

Host Plant Resistance to Insects in Integrated Pest Management in Vegetable Crops¹

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ABSTRACT Host plant resistance to insects (PRI) is an underutilized pest management strategy in vegetable production. Increased pressures to reduce pesticides, and changes in technology now increase the economic viability and probable role of PRI in vegetable pest management. This is reflected in the relatively recent release of several insect-resistant varieties and breeding lines. The attention PRI now receives in extension publications is also increasing. There is room to improve research and extension documentation to assist producers in making better use of the available resistance to insects in vegetable crops. In the short term, existing varieties can be screened more extensively and quantitative information provided to producers. In the long term, variety specific recommendations for the use of chemical controls, and other management tactics in conjunction with PRI will be beneficial. Awareness of varietal susceptibility to insect pests will increase the incentives to private breeders to eliminate extremely susceptible material from their breeding programs. Trends in these directions can already be seen in the industry. Support for the research necessary to exploit PRI in vegetables will be required from public sources, as part of the alternatives to pesticides, and from private breeders and producers who stand to benefit from the development of variety-specific recommendations and impartial comparison of varieties.

KEY WORDS Vegetables, host plant resistance, integrated pest management.

In several cereal and forage crops, host plant resistance to insects (PRI) has been an extremely successful technique for suppressing pest populations or damage. In contrast, there has been much less use of this method for the management of insect pests in commercial vegetable production (Smith 1989).

This lack of utilization of PRI in vegetable production is in spite of the fact that insect resistance has been a goal of vegetable breeders and entomologists at least since the first publication concerning resistance in sweet corn to the corn earworm *Helicoverpa zea* (Boddie) (Collins and Kempton 1917). Review of this

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extensive literature is beyond the scope of the present report. Readers are referred to the reviews of Painter (1951), Kennedy (1978), Smith (1989), and Stoner (1992) which cover 1100 articles on PRI in vegetables between 1917 and 1991. A great deal of progress has been made identifying sources and understanding the genetics and mechanisms of resistance to important pests in the major vegetable crops. Excellent recent reviews summarize this work in tomato (Farrar and Kennedy 1992), potato (Flanders et al. 1992, Tingey and Yencho in press), cucurbits (Robinson 1992), and common beans (Kornegay and Cardona 1991).

Mostly within the last ten years, several insect-resistant vegetable varieties or advanced breeding lines have been released (Table 1). In addition, variation in insect susceptibility has long been noted and continues to be found in existing vegetable varieties including tomatoes (Wolfenbarger 1966, Fery and Cuthbert 1974, Schuster 1977, Fornazier et al. 1986, Eigenbrode et al. 1993), peppers (Fery and Schalk 1990), carrots (Ellis et al. 1984), sweet corn, (Wiseman et al. 1972, 1978, Story et al. 1983), lettuce (Dunn 1968, Reinink and Dieleman 1989), *Brassica oleracea* crops (Benepal and Hall 1967, Shelton et al. 1983, Stoner 1990, Eigenbrode et al. 1991), watermelons (East and Edelson 1990), other cucurbits, reviewed by Robinson (1992), onions (Ellis et al. 1979, Edelson et al. 1991), and green beans (Eckenrode and Webb 1989). These differences in susceptibility of existing varieties to insects can be great enough to be of potential economic importance.

The poor utilization of the available PRI in vegetables has been attributed largely to economic factors (Stoner 1970, Schalk and Ratchliffe 1976, Smith 1989). The high dollar value per acre of most vegetable crops renders pesticides more cost-effective and acceptable to risk-averse producers. Stringent cosmetic requirements for many vegetable crops increase the incentive for pesticide use to ensure high value, blemish-free products. Cosmetic requirements can also limit usable resistance traits to those that do not affect the appearance of the product. In addition, small seed markets for many vegetable crops limit the potential for private breeders to obtain adequate returns on the investment required to develop insect-resistant vegetable varieties.

Recent changes in this incentive structure, however, have increased the value of PRI in agriculture. These changes include, increased market and regulatory pressure to reduce pesticide use, continuing problems with insect resistance to pesticides, and technological developments in the genetic manipulation of crop plants. The impact of these changes is likely to be especially large in vegetable crops in which PRI is currently underutilized.

A first objective of the present review is to document the increased role of PRI in vegetable pest management that has occurred in recent years in response to these changes. In addition, this review will consider the measures necessary to integrate PRI more effectively in vegetable integrated pest management (IPM). Finally, suggestions will be made for how to support the necessary research for this integration. The crops included in this review include almost all vegetable crops, including the sweet-fruited cucurbits. Most legumes usually harvested dry but occasionally harvested and consumed green (e. g. soybeans) and cassava are excluded. Cowpeas (southern peas) are included because of their importance as a vegetable in the southeastern United States.

