PLANT RESISTANCE TO ARTHROPODS

Plant Resistance to Arthropods

Molecular and Conventional Approaches

by

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Dedication

To Rita, Segen, and Sonder -
the melodies of my life.

Contents

Preface

The theory, study, and practice of plant resistance to arthropods has matured greatly since the publication of R. H. Painter's classic *Plant Resistance to Insects* in 1951. In *Plant Resistance to Arthropods - Molecular and Conventional Approaches,* I have attempted to update the literature in this continually expanding area of arthropod pest management and to synthesize new information about transgenic arthropod resistant crop plants, the molecular bases of arthropod resistance in crop plants, and the use of molecular markers to breed arthropod resistant plants. The information is presented in a step-by-step manner that introduces and describes of the study of plant resistance for students, researchers, and educators.

I am thankful to colleagues around the world for their encouragement and support during the development of this book over the past three years. Special thanks are expressed to Elena Boyko, Steve Clement, Xuming Liu and Lieceng Zhu for their critical reviews of the manuscript. I appreciate the efforts of Clayton Forgey and Annie Nordhus, who formatted different revisions of the text. The project benefited greatly from the efforts of two talented artists. Andrea Kohl, a graphic artist at Northern Michigan University designed the book cover. Robert Holcombe, a graphic designer in the Department of Communications at Kansas State University prepared several line drawings for the text. I appreciate the help of Skylar Martin-Brown, who developed the figures of plant allelochemical structures. Thanks are also due to Sharon Starkey for assistance in location of bibliographic materials and in the preparation of photographic images. I acknowledge the support of the administration of the Kansas State University College of Agriculture for granting me sabbatical leave during which I completed a working draft of the book.

I express special thanks to Frank Davis, for his friendship, guidance and inspiration for the past 30 years. Finally, I thank the many students I have had the privilege to educate during the past 25 past years for their eagerness to learn and their constructive criticisms of my concepts of plant resistance to arthropods.

C. Michael Smith
Manhattan
March 7, 2005

CHAPTER 1

INTRODUCTION

1. WHAT IS PLANT RESISTANCE TO ARTHROPODS?

1.1. Uses of Plant Resistance to Arthropods

The cultivation of plants expressing some form of inherited resistance to an arthropod pest has been practiced for several hundred years. Before the domestication of plants for agricultural purposes, those susceptible to arthropods died before they could produce seed or before their damaged seeds could germinate. In effect, resistant plants survived subject to the laws of adaptation and natural selection. It is probable that early indigenous agricultural systems selected and utilized plants resistant to arthropod pests, since these systems developed production practices based on different crop species, and within species, selected different strains and land races of crops.

Crop domestication began about 10,000 years ago with the cultivation of potato, *Solanum* spp., in South America, and the production of maize, *Zea mays* L., about 6,000 years ago in Central America. Humans began to cultivate curcubits and sunflower, *Helianthus* spp., in North America during this time. By 7,000 BC, wheat, *Triticum aestivum* L., barley, *Hordeum vulgare* L., and lentil, *Lens culinaris* Medik., had become major domestic food crops in the Fertile Crescent of present day Iran, Iraq, Israel, Jordan, Syria, and Turkey, and by 5,000 BC agricultural communities had spread through much of what is now China (Garofalo 1999, Smitha 1998). Approximately 3,000 years ago, physiological differences had developed between a number of cultivars and their wild relatives (Anderson 2000). With the advent of these crop plant domestication systems and the use of rudimentary agricultural practices, farmers selected the seeds to use for future crops. Dicke (1972) describes the selection and development of mulberry, *Morus rubra* L., that yielded high populations of the silkworm moth, *Bombyx mori* (L.), and fine quality silk. In this instance, arthropod susceptibility was actually selected for instead of resistance.

During the eighteenth and early nineteenth centuries, insect resistant cultivars of wheat and apples were first developed and cultivated in the United States. As early as 1788, early maturing wheat cultivars were grown in the United States to avoid infestation by the Hessian fly, *Mayetiola destructor* (Say) (Chapman 1826). A few years later, Havens (1792) identified resistance to the Hessian fly in the wheat cultivar 'Underhill' in New York. Lindley (1831) made recommendations for the cultivation of the apple, *Malus* spp., cultivars 'Winter Majetin' and 'Siberian BitterSweet', because of their resistance to the wooly apple aphid, *Eriosoma lanigerum* (Hausmann).

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In the mid-nineteenth century, plant resistance to an insect played an important role in Franco-American relations. The grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), had been accidentally introduced from North America into the French wine-producing areas about 1860. Within 25 years, *D. vitifoliae* had destroyed nearly one-third (~10 million ha) of the French wine grapes and the French wine industry was devastated. The famous entomologist Charles Valentine Riley recognized that native American grapes, *Vitis labrusca*, were resistant to *D. vitifoliae*. Working with a colleague, J. E. Planchon in France, Riley led efforts to graft French scions of *Vitis vinifera* to resistant *V. labrusca* rootstocks from the Midwestern United States. Planchon's efforts were successful, and the industry recovered. For his efforts, Riley received the French Grand Gold Medal and was named a Chevalier of the Legion of Honor in 1884.

The breeding of arthropod resistant plants became more formalized in the late 19th century, with the rediscovery of Gregor Mendel's basic tenets of heredity and plant hybridization. However, fewer than 100 reports of plant resistance to arthropods were published in the United States during the 19th and early 20th century. In one of the earliest comprehensive reviews of plant resistance to arthropods, Snelling (1941) identified 163 publications dealing with plant resistance in the United States from 1931 until 1940. Since then, numerous reviews have chronicled the progress and accomplishments of scientists conducting research on plant resistance (Beck 1965, Green and Hedin 1986, Harris 1980, Hedin 1978, 1983, Maxwell et al. 1972, Painter 1958, 1968, Smith 1999, Stoner 1998).

