PLANT RESISTANCE TO INSECTS IN THE SOUTHEASTERN UNITED STATES—AN OVERVIEW

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ABSTRACT

Plant resistance to insects is an effective and ideal method for controlling crop pests. The development and use of plant cultivars with resistance to insects and their effects on insect populations is reviewed. Resistant plants may be used as a sole control method or as an adjunct to other control components of integrated pest management. Although demand for the use of resistant cultivars for control of insects is anticipated to increase, graduate training in applied plant resistance is lacking, and only four universities in the southeastern United States have formal graduate courses. Georgia, Louisiana, and Mississippi have major programs of plant resistance to insects with lesser amounts in Florida, North Carolina, and South Carolina. The United States Department of Agriculture's Agricultural Research Service has the largest efforts in plant resistance to insects in the Southeast.

RESUMEN

Un método efectivo e ideal para controlar plagas en cultivos es el uso de plantas resistentes. Se revisa el desarrollo y el uso de variedades resistentes a plaga de insectos y sus efectos en las poblaciones de insectos. Plantas resistentes se pueden usar como el único método de control o como adjunto a otros componentes de control en un sistema integrado de administración de plagas. Aunque se anticipa el aumento en la demanda de variedades resistente a plagas, hay una falta de entrenamiento en el área de la aplicación de resistencia de plantas al nivel de graduados, y solo cuatro universidades en el sudeste de los Estados Unidos ofrecen cursos formales para graduados. Los estados de Georgia, Louisiana y Mississippi tiene grandes programas de resistencia de plantas a plagas de insectos, y la Florida, Carolina del Norte y Carolina del Sur tienen programas menores. El Servicio de Investigación Agrícola del Departamento de Agricultura de los Estados Unidos tiene los mayores programas de estudios de resistencia de plantas a plagas en el sudeste.

Numerous agricultural leaders over the past 25 years have emphasized the need for nonchemical control of insect pests. However, Headley (1979) predicted that chemical control would have a major role in pest management in high value crops until 1992 and then the trend for nonchemical control methods would increase (Table 1). He also predicted that resistant cultivars would have a major role in controlling pests in grain crops until 1992 and that a demand for their use would sharply increase in all crops after that time. The recent ARS budget increases for biocontrol and ground water quality emphasize the need for more nonchemical pest control research to minimize reliance on chemical pesticides for pest control. Plant resistance to insects, integrated with other biocontrol strategies, should be one of the principle means of nonchemical control of pests.

The growing of cultivars resistant to insect pests has been acclaimed the most effective and ideal method of combating pests that attack plants (Luginbill 1969). The use of resistant cultivars, either alone or in combination with other integrated pest manage-

TABLE 1. PREDICTIVE COMPONENTS OF FUTURE PEST CONTROL*.

Pest control technique	Probable use to 1992	Trend in use
Chemical methods		
Insecticides	Major	Declining
Mechanical methods	Minor	Declining
Biological methods		
Parasites & predators	Minor	No change
Bacteria	Minor	Increasing
Viruses	Not significant	Increasing
Pheromones	Not significant	No change
Resistant varieties	Major	Increasing
Pest genetics	Minor	Declining
Cultural methods		
Crop rotation	Minor	Declining
Trap crops	Minor	No change

*Modified from Headley 1979.

ment systems, provides crop protection that is biologically, ecologically, economically, and socially feasible (Teetes 1985). Resistant cultivars are nonpolluting to our environment and may be grown at no extra expense to the farmer.

The use of insect-resistant plants is usually associated with reduced crop damage by pests (Painter 1951). Painter attributed resistance to heritable qualities of the plant. A resistant plant is always resistant to a specific pest species under given environmental conditions; if the environment changes, the level of resistance may or may not change. Mutations in a resistant plant genotype may or may not be resistant, but its predecessor remains resistant to the pest insect. A pest insect species may also form new biotypes while the original insect biotype remains susceptible to the resistant plant genotype. Hence, resistance in plants to insects is probably more stable than given credit. Conversely, insect pests are genetically diverse, as evidenced by the number of biotypes in certain crop-insect relationships, i.e., the Hessian fly.

Painter (1968) proposed three mechanisms of resistance: non-preference, antibiosis, and tolerance. (1) Nonpreference denotes a group of plant characters and insect responses that lead an insect away from a plant or plant part for oviposition, for food, or for shelter, or for any combination of the three (Painter 1951, 1968). Painter (1968) delineated nonpreference into two distinct actions of choice by insects among cultivars: (a) a choice to oviposit, establish, or feed when several cultivars are grown or (b) a choice to oviposit, establish, or feed when only one cultivar is present. Owens (1975) further described these two uses of nonpreference as relative or absolute. (2) Antibiosis is the mechanism of resistance that produces those adverse effects on the insect life history which result when a resistant plant is used for food (Painter 1951). The effects of an insect feeding on a plant with this type resistance may be death of the neonate larva or nymph, reduced food consumption that results in a smaller size or lower weight, increased developmental time, low food reserves, death in the prepupal stage, and/or reduced fecundity (Owens 1975). (3) Tolerance to insect damage is a resistance mechanism that allows the plant to grow and reproduce or repair injury in spite of supporting a density of insects approximately equal to what would be damaging to a susceptible cultivar (Painter 1951).

