible (resistant plant) interactions, similar to plant-pathogen interactions (56).

Perhaps the most dramatic shift in research has been the progress made in understanding constitutively expressed arthropod resistance gene products. For example, knowledge of the phenotypic inheritance of Lepidoptera resistance in maize has been greatly improved by a completely new understanding of genes involved in synthesis of DIMBOA (*bx*), maysin (*p1*), and cysteine proteinases (*Mir*). The same is true for genes controlling production of other allelochemicals, including the arcelin α -amylase inhibitor (*Arc1*) in common bean, endophyte-produced alkaloids (*LOL*, *perA*) in grasses, and the steroidal alkaloids acetyl-leptinidine (*AL*) and leptinidine (*Lep*) in potato. Advances in the past decade alone indicate the involvement of numerous plant signaling pathways, primarily the jasmonate pathway, in the production of induced arthropod resistance proteins. Although the balance of interaction between induced and constitutive genes remains unclear, the results of gene silencing experiments reveal essential functions of both (60, 137, 141). Finally, knowledge gained from cloning *Mi-1.2* and *Vat*, both members of the CC-NBS-LRR subfamily of NBS-LRR resistance proteins, has yielded information to facilitate the cloning of other arthropod resistance genes using resistance gene analog (RGA) approaches. For example,

Mir: a gene in maize encoding cysteine proteinases that inhibits larval growth of *Spodoptera frugiperda*

Arcelin α -amylase inhibitor (*Arc1*): a gene in common bean encoding arcelin, an α -amylase inhibitor inhibiting larval growth of *Zabrotes subfasciatus*

***Lep* (leptinidine) and *AL* (acetyl-leptinidine)**: genes encoding nonglycosylated steroidal alkaloids from foliage of wild potato, *Solanum chacoense*, that inhibit feeding of *Leptinotarsa decemlineata*



Arthropod virulence:

a mutation of an arthropod avirulence gene(s) that results in a plant's loss of ability to recognize the presence of the arthropod

the *AIN*, *AKR*, and *TRR* aphid resistance genes in barrel medic are located in RGA clusters that are highly similar to the CC-NBS-LRR subfamily (63 and **Supplemental References**), strongly suggesting that these genes are also NBS-LRR resistance proteins. Comparative analyses of these aphid resistance genes will greatly expand the genomic understanding of what constitutes an arthropod resistance gene.

Given these significant genetic and genomic advances, to what extent have molecular genetic and genomic innovations benefited producers and consumers through the delivery of arthropod-resistant crops? Field integration of rice, sorghum, and wheat arthropod resistance genes into IPM in Asia, Australia, and North America, and to a limited extent Europe, has increased steadily for the past 50 years. Aside from these three major cereal food crops, however, the actual integration of arthropod-resistant cultivars, biological control agents, and cultural control practices has not occurred at the farm level, mainly because of continued but often unnecessary use of synthetic insecticides. The use of VOCs to recruit pest-arthropod natural enemies and synergize field resistance could be developed as an IPM tool to alleviate this dilemma.

Molecular markers are facilitating and improving our ability to develop and deliver arthropod-resistant crops. This is clearly demonstrated by more than 100 arthropod resistance loci and linked markers that have been identified and used to generate numerous crop-plant genetic linkage maps. Many of these markers are used to track arthropod resistance via MAS in breeding lines for deployment in cultivars. This is especially true at CGIAR centers (ICARDA, ICRISAT, and IRR) where MAS has been used to breed arthropod-resistant crop cultivars and continues to be used to identify different genes in new sources of resistance. Importantly, several markers in **Table 1** have been linked to specific resistance categories and in several cases to allelochemical or biophysical traits. This knowledge offers HPR researchers the capability of deploying resistant cultivars with broader, more durable resistance that reduces the occurrence of arthropod virulence.

Although these data reflect steady progress, QTL must be used more broadly to identify plant arthropod resistance genes, especially to identify and deploy arthropod-resistant cultivars of cool-season food legumes (chickpea, faba bean, lentil, pea) in the semitropical areas of the world currently undergoing rapid population growth. The challenges of developing cultivars with arthropod resistance from wild species remain (28), but transgenic technology has decreased these difficulties. An improved understanding of constitutive and induced gene expression, and the use of plant and arthropod genomic tools associated with gene manipulation, now provide many opportunities to more efficiently develop arthropod-resistant plants. Therefore, the outlook for confronting future challenges of HPR is bright. Nevertheless, the development of durable, higher-yielding arthropod-resistant crop cultivars for global agriculture and their integration into IPM programs will succeed only through interdisciplinary collaborations among entomologists, plant breeders, and molecular biologists.

SUMMARY POINTS

1. Plant genetic diversity resulting from selective pressures due in part to arthropod herbivory provided humans cultivatable food crops with which to form agrarian societies about 10,000 years ago. Conventional plant breeding has since been used to develop hundreds of arthropod-resistant crop cultivars that currently provide major ecological and economic benefits to global agriculture.
2. Arthropod-resistant plants function by producing allelochemical and biophysical plant traits that adversely affect arthropod behavior and survival or that allow plants to tolerate arthropod damage.