PRI in Vegetable Pest Management Recommendations

Older extension literature sometimes included information on vegetable variety susceptibility to insects (e. g. North Carolina Agricultural Extension Service 1972). Mention of PRI has been rare in recent years, but is increasing. Recommendations from New York (Cornell University Cooperative Extension 1992), Wisconsin (University of Wisconsin 1990), Minnesota (Hutchison 1993), the midwestern states (Purdue University Cooperative Extension Service 1993), and New England (Anonymous 1990) all include some information on insect susceptibility of vegetable varieties. The information provided in these publications typically is qualitative and mentions a few varieties: e. g. "A comparison of two major kidney bean varieties shows that 'Redcloud' is more tolerant to leaf hopper feeding than 'California Light Red'" (Cornell University Cooperative Extension 1992, p. 40) and "Butternut squash is more resistant to SVB (Squash vine borer) than many varieties" (Hutchison 1993, p. 83).

Occasionally, qualitative susceptibility ratings for the majority of favored varieties of a particular crop are provided. For example, onion thrips susceptibility of cabbage varieties in New York, monitored since the early 1980's has been used to construct susceptibility ratings for more than 20 fresh market, processing, and storage varieties of cabbage. These ratings are published in pest management recommendations for New York (Cornell University Cooperative Extension 1992) and included in those of Minnesota (Hutchison 1993). Similarly, recommendations for chemical control of green peach aphid, *Myzus persicae* (Sulzer), and the potato leafhopper, *Empoasca fabae* (Harris) in Wisconsin include the suggestion to adjust the treatment thresholds developed on 'Russet Burbank' upward or downward on the basis of relative susceptibility ratings for 19 other varieties (University of Wisconsin 1990).

Sometimes pest damage sustained by several varieties in field experiments is reported. Yield (% jumbo bulbs) and *Thrips tabaci* Lindeman populations on 10 commonly grown onion varieties with uncontrolled thrips populations and after treatment with cypermethrin, permit producers to assess tolerance of some of these varieties (Edelson et al. 1991). Damage to 41 varieties of sweet corn by European corn borer, *Ostrinia nubilalis* (Hübner), is reported in the Minnesota Vegetable Production Guide; the reported percentage of ear damaged ranged from 2% - 10% (Hutchison 1993). Corn earworm damage to 21 varieties treated and untreated with insecticides provide Oklahoma producers with information on levels of antibiosis and tolerance to this pest. Populations of *Tetranychus urticae* Koch on seven watermelon varieties under controlled (six to forty-fourfold variation) have been published for producers in Oklahoma (East and Edelson 1990).

Rarely, information provided to producers includes quantitative recommendations for pesticide use on different varieties. The best example of which these authors are aware has been developed by P. R. Ellis and colleagues at Horticulture Research International at Wellesbourne, England. Among the 15 varieties of carrots identified with partial levels of resistance to carrot rust fly, *Psila rosae* (F.), Nantes type 'Sytan' consistently is 50% less damaged than susceptibles (Ellis et al. 1984, Ellis 1992). This difference has been translated into recommendations for pretreatment of the soil with reduced amounts of

chlorfenvinphos on 'Sytan'. Thirty mg AI/m row of crop will provide 95% damage-free roots in 'Sytan' as compared with 80 mg in 'Danvers Half-Long 126'. Publication of these recommendations in a producer journal (Ellis et al. 1990) has helped promote the use of 'Sytan'.

Impact of PRI in Pest Management in Vegetables

The impact of PRI on vegetable pest management is apparently limited. As far as is known, released resistant varieties (Table 1) are grown only to a limited extent. Based on the amount of registered seed sold, 'Excel' sweet potato is grown on about 2,000 ha in the U. S. annually. 'Regal' and 'Sumor' seeds are also sold in small amounts in the U.S., but this is apparently primarily for home garden use. 'Hi-Dry' has become a very popular variety in the Philippines, but estimates of the amount of the variety used there are not available (P. D. Dukes, U.S.D.A./A.R.S. Vegetable Research Lab, Charleston, South Carolina, personal communication). Aphid-resistant netted muskmelon 'Mainpack' is being grown on a small scale (total of approximately 500 ha based on seed sales) by commercial producers in northern California and Texas. Acceptance of the sweet potato varieties has been slow because they have a lighter color periderm as compared with popular susceptible varieties. The 'Mainpack' melon is less desirable because it is relatively small (18-23 per carton vs. 12 per carton for preferred varieties).

There are indications that producers consider available information on insect susceptibility when choosing varieties. For example, in south Texas the 'Grano 502' onion has largely replaced thrips-susceptible '1015Y' (J. V. Edelson, Oklahoma State University, personal communication). The use of watermelon and sweet corn varieties in Oklahoma has been influenced by published data on insect pest susceptibilities (B. Cartwright, Oklahoma State University, personal communication; Crummett 1992). In New York and other northern states, producers have increased their use of cabbage varieties for storage and fresh market that are less susceptible to *Thrips tabaci* (A. M. Shelton, Cornell University, personal communication). In Europe and parts of Britain, lettuce varieties with resistance to *Pemphigus bursarius* (L.) are reportedly favored (P. R. Ellis, Wellesbourne, Warwick, U. K., personal communication). Unfortunately data are not available to document these reported shifts in varietal use.