The first book on the subject, *Plant Resistance to Insect Pests* was written by R. H. Painter (1951), the founder of this area of research in the United States. In Russia, Chesnokov (1953) published the first review of techniques on the subject, *Methods of Investigating Plant Resistance to Pests.* In the late 1970's, research activities in plant resistance intensified and several additional books on the subject were published, including those of Rosetto (1973) *Resistencia de plantas a insetos,* Russell (1978) *Plant Breeding for Pest and Disease Resistance*, Lara (1979) *Principos de resisencia de plants a insetos,* Panda (1979) *Principles of Host-Plant Resistance to Insects,* Maxwell and Jennings (1980) *Breeding Plants Resistant to Insects*, and the first edition of this text. In one of the few publications of its type, Mattson et al. (1988) developed *Mechanisms of Woody Plant Defenses Against Insects: Pattern for Search*. In 1994, I collaborated with Z. R. Khan and M. D. Pathak to publish an updated techniques book, *Techniques for the Evaluation of Insect Resistance in Crop Plants* (Smith et al. 1994).

In the last decade alone, the treatment of the subject of plant resistance has broadened to include several new perspectives. These include the evolutionary responses of pathogens and pests to plant resistance (Fritz and Simms 1992) and an edited volume completely dedicated to the economic benefits of resistance (Wiseman and Webster 1999). Panda and Khush (1995) developed an excellent updated overview of the literature, while Ananthakrishnan (2001) compiled a contemporary collection of contributions dealing specifically with the allelochemistry of resistant plants. The area of induced plant defense to herbivore and pathogen challenge has expanded

greatly with an increasing number of reports of the identification of expressed resistance genes and gene products (see Chapter 9). These have been exceptionally well documented in reviews edited by Agrawal et al. (1999), Baldwin (1994), Chadwick and Goode (1999), Karban and Baldwin (1997) and Kessler and Baldwin (2002).

Research involving the development and use of arthropod resistant crop cultivars has led to significant crop improvements in the major food producing areas of the world in the past 50 years. These improvements include significantly improved food production, contributions toward the alleviation of hunger and improved human nutrition (Khush 1995). One of the most spectacular successes of the use of arthropod resistant crops occurred during the "Green Revolution" in tropical Asia during the 1960s, when high-yielding pest-resistant cultivars of rice, *Oryza sativa* (L.), were introduced into production agriculture. The continued growth of such cultivars has made significant improvements to the economies of several south and Southeast Asian countries, such that many countries that were previously food importers are now food exporters. One cultivar, IR36, developed and produced during the 1970's in Southeast Asia, provided approximately $1 billion of additional annual income to rice producers (Khush and Brar 1991).

Over 500 cultivars, plant material lines, or parent lines of food and fiber crops have been developed and registered in the United States since 1975 (reviewed in Smith 1989 and Stoner 1996). This germplasm has been produced through the cooperative efforts of entomologists and plant breeders employed by state agricultural experiment stations, the United States Department of Agriculture Agricultural Research Service, and private industry. Presently, hundreds of resistant cultivars are grown in the United States other major crop production areas of the World. Over one-half of the cultivars developed are maize, wheat, and *Sorghum bicolor* (L.) Moench, - the major world cereal grain food crops. For example, over one-half of all U. S. commercial maize cultivars have some resistance to the corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Barry 1969). Over 75% of the maize cultivars have some resistance to the first and second generation of the European corn borer, *Ostrinia nubilalis* Hubner (Barry and Darrah 1991). Most of the U. S. cultivars of soybean, *Glycine max* (L.) Merr., have resistance to the potato leafhopper, *Empoasca fabae* (Harris), and many alfalfa cultivars of alfalfa, *Medicago sativa* L., have resistance to a complex of pest aphids (Wilde 2002).

Many of the cultivars described above were developed in collaborations with by researchers at International Agricultural Research Centers that comprise the Consultative Group for International Agricultural Research (Figure 1.1). Hundreds of cultivars of maize, potato, *Solanum tuberosum* L., rice, sorghum, and wheat, and have been developed at these centers, and many possess resistance to the major arthropod pests of each crop. Often, detailed knowledge about the type and nature of resistance has been determined. Clement and Quisenberry (1999) reviewed an outstanding comprehensive collection of the existing global genetic resources in arthropod-resistant crop plants (see Chapter 5).

Figure 1.1. Locations of International Agricultural Research Centers comprising the Consultative Group for International Agricultural Research.

2. ADVANTAGES OF PLANT RESISTANCE TO ARTHROPODS

The economic advantage that arthropod resistant cultivars offer producers is genetically incorporated arthropod control for the cost of the seed alone. Even if only moderate levels of resistance are combined with pesticide applications, the costs of insecticidal control and insecticide residue problems are greatly reduced. Schalk and Ratcliffe (1976) estimated that approximately 319,000 tons of insecticides (approximately 37% of the total insecticides applied during the 1960s) were saved annually through the planting of insect resistant cultivars of alfalfa, barley, maize and sorghum in the U. S. This amount is now likely greater, because the greatly increased use of transgenic cultivars of insect-resistant maize and cotton, *Gossypium hirsutum* L*.,* has further reduced pesticide applications in several countries (see Chapter 10). For example, insecticide use for *O. nubilalis* control in the U. S. dropped approximately 30% after the commercialization of *Bt* maize in North America (Rice and Pilcher 1998). Added ecological benefits of such reduced or eliminated pesticide applications are cleaner water supplies and reduced mortality of beneficial arthropod populations.

