

Tritrophic interactions in the management of *Spodoptera exigua* and other pests on celery

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HISTORICAL PERSPECTIVES ON TRITROPHIC INTERACTIONS IN IPM

Historically, pest managers assumed that host plant resistance and biological control were compatible and largely independent pest management strategies (1,2). One early theoretical approach reflecting this view was derived from deterministic mathematical models of host-parasitoid interactions. Those models show that effective control by natural enemies is enhanced when the rate of increase of the host population is reduced (3,4,5,6,7). Such a prediction assumes that the host plant affects only the growth rate of the prey population and not the attractiveness or quality of prey individuals for discovery and utilization by natural enemies. A substantial number of cases are now known where the assumption of uniformity of the prey population on different host plants either does not hold or has limited applicability (8,9,10,11,12).

Unfortunately, there have been relatively few attempts to translate results of short-term studies on the effects of host plants on particular life history parameters of natural enemies into changes in herbivore-natural enemy population dynamics. Such population studies are essential, for results from short-term laboratory studies may be misinterpreted. For example, while plant resistance led to a reduction in the size and number of parasitoids from greenbugs (13), host plant resistance did not disrupt biological control. In fact, overall plant damage was least, and greenbug populations were smallest, on resistant varieties in the presence of parasitoids (13). Despite their reductions in size and density, the parasitoids were more effective in suppressing aphids on resistant

compared with susceptible plants.

Similarly, while Kauffman & Flanders (14) reported an increase in development time, reduced survival, and reduced reproduction of *Pediobius foveolatus* Crawford (Hymenoptera: Eulophidae) when reared on Mexican bean beetles, *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae), on resistant soybeans, the population growth potential of the parasitoid was reduced less than was that of the host. Thus, despite the negative impact on individual life history parameters, the intrinsic rate of increase of the parasitoid was greatest relative to that of its host on the resistant cultivar. Even though host plant resistance and biological control might be judged antagonistic at the individual level, host plant resistance and biological control are expected to be compatible at the population level in this system. Using a modeling approach based upon energy flow, Gutierrez (15) also concluded that, in general, the net effect of host plant resistance would be beneficial to natural enemies if host plant resistance suppressed herbivore populations more than natural enemy populations. Thus, the compatibility of host plant resistance and biological control cannot be predicted simply from measuring the effect of host plant resistance on life history parameters or population growth of the natural enemy. Corresponding data on the herbivore are equally essential. Ideally, research to understand the combined and interacting effects of host plant resistance and biological control in pest management would include multigenerational experiments to determine the growth rates of both herbivore and natural enemy on both resistant and susceptible crop

varieties.

In order to better understand the consequences of host plant variation on population dynamics of herbivore and natural enemy, Hare (12) developed five models of responses based upon the statistical form of the interaction between host plant resistance and biological control on equilibrium pest density. These models have been useful in resolving some of the confusion in the use of the term, "compatibility" between host plant resistance and biological control in applied systems (9). Four of these models are reviewed below.

A purely additive relationship between host plant resistance and natural enemies occurs when the incremental numerical reduction in equilibrium herbivore density caused by natural enemies is independent of that caused by host plant resistance and uniform at all levels of host plant resistance. Therefore, the expected equilibrium pest density due to host plant resistance and natural enemies can be predicted simply from the combined effects of both acting independently. Additive relationships preclude any biological or statistical interaction.

In a simple synergistic model, the incremental reduction in equilibrium herbivore density caused by natural enemies is relatively greater at high host plant resistance levels than at low. This form of interaction is obviously compatible in a pest management program and the ideal model to be sought.

A mildly antagonistic model specifies that the reduction in equilibrium herbivore density due to host plant resistance and natural enemies is less than would be calculated if the interaction were additive. Such mildly antagonistic interaction may also be a "compatible" interaction in pest management, if not the most desirable, because the reduction in equilibrium pest density due to both factors is still greater than that due to either alone.

When the antagonism is more severe, the reduction in equilibrium herbivore density once caused by natural enemies is now replaced by that of host plant resistance. Hare (12) termed this a disruptive model. Such an interaction would be expected when natural enemies are more susceptible than herbivores to plant resistance mechanisms (e.g. 16,17,18). This form of interaction would be incompatible from low to intermediate host plant resistance levels, and there would be essentially no interaction at high host plant resistance levels

due to the high mortality suffered by natural enemies.

An important point to recognize is that all models except the disruptive model show qualitative compatibility between host plant resistance and biological control. The only difference between the additive, synergistic, or mildly antagonistic models is whether the magnitude of pest population reduction differs from that predicted assuming host plant resistance and biological control imposed independent sources of mortality.

Several studies exploring the form of the interaction between resistant crop varieties and natural enemies in a number of crops were evaluated and are presented in Table 1. Antagonistic interactions were found in eight of 30 involving parasitoids (26.7%) while a synergistic relationship was found in only three (10.0%). No clear interactions (i.e. additive relationships) were found in 13 (43.3%). In the remaining three cases, the form of the relationship varied with the resistance level of the cultivars employed.

All of the clearly disruptive interactions involved parasitoids attacking hosts on wild tomato plants (*Lycopersicon hirsutum* f. *glabratum*) with trichome-based resistance to *Manduca sexta* (L) and other insect species, and a second, non-trichome based mechanism conferring partial resistance to *Helicoverpa zea* (Boddie) and *Heliothis virescens* (F.). In a number of studies, Kennedy and co-workers showed that the methyl ketones causing the trichome-based resistance were toxic or deleterious to several species of insect parasitoids (34,18, and references therein). In the field, the deleterious impact on the natural enemies of *H. zea* and *H. virescens* was sufficiently great that the densities of these two insect pests were similar, if not higher, on the partially resistant plants (18).

Host plant resistance appears to be quite compatible with the biological control provided by generalist predators, as most studies to date indicate an additive relationship between host plant resistance and predation. In several systems, however, mild antixenosis caused increased movement of prey and presumably facilitated their discover and capture. Brown rice planthoppers, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae), suffered heavier predation by the spider, *Lycosa pseudoannulata* (Bosenberg et Strand) (Araneida: Lycosidae) on non-preferred rice

Table 1: Effect of Host Plant Resistance in Cultivated Crops on Natural Enemies of Selected Insect Pests.

