1988

Compatibility of Biological Control With Host Plant Resistance and Insecticidal Control in Soybeans.

David Boyd Orr

Louisiana State University and Agricultural & Mechanical College

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Compatibility of biological control with host plant resistance and insecticidal control in soybeans

Orr, David Boyd, Ph.D.

The Louisiana State University and Agricultural and Mechanical Col., 1988
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UMI
COMPATIBILITY OF BIOLOGICAL CONTROL WITH HOST PLANT RESISTANCE AND INSECTICIDAL CONTROL IN SOYBEANS

A Dissertation
Submitted to the Graduate Faculty of the Louisiana State University Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy in The Department of Entomology

by
David Boyd Orr
B.S., Simon Fraser University, 1983
M.S., Louisiana State University, 1985
May, 1988
First, I wish to express my sincere gratitude to my major professor, Dr. David J. Boethel, for allowing me to work independently while providing guidance, constructive criticism, and enthusiastic support. The assistance, suggestions and review of manuscripts by the members of my advisory committee, Drs. Elvis A. Heinrichs, Ronald M. Knaus, Sharron S. Quisenberry, and Thomas C. Sparks are gratefully acknowledged. I also express sincere gratitude to Dr. John S. Russin for his many helpful discussions and reviews. I appreciate the assistance of J. Sanmugam, S. Gonzales, and M.R. Riggio in feeding leaves to seemingly endless numbers of soybean loopers. The help provided in the field by Gavin Falconi is greatly appreciated.

I would also like to make a special thanks to Dr. Mark Winston who first inspired my interest in entomology, and Dr. John H. Borden for making that interest grow. Finally, I would like to thank my family and friends for their support and encouragement throughout my graduate studies.
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ABSTRACT

Studies were conducted to investigate the influence of both plant resistance and insecticidal controls used in soybean on several natural enemies of pest insects. There were two major objectives to this research: 1) to examine the effects of an insect herbivore-resistant soybean genotype on relationships between four levels of a trophic system 2) to determine the influence of the primary insecticides applied to control Louisiana soybean insect pests on survival of a major biological control agent of stink bugs.

In the first study, pre-imaginal development of the predatory pentatomid, *Podisus maculiventris* (Say), was affected by soybean antibiosis in a manner similar to that of its lepidopteran prey, *Pseudoplusia includens* (Walker). Pre-imaginal development time and mortality were increased, and cumulative weight gain reduced on resistant foliage. Reproductive capacity of *P. maculiventris* reared on *P. includens* larvae fed resistant soybean generally was unaffected, although progeny production was delayed and extended slightly. Pre-imaginal development and adult emergence of the egg parasitoid *Telenomus podisi* Ashmead from eggs of *P. maculiventris* reared on *P. includens* larvae fed resistant soybean were unaffected. However, overall reproductive capabilities of this parasitoid were reduced.

In the second study, adult egg parasitoids, *Trissolcus basalis* (Wollaston), were minimally affected by permethrin field applications, while methyl parathion had an adverse but short-lived effect on parasitoid survival. High levels of adult mortality were observed only within the first 12 hours following spray application. Neither
insecticide affected emergence of parasitoids from their host eggs, suggesting that stink bug eggs provided a barrier to insecticide penetration. However, parasitoids apparently contacted insecticide residues when chewing through host egg shells to emerge, resulting in some post-emergence mortality caused by methyl parathion. Three factors affected the degree of this mortality: 1) parasitoid developmental stage at time of insecticide application, 2) position of parasitized egg masses in the soybean canopy, and 3) parasitoid gender.

Results from these studies suggest the potential for incompatibility of some biological control agents with insect-resistant soybean, but also demonstrate the compatibility between an important natural enemy and current insecticidal controls applied to Louisiana soybean.
INTRODUCTION

Soybean Insect Pests

Soybeans have risen in prominence from being of incidental importance as a hay crop at the beginning of this century to become a leading agricultural export of the United States, and vital to the economy of this country (Probst & Judd 1973). The increased importance of this crop has stimulated greater attention to losses incurred by pests, including insects.