Although producers evidently realize some benefits from growing more resistant varieties, as indicated by their apparent increased use, these benefits may be in the form of reduced risk of crop loss, or additional profitability, rather than in pesticide savings. The use of resistant or less susceptible varieties does not necessarily constitute effective integration into IPM. Pesticide savings are probably negligible except where variety-specific guidelines are available and their use encouraged. For most resistant vegetable varieties such guidelines have not been developed, and without them risk-averse producers are more likely to use full doses of insecticides or standard treatment thresholds.

Table 1. Vegetable varieties or released breeding lines deliberately selected for resistance to arthropod pests.

Crop	Variety or Breeding Line	Pests	Source ^a
Cabbage, <i>Brassica oleracea</i> L. var. <i>capitata</i>	NY IR 9602, NY IR 8329, NY IR 9605	<i>Trichoplusia ni</i> (Hübner), <i>Pieris rapae</i> (L.), <i>Plutella xylostella</i> (L.)	Dickson et al. 1984
Cowpea or Southern pea, <i>Vigna unguiculata</i> (L.)	CR 17-1-13, CR 18-13-1, CR 22-2-21 'Carolina Cream' 'Santee Early Pinkeye' 'Carolina Crowder' 'Bettergo Blackeye' TVx3236 ICV1, ICV3, ICV8 ICV11	<i>Chalcodermus aneneus</i> Boheman " " " " thrips foliar pests <i>Aphis craccivora</i> Koch	Cuthbert and Fery 1975 Fery and Dukes 1984 Fery and Dukes 1990 Fery and Dukes 1992 Fery and Dukes 1993 Singh and Ntare 1985 Pathak and Olela 1986 Pathak and Olela 1986
Cucumber, <i>Cucumis sativus</i> L.	Wisconsin 2757	<i>Acalymma</i> spp. and <i>Diabrotica</i> spp.	Peterson et al. 1982
Lettuce, <i>Lactuca sativa</i> (L.)	Iceberg type 'Beatrice'	<i>Pemphigus bursarius</i> (L.)	Nickersons, Thompson and Morgan Seed Co.
	Butterhead types 'Ardente', 'Conny', 'Continuity', 'Debby', 'Mussette', 'Sabine', 'Sigmaball', 'Sigmadeep', 'Sigmahead', 'Tina'	"	Various Seed Companies
	Crisp types 'Grand Rapids', 'Lakeland'	"	"

Table 1. Continued.

Crop	Variety or Breeding Line	Pests	Source ^a
Sweet Potato, <i>Ipomoea batatas</i> L.	'Regal'	WDS and <i>C. confinis</i>	Jones et al. 1985
	'Sweet Red'	WDS only	Collins & Moyer 1987
	'Pope'	"	Collins & Moyer 1982
	'Hi-Dry'	"	Hamilton et al. 1985
	'Beauregard'	"	Rolston et al. 1987
Tomato, <i>Lycopersicon esculentum</i> Mill.	'Kewalo'	white grubs only	Hall & Harmon 1989
			Paterson et al. 1984
Turnip, <i>Brassica campestris</i> L.	'Charlestowne', 'Roots'	<i>Tetranychus telarius</i> (L.)	Gilbert et al. 1974
		<i>Hyadaphis erysimi</i> (Kaltenbach)	Robbins & Cuthbert 1980

^a Reference for release or name of seed company marketing the variety

^b WDS = Wireworm, *Diabrotica*, *Systema* complex: *Conoderus falli* Lane, *C. vespertinus* F., *Diabrotica batatae* Le Conte, *D. undecimpunctata howardi* Barber, *Systema blanda* Melsheimer, *Systema elongata* F.

Improving Integration of PRI into Vegetable IPM: Short Term Challenges

As pressures increase to reduce the use of pesticides in agriculture, especially vegetable production, the potential value of insect resistance in vegetable crops will increase. Even partial levels of resistance will have considerable value. The challenge to entomologists will be to facilitate this exploitation by identifying and quantifying resistance and providing guidelines to help producers realize pesticide savings by using resistant varieties. Wherever resources allow, differences in varietal susceptibility should be documented and disseminated as part of the regional extension literature on pest management for vegetables. The extension reports cited in the above sections can be improved and expanded to include more commodities and pests, and more quantitative information. In some geographic areas, the first steps towards exploiting PRI in IPM have yet to be taken. There is no mention of PRI in the major vegetable pest management publications from California (University of California Statewide Integrated Pest Management Project 1990, University of California Cooperative Extension 1992, University of California 1993), Arizona (Minkenberg et al. 1993) the Pacific Northwest (Fisher et al. 1990), or Florida (Maynard 1987), which together include 60% of the commercial vegetable crop acreage in the United States (United States Department of Agriculture 1992).

It will be beneficial in many cases to disseminate some of this information nationally. The newly expanded and renamed *Insecticide and Acaricide Tests (Arthropod Management Tests)* accepts reports of varietal susceptibility tests and reports of resistance breeding efforts, in addition to the traditional chemical trials. *Arthropod Management Tests* is widely used by extension specialists and other applied entomologists. Since many varieties are used inter-regionally, (e. g. cabbage varieties in northern states, some tomato varieties in California and Florida), reports under one cover of varietal trials in different regions will facilitate and improve the identification of the most resistant varieties.