3. Incompatible interactions between resistant plants and arthropods are mediated by both constitutively produced resistance proteins and proteins produced via jasmonate- and other signaling pathways following induction by arthropod herbivory.
4. Two arthropod resistance genes have been cloned and are members of the CC-NBS-LRR subfamily of NBS-LRR resistance proteins. *Mi-1.2* (wild tomato) exhibits multispecies insect and nematode resistance, and *Vat* (melon) expresses aphid resistance. Aphid resistance genes in barrel medic are located in RGA clusters that are highly similar to the CC-NBS-LRR subfamily.
5. More than 100 monogenic and polygenic arthropod plant resistance gene loci and their linked markers have been characterized by molecular mapping, and several are in use to track resistance via MAS in breeding lines for deployment in cultivars.
6. Arthropod-resistant cultivars of rice and sorghum are major components of IPM programs in Asia, Australia, and North America, and resistant raspberry and wheat cultivars are near integration in Europe and North America, respectively. For the majority of food and fiber crops, however, arthropod-resistant cultivars have not been integrated into other IPM methods.
7. Numerous opportunities exist to use advances in molecular technology to more efficiently identify, track, and manipulate arthropod resistance genes in arthropod-resistant cultivars. Integration of such cultivars into IPM programs with biological, chemical, and cultural control tactics will succeed only through interdisciplinary collaborations.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

1. Alam SN, Cohen MB. 1998. Detection and analysis of QTLs for resistance to the brown planthopper, *Nilaparvata lugens*, in a double-haploid rice population. *Theor. Appl. Genet.* 97:1370–79
2. Alston FH, Phillips KL, Evans KM. 2000. A *Malus* gene list. *Acta Hort.* 538:561–70
3. Barry D, Alfaro D, Darrah LL. 1994. Relation of European corn borer (Lepidoptera: Pyralidae) leaf-feeding resistance and DIMBOA content in maize. *Environ. Entomol.* 23:177–82
4. Bateman RM, Crane PR, DiMichele WA, Kenrick PR, Rowe NP, et al. 1998. Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. *Annu. Rev. Ecol. Syst.* 29:263–92
5. Baum JA, Bogaert T, Clinton W, Heck GR, Feldmann P, et al. 2007. Control of coleopteran insect pests through RNA interference. *Nat. Biotechnol.* 25:1322–26
6. Berzonsky WA, Ding H, Haley SD, Harris MO, Lamb RJ, et al. 2010. Breeding wheat for resistance to insects. *Plant Breed. Rev.* Vol. 22. doi: 10.1002/9780470650202.ch5
7. Birch ANE, Jones AT, Fenton B, Malloch G, Geoghegan I, et al. 2002. Resistance-breaking raspberry aphid biotypes: constraints to sustainable control through plant breeding. *Acta Hort.* 585:315–17
8. Blair MW, Muñoz C, Buendía HF, Flower J, Bueno JM, Cardona C. 2010. Genetic mapping of microsatellite markers around the arcelin bruchid resistance locus in common bean. *Theor. Appl. Genet.* 121:393–402