Soybeans are grown over a broad geographical range in the U.S. and consequently encounter a diversity of insect pests. Twenty-four species or species complexes are recognized as pests of soybean in this country (Kogan 1980). However, more than 80% of the damage is caused by seven of these species, which are grouped into three complexes: 1) lepidopterous defoliators, including the velvetbean caterpillar, Anticarsia gemmatalis Hübner, the soybean looper, Pseudoplusia includens (Walker), and the green cloverworm, Plathypena scabra (F.); 2) coleopterous defoliators, including the Mexican bean beetle, Epilachna varivestis (Mulsant), and the bean leaf beetle, Cerotoma trifurcata (Forster); and 3) pod-feeding pentatomids, including the southern green stink bug, Nezara viridula (L.), and the green stink bug, Acrosternum hilare (Say) (Kogan 1980). In Louisiana, the most important soybean insect pest complexes are the pod-feeding pentatomids and the lepidopterous defoliators (Newsom et al. 1980).
Management Tactics

Presently, the use of conventional insecticides is the only satisfactory means of soybean insect pest control in the United States (Newsom 1980). For stink bugs and lepidopterous pests in Louisiana soybeans, this most commonly includes the application of methyl parathion and permethrin, respectively (Tynes & Boethel 1987). While chemical control has been effective and economical, concern has been expressed over the possible misuse of pesticides in soybeans similar to that which has occurred in other agroecosystems (Newsom 1970, Newsom et al. 1980). This concern has, in part, prompted research on other pest management tactics for soybeans.

An alternative tactic is biological control, including both natural and classical aspects. One approach in using biological control as a pest management tool in soybeans is conservation of indigenous natural enemy fauna, thus exploiting the natural control which they provide. This has been attempted mainly through the development of sound economic thresholds for pests, and somewhat through the recommendation of more selective insecticides (Newsom et al. 1980).

A second way in which biological control has been studied for use in soybeans has been through the classical approach, i.e., the importation and release of exotic natural enemies (Jones et al. 1983). This method has potential for controlling a number of pest species, and it seems to be particularly promising for control of stink bugs (Jones et al. 1983, Orr et al. 1986).

Another tactic increasingly studied as an integral component of an overall pest management program for soybean insect pests is host plant resistance. This tactic is considered to have more potential for
development as a key component of a successful soybean IPM system than any other tactic or strategy (Newsom et al. 1980).

Hundreds of plant introductions (PI's) have been screened for resistance to foliage-feeding insects (Newsom et al. 1980) and, of these, three genotypes (PI171451, PI227687, PI229358) have been used as sources of resistance in breeding programs (Sullivan 1984). However, the mechanisms of resistance have been well-studied only in PI227687. This genotype exhibits a high level of chemical antibiosis to a wide range of foliage feeding insects (Smith 1985). Other genotypes have been screened for stink bug resistance, and PI171444 has been identified as a possible candidate source of resistance (Gilman et al. 1982, Kester et al. 1984).

While work is progressing toward development and release of soybean cultivars with multiple pest resistance, such a release has yet to be made (Sullivan 1984). The major barrier appears to be development of a cultivar with yield equal to or better than current commercial cultivars (Sullivan 1984).

**Interactions Between Management Tactics**

Whenever two or more pest management tactics are employed simultaneously in a system, the possibility exists for interactions to occur between tactics. To minimize any antagonistic interactions and to capitalize on any additive or synergistic interactions which may occur, the relationships between pest management tactics should be carefully examined.

Soybeans in Louisiana support an abundance of generalist predators which attack both pentatomid and lepidopterous pests. Among these
predators are a complex of hemipteran species, a complex of spider species, and the red imported fire ant (Turnipseed 1973, Dietz et al. 1976, Stam et al. 1987). In addition, a variety of parasitoids in Louisiana have been reported to attack the various stages of *A. gemmatalis* (Hinds & Osterberger 1931), *P. includens* (Daigle 1986), and *P. scabra* (Daigle et al. 1988). Several parasitoids also have been reported to attack stink bugs, with the majority attacking eggs (Orr et al. 1986) and others attacking larger nymphs and adults (McPherson et al. 1982).