Increased awareness of variation in varietal susceptibility to insects will add an incentive to seed companies to monitor their breeding material and new varieties. As has already occurred in some crops, producers and pest managers will avoid known insect-susceptible varieties. Presently, many seed companies conduct all breeding under prophylactic insecticidal protection, and only a few permit natural insect infestations in their breeding material to facilitate elimination of very susceptible types.

Improving Integration of PRI into Vegetable IPM: Long Term Challenges

A full integration of PRI into IPM will require interfacing with all the other available controls. These include chemical pesticides, microbials, and biological control. Ideally, as more varieties with resistance are identified or developed and deployed, the efficiency of this interfacing should be improved. In the next sections, the challenges of increasing the integration of PRI in vegetables into a multifaceted IPM approach are considered.

Integrating PRI and Chemical Insecticides

At least in the foreseeable future, PRI and chemical insecticides will frequently be used in conjunction for vegetable production. This is because most vegetable crops, as mentioned earlier, have stringent quality requirements necessitating protection not normally provided by PRI alone. The most commonly used protections, and those best understood by producers, are chemical pesticides. Variety-specific rates or treatment thresholds can help producers extract the maximum value from insect resistant varieties.

Treatment thresholds and recommendations. Since their conception, it has been recognized that economic injury levels (EIL) and economic thresholds (ET) would depend on crop variety (Stern 1973). Many types of plant resistance potentially will affect thresholds. This can be illustrated with the help of the formalism proposed by Pedigo et al. (1986). The EIL, or pest density at which the cost of control is equal to the value of crop injury can be expressed as

$$EIL = C/VDIK$$

where C = cost of a control measure per unit of production of the crop (e. g. \$/ha), V = value per unit of produce (e. g. \$/kg), D = damage per pest per unit production (e.g., percent defoliation/pest/ha), I = economic injury per unit of damage (e.g., kg produce lost/ha/percent defoliation), K = efficiency of the control measure (proportion killed). The EIL is expressed in pest/unit of production.

The ET is the pest population density at which action must be taken to prevent the EIL from being reached. The ET is more difficult to estimate because it is predictive and therefore probabilistic. As a result, true ETs have been estimated less frequently than EILs (Pedigo et al. 1986).

EILs and ETs will be differently affected by resistance in each of the three modalities described by Painter (1951):

Antibiosis: Traits reducing the survival, development or reproduction of pest insects utilizing the plant.

Nonpreference (Antixenosis [Kogan and Ortman 1978]): Traits reducing insect oviposition or colonization of the plant.

Tolerance: Traits resulting in the plant sustaining reduced damage compared to susceptible plants infested at the same pest density.

Parameters printed in boldface italics and underlined are potentially affected by each of these modalities:

$$\begin{array}{l} \text{ANTIBIOSIS} \\ \underline{\text{EIL}} - C/\underline{\text{VDIK}} \quad \underline{\text{ET}} \end{array}$$

$$\begin{array}{l} \text{ANTIXENOSIS} \\ \text{EIL} - C/\text{VDIK} \quad \underline{\text{ET}} \end{array}$$

$$\begin{array}{l} \text{TOLERANCE} \\ \underline{\text{EIL}} - C/\underline{\text{VDIK}} \quad \underline{\text{ET}} \end{array}$$

Antibiosis will usually have no effect on the EIL. Rather, pest populations are less likely to reach the EIL on the resistant crop. If an antibiotic trait reduces the feeding of the damaging stage, however, then damage per insect (D) may be lowered. If antibiotic resistance traits affect the efficacy of pesticides (K) (see section below), the EIL could be directly influenced by antibiosis. Antibiosis will affect the ET, if not the EIL, by reducing population growth rates, or reducing the proportion of sampled pests surviving to the damaging stage.

Antixenosis should normally not affect the EIL or the ET. Pest densities are merely less likely to reach these densities. However, if the sampled stage is the ovipositing, or colonizing reproductive stage, the ET will be raised on an antixenotic variety.

Tolerance raises the EIL by affecting either the damage to the crop per unit of pest density (D), the relationship between damage and economic injury (I), or both.

Many resistant varieties have elements of more than one of the three modalities (Cuthbert and Fery 1975, Singh 1987, Birch 1988, Edelson et al. 1991, Sharma 1993). Thus, in most instances host plant resistance can be expected to affect EILs, ETs, or both to some degree. Nevertheless, there are only a few examples of variety-specific EILs or ETs in any crop. The best examples are the ETs for sorghum midge on midge-resistant sorghum (Hallman et al. 1984) and the variety-specific EILs developed for the bollworm and tobacco budworm (*Helicoverpa zea* Boddie) and *Heliothis virescens* F. on cotton (Zummo 1984, Ring et al. 1993). The only published example in vegetables, variety-specific EILs for the variegated cutworm, (*Peridroma saucia* (Hübner), on potatoes (Shields et al. 1985) are currently not in use.