19. Association mapping used to determine a QTL that colocalizes with most structural *bx* genes of the DIMBOA pathway.

9. Blair MW, Muñoz C, Garza R, Cardona C. 2006. Molecular mapping of genes for resistance to the bean pod weevil (*Apion godmani* Wagner) in common bean. *Theor. Appl. Genet.* 114:913–23
10. Blake NK, Stougaard RN, Weaver DK, Sherman JD, Lanning SP, et al. 2010. Identification of a quantitative trait locus for resistance to *Sitodiplosis mosellana* (Géhin), the orange wheat blossom midge, in spring wheat. *Plant Breed.* 130:245–30
11. Boethel DJ. 1999. Assessment of soybean germplasm for multiple insect resistance. See Ref. 30, pp. 101–30
12. Bohn M, Groh S, Khairallah MM, Hoisington DA, Utz HF, Melchinger AE. 2001. Re-evaluation of the prospects of marker-assisted selection for improving insect resistance against *Diatraea* spp. in tropical maize by cross validation and independent validation. *Theor. Appl. Genet.* 103:1059–67
13. Boissot N, Thomas S, Sauvion N, Marchal C, Pavis C, Dogimont C. 2010. Mapping and validation of QTLs for resistance to aphids and whiteflies in melon. *Theor. Appl. Genet.* 121:9–20
14. Botha A-M, Lacock L, van Niekerk C, Matsioloko MT, du Preez FB, et al. 2006. Is photosynthetic transcriptional regulation in *Triticum aestivum* L. cv. ‘TugelaDN’ a contributing factor for tolerance to *Diuraphis noxia* (Homoptera: Aphididae)? *Plant Cell Rep.* 25:41–54
15. Bouton J. 2009. Deployment of novel endophytes in the tall fescue commercial seed trade. In *Tall Fescue for the Twenty-First Century*, ed. HA Fribourg, DB Hannaway, CP West, pp. 367–75. Madison: Am. Soc. Agron., Crop Sci. Soc. Am., Soil Sci. Soc. Am. 540 pp.
16. Boyko EV, Smith CM, Thara VK, Bruno JM, Deng Y, et al. 2006. Molecular basis of plant gene expression during aphid invasion: Wheat *Pro*- and *Pti*-like sequences are involved in interactions between wheat and Russian wheat aphid (Homoptera: Aphididae). *J. Econ. Entomol.* 99:1430–45
17. Brooks TD, Bushman BS, Williams WP, McMullen MD, Buckley PM. 2007. Genetic basis of resistance to fall armyworm (Lepidoptera: Noctuidae) and southwestern corn borer (Lepidoptera: Crambidae) leaf-feeding damage in maize. *J. Econ. Entomol.* 100:1470–75
18. Bus VGM, Chagné D, Bassett HCM, Bowatte D, Calenge F, et al. 2008. Genome mapping of three major resistance genes to woolly apple aphid (*Eriosoma lanigerum* Hausm.) *Tree Genet. Genomes* 4: 233–36
19. **Butrón A, Chen YC, Rottinghaus GE, McMullen MD. 2010. Genetic variation at *bx1* controls DIMBOA content in maize. *Theor. Appl. Genet.* 120:721–34**
20. Cardinal AJ, Lee M. 2005. Genetic relationships between resistance to stalk-tunneling by the European corn borer and cell-wall components in maize population B73xB52. *Theor. Appl. Genet.* 111:1–7
21. Carena MJ, Glogoza P. 2004. Resistance of maize to the corn leaf aphid: a review. *Maydica* 49:241–54
22. Casteel CL, Walling LL, Paine TD. 2006. Behavior and biology of the tomato psyllid, *Bactericera cockerelli*, in response to the *MI-1.2* gene. *Entomol. Exp. Appl.* 121:67–72
23. Castro AM, Vasicek A, Manifiesto M, Giménez DO, Tacaliti MS, et al. 2005. Mapping antixenosis genes on chromosome 6A of wheat to greenbug and to a new biotype of Russian wheat aphid. *Plant Breed.* 124:229–33
24. Castro AM, Worland AJ, Vasicek A, Ellerbrook C, Giménez DO, et al. 2004. Mapping quantitative trait loci for resistance against greenbug and Russian wheat aphid. *Plant Breed.* 121:361–66
25. Cevik V, King GJ. 2002. Resolving the aphid resistance locus *Sd-1* on a BAC contig within a sub-telomeric region of *Malus* linkage group 7. *Genome* 45:939–45
26. Chen M-S. 2008. Inducible direct plant defense against insect herbivores: a review. *Insect Sci.* 15:101–14
27. Cheung WY, Di Giorgio L, Ahman I. 2010. Mapping resistance to the bird cherry-oat aphid (*Rhopalosiphum padi*) in barley. *Plant Breed.* 129:637–46
28. Clement SL. 2002. Insect resistance in the wild relatives of food legumes and wheat. In *Proc. Australas. Plant Breed. Conf., 12th, Perth, Sept. 15–20*, ed. JA McComb, pp. 287–93. Perth: Australas. Plant Breed. Assoc.
29. Clement SL, Cristofaro M, Cowgill SE, Weigand S. 1999. Germplasm resources, insect resistance, and grain legume improvement. See Ref. 30, pp. 131–48
30. Clement SL, Quisenberry SS, eds. 1999. *Global Plant Genetic Resources for Insect-Resistant Crops*. Boca Raton, FL: CRC Press. 295 pp.