Pest	Natural Enemy	Resistant Plant	Mode of Resistance	Effect on Natural Enemy	Comments	Reference
Parasitoids						
<i>Diuraphis noxia</i>	<i>Diaretiella rapae</i>	Wheat (<i>Triticum aestivum</i> L.)	Tolerance	additive	Similar levels of aphid suppression on resistant and susceptible varieties	19
<i>Diuraphis noxia</i>	<i>Diaretiella rapae</i>	Triticale (<i>Triticosecale</i>)	Antibiosis	antagonistic	Reduced parasitoid size and growth rate	19
<i>Pseudophusia includens</i>	<i>Copidosoma truncatellum</i>	Soybean (<i>Glycine max</i> L.)	Reduced survival and growth.	antagonistic	Increased parasitoid development time.	20
<i>Pseudophusia includens</i>	<i>Microplitis demolitor</i>	Soybean	Lengthened development time, reduced weight.	antagonistic	Reduced parasitoid survival, reduced number of available prey.	21
<i>Pseudophusia includens</i>	<i>Voria ruralis</i>	Soybean	Reduced survival	syn/ant, varied with resistance level	Reduced parasitoid puparia per host, reduced pupal weight, increased host death prior to parasitoid emergence.	22
<i>Epilachna varivestis</i>	<i>Pediobius foveolatus</i>	Soybean	Lengthened development time reduced survival, reduced egg production.	antagonistic	Possibly a compatibility of BC with HPR.	14
<i>Epilachna varivestis</i>	<i>Pediobius foveolatus</i>	Soybean	Reduced survival, growth and weight.	add/ant	Male-biased sex ratio on one cultivar, no effects on others.	23
<i>Heliothis</i> sp.	<i>Microplitis croceipes</i>	Soybean	Antibiosis, reduced growth.	syn/ant varied with resistance level	Increased development time, reduced parasitoid adult weight.	24
<i>Nezara viridula</i>	<i>Telenomus chloropus</i>	Soybean	Mild antibiosis and antixenosis.	antagonistic	Reduced survival reduced total fecundity of egg parasitoid.	25
<i>Spodoptera frugiperda</i>	<i>Campoletis sonorensis</i>	Maize (<i>Zea mays</i> L.)	Reduced growth	antagonistic	Increased parasitoid development time.	26
<i>Spodoptera frugiperda</i>	<i>Campoletis</i> sp.	Maize	Antixenosis.	synergistic	Increased parasitization rate.	27
Four Lepidoptera species	<i>Apanteles marginiventris</i> ,	Soybean	Reduced survival, reduced growth, and lengthened development time.	additive	No differences in parasitism levels across cultivars.	28
<i>Schizaphis</i>	<i>Lysiphlebus</i>	Barley	Reduced population	antagonistic	Fewer and smaller	13

Table 1 (continued)

<i>graminum</i>	<i>testaceipes</i>	(<i>Hordium vulgare</i> L.), Sorghum (<i>Sorghum bicolor</i> L.)	growth, reduced size.		mummies, but not disruptive.	
<i>Schizaphis graminum</i>	<i>Lysiphlebus testaceipes</i>	Oat (<i>Avena sativa</i> L.)	Reduced population growth.	additive	No effect on parasitoid survival, sex ratio, or development time.	29
<i>Aphis gossypii</i>	<i>Lysiphlebus testaceipes</i> , and others	Cantaloupe (<i>Cucumis melo</i> L.)	Antibiosis and/or antixenosis.	additive	Parasitization level independent of aphid density across cultivars.	30
<i>Acyrtosiphon pisum</i>	various	Alfalfa (<i>Medicago sativa</i> L.)	Reduced population growth, or predator numbers.	additive	No variation in parasitism rates	31
<i>Myzus persicae</i>	<i>Aphidius matricariae</i>	Chrysanthemum (<i>Chrysanthemum</i> sp.)	Reduced population growth.	additive	No effect of density on searching behavior or apparent effect on parasitoid population growth.	32
<i>Bruchus pisorum</i>	<i>Eupteromalus leguminis</i>	Pea (<i>Pisum sativum</i> L.)	Antixenosis.	synergistic	Increased parasitization.	33
<i>Helicoverpa zea</i>	<i>Archytas marmoratus</i>	Tomato (<i>Lycopersicon hirsutum</i> f. <i>glabratum</i>)	Antibiosis	disruptive	Plant toxic to tachinid larvae	34
<i>Helicoverpa zea</i>	<i>Eucelatoria bryani</i>	Tomato	Antibiosis	additive	No effect on tachinid parasitoid	34
<i>Helicoverpa zea</i> , <i>Heliothis virescens</i>	<i>Tricogramma</i> spp.	Tomato	Antibiosis	disruptive	parasitoid inhibited more by glandular trichomes than host.	18
<i>Manduca spp.</i>	<i>Telenomus sphingis</i>	Tomato	Antibiosis	disruptive	parasitoid inhibited more by glandular trichomes than host.	18
<i>Helicoverpa zea</i> ,	<i>Camponotus sonorensis</i> .	Tomato	Antibiosis	antagonistic	parasitoid inhibited more by glandular trichomes than host.	18
<i>Helicoverpa zea</i> , <i>Heliothis virescens</i>	<i>Cotesia marginiventris</i> .	Tomato	Antibiosis	additive	parasitoid not strongly affected by host plant resistance	18
<i>Heliothis virescens</i>	<i>Cardiochiles nigriceps</i>	tomato	Antibiosis	additive	parasitoid not affected by host plant resistance	18
<i>Oulema melanopus</i>	<i>Anaphes flavipes</i>	Wheat	Antibiosis, Antixenosis	additive	pubescent wheat had no effect on egg parasitoid.	35
<i>Oulema melanopus</i>	<i>Tetrastichus julius</i> , <i>Diaparsis temporalis</i> , <i>Lemo- phagous curtus</i> .	Wheat	Antibiosis, Antixenosis	additive	pubescent wheat had no effect on larval parasitoids.	36
<i>Heliothis</i>	<i>Camponotus</i>	Cotton	Antibiosis,	additive	Similar degrees of	37

Table 1 (continued)