Preliminary data necessary for estimating EILs have been developed for some insect-resistant varieties or breeding lines of vegetables. For example, yield-loss relationships have been estimated for arthropod pests on resistant varieties or breeding lines of potato (Sanford and Ladd 1986, Tingey and Yencho in press), sweet potato (Cuthbert and Fery 1979, Rolston et al. 1981, Mullen 1984, Jones et al. 1987b), sweet corn (Story et al. 1983), beans (Eskafi and Van Schoonhoven 1981), and field peas (Soroka and Mackay 1990). These data, sometimes developed during research to understand resistance mechanisms, can be used to construct treatment recommendations for producers.

Sampling. In order to apply EILs and ETs, sampling plans must be developed to estimate pest densities. These are usually developed on the most commonly grown susceptible varieties and often rely on assumptions about the distribution of pests within or among plants in the crop. However, these assumptions may not be valid on resistant varieties.

To reduce labor requirements, plants are often subsampled to estimate whole-plant densities (Trumble 1994). However, there are examples of resistance substantially affecting the distribution of pests within the plant. Onion thrips are located predominantly on frame leaves of some resistant cabbage genotypes but distributed over the entire plant on susceptibles (Stoner and Shelton 1988). Distribution of the sweetpotato weevil, *Cylas formicarius elegantulus* (Summers), differs significantly within vines of partially resistant and susceptible sweet potato cultivars (Jansson et al. 1987). The effects of

resistant varieties on within-plant distribution of pests rarely have been investigated. Assumptions about the within-plant distribution of pests on resistant varieties must be examined before applying subsampling methods developed on susceptible varieties.

The use of tissue-specific promoters has been proposed to regulate the within-plant expression of genes for insect resistance factors such as *Bt* toxins. Recent studies indicate that *Heliothis virescens* larvae discriminate against diets containing low concentrations of *Bt* endotoxins, suggesting that this strategy for reducing selection for resistance to the toxins could be successful (Gould 1988, Gould et al. 1991). If this method is implemented, it will obviously influence plant subsampling procedures.

Sequential sampling plans designed to determine if pests have exceeded treatment thresholds also depend on assumptions about the spatial distribution of insects among the sample units. These plans are particularly sensitive to the degree of aggregation, quantified using the regression methods of Iwao or Taylor, or with the k of the negative binomial distribution (Shelton and Trumble 1991). The degree of aggregation must be estimated to develop the decision-making model (Allen et al. 1972). Pest spatial distributions have been shown to be sensitive to pest density, geographic location (Trumble et al. 1987), insecticide treatments (Trumble 1985), and crop phenology (Matin and Yule 1984). Although there is evidence that sampling plans for spider mites based on 'generic' dispersion indices can be robust (Jones 1990), large enough differences from the assumed dispersion characteristics do occur and can affect the performance of a decision rule (Trumble et al. 1989). Data comparing pest aggregation on different varieties of the same crop under controlled conditions have not been published, but it is probable that some plant resistance traits influence pest aggregation. For example, traits eliciting nonacceptance, which causes feeding stages to disperse (Eigenbrode and Shelton 1990), might reduce spatial aggregation. Antixenosis, which reduces the acceptability of the crop for oviposition, may cause more frequent movement between ovipositions, or may cause eggs to be retained longer, respectively increasing or decreasing the aggregation of eggs. The tendency for border areas of fields to have higher populations of some pests, which often justifies stratified sampling, may not occur on antixenotic crop plants.

The planting of a mixture of genotypes with different modes of resistance, or the mixing of resistant and susceptible genotypes in a single field (multilining) to provide a refuge for nonadapted pests, has been proposed to slow pest adaptation to the resistance (Gould 1986). Differential mortality on susceptible and resistant plants, as well as behavioral discrimination by the insects, mentioned earlier, would obviously affect the insect distribution in such a mixed planting.

The potential effects of multilining on a sequential decision-making rule can be simulated. Assume on a particular susceptible crop a pest distribution approximates a negative binomial with average $k = 9$. In a mixture containing 80% resistant plants and 20% susceptibles, if the susceptible plants in the multiline have about four times the infestation levels as resistant plants, the negative binomial k will average 1.3 (calculated from simulated data). The 'SPRT' program (Nyrop 1992) can be used to calculate the impact of this change