Arthropod resistance is of practical value even if improved resistant cultivars are not developed. Wightman et al. (1995) studied responses of chickpea, *Cicer arietinum* L., to *Helicoverpa armigera* (Hubner) larval feeding damage in southern India, in the presence or absence of insecticides. Although a *Helicoverpa* resistant landrace does not yield as much as a susceptible landrace or susceptible cultivar, when insecticides are applied the resistant landrace provides profits to producers when they cannot afford to purchase insecticides (Figure 1.2). In some cases, there is no synergistic benefit from insecticides on net crop yield or value and the need for insecticides is eliminated (Buntin et al. 1992, van den Berg et al. 1994).
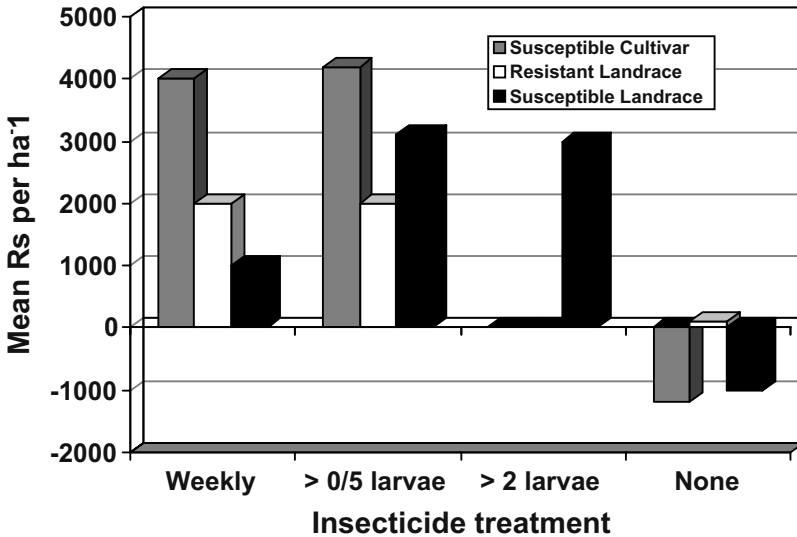
Figure. 1.2. Net Indian farm income for three cultivars of Cicer arietinum grown under four insecticide treatments to control Helicoverpa armigera. Reprinted from Crop Protection, Vol. 14, Wightman, J. A., M. M. Anders, V. R. Rao, and L. M. Reddy. 1995. Management of Helicoverpa armigera (Lepidoptera: Noctuidae) on chickpea in southern India: thresholds and the economics of host plant resistance and insecticide application. Pages 37 - 46, Copyright 1995, Butterworth Heinemann, Inc., with permission from Elseiver.

Regardless of the level of resistance, pest economic threshold levels and economic injury levels require adjustment when resistant cultivars are employed in integrated pest management systems, in order to make insecticide use decisions involving pest resistant cultivars (Teetes 1994, Sharma 1993).

Arthropod resistant cultivars also yield much higher returns per dollar invested than those spent on insecticide development. Luginbill (1969) demonstrated that arthropod resistant varieties of alfalfa, maize and wheat produced in the U. S. during the 1960s yielded a 300% return per research dollar invested. More specifically, *M. destructor*-resistant U. S. wheat cultivars developed during the same period of time yielded a 120-fold higher return of return than did the development of insecticides (Painter 1968). More contemporary research indicates that *M. destructor* resistance in wheat cultivars in Morocco provides a 9:1 return on investment of research funds (Azzam et al. 1997).

Recent economic analyses have provided additional information about the value of plant resistance. The value of research to develop sorghum hybrids with resistance to the greenbug, *Schizaphis graminum* (Rondani), biotype E in the U. S. was estimated to be from $113 million to $389 million per year, depending on whether the provisions of 1989 U. S. farm legislation were considered (Eddleman et al. 1999).

Table 1.1. Estimated annual value of producing Phaseolus *lines with tolerance to* Empoasca
krameri *in Central American agriculture* [a]

Phaseolus line	Value ($ per hectare)		
	Net benefit of control	*Losses (no control)*	*Benefit of resistance*
EMP187	1,094	317	559
EMP188	1,184	438	526
EMP186	990	302	469
Susceptible	880	662	---

[a] *from Heinrichs and Adesina (1999). Reprinted with permission from Thomas Say
Publications in Entomology: Proceedings. Copyright 1999, Entomological Society of
America.*
[b] *($ benefit of resistance - $ benefit of susceptibility) + ($ loss on susceptibility - $ loss on
resistance)*

In Asia, Africa, and Latin America, the value of arthropod resistant cultivars of
and chickpea, sorghum and pearl millet, *Pennisetum glaucum* (L.) R. Br., is
estimated to be worth more than $580 million per year (Heinrichs and Adensina 1999).
Cardona and Cortes (1991) estimated resistance in *Phaseolus* to the leafhopper
Empoasca krameri Ross and Moore, in Latin America to be approximately $500
per acre per year (Table 1.1). Based on a survey of U. S. alfalfa production, Berberet
et al. (1999) estimated that the increase in annual gross income to producers from the
use of multiple disease and arthropod resistant alfalfa to be approximately $300
million per year. The current economic value of all arthropod resistant cultivars of
wheat is slightly more than $250 million per year (Smith et al. 1999). The value of
transgenic resistant crops is just beginning to be recognized. Eddleman (1995)
estimated that the global economic benefit of commercial cotton cultivars containing
the toxin gene from the bacteria *Bacillus thuringiensis*, (see Chapter 10) to be valued at
between $570 million and $730 million per year, depending on whether insecticide
use continued for secondary species of pest Lepidoptera. The current total estimated
global value of arthropod resistant cultivars is approximately $1.18 billion (Table
1.2).

The effects of deploying resistance genes accumulate over time.   In general, the
longer they remain effective, the greater the benefits of their use (Robinson 1996).
These effects were thoroughly documented as arthropod resistant *O. sativa* cultivars
were placed into production in Southeast Asia in the 1970s. In both the Philippines
and Indonesia, yield losses of crops planted with arthropod resistant cultivars were
approximately one-half of the losses in crops planted with non-resistant cultivars
(Panda 1979, Waibel 1987). Wiseman (1999) demonstrated that even low-level resistance
to the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), in the silks of maize
significantly reduced *S. frugiperda* growth and fecundity in only five generations.

Resistant cultivars improve the efficiency of predators, parasites and arthropod
pathogens by decreasing the vigor and physiological state of the pest arthropod. The
effects of many resistant crop cultivars have no detrimental effects and in some
cases, have additive or synergistic effects on the actions of pest arthropod predators
and parasites. (Eigenbrode and Trumble 1994, Quisenberry and Schotzko 1994).