The influence of insecticides on natural enemies in soybeans has been examined to some degree. Studies have addressed the impact of some foliar insecticides on populations of hemipteran predators in soybean (Turnipseed 1972, Walker et al. 1974, Turnipseed et al. 1975, Heinrichs et al. 1979, Marston et al. 1979, McPherson et al. 1979, Morrison et al. 1979, Wilkinson et al. 1979, Layton & Boethel 1986). Methyl parathion was utilized in many of these studies, and, in all cases in which it was used, it was highly toxic to hemipteran predators. Permethrin, on the other hand, was relatively non-toxic in one case to *Podisus maculiventris* (Say) and *Geocoris punctipes* (Say) (Wilkinson et al. 1979) but harmful in others to nabids and *Hippodamia convergens* (Guerin-Meneville) (Wilkinson et al. 1979, Layton & Boethel 1986). In some cases, the loss of hemipteran predators due to foliar insecticide application was believed to have resulted in resurgence in population levels of some lepidopteran (Shepard et al. 1977, Morrison et al. 1979), and pentatomid pests (D.J. Boethel, unpublished data).

Although little specific information is available, it appears the spider complex is affected in a similar, adverse manner by methyl
parathion (Turnipseed et al. 1975). The manner in which fire ants are affected by these pesticides has not been addressed.

Parasitoids in general are more difficult to sample (Marston 1980) and, perhaps partly because of this, their response to insecticides in soybeans has received much less attention. Wilkinson et al. (1979) found a range of effects by several organophosphates and synthetic pyrethroids on the lepidopteran parasitoid *Cotesia (=Apanteles) marginiventris* (Cresson) in a laboratory study. They found permethrin to be moderately toxic to this parasitoid. Marston et al. (1979), on the other hand, observed little effect of carbaryl + malathion applications on total chalcid wasp species in field samples. It remains, however, that much work must be done in this area to gain an understanding of how insecticides impact the parasitoid fauna in soybeans.

The potential utility of host plant resistance in an IPM system is based partly on the assumption that it is compatible with other control tactics (Newsom et al. 1980). However, this assumption of compatibility may not necessarily be sound (see Boethel & Eikenbary 1986, for a review of this topic). In soybean, several studies have addressed this issue. These studies have shown that natural enemies with a wide range of life history strategies can be adversely affected by insect-resistant soybean. These include larval parasitoids of both Lepidoptera (Yanes & Boethel 1983, Powell & Lambert 1984, Grant & Shepard 1985, Rogers & Sullivan 1987) and Coleoptera (Kauffman & Flanders 1985, Dover et al. 1987), an egg-larval parasitoid of Lepidoptera (Orr & Boethel 1985, Beach & Todd 1986), and an egg parasitoid of Pentatomidae (Orr et al. 1985). At the time the research described in this dissertation was
conducted, no published report had addressed the impact of insect-resistant soybean on predators or on natural enemies at the fourth trophic level. However, following publication of Chapter I of this dissertation, a study (Rogers & Sullivan 1986) showed that a hemipteran predator, G. punctipes, was affected adversely by soybean antibiosis.

The development of various tactics for an IPM program often may occur independently of the others. There is a real need to address the interactions between the various IPM tactics to not only avoid antagonistic interactions, but also to capitalize on the additive or synergistic ones. Complementary action of the various tactics will produce a more stable and truly integrated pest management program for insect pests of soybeans. The research presented herein further addresses the question of how host plant resistance and insecticidal controls influence biological control in soybeans.


Grant, J.F., & M. Shepard. 1985. Influence of three soybean genotypes on development of Voria ruralis (Diptera: Tachinidae) and on foliage consumption by its host, the soybean looper (Lepidoptera: Noctuidae). Fla. Entomol. 68: 672-677.


responses and field control of seven pentatomids, associated with soybean, exposed to methyl parathion. Environ. Entomol. 8: 1041-1043.