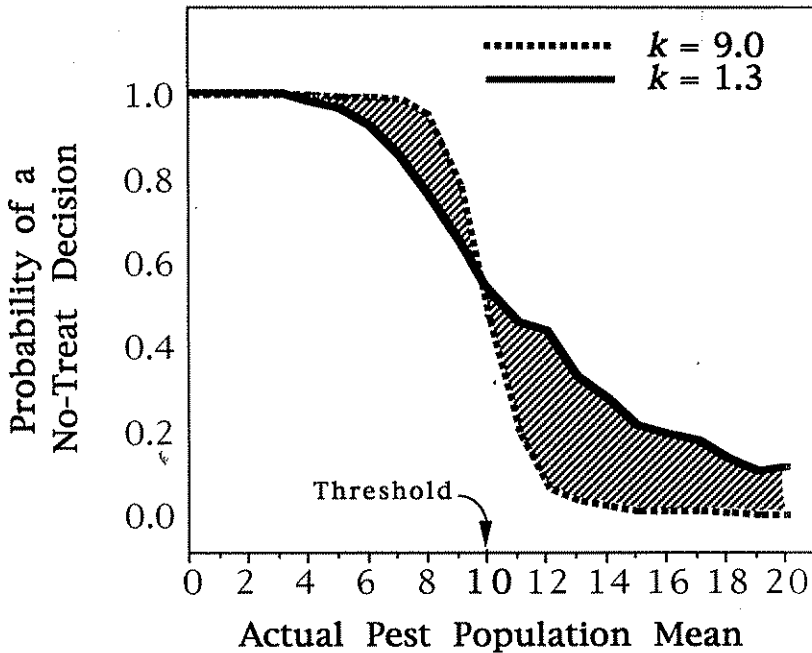


Fig. 1. Operational characteristics of a binomial sequential sampling plan on a monoculture (negative binomial $k = 9.0$), and on a 8:2 resistant:susceptible multiline (negative binomial $k = 1.3$), when aggregation characteristics of the pest were assumed to be the same as the monoculture in both planting arrangements.

in pest aggregation on the operating characteristics of a sampling program based on Wald's sequential probability ratio test (Wald 1947). Figure 1 shows the operation characteristic curves for the sampling plan on a simulated population with $k = 9$ (broken line) or $k = 1.27$ (solid line), using a plan built on an assumed $k = 9$. The curve shows the probability of selecting the null hypothesis (below threshold-do not treat) with α and β levels set to 0.1, and the economic threshold set at 10. Each point on the curve was determined with 500 iterations of the decision rule at each of these actual population means. Deviations from a perfect step form with a vertical inflection at the threshold are misclassifications. The increase in incorrect treatment decisions, resulting from a failure to account for the change in pest aggregation, is presented by the shaded area between the OC curves in Fig. 1. Where such sampling plans are used in conjunction with PRI, it will be necessary to ascertain that resistant varieties, in monocultures or multilining strategies, do not affect spatial distributions enough to affect sampling plans.

PRI \times pesticide interactions. Variable efficacy of arsenical on resistant crop varieties was reported in several articles considered by Painter (1951), and

has since been observed in numerous studies for synthetic organic insecticides. This area was reviewed recently by Van Emden (1991) and by Smith (1989). Host plant resistance is usually neutral (Chalfant 1965, Selander et al. 1972, Creighton et al. 1975, Leonard et al. 1989) or enhances pesticide efficacy (Chalfant and Brett 1967, Heinrichs et al. 1984, Rose et al. 1988). However, there are examples of antagonism in vegetables. Abro and Wright (1989) found that topical toxicity of abamectin and cypermethrin to *Plutella xylostella* (L.) was higher on partially resistant cabbages than on susceptibles, but toxicity of ingested residues was higher on the susceptible cabbages. The antagonism was attributed to reduced ingestion of the toxins on the resistant plants. Kennedy (1984) showed that the tomato antibiotic factor 2-tridecanone induced increased tolerance to the insecticide carbaryl in *Helicoverpa zea*.

Insect resistance traits may affect the efficacy of pesticides by mechanically affecting coverage, or through physiological effects on the target pest. These include induction of detoxifying enzymes in insect guts (Ahmad et al. 1986), changes in feeding rates affecting pesticide ingestion (Abro and Wright 1989), reduced body size or general vigor increasing insecticide susceptibility. The potential for interactions between chemical insecticides and PRI should be considered when variety-specific EILs are being developed. These interactions impact K (proportion killed) in the EIL expression above and can therefore increase or decrease ETs on resistant crops vs susceptible crops.

Integrating PRI and Microbials

Bt endotoxins applied as insecticides are apparently generally compatible with PRI. Efficacy of the endotoxins is equal or greater on resistant varieties as compared with susceptible varieties (Hare 1992). There is evidence that allelochemicals associated with resistance can potentiate *Bt* endotoxins (Felton and Dahlman 1984, Ludlum et al. 1991, Trumble et al. 1991, Meade and Hare 1993). Almost all the examples in this literature are on vegetables or concern allelochemicals prominent in vegetable crops. There is a potential for reduced efficacy of the *Bt* toxin if less is ingested during feeding on a less preferred crop, but this has not yet been demonstrated (Meade and Hare 1993). An unexplored area is the interaction between *Bt* toxins expressed in transgenic plants and allelochemicals in these plants.

On the other hand, plant allelochemicals or plant resistance can have a negative effect on the toxicity of insect pathogens including pathogenic fungi and nuclear polyhedrosis viruses (Hare and Andreadis 1983, Felton et al. 1987, Felton and Duffey 1990). The possibility that PRI and insect pathogens may be antagonistic should be examined when these elements are combined in IPM.