<i>virescens</i>	<i>sonorensis</i> (<i>Gossypium hirsutum</i> L.)		Antixenosis resistant and susceptible		parasitization on cultivars.	
<i>Aphis gossypii</i>	<i>Lysiphlebus testaceipes</i>	Cotton	reduced population growth on smooth-leaved cultivars.	additive	No effect of pubescence on parasitism rates	38
<i>Helicoverpa zea</i>	<i>Trichogramma pretiosum</i>	Cotton	antixenosis	synergistic	Glabrous plants are both non-preferred by the host, and host eggs suffer greater parasitization.	39
Predators						
<i>Nephotettix virescens</i>	<i>Lycosa pseudoannulata</i> (<i>Oryza sativa</i> L.)	Rice	Reduced oviposition and survival.	additive	Predatory spider.	40
<i>Nephotettix virescens</i>	<i>Cyrtorhinus lividipennis</i>	Rice	Reduced oviposition and survival.	additive	Predatory bug.	40
<i>Sogatella furcifera</i>	<i>Lycosa pseudoannulata</i>	Rice	Reduced survival.	additive	All predators cause ca. 30% additional mortality on all varieties.	41
<i>Sogatella furcifera</i>	<i>Cyrtorhinus lividipennis</i>	Rice	Reduced survival.	additive	"	"
<i>Sogatella furcifera</i>	<i>Harmonia octomaculata</i>	Rice	Reduced survival.	additive	"	"
<i>Sogatella furcifera</i>	<i>Paederus fuscipes</i>	Rice	Reduced survival.	additive	"	"
<i>Nilaparvata lugens</i>	<i>Lycosa pseudoannulata</i> , and others	Rice	Mild antixenosis, reduced survival.	synergistic	Increased predation rate due to increased prey movement.	42
<i>Anticarsia gemmatilis</i>	<i>Geocoris punctipes</i>	Soybean	Reduced growth rate.	antagonistic	Reduced growth rate and survival.	43
<i>Pseudoplusia includens</i>	<i>Geocoris punctipes</i>	Soybean	Reduced growth rate.	antagonistic	Reduced growth rate.	43
<i>Pseudoplusia includens</i>	<i>Podisus maculiventris</i>	Soybean	Lengthened development time, reduced growth.	antagonistic	Similar effects on predator as on host	44
<i>Spodoptera frugiperda</i>	<i>Orius insidiosus</i>	Maize	Antibiosis, antixenosis	synergistic	Increased predation	45
<i>Helicoverpa zea</i>	<i>Orius insidiosus</i>	Maize	Reduced growth	synergistic	Increased predation	45
<i>Helicoverpa zea</i>	<i>Chrysopa rufilabris</i>	Cotton	antixenosis	synergistic	Glabrous plants are both non-preferred by the host, and host eggs suffer greater predation by young larvae, but not older larvae.	39

Table 1 (continued)

<i>Tetranychus urticae</i>	<i>Phytoseiulus persimilis</i>	Soybean	50% reduction in mite egg production	additive	No interaction between host plant resistance and predation on host mite population density.	46
<i>Tetranychus</i> spp.	Three predators	Cotton	Lower mite fecundity	additive	Similar suppression of mites on resistant and susceptible cultivars.	47
<i>Acyrtosiphon pisum</i>	<i>Hippodamia convergens</i>	alfalfa	reduced aphid fecundity	additive	Aphid consumption and beetle larval development did not differ between cultivars.	48
Pathogens						
<i>Spodoptera exigua</i>	<i>Bacillus thuringiensis</i> (<i>Apium graveolens</i> L.)	Celery	Antibiosis, Reduced growth rate.	additive	No interaction between host plant resistance and Bt on larval mortality.	49
<i>Trichoplusia ni</i>	<i>Bacillus thuringiensis</i>	Celery	Antibiosis, reduced growth rate.	additive	No interaction between host plant resistance and Bt on larval mortality.	49
<i>Helicoverpa zea</i>	<i>Bacillus thuringiensis</i>	Soybean	Reduced growth rate	synergistic	Increased dose-specific mortality.	50
<i>Helicoverpa zea</i>	<i>Bacillus thuringiensis</i>	Soybean	Reduced survival.	synergistic	Death at earlier age.	51
<i>Heliothis virescens</i>	<i>Bacillus thuringiensis</i>	Cotton	Antixenosis.	synergistic	Increased host mortality.	52
<i>Helicoverpa zea</i>	<i>Nomuraea rileyi</i>	Soybean	Reduced survival.	synergistic	Death at earlier age.	51
Four Lepidoptera species.	<i>Nomuraea rileyi</i>	Soybean	Antibiosis.	additive	No effect on other pathogens.	53
<i>Aphis gossypii</i>	<i>Neozygites fresenii</i>	Cotton	reduced population growth on smooth-leaved cultivars	additive	No effect of pubescence on fungal infestation rates.	38
<i>Pseudoplusia includens</i>	Nuclear Polyhedrosis virus	Soybean	Antibiosis, antixenosis	additive	Similar population reductions by the virus on resistant and susceptible soybean.	54
<i>Anticarsia gemmatilis</i>	Nuclear Polyhedrosis virus	Soybean	Antibiosis, antixenosis	additive	Similar population reductions by the virus on resistant and susceptible soybean.	54
<i>Helicoverpa zea</i>	Cytoplasmic Polyhedrosis virus	Maize	antibiosis	additive	Effects of host plant resistance and virus were independent for survival and synergistic for developmental rate.	55

cultivars (42), and both fall armyworms and corn earworms were more heavily attacked by *Orius insidiosus* (Hemiptera: Anthocoridae) (Say) on non-preferred maize varieties (45).