31. Clement SL, Wightman JA, Hardie DC, Bailey P, Baker G, McDonald G. 2000. Opportunities for integrated management of insect pests of grain legumes. In *Linking Research and Marketing Opportunities for Pulses in the 21st Century, Proc. Third Int. Food Legumes Res. Conf.*, ed. R Knight, pp. 467–80. Dordrecht, The Netherlands: Kluwer. 711 pp.
32. Couldridge C, Newbury HJ, Ford-Lloyd B, Bale J, Pritchard J. 2007. Exploring plant responses to aphid feeding using a full *Arabidopsis* microarray reveals a small number of genes with significantly altered expression. *Bull. Entomol. Res.* 97:523–32
33. Dogimont C, Chovelon V, Tual S, Boissot N, Rittener V, et al. 2008. Molecular diversity at the *Vat/PM-W* resistance locus in melon. In *Proc. EUCARPIA Genet. Breed. Cucurbitaceae, IXtb*, ed. M Pitrat, pp. 219–28. Avignon: INRA
34. Doss RP, Oliver JE, Proebsting WM, Potter SW, Kuy S-R, et al. 2000. Bruchins: insect-derived plant regulators that stimulate neoplasm formation. *Proc. Natl. Acad. Sci. USA* 97:6218–23
35. Duan CX, Su N, Cheng ZJ, Lei CL, Wang JL, et al. 2010. QTL analysis for the resistance to small brown planthopper (*Laodelphax striatellus* Fallén) in rice using backcross inbred lines. *Plant Breed.* 129:63–67
36. Easton S, Tapper B. 2005. *Neotyphodium* research and application in New Zealand. In *Neotyphodium in Cool-Season Grasses*, ed. CA Roberts, CP West, DE Spiers, pp. 35–42. Oxford: Blackwell. 379 pp.
37. Edwards O, Singh KB. 2006. Resistance to insect pests: What do legumes have to offer? *Euphytica* 147:273–85
38. Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586–608
39. Evans KM, Govan CL, Fernández-Fernández F. 2008. A new gene for resistance to *Dysaphis pyri* in pear and identification of flanking microsatellite markers. *Genome* 51:1026–31
40. Franzmann BA, Hardy AT, Murray DAH, Henzell RG. 2008. Host-plant resistance and biopesticides: ingredients for successful integrated pest management (IPM) in Australian sorghum production. *Aust. J. Exp. Agric.* 48:1594–600
41. Frei A, Blair MW, Cardona C, Beebe SF, Gu H, Dorn S. 2005. QTL mapping of resistance to *Tbrrips palmi* Karny in common bean. *Crop Sci.* 45:379–87
42. Fritz RS, Simms EL, eds. 1992. *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. Chicago: Univ. Chicago Press. 590 pp.
43. Futuyma DJ, Agrawal AA. 2009. Macroevolution and the biology diversity of plants and herbivores. *Proc. Natl. Acad. Sci. USA* 106:18054–61
44. Gassmann AJ, Carrière Y, Tabashnik BE. 2009. Fitness costs of insect resistance to *Bacillus thuringiensis*. *Annu. Rev. Entomol.* 54:147–63
45. Gatehouse JA. 2008. Biotechnological prospects for engineering insect-resistant plants. *Plant Physiol.* 146:881–87
46. Gharalari AH, Fox SL, Smith MAH, Lamb RJ. 2009. Oviposition deterrence in spring wheat, *Triticum aestivum*, against orange wheat blossom midge, *Sitodiplosis mosellana*: implications for inheritance of deterrence. *Entomol. Exp. Appl.* 133:74–83
47. Groot AT, Dicke M. 2002. Insect transgenic plants in a multi-trophic context. *Plant J.* 31:387–406
48. Guo B, Butrón A, Scully BT. 2010. Maize silk antibiotic polyphenol compounds and molecular genetic improvement of resistance to corn earworm (*Helicoverpa zea* Boddie) in *sh2* sweet corn. *Int. J. Plant Biol.* 1:13–18
49. Herselman L, Thwaites R, Kimmins FM, Courtois B, van der Merwe PJA, Seal SE. 2004. Identification and mapping of AFLP markers linked to peanut (*Arachis hypogaea* L.) resistance to the aphid vector of groundnut rosette disease. *Theor. Appl. Genet.* 109:1426–33
50. Hill CB, Kim K-S, Crull L, Diers BW, Hartman GL. 2009. Inheritance of resistance to the soybean aphid in soybean PI200538. *Crop Sci.* 49:1193–200
51. Holden J, Peacock J, Williams T. 1993. *Genes, Crops and the Environment*. Cambridge/New York: Cambridge Univ. Press. 162 pp.
52. **Howe GA, Jander G. 2008. Plant immunity to insect herbivores. *Annu. Rev. Plant Biol.* 59:41–66**
53. Huang J, McAuslane HJ, Nuessly GS. 2003. Resistance in lettuce to *Diabrotica balteata* (Coleoptera: Chrysomelidae): the roles of latex and inducible defense. *Environ. Entomol.* 32:9–16
54. Hutchison WD, Burkness EC, Mitchell PD, Moon RD, Leslie TW, et al. 2010. Areawide suppression of European corn borer with *Bt* maize reaps savings to non-*Bt* maize growers. *Science* 330:222–25

52. Describes the roles of jasmonate signaling in coordinating direct and indirect plant responses to herbivory.



56. First in-depth analysis of gene-for-gene plant resistance to piercing-sucking insects.

59. Integrated review of transcriptional changes in plants exhibiting constitutive and induced arthropod resistance.

63. Aphid resistance genes in barrel medic occur in clusters very similar to the CC-NBS-LRR subfamily of NBS-LRR resistance proteins that includes *Mi-1.2* and *Vat*.