Table 1.2. Net annual global economic value of arthropod resistant crop cultivars

Crop	Pest(s)	Location	$ (x million)
Gossypium hirsutum	Lepidoptera larvae	World	570 [b]
Medicago sativa	Aphids	United States	300 [a]
Oryza sativa	Leafhoppers	Asia	1,000
Sorghum bicolor	*Schizaphis graminum*	United States	113 [c]
Triticum aestivum	*Aceria tosichella*	North America	150
	Mayetiola destructor	United States	17
	Diuraphis noxia	United States	13
	Cephus cinctus	United States	12 [d]

[a] *Assumes a 60% area of planting multiple pest (disease and insect) resistant cultivars*
[b] *Assumes insecticide use remains constant for non-target pest species*
[c] *Assumes no 1989 U. S. farming legislation provisions*
[d] *Assumes 3.5% annual rate of inflation of 1948 estimate of $3.8 million*

The additive effects of resistance genes and arthropod pathogens have been reviewed previously (Smith 1999). For example, results of Wiseman and Hamm (1993) demonstrate how nuclear polyhedrosis viruses increase the mortality of corn earworm, *Helicoverpa zea* Boddie, larvae fed silk tissue of a resistant maize cultivar (Figure 1.3). The use of resistant cultivars to maximize cultural control tactics such as early-planted cultivars, trap crops, and early maturing cultivars is well documented in several crops (Maxwell 1991). The planting of early-maturing, arthropod-resistant cultivars has been shown to reduce populations of several key pests in rice. Trap cropping, a practice used to attract pest arthropod populations and then destroy them, is synergistic when used in combination with arthropod resistant cultivars of cotton, rice and soybean.

In addition to synergizing traditional pest management tactics, there are also several advantages of resistant plants themselves over biological, chemical and cultural controls. Insecticides applied at recommended rates often kill biological control organisms, but resistant cultivars do not, and are compatible with insecticide use. Where biocontrol organisms depend on the sustained density of hosts or prey to remain effective, resistant cultivars function independently of arthropod density and operate at all pest population levels (Panda and Khush 1995). Expanded discussions of the integration of resistant cultivars with biological control organisms, chemical control, and cultural control tactics in integrated pest management systems are presented in Chapter 12.

Resistant cultivars have also been shown to impede the spread of arthropod-vectored plant diseases, by reducing the population growth of disease vectors (see reviews by Kennedy 1976, Gibson and Plumb 1977, Maramorosch 1980). In a 9 year study, Harvey et al. (1994) demonstrated how resistance in *Triticum aestivum* to the wheat curl mite, *Aceria tosichella* Keifer, the vector of wheat streak mosaic virus, reduced

virus incidence by as much as 50%. Kishaba et al. (1992) demonstrated similar results (31% - 74% reduction) in the reduction of the transmission of water-melon mosaic virus through the use of breeding lines of muskmelon, *Cucumis melo* L., resistant to the melon aphid, *Aphis gossypii* Glover. Kobayashai et al. (1993) evaluated the resistance of several *Oryza* species to the green rice leaf-hopper, *Nephotettix virescens* (Distant), and the green rice leafhopper, *Nephotettix nigropictus* (Stål), as vectors of rice tungro virus. In several of the species evaluated, reduced infection by the virus was related to the resistance to either of the two vectors.
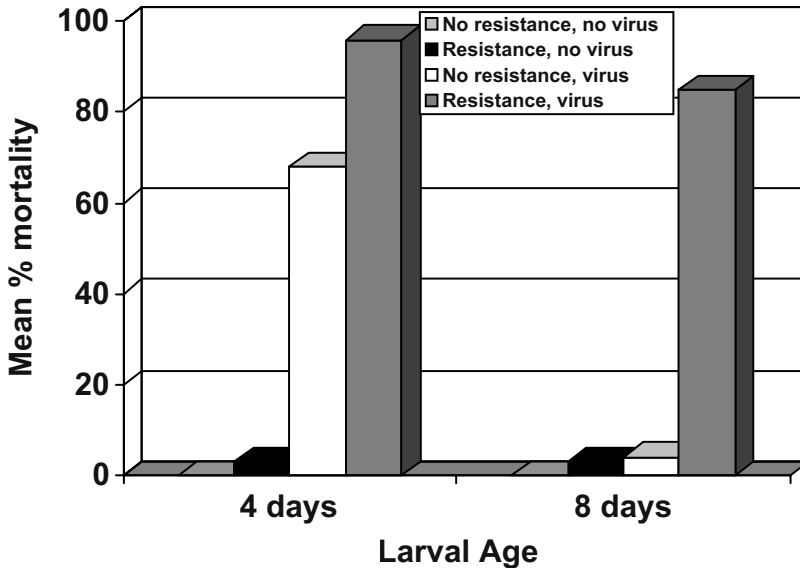

Figure 1.3. Mortality of Helicoverpa zea larvae feeding on artificial diets with (Resistance) and without (No Resistance) silks of the resistant maize cultivar 'Zapalote Chico' and exposed to Elcar (no virus - 0, virus - 1330 polyhedral occlusion bodies). Reprinted from Biological Control, Vol. 3. Wiseman, B. R., and J. J. Hamm. 1993. Nuclear polyhedrosis virus and resistant corn silks enhance mortality of corn earworm (Lepidoptera, Noctuidae) larvae. Pages 337-342, Copyright 1993, Academic Press Inc., with permission from Elseiver.

3. DISADVANTAGES OF PLANT RESISTANCE TO ARTHROPODS

Arthropod resistant cultivars have some disadvantages. In some cases, the level of resistance is incompatible with biological control agents (Bottrell et al. 1998). In arthropod-resistant cultivars of some crops, high densities of plant trichomes and high concentrations of resistance-bearing allelochemicals have been shown to impart detrimental effects on the biology of beneficial arthropod predators and parasites, as well as arthropod pathogens. Negative interactions between insecticides and some resistant cultivars also exist. When arthropods are fed foliage containing high levels

of allelochemicals that mediate resistance in some crops, they are better able to detoxify insecticides and miticides (Ghidiu et al. 1990).

Developing a cultivar resistant to a single arthropod species traditionally has required three to five years, and may require ten years or longer for a complex of several arthropods. These intervals have shortened somewhat with the now common use of tropical and subtropical winter nurseries to increase the number of plant generations that can be produced each year. Many crops are grown over broadly diverse geographic ranges, soil types and environmental conditions, necessitating the deployment of different resistant cultivars for different geographic production regions. From the plant breeder's perspective, even with winter nurseries, regional crop resistance to arthropods may be an expensive and time-consuming objective.