In contrast, two other hemipteran predators, *Geocoris punctipes* (Say) (Hemiptera: Lygaeidae) and *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae) were negatively affected by resistance to caterpillars in soybean. *Geocoris*, which normally feeds on plant material to acquire water, exhibited increased development time and increased nymphal mortality when their diets included foliage from soybean cultivars resistant to the velvetbean caterpillar, *Anticarsia gemmatilis* Hübner (Lepidoptera: Noctuidae), and the soybean looper, *Pseudoplusia includens* (Walker) (Lepidoptera: Noctuidae). Similar increases in mortality and development time occurred when predators were reared on caterpillars that were reared on resistant soybean cultivars (43). Pre-imaginal development of *P. maculiventris* closely paralleled the effect of host plant resistance on *P. includens* reared on resistant and susceptible soybean cultivars; development time was increased and growth rates were reduced on foliage from resistant plants compared to susceptible plants (44). In the latter study, the effects of host plant resistance extended to the fourth trophic level in that the reproductive capacity of the egg parasitoid, *Telenomus podisi* Ashmead (Hymenoptera: Sceleonidae), was reduced when it was reared from eggs of *P. maculiventris* whose prey was *P. includens* reared on resistant soybeans as compared to susceptible soybeans (44). The net outcome of this four trophic level interaction on the overall fitness of any of the individual participants under field conditions remains to be ascertained. In summary, as with many of the parasitoids, and in contrast to most other crops, antibiosis to the insect herbivores of soybean appeared to interact negatively with the predators of those insect herbivores.

Although a number of laboratory studies have shown both positive and negative effects of selected plant chemicals on the efficacy of insect pathogens (reviewed by 56,57), most studies using resistant plant cultivars to date indicate a general compatibility between host plant resistance and biological control by pathogens. In none of the cases out of the 11 that we could evaluate did we find antagonistic

or disruptive interactions. In most studies, the susceptibility of host larvae to pathogens was inversely related to the growth and vigor of the larvae, which itself was directly related to the level of host plant susceptibility.

Unlike entomopathogenic fungi and viruses, vegetative growth of *Bacillus thuringiensis* (Berliner) is not necessary for death of the insect. *B. thuringiensis* spores and endotoxin normally enter via feeding, and, in most susceptible insects death of the insect is caused directly by ingested endotoxin. High midgut pH inhibits spore germination. After partial cleavage by the insect's proteases, the activated toxin causes a swelling of the midgut epithelial cells, disruption of ion transport, and eventual separation and breakdown of the midgut epithelium. Such disruption leads to ion and pH imbalances in the hemolymph, total body paralysis, and eventual death. Spores then germinate within the hemolymph (58,59). Thus, the effect of host plant allelochemicals on solubilization and activation of the endotoxin can be equally important as the direct effects of those allelochemicals on *B. thuringiensis* vegetative growth and sporulation.

It is difficult to predict how particular plant chemicals may influence insect control by *B. thuringiensis*, because previous laboratory studies have shown the full range of antagonistic, synergistic, and additive effects depending upon the host insect and specific chemicals examined (e.g., 57,60,61,62). Our analysis of studies that examined the effect of *B. thuringiensis* on resistant vs. susceptible plants showed that in three of the five cases examined, *B. thuringiensis* interacts synergistically with host plant resistance, in that host insects reared on resistant plants are themselves more susceptible to *B. thuringiensis*. For example, *H. zea* fed a resistant soybean genotype had a 40% lower LD50 to a commercial formulation of *B. thuringiensis* than did insects reared on a susceptible genotype (50). Bell (51) also found that *H. zea* suffered higher total mortality and succumbed at an earlier age when reared on a resistant compared to a susceptible soybean genotype. Similarly, Schuster et al. (52) found *B. thuringiensis* to be more efficacious for *H. virescens* suppression when insects were reared on a high-tannin cotton cultivar than when reared on a low-tannin cultivar. More recently, Meade & Hare (63,49) compared the

susceptibility of *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) and *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) to measured doses of *B. thuringiensis* when reared on genotypes of celery that differed in both laboratory and field. Both insect species were affected similarly by variation among celery genotypes, and there were no interactions between host plant resistance and *B. thuringiensis* dose on insect survival or population density in the field.

TRITROPHIC INTERACTIONS AND CELERY PEST MANAGEMENT

Historical Background

In terms of pesticide usage, the \$300 million a year U.S. celery industry in California, Michigan, Texas and Florida is faced with significant societal and biological problems (64,65). Concerns about the pollution of ground water and fears of increased cancer risks have stimulated an increase in legislation dealing with pesticides. For the past few years, twenty or more new agriculturally-related bills have been introduced in California in each year (66). Nearly all of these would require further restrictions on the use of chemicals for insect control. In some cases these restrictions have reduced pesticide use, but in celery these laws paradoxically have served to increase use due to development of pesticide resistance (67). Along with this increased use of petroleum-based pesticides has been a concern that the solvents they are mixed with may be contributing to air pollution.

These problems are exacerbated by the declining availability of efficacious insecticides. Insecticide resistance is increasing exponentially (68). Because growers are rarely altruistic, their tendency has been to exploit each new compound to maximum commercial advantage, with the expectation that their neighbors will do the same. Thus, while conservation of pesticides is in their best long term interests, the growers practices are frequently driven by the concern that even if they employ conservation strategies, pesticides will rapidly lose effectiveness due to extensive use by others. This would, of course, put conservation-minded producers at a significant competitive disadvantage.

Occasionally the lack of efficacious pesticides results in catastrophic crop losses. In California, the rapid development of

resistance to all available pesticides by the leafminer, *Liriomyza trifolii* (Burgess), resulted in losses of over \$20 million in a single year (69). Similar problems have been identified for the beet armyworm, *S. exigua*, which has become a major pest of most vegetable and many field crops in California (70).

As a result of these concerns, the celery industry appears willing to adopt less pesticide intensive systems. Certainly the industry is supporting considerable research into IPM and low pesticide use strategies (71). However, any such system ideally must be at least as profitable as the current chemical tactics. Growers might accept some losses in yield if overall net profits were similar. If the pesticide example noted previously offers a lesson, it is that programs that result in even short term competitive disadvantages will not be adopted. Therefore, for effective implementation, any proposed new management strategies must include economic analyses which document the profitability of the proposed program.

In order to develop such an IPM program, the key components of the celery production system must be understood. In addition, the interactions between these constituents must be known, or substantial problems will result. The remainder of this chapter initially focuses on the key components of the celery system and their interactions. The chapter concludes with the incorporation of these components into an economically-viable IPM program for celery.

Biological problems in celery production

Linear Furanocoumarins

Celery can be rendered unmarketable by diseases, arthropods, and the presence of unacceptable levels of linear furanocoumarins. The three linear furanocoumarins common in celery; psoralen, bergapten and xanthotoxin, are undesirable because of their carcinogenic, mutagenic (72,73) and photodermatitic activities (74,75, and references therein). These compounds are believed to have evolved in Apiaceae and several other plant families as a protective measure against mutagenic UV radiation (76,77), plant pathogens (77,78), nearby plants (77,80), and insect herbivory (75, and references therein, 81).