55. Hwang CF, Bhakta AV, Truesdell GM, Pudlo WM, Williamson VM. 2000. Evidence for a role of the N terminus and leucine-rich repeat region of the *Mi* gene product in regulation of localized cell death. *Plant Cell* 12:1319–29
56. Kaloshian I. 2004. Gene-for-gene disease resistance: bridging insect pest and pathogen defense. *J. Chem. Ecol.* 30:2419–38
57. Kaloshian I, Walling L. 2005. Hemipterans as pathogens. *Annu. Rev. Phytopathol.* 43:491–521
58. Kennedy GG, Barbour JD. 1992. Resistance variation in natural and managed systems. See Ref. 42, pp. 13–41
59. Kessler A, Baldwin IT. 2002. Plant responses to insect herbivory: the emerging molecular analysis. *Annu. Rev. Plant Biol.* 53:299–328
60. Kessler A, Halitschke R, Baldwin IT. 2004. Silencing the jasmonate cascade: induced plant defenses and insect populations. *Science* 305:665–68
61. Kielkiewicz M. 2002. Influence of carmine spider mite *Tetranychus cinnabarinus* Boisd. (Acarida: Tetranychidae) feeding on ethylene production and the activity of oxidative enzymes in damaged tomato plants. In *Acarid Phylogeny and Evolution: Adaptation in Mites and Ticks—Proc. IV Symp. Eur. Assoc. Acarol.*, ed. F Bernini, R Nannelli, G Nuzzaci, E de Lillo, pp. 389–92. Dordrecht, The Netherlands: Kluwer. 452 pp.
62. Kim K-S, Hill CB, Hartman GL, Mian MAR, Diers BW. 2008. Discovery of soybean aphid biotypes. *Crop Sci.* 48:923–28
63. Klingler JP, Nair RM, Edwards OR, Singh KB. 2009. A single gene, *AIN*, in *Medicago truncatula* mediates a hypersensitive response to both bluegreen aphid and pea aphid, but confers resistance only to bluegreen aphid. *J. Exp. Bot.* 60:4115–27
64. Knodel J, Shanower T, Beauzay P. 2010. Integrated pest management of wheat stem sawfly in North Dakota. *N. D. Ext. Serv. Bull.* E-1479. 8 pp.
65. Kutil BL, Greenwald C, Liu G, Spiering MJ, Schardl CL, Wilkinson HH. 2007. Comparison of loline alkaloid gene clusters across fungal endophytes: predicting the co-regulatory sequence motifs and the evolutionary history. *Fungal Genet. Biol.* 44:1002–10
66. Lanning SP, Fox P, Elser J, Martin JM, Blake NK, Talbert LE. 2006. Microsatellite markers associated with a secondary stem solidness locus in wheat. *Crop Sci.* 46:1701–93
67. Lapitan NLV, Li YC, Peng JH, Botha AM. 2007. Fractionated extracts of Russian wheat aphid eliciting defense responses in wheat. *J. Econ. Entomol.* 100:990–99
68. Lapitan NLV, Peng J, Sharma V. 2007. A high-density map and PCR markers for Russian wheat aphid resistance gene *Dn7* on chromosome 1RS/1BL. *Crop Sci.* 47:811–20
69. Li Y, Zou J, Li M, Bilgin DD, Vodkin LO, et al. 2008. Soybean defense responses to the soybean aphid. *New Phytol.* 179:185–95
70. Lin C, Chen C-S, Horng S-B. 2005. Characterization of resistance to *Callosobruchus maculatus* (Coleoptera: Bruchidae) in mungbean variety VC6089A and its resistance-associated protein VrD1. *J. Econ. Entomol.* 98:1369–73
71. Liu X, Bai J, Huang L, Zhu L, Liu X, et al. 2007. Gene expression of different wheat genotypes during attack by virulent and avirulent Hessian fly (*Mayetiola destructor*) larvae. *J. Chem. Ecol.* 33:2171–94
72. Liu XM, Smith CM, Gill BS, Tolmay V. 2001. Microsatellite markers linked to six Russian wheat aphid resistance genes in wheat. *Theor. Appl. Genet.* 102:504–10
73. Luckmann WH, Metcalf RL, eds. 1994. *Introduction to Insect Pest Management*. New York: Wiley. 650 pp. 3rd ed.
74. Malik R, Brown-Guedira GL, Smith CM, Harvey TL, Gill BS. 2003. Genetic mapping of wheat curl mite resistance genes *Cmc3* and *Cmc4* in common wheat. *Crop Sci.* 43:644–50
75. Matteson PC. 2000. Insect pest management in tropical Asian irrigated rice. *Annu. Rev. Entomol.* 45:549–74
76. McCreight JD. 2008. Potential sources of genetic resistance in *Lactuca* spp. to the lettuce aphid, *Nasanovia ribisnigri* (Mosely) (Homoptera: Aphididae). *HortScience* 43:1355–58
77. McMenemy LS, Mitchell C, Johnson SN. 2009. Biology of the European large raspberry aphid (*Amphorophora idaei*): its role in virus transmission and resistance breakdown in red raspberry. *For. Entomol.* 11:61–71