Resistance is commonly identified in wild, undomesticated species of plants or landraces that may have only distant taxonomic relations to the crop species under improvement. It is not unusual for these plants to have poor yield, poor plant type, or disease susceptibility. Some of these problems may be eliminated with the adaptation and use of embryo rescue and related plant tissue culture techniques. For the most part, however, the incorporation of resistance from wild species of plants into domestic crop plants is a long-term process.

Arthropod resistant cultivars that rely on the effects of a single, major gene often promote the development of populations of individuals possessing genes virulent to plant resistance genes (see Chapter 11). The use of monogenic resistance often leads to a pattern of sequential gene release, with each new cultivar possessing a different gene or gene arrangement, in order to stay a step ahead of the continuously mutating genetic machinery of the pest arthropod. The development of cultivars with polygenic resistance, to delay biotype development, requires years longer to accomplish. Cultivars with moderate levels of multigene resistance to stem boring Lepidoptera have been used in Asian rice production and North American maize production for many years without the development of resistance-breaking borer biotypes (Heinrichs 1986). Different aspects of the gene-for-gene interaction between arthropod biotypes and plant resistance genes are fully discussed in Chapter 11.

4. DEFINITIONS

By definition, **plant resistance to arthropods** is the sum of the constitutive, genetically inherited qualities that result in a plant of one cultivar or species being less damaged than a susceptible plant lacking these qualities. Plant resistance to arthropods must always be measured on a relative scale, with the degree of resistance based on comparison to susceptible control plants that are more severely damaged or killed under similar experimental conditions, as well as resistant control plants with a known, predetermined level of resistance. Relative measurements are necessary, since resistance is influenced by environmental fluctuations occurring over both time and space. In the terms of the plant resistance researcher, susceptibility is the inability of a plant to inherit qualities that express resistance to arthropods.

Induced resistance to arthropods is expressed in plants damaged by pest feeding or oviposition. This damage activates **defense response (DR)** genes and the redirection of normal cell maintenance genes to plant defense. Damaged plants produce **elicitors** that activate plant gene expression and the synthesis of volatile and non-volatile allelochemicals such as proteinase inhibitors, phenolics, and enzymes involved in the different types of plant defense (Agrawal et al. 1999). Several plant signaling pathways, including those driven by jasmonic acid, salicylic acid, ethylene and abcissic acid orchestrate the induction of plant defenses to arthropod attack (Walling 2000). Induced arthropod resistance, first demonstrated in apple by Bramstedt (1938), has been demonstrated in over 100 species of the major plant taxa (Karban and Kuc 1999). A complete discussion of induced resistance and the plant genes expressed as a result of the induction process is provided in Chapter 9.

Pseudo- or false resistance may occur in normally susceptible plants for several different reasons. Plants may avoid arthropod attack due to earlier than normal phenological development and resultant unsuitability for arthropod development. False resistance may occur as a result as a result of temporary variations in temperature, daylength, soil chemistry, plant or soil water content, or internal plant metabolism. Finally, normally susceptible plants may appear resistant as a result of simply escaping damage due to incomplete arthropod infestations.

Associational resistance occurs through the practice of intercropping, when normally susceptible plants grow in association with a resistant plant, and derive protection from arthropod predation. The diversionary or delaying actions of mixtures of plant species can help slow the development of pest arthropod populations in general, and may also help prevent the development of arthropod biotypes (Chapter 11) that develop virulence to plant resistance genes. A specialized type of associational resistance has been shown to exist in Graminaceous crops infected with fungal endophytes that produce alkaloids that kill or delay the development of pest arthropods (Breen et al. 1994, Clement et al. 1994). An in-depth discussion of endophyte-arthropod resistance interactions is provided in Chapter 7.

Overall, intercropping has positive implications for arthropod resistance. Thrips populations are much lower in polycultures of sorghum and cowpea, mungbean, than in either crop grown in monoculture (Ampong-Nyarko et al. 1994). Similar reductions have been reported for pest aphid populations in sorghum-soybean mixtures and *Phaseolus* spp.-maize mixtures (Bottenberg and Irwin 1991, 1992), and for populations of the flea beetle, *Phyllotreta cruciferae* (Goeze), on mixtures of *Vicia* and broccoli, *Brassica oleracea* L. (Garcia and Altieri 1992). Khan et al. (1997) developed a very specialized intercropping system consisting of molasses grass, *Melinis minutiflora,* and maize for management of the maize stem borers *Busseola fusca* Fuller and *Chilo suppressalis* (Walker). The molasses grass crop repels borer larvae and adults, and attracts significantly more parasites to borers infesting maize, resulting in significant (~10 fold) reductions in borer damage.

Because plant-arthropod-environment interactions vary widely, no single management tactic, including plant resistance, is universally effective. In at least one instance, intercropping has been shown to have a negative effect on a resistant

cultivar, where intercropping of cowpea and maize diminishes resistance in cowpea to the cowpea borer, *Maruca testulalis* (Geyer) (Gethi et al. 1993). From a practical standpoint, associational resistance may be imitated by the development of plant cultivars based on several different sources of resistance, or mixtures of resistant and susceptible cultivars. An expanded discussion of crop and gene mixtures is presented in Chapter 8.

5. RESISTANCE CATEGORIES

Three types of plant resistance to arthropods are commonly referred to in plant resistance literature. These resistance types were originally defined by Painter (1951) as mechanisms (Figure 1.4), and were more accurately termed functional categories by Horber (1980). Although I originally termed these categories functional modalities of resistance (Smith 1989) there are several reasons for them to be referred to as categories. By definition*,* a category is a general class or group, and a modality is a classification or form. Conversely, a mechanism is a fundamental physical or chemical process involved in or responsible for an action, reaction or other natural phenomenon. The term basis refers to the foundation or principal component of anything. Thus, the terms category and modality refer to the way a group of items are classified, while the terms basis and mechanism denote the principal process governing a natural phenomenon.