In most commercial celery plants, the collective concentrations of these compounds

in healthy petioles are quite low, generally less than 4 µg/g per g fresh weight in the petioles (82). Concentrations tend to be somewhat higher in the leaves (~ 12 µg/g) (83), which are typically not marketed except at organic food stores and farmer's markets. The level in petioles is usually well below the concentration believed to cause either acute dermatitis (18 µg/g) (84) or chronic dermatitis (7 µg/g) (85).

However, a variety of stress-inducing factors (UV light, plant pathogens, cold temperatures, wilting, mechanical damage, pollution, etc.) have been shown to increase the linear furanocoumarins in celery (86, and references therein). Not surprisingly, breeders developing resistance to *Fusarium* spp. root pathogens have unintentionally selected for celery plants high in furanocoumarins; foliar concentrations in some resistant lines exceeded 400 µg/g (87). Thus, because these compounds can be readily selected for in a breeding program, and because they have substantial activity against key insect pests of celery (88,89), the concentrations of these compounds must be monitored in any breeding program for insect resistance. Some recent studies, however, have determined that some celery lines have promising modes of resistance to insect pests which are not based on the linear furanocoumarins (60,90).

Insect Pests of celery

Spodoptera exigua (Hübner), the beet armyworm, is a polyphagous noctuid moth that was introduced into North America in the mid 1800s (reported as *Laphygma exigua* Hübner)(91). In California, this species is consistently the primary insect pest of celery. Although adults can be found throughout the year in central and southern California, major emergences and migration flights are usually recorded in the spring through late summer (92). They typically lay masses of 20 to 120 eggs, and cover them with light colored scales. This gives the egg masses a distinctive cottony appearance and protects them from egg parasitoids such as *Trichogramma* spp. (93). Up to 600 or more eggs can be laid by each female over a 7 -8 d period (94). The early instars are positively phototactic, often feeding gregariously on celery for the first instar (95). Larger instars are quite mobile, but negatively phototactic. Thus, later instars generally hide in the center of the celery plant where they

damage the petioles. After 5 -7 6 instars, the larvae burrow into the soil to pupate. The pupal stage persists 7 to 10 days, but may be much longer at cooler temperatures (94). Although newly emerged adults can be found throughout the year in Central and Southern California, major emergences and migration flights are usually recorded in the spring through late summer.

Early instars feed on the leaves of celery but rarely cause substantial economic losses; the celery plant can compensate for a substantial amount of leaf damage (96,97). However, the larger larvae will feed on petioles and can cause significant crop loss. Large larvae are quite mobile, and have been observed to travel extended distances, feeding on several plants in a 24 h period (98,99). If petioles near the outside of the plants are damaged, they can be removed. If damage occurs in a centrally located petiole the plant must often be discarded.

L.trifolii is an important secondary pest of celery which causes crop losses through growth reduction resulting from mining of either the leaves or petioles. When populations are low to moderate (less than 25% of the leaves mined), the primary effect is slowed growth or stunting of the celery plant (97). A single mine can reduce photosynthetic production of a leaf by over 40% (100). Because growers in California plant in late summer just after a mandated celery-free period, and the best market prices generally occur during the holidays prior to the new calendar year, leafminer feeding which extends the harvest date by three to six weeks can have significant impact on profitability of the crop. If populations reach high levels (>25% of leaves mined), the insects begin to oviposit in the petioles. If this occurs losses can be catastrophic (101).

Other insects are occasional pests of celery. *Trichoplusia ni* (102), the black bean aphid (103), *Listronotus oregonensis* LeConte and possibly *L. texanus* (Stockton) (104) can be locally important. Although the leafminer, *L. huidobrensis*, has been present for at least 40 years in California, this species has become a significant pest only relatively recently (105), but appears to be increasing in importance.

Biological control agents

Bacillus thuringiensis (Berliner)

The insect pathogen, *B. thuringiensis*, is

a widely used bacterium produced commercially for suppression of a variety of insect pests. The isolate *B. thuringiensis* var. *kurstaki*, is commonly used in celery for control of lepidopterous pests, including *S. exigua* (106). A great deal of information is available on the toxicity of various proteins, the search for new isolates, and genetic engineering of key proteins into crop plants (107, and references therein). This information will not be repeated here. Instead we will briefly report on the difficulty of use of this pathogen in commercial vegetable production.

Bacillus thuringiensis has not been a panacea for insect control in vegetables such as tomatoes and celery. On the contrary, this material often does not provide the level of control offered by many chemical pesticides such as the organophosphates or the pyrethroids. Years of testing reported in such journals as the Entomological Society of America's Insecticide and Acaricide Tests (now Arthropod Management Tests) show that in a regularly scheduled application program, many other pesticides provide significantly better suppression of pest insects. More importantly, anecdotal information suggests many growers tried *B. thuringiensis* in past years in scheduled control programs, and found that in commercial production the control was not equivalent to other insecticides. This lack of success could, in part, be attributed to the need for accurate timing of the application of *B. thuringiensis* to susceptible life stages, as well as the relatively short residual activity of the material (107). Not surprisingly, there is some resistance to using *B. thuringiensis*, even though recent advances in formulations and isolate selection have improved efficacy (108). Nonetheless, several commercially-viable control programs have been developed and implemented for vegetables based on *B. thuringiensis* (109,110), proving that these limitations can be overcome.

Parasitoids

Surprisingly few parasitoids are effective at economically suppressing populations of *S. exigua* (111,112,113). In fact, percent parasitism rarely exceeded 30% in the California studies.

On the other hand, leafminer parasitoids can provide economic levels of suppression in celery and other crops. Generally, a complex

of parasite species is present, with one or two species dominating (114). Often, leafminers only occur at damaging levels when their associated parasitoids are killed by pesticide applications aimed at *S. exigua*. The literature contains many reports that insecticides will generate outbreaks of *Liriomyza* species. Hills and Taylor (115) were the first to document this problem with reports that *Liriomyza* species populations increased and parasite populations decreased following DDT application. This same resurgence effect has since been demonstrated for methoxychlor, dieldrin, endrin and lindane (116), for parathion, ethion and diazinon (117), for permethrin (118), methomyl, (97,119,120) and a variety of other compounds (121,122).