Integrating PRI and Biological Control

Interactions between PRI and biological control have been the subject of a large amount of research. Hare (1992) provides an excellent review. Of the 16 cases of classical biological control used in combination with PRI in crop plants reviewed by Hare, six reported antagonistic interactions, two reported synergistic interactions, five reported additive effects, and in three systems the

type of interaction depended on the level of plant resistance. No general principles exist to predict these effects. The type of interaction depends on the mechanisms of resistance and how these affect the biology of the pest, the predator or parasitoid, and their interactions. There have been considerable theoretical discussion and research about the potential interactions at the tritrophic level (see Boethel and Eikenbary 1986, and Van Emden 1991 for additional references). At any rate, the effects can potentially be large, indicating that the possibility of antagonism should be considered during the development and deployment of PRI.

Plant breeders could even develop varieties deliberately designed to enhance the efficacy of biological control agents. An interesting example of the use of plant breeding to enhance biological control in vegetables is summarized by Van Lenteren (1991) and illustrates the feasibility of such an approach. Biological control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), by *Encarsia formosa* Gahan is effective on tomatoes but is ineffective on cucumber. This is apparently because cucumber is a very good host plant for the whitefly, and because the extreme hairiness of the leaves of most cucumber varieties (about 380 hairs per cm²) reduces the walking speed and searching efficiency of the wasps. Hairless mutants were identified but it was discovered that wasp foraging efficiency on these types was also inefficient because the wasps moved too quickly and missed many whitefly larvae. A series of experiments demonstrated that on "half-haired" genotypes (about 160 hairs per cm²), selected by breeders, *E. formosa* efficiency was maximized in terms of searching efficiency and parasitization rates (Van Lenteren 1991). As a result of this work, commercial breeders in the Netherlands are working to develop greenhouse cultivars with leaf hairiness compatible with *E. formosa*. It would be interesting to combine partial levels of resistance to the whitefly with "half-hairiness" to obtain even better control of *Trialeurodes vaporariorum* on cucumber in greenhouses.

Integrating PRI into a Complete IPM System

A complete IPM system combines several pest management methods to achieve stable low pest populations with a minimum use of insecticides. PRI can be used in concert with chemical controls, cultural adjustments, biological controls, or any combination of these. Ellis et al. (1990) recommended growing the resistant carrot 'Sytan' with reduced insecticides for spring plantings, which are at greater risk of attack by *Psila rosae* in the U. K. Summer plantings of more susceptible cultivars can be planted without insecticidal protection against this pest. A similar potential may exist in fresh market tomato varieties varying in their susceptibility to *Spodoptera exigua* (Hübner) in California (Eigenbrode et al. 1993). Varieties with the greatest susceptibility could be planted for harvest before the heaviest *Spodoptera exigua* infestations in the late summer and fall. More resistant varieties could be grown for the fall harvest and treated with insecticides at lower rates than required for more susceptible varieties. There are certainly many creative solutions to pest problems that can and should be developed using PRI.

Problems with PRI in Vegetable IPM

Most crops are subject to attack by multiple pests. Multiple pest resistance is achievable in some cases (e. g. sweet potato, Schalk et al. 1990), but difficult. In other cases, available resistance mechanisms carry trade-off linkages that cannot be broken. For example, glossy-leaf resistance to Lepidoptera in glossy *Brassica* has the liability of increased susceptibility to flea beetles *Phyllotreta* spp. and possibly *M. persicae* (Stoner 1990, Bodnaryk 1992). Presently, the flea beetles can be easily controlled with available insecticides. If control problems develop for these insects, it may be difficult to find a solution with PRI. The need to apply pesticides to control pests that remain destructive on the resistant crop could eliminate much of the potential benefit of PRI, including conservation of beneficial insects. Breeding for arthropod resistance must be conducted with cognizance of the crop's pest complex and existing strategies available for management.

As Kennedy et al. (1987) correctly pointed out, PRI which increases the complexity of pest management, and thus potentially the cost, will not be readily adopted and may not be economically viable. If pests are routinely managed with prophylactic sprays on a susceptible crop, but exceed thresholds intermittently on a resistant crop, the value of PRI will be offset by the requirement for increased monitoring. Many of the potential approaches to integration outlined herein involve potential additional increases in pest management complexity. Although it is important to consider the complex interactions between the elements of IPM, the final system must be designed for greatest simplicity for the producer. Producers can be expected to choose the simplest approach to pest management that provides good economic returns, and this may not mean using PRI to reduce pesticide use. Economic analyses sometimes indicate that the best net returns for producers are obtained by using the resistant crop with the traditional insecticide treatments (Nangju et al. 1979, Teetes et al. 1986).

Choice of variety by producers is affected by many considerations, including earliness, appearance, familiarity, and adaptation to local growing conditions. In some cases, the variety is mandated by processors for whom the producer has contracted to produce the crop. Insect resistance will usually be a minor consideration. Producers' and processors' willingness to adopt integrated PRI and other alternatives will likely increase when pesticide efficacy falls due to resistance and when legislation removes some of the more effective compounds from registration.

Insect resistance that relies on elevated concentrations of allelochemicals in crop plants may pose health risks to consumers, especially in vegetables that may be eaten after minimal processing. Plant breeders will have to work closely with food scientists to make sure that a great deal of effort is not wasted developing resistant varieties unsafe for human consumption. This potential problem is discussed elsewhere (Ames and Gold 1990).