78. Mian MAR, Kang S-T, Beil SE, Hammond RB. 2008. Genetic linkage mapping of the soybean aphid resistance gene in PI 243540. *Theor. Appl. Genet.* 117:955–62
79. Miklas PN, Kelly JD, Beebe SE, Blair MW. 2006. Common bean breeding for resistance against biotic and abiotic stresses: from classical to MAS breeding. *Euphytica* 147:105–31
80. Mitchell C, Johnson SN, Gordon SC, Birch ANE, Hubbard SF. 2010. Combining plant resistance and a natural enemy to control *Amphorophora idaei*. *BioControl* 55:321–27
- 81. Mithöfer A, Boland W. 2008. Recognition of herbivory-associated molecular patterns. *Plant Physiol.* 146:825–31**
82. Mittal S, Dahleen LS, Mornhinweg D. 2008. Locations of quantitative trait loci conferring Russian wheat aphid resistance in barley germplasm STARS-9301B. *Crop Sci.* 48:1452–58
83. Mornhinweg DW, Bregitzer PP, Porter DR, Peairs FB, Baltensperger DD, et al. 2009. Registration of ‘Sidney’ spring feed barley resistant to Russian wheat aphid. *J. Plant Reg.* 3:214–18
84. Myers GO, Fatokun CA, Young ND. 1996. RFLP mapping of an aphid resistance gene in cowpea (*Vigna unguiculata* L. Walp). *Euphytica* 91:181–87
85. Ni X, Li X, Chen Y, Guo F, Feng J, Zhao H. 2010. Metamorphosis of cisgenic insect resistance research in the transgenic crop era. In *Recent Advances in Entomological Research: From Molecular Biology to Pest Management*, ed. T-X Liu, L Kang, pp. 157–69. Beijing: High. Educ. Press. 500 pp.
86. Nombela G, Williamson VM, Muñoz M. 2003. The root-knot nematode resistance gene *MI-1.2* of tomato is responsible for resistance against the whitefly *Bemisia tabaci*. *Mol. Plant-Microbe Interact.* 16:645–49
87. Osborn TC, Blake T, Gepts P, Bliss FA. 1986. Bean arcelin 2. Genetic variation, inheritance and linkage relationships of a novel seed protein of *Phaseolus vulgaris* L. *Theor. Appl. Genet.* 71:847–55
88. Painter RH. 1951. *Insect Resistance in Crop Plants*. Lawrence: Univ. Kans. Press. 520 pp.
89. Panaccione DG, Johnson RD, Wang J, Young CA, Damrongkool P, et al. 2001. Elimination of ergovaline from a grass-*Neotyphodium* endophyte symbiosis by genetic modification of the endophyte. *Proc. Natl. Acad. Sci. USA* 98:12820–25
90. Panda N, Khush GS. 1995. *Host Plant Resistance to Insects*. Wallingford, UK: CABI/IRRI. 431 pp.
91. Pascal T, Pfeiffer F, Kervella J, Lacroze P, Sauge MH. 2002. Inheritance of green peach aphid resistance in the peach cultivar ‘Rubira’. *Plant Breed.* 121:459–61
92. Pechan T, Jiang B, Steckler D, Ye L, Lin L. 1999. Characterization of three distinct cDNA clones encoding cysteine proteinases from maize (*Zea mays* L.) callus. *Plant Mol. Biol.* 40:111–19
93. Popay AJ. 2009. Insect pests. In *Tall Fescue for the Twenty-First Century*, Agron. Monogr. 53, ed. HA Fribourg, DB Hannaway, CP West, pp. 129–49. Madison: ASA, CSSA, SSSA. 540 pp.
94. Porter DR, Burd JD, Mornhinweg DW. 2007. Differentiating greenbug resistance genes in barley. *Euphytica* 153:11–14
95. Posey FR, White WH, Reay-Jones FPF, Gravois K, Salassi ME, et al. 2006. Sugarcane borer (Lepidoptera: Crambidae) management threshold assessment on four sugarcane cultivars. *J. Econ. Entomol.* 99:966–71
- 96. Potter DA, Stokes JT, Redmond CT, Schardl CL, Panaccione DG. 2008. Contribution of ergot alkaloids to suppression of a grass-feeding caterpillar assessed with gene knockout endophytes in perennial ryegrass. *Entomol. Exp. Appl.* 126:138–47**
97. Qaim M, Zilberman D. 2003. Yield effects of genetically modified crops in developing countries. *Science* 299:900–2
98. Qiu Y, Guo J, Jing S, Zhu L, He G. 2010. High resolution mapping of the brown planthopper resistance gene *Bph6* in rice and characterizing its resistance in the 9311 and Nipponbare near isogenic backgrounds. *Theor. Appl. Genet.* 121:1601–11
99. Rahman ML, Jiang W, Chu SH, Quiao Y, Ham T-H, et al. 2009. High-resolution mapping of two rice brown planthopper resistance genes, *Bph20(t)* and *Bph21(t)*, originating from *Oryza minuta*. *Theor. Appl. Genet.* 119:1237–46
100. Ratcliffe RH, Cambron SE, Flanders KL, Bosque-Perez NA, Clement SL, Ohm HW. 2000. Biotype composition of Hessian fly (Diptera: Cecidomyiidae) populations from the southeastern, midwestern, and northwestern United States and virulence to resistance genes in wheat. *J. Econ. Entomol.* 93:1319–28
101. Rector BG, All JN, Parrott WA, Boerma HR. 2000. Quantitative trait loci for antibiosis resistance to corn earworm in soybean. *Crop Sci.* 40:233–38