Fortunately, in the absence of pesticides which kill the parasitoids, the leafminer is generally held below threshold levels. Most of the currently available documentation is from tomatoes (109, and references therein,120), but some confirming data have been collected from celery as well (64,96,100). However, even when the parasitoids are locally effective, occasional outbreaks of *L. trifolii* can occur. A typical scenario is the harvesting of a nearby field, which drives large numbers of adult *L. trifolii* into an adjacent crop, temporarily overwhelming the biological control agents. In situations such as this, the availability of a pesticide which controls leafminers without substantially damaging the parasitoid population can be critical (123).

Interactions of biological components in the celery system

Linear furanocoumarins, *S. exigua* and *L. trifolii*

There is little evidence that linear furanocoumarins have any physiological or behavioral effects on *L. trifolii* at the concentrations that occur in commercial celery. In fact, there is evidence that there is no correlation between *L. trifolii* density and linear furanocoumarin concentration in celery leaves (87). Even leaf concentrations exceeding 250-300 µg/g fresh weight did not significantly reduce adult emergence (87).

On the other hand, *S. exigua* is strongly affected physiologically by the presence of linear furanocoumarins. Increasing concentrations of these compounds in artificial diets decreases larval weights, extends generation time and results in higher

mortality (89). In field-grown celery, plant growth stage, season of planting, and commercial genotype interact to affect *S. exigua* development (124). Although a number of factors could contribute to the variability observed in developmental rate, previous research has shown that furanocoumarin concentrations in celery also fluctuate with season and genotype (82,88). In addition, exposure to short wave UV light can enhance the impact of linear furanocoumarins, but such exposure is not required for negative effects to manifest (125). The extent of the biological response of *S. exigua* to individual furanocoumarins or combinations of these chemicals is impacted by the pesticide resistance status of the insect; more insecticide-susceptible insects are more strongly affected by furanocoumarins (126). As a result of this variability, predicting developmental rates and mortality of *S. exigua* feeding on celery is not a simple process. Therefore, most celery producers rely on weekly or twice weekly scouting for larvae.

The behavior of *S. exigua* is also influenced by linear furanocoumarins. An avoidance response by insects can have substantial implications for host plants (127). This response is particularly important for insects, like *S. exigua*, which are highly mobile (98), and for plants like celery which are frequently found in close association with the herbivore's preferred weed host (99). Even the relatively low concentrations of furanocoumarins occurring in celery petioles elicits a significant deterrent response from *S. exigua* (128).

This effect may be exacerbated by the determination that herbivory by *S. exigua* on celery can elicit additional production of furanocoumarins. Feeding at high densities (10/plant) of *S. exigua* larvae resulted in enhanced production of furanocoumarins in the leaves of celery (Fig. 1, see figure caption for experimental design). Both psoralen and bergapten showed significant increases in concentrations (bergapten, $F_{2,27} = 6.39$, $P < 0.004$; psoralen, $F_{2,27} = 2.7$, $P < 0.05$). However, five larvae/plant did not produce a significant effect. In addition, the much lower concentrations of linear furanocoumarins in the petioles did not show significant differences among herbivory levels. Lower concentrations of linear furanocoumarins in petioles are typical of commercial celery

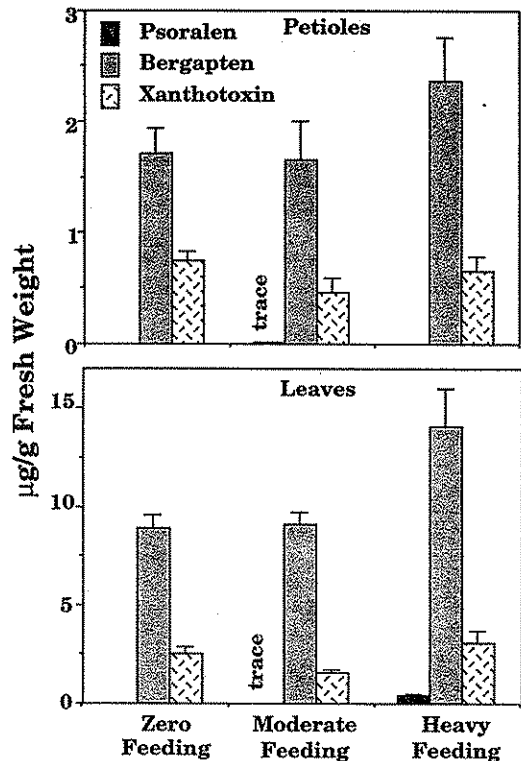


Figure 1. Psoralen, bergapten and xanthotoxin levels in petioles and leaves of celery fed upon by *S. exigua*. Feeding levels of moderate and high correspond to five and ten third instars/plant, respectively. Lines above bars delineate standard errors of the mean. The plants used in the experiment, cv 'Tall Utah 52-70R', were standardized to the extent possible. Ten replicates each of 0, 5, and 10 third instar *S. exigua* were caged on standardized 52-70R celery plants. The insects were allowed to complete development before petiole and leaf samples were randomly chosen from each test plant. Because leaf and petiole location influences furanocoumarin concentration (83), samples were standardized by limiting selections to only mature leaves and petioles that had not yet begun to senesce.

(83,89). No claims are made that this observation supports the evolution of furanocoumarin production in plants. There

is ample evidence in the literature that induced chemical defenses that benefit plants and appear to be stimulated by insects are frequently coincidental, rather than specifically targeted at herbivores (129,130). In fact, the density of third instars required to generate an increase in furanocoumarin production in our study is quite high, and the response is several orders of magnitude below that reportedly induced by disease incidence (131,132) or air pollution (86). Thus, the insect population level required to create a significant response in our tests suggests that insect feeding may simply reinforce a generalized wound response. Nonetheless, avoiding high densities of *S. exigua* should be a priority in commercial production, even if the crop is destined for processing.