The basic triad of the mechanisms of resistance proposed by Painter (1951) is usually delineated by specifically designed experiments to demonstrate the independence of the three components; however, resistant cultivars often possess combinations of these resistance mechanisms, especially with regard to nonpreference and antibiosis. With a combination of resistance mechanisms, a cultivar that is nonpreferred does not require the same level of antibiosis or tolerance that a more preferred cultivar must possess to have the same level of resistance. Thus, different cultivars may possess the same levels of resistance with different mechanisms of resistance and/or levels of the resistance components.

Plant resistance to insects received a lot of attention and support shortly after the late Rachael Carson published her book, "Silent Spring," even though she did not mention the use of resistant cultivars as a means of nonchemical control of insect pests. This was probably because the resistant plant's effect is not as dramatic and its effects on insects are not as visible as those of other control measures (Luginbill 1969). However, agricultural leaders recognized the importance of resistant cultivars as the most successful and least heralded of all the natural methods of insect control (Holcomb 1970). Dahms (1972a) reported that more than 100 varieties or inbreds with resistance to insects have been released, with resistance to more than 25 insect species. Today, probably more than 500 cultivars with resistance to more than 50 insect species or biotypes have been developed and released.

The development and use of resistant cultivars should be the foundation or "hub" of any crop protection scheme. Before 1951, the production of sweet corn was unprofitable in the Southeast, even with the use of pesticides. However, in 1951 'Ioana' sweet corn was released with low to intermediate levels of resistance to corn earworm. This allowed growers to produce sweet corn without pesticides. Today, higher levels of resistance in sweet corn are available to growers, as evidenced by the fact that 'Ioana' is used in our studies as a susceptible check. Use of resistant cultivars has certainly been profitable to the grower. Luginbill (1969) quoted a return value to the grower of $300 for each $1 invested in research and development of resistant plants. McMillian & Wiseman (1972) also estimated that for each $1 invested by the USDA for the period from 1950 through 1970 on research on resistance in corn to *Heliothis zea* (Boddie), $20 was returned to the grower in the form of an increase in corn yield.

Historically, insect-resistant cultivars have been more widely used for crops where plant resistance was the only method of protection from losses caused by insects (Wiseman 1982). One of the earliest records of the use of an insect resistant variety was that of Havens (1792) who reported that the wheat variety 'Underhill' was planted to avoid losses caused by the Hessian fly, *Mayetiola destructor* (Say). Today, growing resistant wheat cultivars is the primary method for controlling the Hessian fly worldwide. The Purdue-USDA small grains improvement program has estimated a $3.4 billion increase in farm income attributable to improved cultivars with resistance to this insect (Roberts et al. 1988). The annual return exceeded $4.6 million per scientific year invested, calculated over a 64-year period of the program. Buntin & Raymer (1989) reported an economic benefit of using resistant wheat cultivars to control the Hessian fly averaged $104/ha in Georgia.

Grape stocks resistant to *Phylloxera* spp. were first grown commercially in Europe in 1870, and U.S. grape stocks were subsequently shipped to France to save the wine industry from *Phylloxera* (Painter 1951). 'Rescue', a resistant wheat cultivar, rescued the wheat growers of the Northern Plains of the U.S. and Canada from the wheat stem sawfly, *Cephus cinctus* (Norton) (Luginbill 1969). In addition, the planting of some 8.6 million hectares of corn hybrids resistant to the European corn borer, *Ostrinia nubilalis* (Hübner), is a present day example of the adoption and wide use of a resistant cultivar in some crop-insect relationships (Schalk & Ratcliffe 1976).

Dr. R. G. Dahms (personal communication, 1972) stated that in 1951, in the U.S., resistant grain and forage cultivars were available only for limiting losses to the corn earworm in dent corn and to the Hessian fly in wheat (Table 2). By 1971, U.S. growers had dent corn resistant to corn earworm and European corn borer, alfalfa cultivars resistant to spotted alfalfa aphid, *Therioaphis maculata* (Buckton), wheat cultivars

TABLE 2. INSECT CONTROL METHODS USED BY THE FARMER IN 1951 TO CONTROL EIGHT IMPORTANT PESTS*.