Orr D.B., & D.J. Boethel 1985. Comparative development of Ccpidosoma
truncatellum (Hymenoptera: Encyrtidae) and its host, Pseudoplusia includens (Lepidoptera: Noctuidae), on resistant and susceptible soybean genotypes. Environ. Entomol. 14: 612-616.


Agronomy, Madison.


CHAPTER I

Influence of Plant Antibiosis
Through Four Trophic Levels

This chapter is written in the style of
Oecologia
and is published in this journal
Vol. 70 pp 242-249
ABSTRACT

The effects of an insect herbivore-resistant soybean genotype on relationships between four levels of a trophic system were examined in the laboratory using both greenhouse and field-grown plants.

Pre-imaginal development of the predatory pentatomid, *Podisus maculiventris* (Say), was affected by soybean antibiosis in a manner similar to that of its lepidopteran prey, *Pseudoplusia includens* (Walker). Pre-imaginal development time was increased, and cumulative weight gain tended to be reduced on both greenhouse and field-grown resistant foliage; although mortality was increased on greenhouse-grown resistant foliage, it appeared unchanged on field-grown foliage.

Reproductive capacity of *P. maculiventris* reared on *P. includens* larvae that were fed resistant soybean generally was unaffected, although peak progeny production was delayed and extended slightly. Pre-imaginal development and adult emergence of the egg parasitoid *Telenomus podisi* Ashmead from eggs of *P. maculiventris* reared on *P. includens* larvae that were fed resistant soybean were unaffected. However, the overall reproductive capabilities of this parasitoid were reduced. Our results demonstrate that plant antibiosis can influence the biology of organisms over four trophic levels, thus documenting a relationship heretofore undescribed. Determination of the final outcome of the interaction between plant resistance and biological control is difficult. The four trophic level model reported in this study further illustrates the complexity which hinders a general understanding of these interactions.
INTRODUCTION

That predators and parasitoids can be affected by the non-cultivated host plants of their prey/host has been documented in a number of cases (Price et al. 1980). Cultivated host plants which are herbivore-resistant also have been shown to have significant effects on natural enemies (see Boethel and Eikenbary 1986). Both host plant resistance and biological control, when solely implemented, have been shown to be very effective measures in the control of arthropod pests (Maxwell and Jennings 1980, Huffaker and Messenger 1976). Whether the interaction between these two pest management tactics acts to the benefit or detriment of natural enemies appears to depend upon the particular system and its components. For example, when herbivore development is slowed as a result of the action of digestibility reducers or other sublethal resistance factors, natural enemies may exert greater effects on their prey/host because of increased exposure time of susceptible host stages (e.g., Starks et al. 1972, Feeny 1976, Bouton et al. 1986). However, where a non-specific resistance mechanism is involved, natural enemies may be affected adversely while their hosts may or may not be (e.g. Flanders 1942, Rabb and Bradley 1968, Campbell and Duffey 1979, Obrycki et al. 1985).

Detailed information concerning interactions between host plant resistance and biological control agents on agricultural crops, including soybean, Glycine max (L.) Merrill, is still relatively sparse. Research has been done previously on several different insect trophic systems using different resistant soybean genotypes. Both reduced adult emergence and fecundity were experienced by the egg parasitoid,
Telenomus chloropus Thomson, when pre-imaginal development occurred in eggs produced by the southern green stink bug, Nezara viridula (L.), which had been reared on pods of the stinkbug-resistant soybean genotype 'PI171444' (Orr et al. 1985a). Kaufman and Flanders (1985) found that the Mexican bean beetle (MBB)-resistant soybean cultivar 'Cutler 71' reduced both the survival and number of progeny produced per host by the MBB parasitoid, Pediobius foveolatus Crawford.

Other work has concentrated on the soybean plant introduction 'PI227687'. This genotype displays a high level of resistance to 16 different insect pests including the soybean looper, Pseudoplusia includens (Walker) (Smith 1985). Resistance of this soybean genotype to P. includens is a form of antibiosis with an apparent chemical basis and is manifested through reduced larval growth rates and increased mortality (Smith 1985).