Bacillus thuringiensis, S. exigua and L. trifolii

Toxic proteins from *B. thuringiensis* have been reported to influence larval feeding behavior (133, and references therein). In most cases, larvae receiving sublethal doses slowed their rate of intake, thus increasing developmental time. Relatively few publications are available that specifically examine the behavioral responses of *S. exigua* to *B. thuringiensis*. However, Berdegue et al. (134) did report that first and third instar *S. exigua* could detect and, if given a choice, would avoid the Cry1C protein. Further, larvae preferred the control diet over diets with a variety of concentrations of the commercial formulation, inclusion bodies (protoxin), or Cry1C toxin (activated toxin). The fact that *S. exigua* can detect and avoid Cry1C toxin could have important implications for management of this pest. It is unlikely that celery plants sprayed with *B. thuringiensis* would have equal coverage throughout the plant. Therefore, coverage which favors the leaves could actually drive the larvae to feed on the petioles. In the case of transgenic plants which have variable expression of *B. thuringiensis* toxins within the plant, *S. exigua* larvae may selectively feed on those plant parts with the least expression. Finally, if attractive weed hosts are present in the field, larvae could feed on these during the smaller, more susceptible instars. Thus, higher than expected pest populations would result from the use of transgenic plants if larval behavioral responses were not taken into consideration.

There is also good evidence from celery

that plant genotype and environmentally induced host plant variation will affect the efficacy of *B. thuringiensis* for *S. exigua* (60,62). Larvae fed preferred celery genotypes ate more and subsequently received larger doses of *B. thuringiensis*. In this particular case, other factors associated with the host plant were mediating efficacy, as larvae receiving larger doses actually survived better. They conclude that host plant resistance and *B. thuringiensis* are acting additively against *S. exigua* in their system.

There is no evidence that *L. trifolii* is affected in any way by application of commercial formulations containing the Cry1C toxin of *B. thuringiensis*. This is not surprising because Cry1C is reportedly active only against lepidoptera (107).

Linear furanocoumarins and B. thuringiensis

Relatively few studies are available on the *in vivo* impact of plant defensive compounds on efficacy of *B. thuringiensis* (135). Most compounds appear to reduce the activity of pathogen (136,137,138). This is of concern because linear furanocoumarins are known to be antibacterial (139). Thus, these is some concern that ingesting furanocoumarins and *B. thuringiensis* concurrently would lead to reduced intoxication. In addition, some furanocoumarins act as antifeedants for *Spodoptera* spp. (81,140), even at levels found in commercial celery (128). Plant compounds which reduce the rate of food intake would also reduce the ingestion rate of *B. thuringiensis*; with detrimental effects on efficacy (141).

However, these concerns are unfounded. Studies designed to examine the physiological responses of *S. exigua* to various linear furanocoumarins in concert with *B. thuringiensis* found no antagonistic interactions (125). In fact, increases in larval developmental times and decreases in survival were additive. Thus, at least for the commercial celery system, these control factors are compatible.

Parasitoids, B. thuringiensis, and linear furanocoumarins

Navon (137) reports a series of studies showing that *B. thuringiensis* has minimal negative impact on parasitoids and predators. In three of eight studies, he found the interactions were synergistic. Only one study indicated that antagonistic effects were

occurring. Unfortunately, no published work was found showing the impact of *B. thuringiensis* on parasitoids of *S. exigua* in celery. However, these is ample evidence suggesting that *B. thuringiensis* has essentially no negative effect on parasitoids of *L. trifolii* (109,110).

Little information is available on the effects of linear furanocoumarins on parasitoids. In the one study found, the impact of the furanocoumarins found in celery were examined for effect on the polyembryonic parasitoid *Copidosoma floridanum* (Ashmead) attacking *T. ni* (142). Increasing furanocoumarin concentrations reduced survival of *C. floridanum* substantially more than for its host, *T. ni*. There was no significant differences in the number of reproductive parasitoid larvae among treatments. This indicated that linear furanocoumarins did not interfere with polyembryonic development of *C. floridanum*, but exerted toxicity after the parasitoid larvae began feeding on host tissue. Because of the differential effects on the host and parasitoid, linear furanocoumarins can mediate this host-parasitoid relationship through direct effects on the parasitoid, and not merely as a consequence of their effect on the host. No published reports could be found regarding the impact of furano-coumarins on parasitoids of *L. trifolii*.

Development and Validation of an IPM program for celery

The program

The primary objectives of this work were to develop and validate an IPM program designed for use in California's celery industry. In addition, an economic analysis comparing the benefit of the use of standard pesticide practices currently in use in California with an low-input IPM program was evaluated. The IPM program is based on scouting using treatment thresholds, protecting naturally occurring parasites of the leafminer, and threshold-driven applications of an insect pathogen. As noted, in some years the trials also included other pesticides. All experiments allowed the assessment of insect damage, crop yields (and subsequent determination of crop value). With this information, the costs of control programs and net profits resulting from each approach could be calculated. These studies are summarized

mostly from Trumble et al. (143) and Trumble (144); these manuscripts provide considerably more detail on the experimental designs and methodology.

In the initial tests on the University of California's South Coast Research and Extension Center operation, three treatments were evaluated in a randomized complete block design: a chemical standard approach using scheduled treatments (methomyl plus permethrin), an IPM treatment consisting of *B. thuringiensis*, and abamectin as needed; and an untreated control treatment. Pesticides and numbers of applications used in the chemical standard approach were based on average pesticide use data for California (145). *B. thuringiensis* was selected for the IPM program because, as noted earlier, this pathogen has minimal effect on leafminer parasites. Abamectin was chosen for any needed leafminer control as this compound provides good suppression with minimal effect on associated parasites (96).

Following the successful tests on the field station, a large scale grower validation trial was conducted in a commercial planting of cultivar 'G20' celery in Ventura County CA. This large plot design only had two treatments, the grower standard and the IPM program.

Field trials and validation

The experimental plantings of celery (cultivar 'Tall Utah') were established at the University of California's South Coast Research and Extension Center in Orange County, CA during the fall seasons of 1992 and 1993. Celery was transplanted in late August in both years, grown using local commercial practices, and harvested in December. In the Ventura Co. study, the commercial firm was responsible for all aspects of growing, pesticide application and harvesting.

Determination of the need for pesticide applications was based on weekly sampling. *L. trifolii* populations were evaluated by weekly counts of leafminer larvae and puparia in four, 10 x 20 cm styrofoam trays per replicate, when the plants reached a suitable height. Fifteen leafminers per tray per week was the action threshold for treatment. Weekly evaluations of populations of *S. exigua* larvae were based on the numbers in 10 plants per replicate (field station) or 80 plants per replicate (commercial farm). One larva per 10 plants was used as a threshold for treatment.