Antibiosis ⟷ **Antixenosis**
adverse effects on   adverse effects on
insect survival   insect behavior

— —

Tolerance
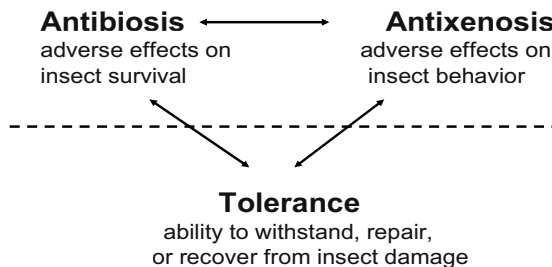ability to withstand, repair,
or recover from insect damage

Figure 1.4. The antibiosis, antixenosis and tolerance categories (originally described as mechanisms) of plant resistance to insects. (from Painter 1951)

Many examples demonstrate how resistant plants categorized or classified as exhibiting antibiosis or antixenosis, while the plants themselves demonstrate tolerance as a third type of resistance, independent of arthropod effects. In contrast to Painter's original use, the term mechanism should be used to describe the underlying chemical or morphological plant processes that, where known, are

responsible for the (negative) reaction of arthropods to resistant plants. To describe the outcome of arthropod-plant interactions, the term category should be used to refer to antibiosis, antixenosis and other as of yet undefined types of plant-arthropod interactions, observed as responses of arthropods to a plant resistance mechanism. The effects of resistant plants on arthropods can be manifested as **antibiosis**, in which case the biology of the pest arthropod is adversely affected; or as **antixenosis**, in which the plant acts as a poor host and the pest then selects an alternate host plant. The inherent genetic qualities of the plant itself may provide it the ability to withstand or recover from insect damage, in which case it is said to express **tolerance** to the pest. The inter-relationship of the three categories is illustrated in Figure 1.4. As indicated previously, these terms have been accepted because of conceptual convenience, but they are not always biologically discrete entities.

Often the antibiosis and antixenosis categories of resistance overlap, because of the difficulty involved in designing experiments to delineate between the two. For example, if an arthropod confined to a resistant plant fails to gain weight at the rate it normally does on a susceptible plant, it might be assumed that the lack of weight gain is due to the presence of antibiotic properties in the plant. However, the lack of weight gain may also be due to the presence of a physical or chemical feeding deterrent with strong antixenotic properties. This deterrent may initiate aberrant behavior in the test arthropod that results in a weakened physiological condition that could be assumed to be the result of an antibiotic effect. In Painter's words "There is increasing evidence that many examples formerly thought to be antibiosis actually are extremely high levels of nonpreference. It has been impossible to determine whether young, tiny insects have starved to death or been poisoned." (Painter 1968).

Combinations of antibiosis and antixenosis are reported often, as a result of researchers conducting very detailed experiments that have delineated the contributions of each category of resistance. A cursory survey of the literature indicates that antibiosis and antixenosis occur together across many plant taxa, including major cereal crops, food legumes, forages, fruits, ornamental plants and vegetables. In a few instances, all three categories have been shown to operate simultaneously. Aphid resistance in barley, sorghum, wheat and sugarcane, a complex hybrid of *Saccharum* species, involves antibiosis, antixenosis and tolerance (Castro et al. 1996, Hawley et al. 2003, White 1990). Resistance in maize to the pink stem borer, *Sesamia nonagrioides* Lef., also involves each of the three categories (Butrón et al. 1998). Bodnaryk and Lamb (1991) noted that all three categories of resistance operate in the resistance of yellow mustard, *Sinapis alba* L., to the flea beetle, *Phyllotreta cruciferae* (Goeze). Detailed descriptions and discussions of each of the three categories and the methodologies involved in investigating them are presented in Chapters 2, 3, 4, and 6.

The practice of identifying and cultivating plants with arthropod-resistant qualities is an ancient one that we continue to use and improve for use in modern crop pest management systems. The use of resistant crop cultivars has been and continues to be necessitated by the continual development of arthropod populations with genetic resistance to chemical pesticides and plant resistance genes, and by a continual need to produce crops with fewer pesticides and at lower production costs.

A major advantage in the cultivation of arthropod-resistant crops is that their production costs are lower, due to the fact that some or all of the arthropod control costs are incorporated into the seeds or clones themselves. In the following chapters we will investigate how this control is identified, how it is inherited, the techniques used to manipulate it, and how it can ultimately be used to manage arthropod populations in crop pest management systems.

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CHAPTER 2

ANTIXENOSIS - ADVERSE EFFECTS OF RESISTANCE ON ARTHROPOD BEHAVIOR

1. DEFINITIONS AND CAUSES

Antixenosis is a term derived from the Greek word xeno (guest) that describes the inability of a plant to serve as a host to an arthropod. If this situation exists in a plant-arthropod interaction, a potential pest chooses to select an alternate host plant. The term antixenosis resistance was developed by Marcos Kogan and Eldon Ortman (1978) to more accurately describe the nonpreference reaction of arthropods to a resistant plant, and to complement the terminology for antibiosis resistance to arthropods (see Chapter 3). Nonpreference was originally defined by Painter (1951) (see Figure 1.5) as the group of plant characters and arthropod responses that lead to a plant being less damaged than another plant lacking these characters and the arthropod responses to them. Both antixenosis and nonpreference denote the presence of morphological or chemical plant factors that adversely alter arthropod behavior, resulting in the selection of an alternate host plant. Physical barriers such as thickened plant epidermal layers, waxy deposits on leaves, stems, or fruits, or a change in the density of trichomes (plant hairs) on normally susceptible plants may force arthropods to abandon their efforts to consume, ingest or oviposit on an otherwise palatable plant. Resistant plants may also be devoid of or lack sufficient levels of phytochemicals to stimulate arthropod feeding or oviposition, and allow them to escape consumption. Arthropod resistant plants may also possess unique phytochemicals that repel or deter herbivores from feeding or ovipositing. Finally, resistant plants may also contain chemicals that are toxic to arthropods after digestion of plant parts.

2. ARTHROPOD SENSORY SYSTEMS INVOLVED IN HOST SELECTION

Understanding how antixenosis functions in the resistance of a plant to an arthropod requires developing a perception of the arthropod's sensory environment. By taking this approach, we can gain some appreciation of the basic factors governing arthropod perception and integration of external stimuli detected by an arthropod's olfactory, visual, tactile, and gustatory receptors. The following sections describe

each type of stimuli. More detailed discussions should be consulted and studied in reviews by Bernays (1992).