The antibiosis displayed by 'PI227687' towards herbivores also has been shown to have an adverse effect on several natural enemies. Copidosoma truncatellum Dalman, an egg-larval parasitoid of P. includens which requires a relatively long development time within its host, is mainly affected by high host mortality which occurs in the ultimate larval instar (Orr and Boethel 1985). However, the larval parasitoid Microplitis demolitor (Wilkinson), which completes development in earlier instars of P. includens, apparently can escape these effects although adult emergence is reduced (Yanes and Boethel 1983). Powell and Lambert (1984) found that survival and pupal weights of Microplitis croceipes (Cresson) were reduced when pre-imaginal development of this parasitoid occurred in either Heliothis zea (Boddie) or H. virescens (F.) which were fed foliage of 'PI227687' or 'PI229358'. Rogers and
Sullivan (1986) report increased development time and mortality of the predator *Geocoris punctipes* (Say) when prey are fed resistant soybean.

All previous studies concerned with interactions of plants with natural enemies of herbivorous insects have been restricted to only the first three trophic levels. The authors are aware of no published research on the effects host plants may exert through four trophic levels. Consumers at the fourth trophic level attack predators and parasitoids. Therefore, they cross the 'boundary' between beneficial and pest species, and may exert important effects on natural enemy populations (eg. Balduf 1926, Way 1953, Mertins and Coppel 1973).

A trophic system involving four levels exists in Louisiana soybean (Fig. 1). This includes three common insect species: the soybean looper, *P. includens*; the spined soldier bug, *Podisus maculiventris* (Say); and the *P. maculiventris* egg parasitoid, *Telenomus podisi* Ashmead. *P. includens* can be a serious pest of a number of field crops in the southeastern and eastern U.S. (Herzog 1980). *P. maculiventris* is part of a complex of hemipterans which together are the most abundant predators in soybean in the U.S. (Turnipseed and Kogan 1976). *P. maculiventris* eggs are attacked by five parasitoid species in Louisiana, the most important of these being *T. podisi* (Orr et al., 1986).

Mortality incurred by *P. maculiventris* as a result of egg parasitism averaged 26.4% during the 1983 and 1984 soybean growing seasons in Louisiana; ca. 66% of that mortality was due to *T. podisi* alone (Orr et al., 1986).

The purpose of this study was to determine if rearing *P. maculiventris* on *P. includens* larvae that had been fed foliage of the resistant soybean genotype PI227687 would affect the life history of
Fig. 1 - Four level trophic system commonly associated with Louisiana soybean.
the predator and its associated egg parasitoid *T. podisi*. Also, we felt that this system would serve as a model to examine the influence of a resistant plant genotype through four trophic levels, thus documenting a relationship heretofore undescribed.

MATERIALS AND METHODS

Plants

Plants of the insect-resistant genotype 'PI227687' and the insect-susceptible commercial cultivar 'Davis' were grown in both the greenhouse and the field. In the greenhouse, plants were grown from seed treated with commercial *Bradyrhizobium* inoculum (Nitragin) and planted in either plastic or ceramic pots (25 or 35 cm diam.) or galvanized steel wash tubs (100 cm diam.). Field-grown plants were planted at the St. Gabriel Experiment Station, St. Gabriel, La. on 27 Jun., 11 Jul., and 20 Jul., 1985, to ensure that plants of the correct phenological stage were available for experimentation. Plants from both the greenhouse and the field were ca. 6 weeks old when used for these studies. Foliage used for all studies consisted of trifoliates selected from below the third fully-expanded leaf from plant apices and above the third leaf from plant bases (Reynolds and Smith 1985).

Insect Colony Maintenance

*P. maculiventris* colonies were established and maintained either with insects collected from various locations throughout Louisiana...
or their F₁ progeny. Predatory stink bugs were reared in 37.9-liter terraria that were lined with cheesecloth (a preferred ovipositional substrate of *P. maculiventris*). Eggs produced by insects in these colonies were used both to start experimental cohorts and to provide hosts for measuring progeny production by *T. podisi*. Larvae of *P. includens* that had been reared on artificial diet were provided as food for *P. maculiventris*.