The results were encouraging. Pesticide applications were reduced from nine in the chemical standard program (two insecticides per application) to three or four in the IPM approach (one insecticide per application). The IPM program produced significantly fewer *L. trifolii* than the chemical standard (Fig. 2). In 1992, parasite populations were

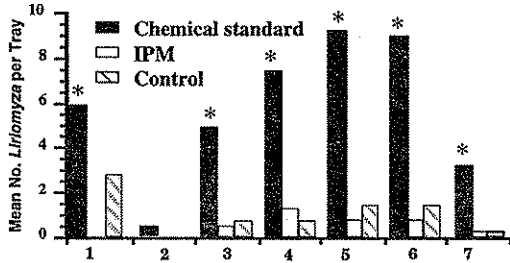


Figure 2. Mean *Liriomyza trifolii* puparia in trays within the chemical standard, IPM and control treatments in 1994. The experimental design is reported in the text. Asterisks above bars indicate significant differences from the IPM plots at the $P < 0.05$ level (Tukey's Honestly Significant Difference Test).

generally quite low (mean < 1 /tray in any treatment). However, in 1993, populations were higher. The numbers of dead adult parasites/tray were substantially higher in the chemical standard (highest mean in 1993 = 5.2/tray) as compared to the IPM treatment (highest mean in 1993 < 0.02 /tray). Similar results were achieved in Ventura Co., with five fewer pesticides applied in the IPM plots.

Economic analyses

Understanding how the economic analyses were conducted is important, and some background information is necessary. Economic data on costs of applications were collected from several sources, including pesticide distributors, farm advisors, and extension publications. For example, the cost of application (excluding pesticides) was estimated at \$39.54/ha per application and included the tractor driver's salary, gas, etc. Pesticide costs per application were: methomyl = \$44.48/ha; pyrethroid = \$56.86/ha; *B. thuringiensis* = \$24.71/ha. Specific costs for

production and marketing are detailed in Trumble et al. (142). All of these costs and other costs of planting, etc. were added to provide a total cost of production. The gross yield of each crop, in boxes of various size classes, was calculated by multiplying the value of each size class of celery by the mean number of boxes produced per treatment. The net profit could then be calculated by subtracting the costs of production from the gross value of the crop for each treatment.

Our economic analyses indicated that the IPM program generated a better net profit than the chemical standard or the control treatments in both 1992 and 1993 (Fig. 3). In 1992, the net profit in the IPM treatment was approximately \$1,500 dollars/ha better than the chemical standard and \$7,000 above the control treatment. In 1993, when the value of celery

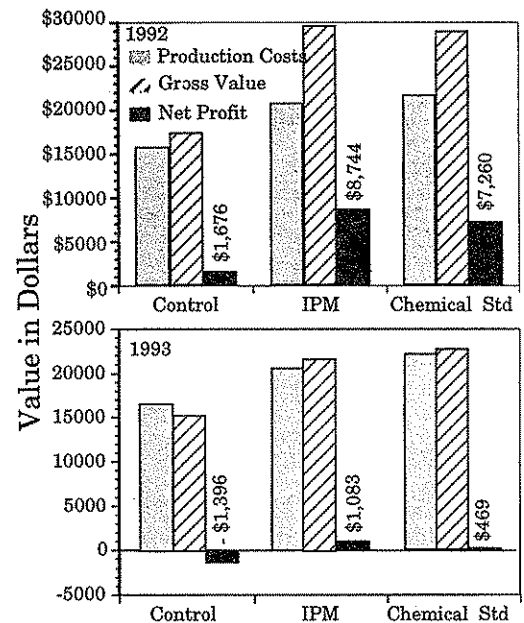


Figure 3. Production costs, gross value and net profits for the control, IPM and chemical standard treatments in 1992 and 1993. Net profit is the cost of production subtracted from the gross value. Numbers above net profit bars are the actual dollar values. Modified from Trumble et al. (142).

was lower, the IPM treatment generated approximately \$600/ha more in net profit. The control treatment lost nearly \$1,400/ha, demonstrating that celery production can be risky.

In the commercial validation trials, the IPM program produced at net profit of about \$400/ha more than the grower's standard (Fig. 4). This occurred in spite of the grower's already conservative approach to pesticide use. Thus, regardless of the year or location of testing, the IPM procedure consistently

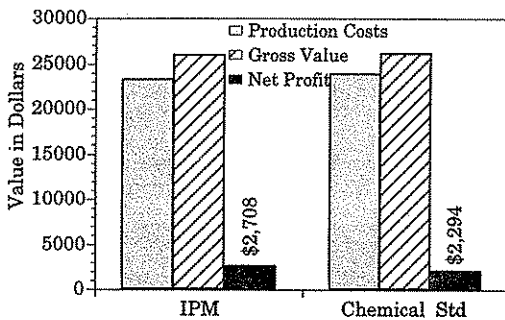


Figure 4. Production costs, gross value and net profits for the IPM and chemical standard treatments in 1995. Net profit is the cost of production subtracted from the gross value. Numbers above net profit bars are the actual dollar values. Modified from Trumble et al. (142).

produced an improved net profit.

Risk assessment

The benefits of the IPM program extend beyond just an improvement in short-term economic return. Certainly, the potential reduction in development of insecticide resistance due to fewer pesticide applications has considerable long-term economic implications. In addition, the IPM approach offers significant advantages for all of the following factors, which were not included in the economic analysis; 1) leafminer populations are largely eliminated by biocontrol agents, 2) soil compaction is minimized because fewer trips are made through the field, 3) there is a substantially reduced potential for environmental

contamination or human health concerns, 4) potential advantages in marketing were not incorporated and, 5) zero reentry intervals allow access to the crop for harvest or maintenance.

Finally, the IPM program releases no solvents into the atmosphere. In 1992 and 1993, the chemical standard approach could be expected to release over 12,000 ml/ha of solvent. Even using the conservative approach of the cooperating grower, over 3,000 ml/ha were released. At this time there is no procedure available for calculating the economic benefit of such reductions. Nevertheless, the benefits derived from solvent reductions as well as the previously mentioned factors are likely to make the economics of the IPM program even more appealing.

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