81. Reviews herbivore-derived signaling compounds eliciting plant HAMPs and ensuing defensive responses.

96. First use of an endophyte gene knockout approach to link a specific endophyte alkaloid with arthropod resistance.



103. Reports cloning of the first plant insect resistance gene (*Mi-1.2*).

102. Renganayaki K, Fritz AK, Sadasivum S, Pammi S, Harrington SE, et al. 2002. Mapping and progress toward map-based cloning of brown planthopper biotype-4 resistance gene introgressed from *Oryza officinalis* into cultivated rice, *O. sativa*. *Crop Sci.* 42:2114–17
103. Rossi M, Goggin FL, Milligan SB, Klaoshian I, Ullman DE, Williamson VM. 1998. The nematode resistance gene *Mi* of tomato confers resistance against the potato aphid. *Proc. Natl. Acad. Sci. USA* 95:9750–54
104. Sadasivum S, Thayumanavan B. 2003. *Molecular Host Plant Resistance to Pests*. New York: Marcel Dekker. 479 pp.
105. Sagredo B, Balbyshev N, Lafta A, Casper H, Lorenzen J. 2009. A QTL that confers resistance to Colorado potato beetle (*Leptinotarsa decemlineata* [Say]) in tetraploid potato populations segregating for leptine. *Theor. Appl. Genet.* 119:1171–81
106. Sandanayaka WRM, Bus VGM, Connolly P. 2005. Mechanisms of woolly aphid [*Eriosoma lanigerum* (Hausm.)] resistance in apple. *J. Appl. Entomol.* 129:534–41
107. Sargent DJ, Fernández-Fernández F, Rys A, Knight VH, Simpson DW, Tobutt KR. 2007. Mapping of *A1* conferring resistance to the aphid *Amphorophora idaei* and *dw* (dwarfing habit) in red raspberry (*Rubus idaeus* L.) using AFLP and microsatellite markers. *BMC Plant Biol.* 7:15
108. Satish K, Srinivas G, Madhusudhana R, Padmaja PG, Nagaraja Reddy R, et al. 2009. Identification of quantitative trait loci for resistance to shoot fly in sorghum [*Sorghum bicolor* (L.) Moench]. *Theor. Appl. Genet.* 119:1425–39
109. Schardl CL, Grossman RB, Nagabhyru P, Faulkner JR, Mallik UP. 2007. Loline alkaloids: currencies of mutualism. *Phytochemistry* 68:980–96
110. Schmelz EA, Engelberth J, Alborn HT, Tumlinson JH, Teal PEA. 2009. Phytohormone-based activity mapping of insect herbivore-produced elicitors. *Proc. Natl. Acad. Sci. USA* 106:653–57
111. Sharma HC. 2009. *Biotechnological Approaches for Pest Management and Ecological Sustainability*. Boca Raton, FL: CRC Press. 526 pp.
112. Sherman JD, Weaver DK, Hofland ML, Sing SE, Buteler M, et al. 2010. Identification of novel QTL for sawfly resistance in wheat. *Crop Sci.* 50:73–86
113. Smith CM. 1989. *Plant Resistance to Insects: A Fundamental Approach*. New York: Wiley. 286 pp.
114. Smith CM. 2004. Plant resistance against pests: issues and strategies. In *Integrated Pest Management: Potential, Constraints and Challenges*, ed. O Koul, GS Dhaliwal, GW Cuperus, pp. 147–67. Wallingford/Cambridge, UK: CABI. 329 pp.
115. Smith CM. 2005. *Plant Resistance to Arthropods: Molecular and Conventional Approaches*. Dordrecht, The Netherlands: Springer. 423 pp.
116. Smith CM. 2010. Biochemical plant defenses against herbivores: from poisons to spices. In *All Flesh is Grass, Plant-Animal Interrelationships Series: Cellular Origins, Life in Extreme Habitats and Astrobiology*, ed. Z Dubinsky, J Seckbach, pp. 1–20. Berlin: Springer. 485 pp.
117. Smith CM, Boyko EV. 2007. The molecular bases of plant resistance and defense responses to aphid feeding: current status. *Entomol. Exp. Appl.* 122:1–16
118. Smith CM, Khan ZR, Pathak MD. 1994. *Techniques for Evaluating Insect Resistance in Crop Plants*. Boca Raton, FL: CRC Press. 320 pp.
119. Smith CM, Liu XM, Wang LJ, Liu X, Chen M-S, et al. 2010. Aphid feeding activates expression of a transcriptome of oxylipin-based defense signals in wheat involved in resistance to herbivory. *J. Chem. Ecol.* 36:260–76
120. Smith MAH, Lamb RJ, Wise IL, Olfert OO. 2004. An interspersed refuge for *Sitodiplosis mosellana* (Diptera: Cecidomyiidae) and a biocontrol agent *Macroglenes penetrans* (Hymenoptera: Pteromalidae) to manage crop resistance in wheat. *Bull. Entomol. Res.* 94:179–88
121. Spiering MJ, Moon CD, Wilkinson HH, Schardl CL. 2005. Gene clusters for insecticidal loline alkaloids in the grass-endophytic fungus *Neotyphodium uncinatum*. *Genetics* 169:1403–14
122. Stewart SA, Hodge S, Ismail N, Mansfield JW, Feys BJ, et al. 2009. The *rap 1* gene confers effective, race-specific resistance to the pea aphid in *Medicago truncatula* independent of the hypersensitive reaction. *Mol. Plant-Microbe Interact.* 22:1645–55
123. Stoeckli S, Mody K, Gessler C, Patocchi A, Jermini M, Dorn S. 2008. QTL analysis for aphid resistance and growth traits in apple. *Tree Genet. Genomes* 4:833–47