2.1. Olfaction

In order to perceive the odors emitted by potential host plants, arthropods rely on an olfactory guidance system controlled by cuticular sense organs known as sensilla basiconica, located on the antennae. Basiconic sensilla are porous, thin-walled structures ranging in length from 10 to 20 um (Figure 2.1). Great diversity exists in the number and arrangement of these sensilla on the antennae of various arthropods.

   The olfactory sensitivity of different arthropod species is instinctively tuned to and controlled by a given qualitative and quantitative blend of odors. Most plant species are unique in their composition of volatile phytochemicals produced by fruiting structures, leaves, roots and stems. Specific groups of odor components in foliage of vegetables such as carrot, leek, onion and potato play important roles in directing arthropod movement to their host plants (Guerin et al. 1983, Leconte and Thibout 1981, Matsumoto 1970, Pierce et al. 1978, Visser et al. 1979). Mustaparta (1975) was one of the researchers to suggest that specific olfactory sensilla respond to specific odor components of a plant's odor "bouquet". Results of more recent research indeed has revealed how arthropods employ olfactory discrimination to determine the differences between unacceptable resistant pants and acceptable susceptible plants (Lapis and Borden 1993, Seifelnasr 1991)

   Vincent Dethier developed original definitions for the effects of phytochemicals based on the responses they elicit in arthropods (Dethier et al. 1960), and the plant resistance research community has incorporated these terms into their working vocabulary. Odors emitted by plants that stimulate arthropod olfactory receptors and cause long-range arthropod movement toward the odors are **attractants**.   In the opposite situation, plants exhibiting antixenosis may produce olfactory **repellents** that cause arthropods to move away from the plants producing the odor. Susceptible plants also emit **arrestant** odors that cause arthropods to stop movement when in close proximity to the odor source. The interplay between the odors emitted by host and non-host plant sources, the regulation of these odors by environmental factors, the perception of the odors by arthropods, and the resultant arthropod behaviors were discussed by Visser (1986) and are summarized in Figure 2.2. Additional experiments (Dickens et al. 1993, Thiery and Visser 1987) have demonstrated many more specifics about the olfactory perception of green leaf volatiles by arthropods.
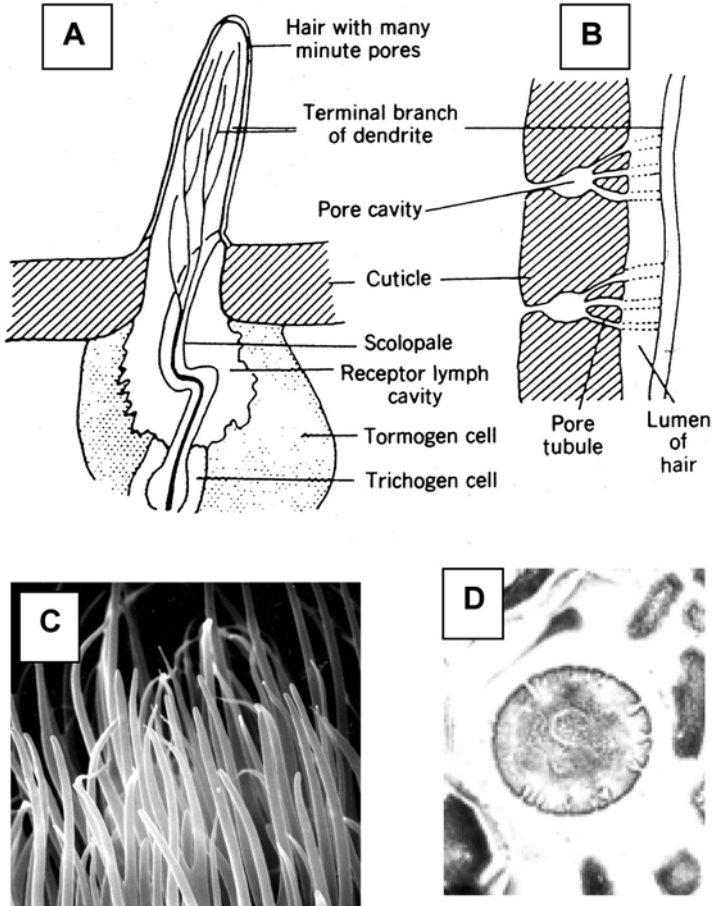
Figure 2.1. Insect sensilla basiconica (A) diagram of sensillum, (B) exploded diagram of hair wall showing pores through which stimulating molecules reach the nerve (dendrite), (C) sensilla basiconica on the antennal club of Lissorhoptrus oryzophilus (4,088X), (D) cross section of sensillum basiconica on the antennal club of L. oryzophilus showing pores in sensillum wall (35,200X). Figures 2.1.a & 2.1.b reprinted from Chapman and Blaney. How animals perceive secondary compounds. In G. A. Rosenthal and D. H. Janzen (Eds.) Herbivores: Their Interaction with Secondary Metabolites, Pages 161-198, Copyright 1979, Academic Press Inc., with permission from Elseiver.
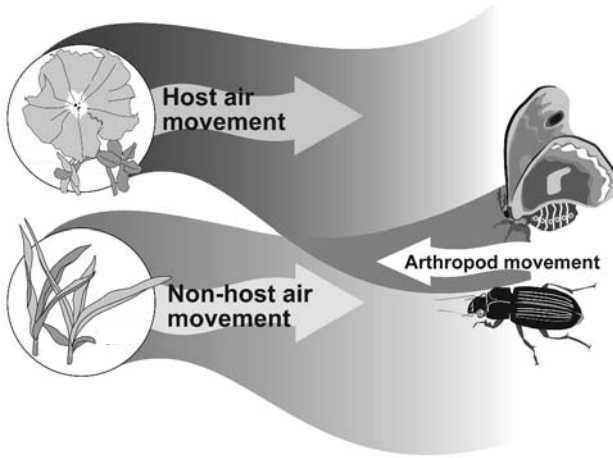
Figure 2.2. Schematic representation of the release of plant volatiles, their dispersion and perception by arthropods, and resultant arthropod behaviors. Host and non-host plants release volatile odor plumes that differ both quantitatively and qualitatively. Perception of the plume by an arthropod is dependent on the olfactory tuning of peripheral antennal sensory receptors. Arthropod orientation and movement to an odor source is governed by a positive anemotaxis (reaction to wind), as well as a positive chemotaxis (directed movement to or away from a chemical stimulus). Positive contact chemoreception of the plant results in the arthropod accepting the plant, followed by feeding and oviposition.