Insect and Crop	Chemical	Cultural	Res. Var.
Corn earworm			
Sweet corn	X	–	–
Dent	–	–	X
European corn borer	X	X	–
Southwest. corn borer	X	X	–
Corn rootworm	–	X	–
Fall armyworm	X	–	–
Spotted alfalfa aphid	X	–	–
Greenbug			
Sorghum	–	–	–
Wheat	X	X	–
Barley	X	X	–
Hessian fly	–	X	X

*From R.G. Dahms (personal communication).

resistant to Hessian fly, and a barley cultivar resistant to the greenbug, *Schizaphis graminum* (Rodani) (Table 3). Dahms then made a prediction that by 1981, U.S. farmers would have grain and forage cultivars resistant to all eight major pests listed in Table 4. This prediction was achieved and surpassed with the release of the first sorghum hybrid with resistance to the sorghum midge, *Contarinia sorghicola* (Coquillett), in July of 1981. However, chemical controls are still needed for second generation European corn borer, Southwestern corn borer, and for control of corn rootworms.

The use of resistant cultivars as a primary control measure has made the use of other control components unnecessary for the management of some insect pests. The results have been rather specific, cumulative, and persistent (Dahms 1972b, Wiseman 1982). Further, Adkisson & Dyck (1980) stated that reduction in pest populations achieved through the use of resistant plants is constant, cumulative, and practically without cost

TABLE 3. INSECT CONTROL METHODS USED BY THE FARMER IN 1971 TO CONTROL EIGHT MAJOR PESTS*.

Insect and Crop	Chemical	Cultural	Res. Var.
Corn earworm			
Sweet corn	X	X	–
Dent	–	X	X
European corn borer	–	X	X
Southwest. corn borer	X	X	–
Corn rootworm	X	X	–
Fall armyworm	X	–	–
Spotted alfalfa aphid	–	–	X
Greenbug			
Sorghum	X	X	–
Wheat	X	X	–
Barley	–	X	X
Hessian fly	–	X	X

*From R. G. Dahms (personal communication).

TABLE 4. PREDICTION OF INSECT CONTROL METHODS USED BY THE FARMER IN 1981 TO CONTROL EIGHT MAJOR PESTS*.

Insect and Crop	Chemical	Cultural	Res. Var.
Corn earworm			
Sweet corn	X	X	X
Dent	–	X	X
European corn borer	–	X	X
Southwest. corn borer	–	X	X
Corn rootworm	–	X	X
Fall armyworm	X	–	X
Spotted alfalfa aphid	–	–	X
Hessian fly	–	X	X
Greenbug			
Sorghum	–	X	X
Wheat	–	X	X
Barley	–	X	X
Sorghum midge			
**Sorghum	X	X	X

*From R.G. Dahms (personal communication).
**First resistant hybrid release in July 1981 by Funk Seeds International.

to the growers. In the future, resistant cultivars developed for the sole component of control for a specific insect will likely possess a high level of resistance, while other cultivars will be developed with lower levels of resistance and will be integrated with other IPM components for the control of pests.

Dahms (1972b) illustrated vividly the theoretical effects of antibiosis on insect populations using four criteria, i.e., rate of reproduction, rate of nymphal development, mortality of nymphs, and length of productive life. Applying the four antibiotic factors cumulatively for the spotted alfalfa aphid, he showed that aphids on 'Lahontan', a resistant alfalfa cultivar, reproduced at a rate of 2.5 per day for 13 days and that nymphs matured in 9 days with 90% mortality, while aphids on 'Chilean', a susceptible alfalfa cultivar, reproduced at a rate of 4 per day for 13 days and nymphs matured in 6 days with only 10% mortality. After 10 days there would be 30 times more aphids on 'Chilean' than on 'Lahontan', and after 50 days 14 million times more aphids would be produced on 'Chilean' than on 'Lahontan'. Similar documentation on the effects of resistance to other insects would be of immense benefit in promoting the use of resistant cultivars.

Resistant cultivars also may be used as an adjunct to other control tactics. Resistant cultivars are, for the most part, compatible with insecticides, biocontrol agents, and cultural control. However, the levels and mechanisms of resistance must be well understood to effectively combine other control tactics with the resistant cultivar (Wiseman 1985).

Researchers in plant resistance have attained a number of goals. However, in the Southeast the results have not been as striking as results in the mid-west, probably because of the overwhelming populations of pests that occur in the Southeast each year that often mask lower levels of resistance to insects or the levels of resistance in the germplasm collections are low. But since we work with two dynamic, ever-changing biological systems, we must not and cannot stop in our search for higher levels of resistance.