The *P. includens* larvae used for the present studies were originally obtained from a laboratory colony which had been reared on an artificial diet and maintained at 27 ± 1°C, 50 ± 10% RH, and at LD 14:10 photoperiod. The diet used was that described by Burton (1969), with brewer's yeast substituted for torula yeast.

Larvae used to rear *P. maculiventris* in experimental cohorts were themselves reared from first instar on leaves from plants of the two genotypes studied. Leaves of either 'PI227687' or 'Davis', which had been rinsed in distilled water and blotted dry, were placed in 50.8 by 20.3 by 7.6 cm. clear plastic bags and infested with *P. includens* larvae. Two discs of 9 cm filter paper moistened with distilled water were placed in each bag which then was inflated and sealed to maintain a high relative humidity to prevent the leaves from wilting. Larvae were transferred to new bags containing fresh leaves at ca. 2-day intervals until fed to stink bugs. Bags were stored at room temperature (25°C) and at ambient photoperiod.

Colonies of *T. podisi* were established and maintained with parasitoids reared from *P. maculiventris* egg masses collected from soybean on the St. Gabriel Experiment Station, St. Gabriel, La. Stink
bug and parasitoid colonies and all experiments were conducted at 27 ± 1°C, 75 ± 5% RH, and at LD 14:10 photoperiod.

P. maculiventris: Pre-imaginal Development

Pre-imaginal development of P. maculiventris was studied using plants grown both in a greenhouse and in the field. Eggs collected ≤12 h after oviposition by feral P. maculiventris females were incubated to eclosion in clear plastic petri dishes (100 by 15 mm). Nymphs then were transferred to cellucotton moistened with distilled water inside a wax-coated paper carton (227 ml) to develop through the non-feeding first instar. Immediately upon molting to the second instar, nymphs were randomly selected from the population to establish two cohorts of 50 insects each for the two host plant treatments. One cohort, labelled "resistant cohort" (RC) was reared on P. includens larvae that were fed 'PI227687' foliage. A second cohort, labelled "susceptible cohort" (SC), was reared on P. includens fed 'Davis' foliage. Size of prey offered nymphs was increased with nymphal size, beginning with second instar P. includens larvae for second instar predators. Sufficient food was provided to ensure satiation of predators throughout development.

P. maculiventris nymphs were reared individually in clear plastic petri dishes (100 by 15 mm). Each petri dish contained a moistened 9-cm disc of filter paper and a leaf section from the resistant or susceptible soybean genotypes. P. includens larvae from colonies reared on respective genotypes were added as needed. Petri dishes were changed every 24 to 48 h, depending on the size of nymphs and larvae present. Beginning with the second instar, nymphs were weighed within two hours
following ecdysis to successive instars (i.e., prior to any feeding activity).

**P. maculiventris: Reproductive Capabilities**

To study adult reproductive characteristics, *P. maculiventris* nymphs (*F₁* progeny of feral stink bugs) were reared as described above using field-grown 'Davis' or 'PI227687' plants. Upon reaching the adult stage, males and females were paired according to age (time of ecdysis) and each pair was placed in a 1.9-liter paper carton that was lined with cheesecloth and covered with clear plastic. Each carton was provided with a bouquet of soybean trifoliates from one of either genotype and a daily supply of *P. includens* larvae from colonies reared on the foliage from respective genotypes. Bouquets were composed of two to four trifoliates, the petioles of which were inserted through a parafilm cover into soaked cellucotton inside a clear plastic cup (30 ml). Cartons were changed daily to collect eggs and record survival, and bouquets were changed every two days.

**T. podisi: Life History**

Egg masses collected from *P. maculiventris* caged pairs were introduced individually on labelled index card strips (5 by 1 cm) to single, mated *T. podisi* females. The *F₁* progeny of feral parasitoids were used to parasitize eggs utilized in this study. After allowing four hours for parasitism, egg strips then were stapled to the inside walls of wax-coated paper cartons (227 ml). Parasitized eggs were incubated in these cartons until one to two days prior to expected
parasitoid emergence (Yeargan, 1980) at which time they were placed in individual clear plastic cups (30 ml). Pre-imaginal development time (i.e., oviposition to adult emergence) and percent emergence of adults were recorded for these parasitoids. Two *T. podisi* females which emerged from the first egg mass produced by each *P. maculiventris* female were removed to be tested for fecundity. An additional five females and all males present were removed for determination of their longevity.