Finally, development and deployment of arthropod resistance must address the potential of arthropod pests to adapt to resistant varieties. Some resistance may be inherently durable, but there will be instances in which precautions must be taken to slow pest adaptation. The importance of this consideration is discussed by Gould (1983) and Kennedy et al. (1987). The emerging theory

concerning the methods of slowing pest adaptation is also reviewed by Wilhoit (1992). Often pest adaptation will be slowed by relying on a variety of pest management methods rather than PRI alone. This will increase the importance of effective integration of PRI into complete IPM systems.

Conclusions

Increased incentives for the development and use of PRI seem likely to have a greater impact in vegetable crops than in other crops. As noted at the outset, pressures for reductions in pesticide use are substantial. Environmental Protection Agency enforcement of the recently amended Federal Insecticide Fungicide and Rodenticide Act requires reregistration of pesticides for use on all crops. Prohibitive costs may prevent pesticide reregistrations for minor crops, many of which are vegetables. Of the 283 agricultural arthropod pests reported to have resistance to pesticides, at least 60 are key pests of vegetable crops (Georghiou and Lagunes-Tejeda 1991). Among the eight most critical insecticide resistance problems listed by Georghiou (1990), five (*Plutella xylostella*, *Bemisia tabaci* [Gennadius], *M. persicae*, *Liriomyza trifolii* [Burgess], and *Leptinotarsa decemlineata* [Say]) attack vegetable crops.

Biotechnology is on the verge of providing new sources of insect resistance in *Bt*-transformed crops. Potatoes will likely be the first transgenic vegetable crop to be deployed expressing the endotoxins of *Bacillus thuringiensis* var *kurstaki* (*Bt*) to confer insect resistance (Meeusen and Warren 1989). Varieties of *Bt*-transgenic potatoes have not been yet released, but field trials with *Bt*-potatoes have produced impressive results, conferring near immunity to the Colorado potato beetle (Boylan-Pett et al. 1992). Other vegetable crops have been transformed with genes for the *Bt* toxins, including tomato (Delannay et al. 1989), brassicas, and sweet corn. In addition, new techniques are certain to increase the efficiency, and therefore reduce the costs, of developing insect resistant crops. Genetic transformation, embryo culture, protoplast fusion, and the use of biochemical and molecular markers will profoundly increase the potential and efficiency of resistance breeding (Meeusen and Warren 1989, Robinson 1992, Stuber 1992, Walters et al. 1992). These changes will certainly affect the progress of public and private research in plant resistance in all crops.

In response to these changes, private seed companies in Europe and North America are investing effort in developing insect resistant varieties of *Brassica* crops, sweet corn, lettuce, melon, tomato, cucumber, carrots and sweet pepper (personal communications with C. Mollema, P. R. Ellis, and representatives of Rogers/Northrup King Co., Asgrow Seed Div. of Upjohn Co., Sunseeds Genetics, Petoseed Co., Sakata Seed America). Some of these companies are considering adding entomologists to their research staffs. Private seed companies have also begun to promote some existing vegetable varieties for their insect resistance. Since control of *Pempighus bursarius*, became problematic in Britain and parts of Europe in the late 1980's, seed companies advertise resistance to the pest in lettuce varieties (Table 1). Resistance to *Psila rosae* in carrot is also advertized by at least one seed company in Britain (S. E. Marshall & Co. Ltd., Wisbech Cambs., United Kingdom). Reduced susceptibility to thrips is an advertised

feature of 'Earlycole' cabbage, produced by Petoseed (Woodland, California). The melon 'Mainpack' (Sunseeds Genetics, Hollister, California) is promoted and packaged as aphid-resistant.

As resistant varieties become available, and incentives for their use become greater, the challenge will be to integrate them successfully and profitably into production. Currently there is limited funding available for deployment of PRI in vegetables. To extract the full value of PRI in vegetables and other crops, however, substantive funding of the necessary research will be needed. Since producers and private breeders would benefit from objective evaluation of resistant varieties and development of guidelines for their use, some of the funding for this research should come from the private sector (e. g. producer groups and private seed companies). Private seed companies are reluctant to develop variety-specific thresholds themselves, not only because of the expense, but because of potential liability considerations. Therefore a cooperative arrangement analogous to that between agrochemical industry and public scientists seems appropriate. Admittedly, the profits to be realized from arthropod resistant crops are less than those for successful agrochemicals. Seed companies currently cannot demand large premiums for insect resistance, and in the future some degree of resistance to arthropods may be necessary just to retain market share, but command no price premium. On the other hand, without objective evaluation and without suitable guidelines to extract the value of plant resistance to arthropods in vegetables and other crops, producers will have little incentive to utilize these new varieties.

In addition, legislated reduction in pesticide use in agriculture, commendable as it may be for reducing the health and environmental risks associated with agriculture, must be coupled with increased expenditures of public funds to develop and implement alternatives to these chemicals. Basic and applied research in PRI, biological control, cultural control methods and other alternatives must be adequately funded to ensure the health of agriculture in the U. S. and elsewhere.

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