2.2. Vision

Prokopy and Owens (1983) described vision in herbivorous arthropods as being governed by their perception of the spectra quality of light stimuli, (i. e. brightness, hue, and saturation of various wavelengths) as well as the dimensions of the objects viewed, and the pattern or shape of the object. During orientation to potential host plants, arthropods simultaneously perceive visual and chemical stimuli (Green et al. 1994). During long-range orientation, an arthropod may use vision for recognition of the shape of an object and utilize olfaction to perceive plant attractants. After approaching the immediate location of the plant, movement to the plant surface is most likely guided by perception of the plant outline. Final contact with the plant surface by many arthropods is due to a positive response to yellow or yellow-green pigments in plant foliage that occurs in the spectral range of from 500 to 580 nm. Roessingh and Stadler (1990) demonstrated a combination of plant shape and color in studies of the oviposition behavior of the cabbage root fly, *Delia radicum* (L.).

In a direct application of this behavior, Broadbent et al. (1990) studied the relationship between flower color in *Chrysanthemum* spp. cultivars and resistance to the western flower thrips, *Frankiniella occidentalis* (Pegande). Thrips displayed a pronounced preference for yellow-flowered cultivars over white- flowered cultivars. Moharramipour et al. (1997) found similar results, noting that barley, *Hordeum vulgare* L., hybrids with green waxless foliage were less preferred by the corn leaf aphid, *Rhopalosiphum maidis* (L.), than hybrids with yellow waxless foliage. Antixenosis resistance has been achieved by genetically altering the color of plant foliage to reflect different wavelengths of light. Some curcubit cultivars with silver leaves reflect more blue and ultraviolet wavelengths of light than green-leaved cultivars, and are resistant to aphids and aphid-vectored diseases (Shifriss 1981).

The red leaf color in cotton, *Gossypium hirsutum* L., is a heritable character that causes antixenotic reactions in adult boll weevils, *Anthonomous grandis* Boheman (Iseley 1928, Jones et al. 1981). Red foliage in some cultivars of cabbage, *Brassica oleracea* var. *capitata* L., imparts antixenosis to alates of the cabbage aphid, *Brevicoryne brassicae* (L.), but this resistance is ephemeral and declines over the life of the plant (Singh and Ellis 1993). The same trend was noted in evaluations of cultivars of crabapple, *Malus ioensis*, (Wood) Britt., for resistance to Japanese beetle, *Popillia japonica* Newman, by Spicer et al. (1995). Cultivars with young red leaves that turned green with maturity were much more susceptible than cultivars with completely green leaves. Reinert et al. (1983) noted a similar preference in oviposition of the larger canna leafroller, *Calpodes ethlius* (Stoll), for cultivars of *Canna* spp. with red foliage over cultivars with green foliage. Fiori and Craig (1987) used the color intensity of birch leaf supernatants to determine degrees of resistance in birch, *Betula lutea* F. Michx., to oviposition by the birch leafminer, *Fenusa pusila* (Lepeletier). Birch species with high levels of oviposition have lower leaf supernatant spectrophotometric absorption rates than species that are resistant.

2.3. Thigmoreception

After an arthropod contacts the plant surface, trichoid sensilla on the body, tarsi, head, and antennae (Figure 2.3) perceive tactile stimuli and supply information about host plant morphology to the arthropod nervous system. Stimuli are received from the leaf or stem surface, or from trichomes, epidermal ridges, or leaf margin notches that trigger genetically controlled sequences of arthropod feeding or oviposition behavior. Plant morphological features may promote positive mechanical stimuli and act as feeding or oviposition stimulants. Changes in the shape, size and number of such plant morphological features may also prevent or disrupt the normal mechanoreceptive process, resulting in deterrency of feeding or oviposition.
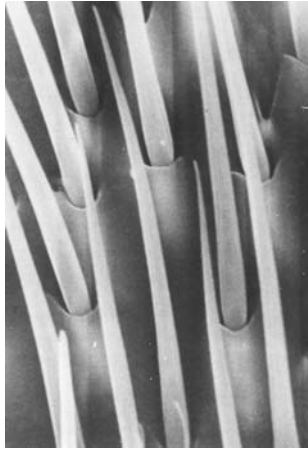
Figure 2.3. Sensilla trichoidea on the antennal club of Hypera meles (2,000X). Reprinted from J. Insect Morphol. & Embryol., Vol. 5. Smith, C. M., J. L. Frazier, L. B. Coons and W. E. Knight. 1976. Antennal morphology of the clover weevil, Hypera meles (F.) Int. J. Insect Morph. and Embryol. Pages 349-355, Copyright 1976, Pergamon Press, Inc., with permission from Elseiver.

A classic example of changing plant morphology to establish arthropod resistance is the breeding of the 'frego' or twisted bract character (Figure 2.4a) from wild genotypes of *Gossypium* into cotton cultivars. Normal cotton buds are tightly enclosed in bracts (Figure 2.4) that create a favorable environment for oviposition and feeding of the boll weevil. The open, twisted condition of the frego bract imparts weevil resistance by removing the positive stimuli that promote the use of normal bracts (Mitchell et al. 1973).
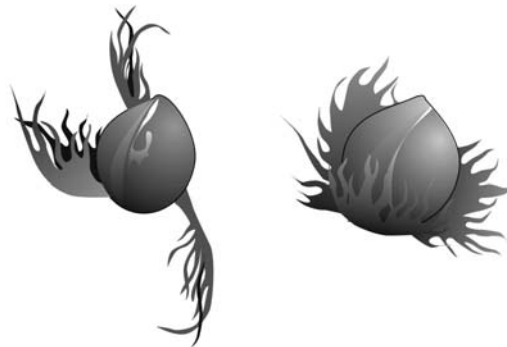

Figure 2.4. Frego (twisted) bract character of a cotton cultivar with resistance to Anthonomous grandis (left) and enclosed bracts of a susceptible cultivar (right).