124. Stout M, Davis J. 2009. Keys to the increased use of host-plant resistance in integrated pest management. In *Integrated Pest Management: Innovation-Development Process*, ed. R Peshin, AK Dhawan, pp. 163–81. New York/Heidelberg: Springer Science + Business Media. 690 pp.
125. Stout MJ. 2007. Types and mechanisms of rapidly induced plant resistance to herbivorous arthropods. In *Induced Resistance for Plant Defence*, ed. D Walters, A Newton, G Lyon, pp. 89–107. Oxford: Blackwell. 271 pp.
126. Sullivan TJ, Rodstrom J, Vandop J, Librizzi J, Graham C, et al. 2007. Symbiont-mediated changes in *Lolium arundinaceum* inducible defenses: evidence from changes in gene expression and leaf composition. *New Phytol.* 176:673–79
127. Tabashnik BE, Carrière Y, Dennehy TJ, Morin S, Sisterson MS, et al. 2003. Insect resistance to transgenic *Bt* crops: lessons from the laboratory and field. *J. Econ. Entomol.* 96:1031–38
128. Tan GX, Weng QM, Ren X, Huang Z, Zhu LL, He GC. 2004. Two whitebacked planthopper resistance genes in rice share the same loci with those for brown planthopper resistance. *Heredity* 92:212–17
129. Tanaka A, Tapper BA, Popay A, Parker EJ, Scott B. 2005. A symbiosis expressed non-ribosomal peptide synthetase from a mutualistic fungal endophyte of perennial ryegrass confers protection to the symbiotum from insect herbivory. *Mol. Microbiol.* 57:1036–50
130. Tao YZ, Hardy A, Drenth J, Henzell RG, Franzmann BA, et al. 2003. Identifications of two different mechanisms for sorghum midge resistance through QTL mapping. *Theor. Appl. Genet.* 107:116–22
131. Teetes GL, Anderson RM, Peterson GC. 1994. Exploitation of sorghum midge nonpreference resistance in sorghum midge (Diptera: Cecidomyiidae) using mixed plantings of resistant and susceptible sorghum hybrids. *J. Econ. Entomol.* 87:826–31
132. Teetes GL, Peterson GC, Nwanze KF, Pendleton BB. 1999. Genetic diversity of sorghum: a source of insect-resistant germplasm. In *Global Plant Genetic Resources for Insect-Resistant Crops*, ed. SL Clement, SS Quisenberry, pp. 63–82. Boca Raton, FL: CRC Press. 295 pp.
133. Thomas J, Fineberg N, Penner G, McCartney C, Aung T, et al. 2005. Chromosome location and markers of *Sm1*: a gene of wheat that conditions antibiotic resistance to orange wheat blossom midge. *Mol. Breed.* 15:183–92
134. Thomas MB. 1999. Ecological approaches and the development of “truly integrated” pest management. *Proc. Natl. Acad. Sci. USA* 96:5944–51
135. Underwood N, Rausher M. 2002. Comparing the consequences of induced and constitutive plant resistance for herbivore population dynamics. *Am. Nat.* 160:20–30
136. Underwood NC, Rausher M, Cook W. 2002. Bioassay versus chemical assay: measuring the impact of induced and constitutive resistance on herbivores in the field. *Oecologia* 131:211–19
137. van Eck L, Schultz T, Leach JE, Scofield SR, Peairs FB, et al. 2010. Virus-induced gene silencing of *WRKY53* and an inducible *phenylalanine ammonia-lyase* in wheat reduces aphid resistance. *Plant Biotechnol. J.* 8:1023–32
138. van Emden HF. 2007. Host-plant resistance. In *Aphids as Crop Pests*, ed. HF van Emden, R Harrington, pp. 447–68. Wallingford, UK: CABI. 717 pp.
139. Waiss AC, Chan BG, Elliger CA, Wiseman BR, McMillian WW, et al. 1979. Maysin, a flavone glycoside from corn silks with antibiotic activity toward corn earworm. *J. Econ. Entomol.* 72:256–58
140. Willcox MC, Khairallah MM, Bergvinson D, Crossa J, Deutsch JA, et al. 2002. Selection for resistance to southwestern corn borer using marker-assisted selection and conventional backcrossing. *Crop Sci.* 42:1516–28
141. Wroblewski T, Piskurewicz U, Tomczak A, Ochoa O, Michelmore RW. 2007. Silencing of the major family of NBS–LRR-encoding genes in lettuce results in the loss of multiple resistance specificities. *Plant J.* 51:803–18
142. Wu K-M, Lu Y-H, Feng H-Q, Jiang Y-Y, Zhao J-Z. 2008. Suppression of cotton bollworm in multiple crops in China in areas with *Bt* toxin-containing cotton. *Science* 321:1676–78
143. Wu Y, Huang Y. 2008. Molecular mapping of QTLs for resistance to the greenbug *Schizaphis graminum* (Rondani) in *Sorghum bicolor* (Moench). *Theor. Appl. Genet.* 117:117–24
144. Yench G, Cohen MB, Byrne PF. 2000. Applications of tagging and mapping insect resistance loci in plants. *Annu. Rev. Entomol.* 45:393–422

124. Discusses use of conventional and molecular tools to better integrate arthropod-resistant crops into IPM programs.

137. Silencing a wheat WRKY transcription factor mediating JA-SA cross-talk, or an inducible phenylalanine ammonia-lyase, reduces aphid resistance.



145. Young CA, Tapper BA, May K, Moon CD, Schardl CL, Scott B. 2009. Indole-diterpene biosynthetic capability of *Epicicloë* endophytes as predicted by *ltm* gene analysis. *Appl. Environ. Microbiol.* 75:2200–11
146. Zhang D-X, Stromberg AJ, Spiering MJ, Schardl CL. 2009. Coregulated expression of loline alkaloid-biosynthesis genes in *Neotyphodium uncinatum* cultures. *Fungal Genet. Biol.* 46:517–30
147. Zhang G, Gu C, Wang D. 2010. A novel locus for soybean aphid resistance. *Theor. Appl. Genet.* 120:1183–91
148. Zhang P, Wang Y, Zhang J, Maddock S, Snook M, Peterson T. 2003. A maize QTL for silk maysin levels contains duplicated Myb-homologous genes which jointly regulate flavone biosynthesis. *Plant Mol. Biol.* 52:1–15
149. Zhu L, Liu X, Liu XM, Jeannotte R, Reese J, et al. 2008. Hessian fly (*Mayetiola destructor*) attack causes a dramatic shift in carbon and nitrogen metabolism in wheat. *Mol. Plant-Microbe Interact.* 21:70–78
150. Zhu LC, Smith CM, Fritz A, Boyko EV, Voothuluru P, Gill BS. 2005. Inheritance and molecular mapping of new greenbug resistance genes in wheat germplasms derived from *Aegilops tauschii*. *Theor. Appl. Genet.* 111:831–37

RELATED RESOURCES

- Núñez-Farfán J, Fornoni J, Valverde PL. 2007. The evolution of resistance and tolerance to herbivores. *Annu. Rev. Ecol. Evol. Syst.* 38:541–66
- Orians CM, Ward D. 2010. Evolution of plant defenses in nonindigenous environments. *Annu. Rev. Entomol.* 55:439–59
- St. Clair DA. 2010. Quantitative disease resistance and quantitative resistance loci in breeding. *Annu. Rev. Phytopathol.* 48:247–68