This symposium reported on programs of plant resistance to insects in the Southeastern United States. Studies on insect nutritional ecology, insect behavior, and plant resistance enhancing biocontrol were discussed. In addition, information was reported

TABLE 5. PUBLICATIONS, NEWSLETTER CONTRIBUTIONS, GERMPLASM RELEASES, AND PLANT RESISTANCE GRADUATES FOR THE SOUTHEASTERN UNITED STATES, 1980-89.[1]

	Total Number of			
State[2]	Publications	Contributions to PRI Newsletter	Germplasm Releases	Graduates
Florida	5	7	0	1
Georgia	149	183	16	0
Louisiana[3]	98	32	0	2
Mississippi	47	5	8	2
N. Carolina	14	8	1	1
S. Carolina	1	6	3	0

[1]Source: Plant Resistance to Insects Newsletter Vol. 6-15, 1980-89. Graduates were reported beginning in 1984.
[2]No reports available from Arkansas or Tennessee.
[3]Most of the publications for 1986-87 originated from the International Rice Research Institute.

on insect rearing and the development and release of resistant germplasm for corn, cotton, grasses, peanuts, soybeans, sorghum, tobacco, and vegetables. Over the past 10 years, most of the resistant germplasm released has been from Georgia, followed by Mississippi and South Carolina. Major efforts in plant resistance have been by USDA's Agriculturel Research Service. Likewise, the most publications and contributions reported via the Plant Resistance to Insects Newsletters came from Georgia, Louisiana, and Mississippi, respectively (Table 5). In addition to the crops previously mentioned, plant resistance research and development on forages, forest trees, rice, sugarcane, and wheat ongoing in the Southeastern States are listed in Table 6. Research on 33 insect species has been reported over the past 10 years (Table 7) (PRI Newsletter Vols. 6-15). There is also some commercial research and development in Tennessee on plant resistance to insects attacking corn. And there are a few programs on biotechnology at the state, federal, and commercial level with its application to plant resistance to insects in the Southeast.

TABLE 6. CROP RESEARCH ON PLANT RESISTANCE TO INSECTS IN THE SOUTHEASTERN UNITED STATES.[1]

Crop	Fla.	Ga.	La.	Miss.	N.C.	S.C.	Tenn.
Corn		X		X			[2]
Cotton		X		X			
Forage		X	X	X	X	X	
Forest					X		
Peanut		X			X		
Rice			X				
Sorghum		X					
Soybean	X	X	X	X	X	X	
Sugarcane	X		X				
Tobacco		X			X	X	
Vegetable	X				X	X	
Wheat		X					

[1]Source: Plant Resistance to Insects Newsletter Vols. 6-15. 1980-89.
[2]No report available but commercial research and development is ongoing.

TABLE 7. LISTING OF INSECTS BY LOCATION RESEARCHED DURING THE PAST 10 YEARS ON PLANT RESISTANCE IN THE SOUTHEASTERN UNITED STATES,[1]

Insect	Insect
Aphids, MS	Rice stink bug, LA
Bean leaf beetle, LA	Rice water weevil, LA
Beet armyworm, MS	Sorghum midge, GA
Caribbean fruit fly, FL	Southern green stink bug, SC
Clover head weevil, MS	Southwestern corn borer, MS, TN
Colorado potato beetle, NC	Soybean looper, GA, LA, MS
Corn earworm, GA, MS, NC	Sugarcane borer, FL
Cowpea curculio, SC	Thrips, NC
Diabrotica sp., LA, SC	Tobacco budworm, MS, NC
Fall armyworm, GA, LA, MS, TN	Tobacco hornworm, NC
Flea beetle, SC	Tomato pinworm, FL
Green cloverworm, GA	Velvetbean caterpillar, GA, LA, MS
Hessian fly, GA	Wireworm, SC
Leaf miner, FL	
Least skipper, LA	
Maize weevil, GA	
Mexican bean beetle, GA, SC	
Pickleworm, SC	
Potato leafhopper, NC	
Pseudoplusia includens, LA	

[1]Source: Plant Resistance to Insects Newsletter, Vols. 6-15. 1980-89.

One weak point in our discipline of plant resistance to insects is the training of graduate students (Table 5). Even though we have numerous plant resistance research programs and several formal courses taught in the U.S., today more than ever before, applied graduate student training in plant resistance to insects is lacking. Most of the training is on the interaction of insects and plants rather than on the development and use of resistant cultivars. In the southeastern U.S., formal plant resistance courses are taught only at Louisiana State University, Mississippi State University, North Carolina State University, and the University of Florida. The University of Florida has the distinction of offering two formal graduate courses.

There are definite bright spots for the future for plant resistance to insects. Examples are the development of resistant cultivars for more crops, development of cultivars with multiple pest resistance such as that reported by Overman (in press), use of resistant cultivars in the management of insect pests on the farm and on an area-wide basis, and utilization of biotechnology and genetic engineering breakthroughs for the development of resistant cultivars. Plant resistance to insects should be the major component in the future for management of insect pests. Better training of graduate students in this area and better documentation on the effects of resistant cultivars on insect populations are two major needs if we are to meet this expectation.

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