*T. podisi* females used for fecundity measurements were placed individually into cylindrical, clear plastic cages (6 by 3 cm). Honey streaked on inside walls of cages served as a food source. A fresh (< 36-h-old) *P. maculiventris* egg mass was provided daily on a labelled index card strip (5 by 1 cm) to each parasitoid female throughout its life. After exposure, egg strips were treated as described above to monitor daily progeny production.

Longevity of *T. podisi* males and females was determined by placing parasitoids in petri dishes (100 by 15 mm, five per dish) that contained a 7 cm disc of moistened filter paper. Honey spread in a thin layer on petri dish lids served as food.

**Data Analysis**

Development time and weight data were compared using Student's *t*-test; mortality and emergence data were analysed using a Chi-square test of significance. Adult reproductive parameters and longevity were analysed using Student's *t*-test. Values of intrinsic rate of increase (*r*) were estimated for both *P. maculiventris* and *T. podisi* in this study by iteratively solving the equation:
where $l_x$ and $m_x$ are the age-specific survival and fecundity rates, respectively, at day $x$ (Birch 1948). Doubling time was determined by the equation $DT = (\ln 2)(r^{-1})$.

RESULTS

**P. maculiventris**: Pre-imaginal Development

Consumption of *P. includens* larvae fed greenhouse-grown 'PI227687' foliage had a pronounced effect on both pre-imaginal development time and mortality of *P. maculiventris*. Time spent in successive instars was consistently longer for RC nymphs than for SC nymphs; however, these differences were significant only for penultimate and ultimate instars (Fig. 2). A similar increase in larval development time was noted for *P. includens* larvae when fed foliage of 'PI227687' as compared to larvae fed 'Davis' foliage (Reynolds *et al.* 1984). Landis (1937) found changes in *P. maculiventris* development time when reared on *Leptinotarsa decemlineata* (Say) fed foliage of different *Solanum* species.

Mortality of RC nymphs increased with each successive instar and during the fifth instar was ca. 10 times greater than that of SC nymphs (Fig. 3). Similar patterns for larval mortality are evident for *P. includens* when reared on 'PI227687' foliage; mortality was considerably higher in the ultimate instar than all others combined (Reynolds *et al.* 1984). SC nymphs incurred lower mortality, and although during their fourth instar mean mortality was ca. doubled when compared to RC nymphs, this difference was not significant. Cumulative weight gain for SC bugs
Fig. 2 - Time required for development through successive instars by \textit{P. maculiventris} when reared on \textit{P. includens} larvae fed susceptible 'Davis' and resistant 'PI227687' greenhouse-grown soybean foliage.
Fig. 3 - Mortality incurred by *P. maculiventris* nymphs in instars two through five when reared on *P. includens* larvae fed susceptible 'Davis' and resistant 'PI227687' greenhouse-grown soybean foliage.
tended to be greater than for RC bugs, but this difference was not significant in any of the four feeding instars or the adult stage (Fig. 4). This is in contrast to the weight gain patterns displayed by _P. includens_ when fed either 'PI227687' and 'Davis' foliage (Yanes and Boethel 1983). Reynolds _et al._ (1984) demonstrated a 43% reduction in maximum weight of _P. includens_ when reared on 'PI227687' as opposed to 'Davis' foliage.

Pre-imaginal development of _P. maculiventris_ was not monitored as closely when this study was repeated using field-grown foliage, because the primary focus was on reproductive capabilities. However, similar trends were observed in the measured developmental parameters (Table 1). When _P. maculiventris_ nymphs were reared on _P. includens_ larvae fed field-grown 'PI227687' soybean foliage, pre-imaginal development time and weight gain were altered, however, mortality was not. Time from egg eclosion to both the fifth instar and adult ecdysis were significantly increased for female but not male _P. maculiventris_. On the other hand, overall survivorship to the adult stage of combined male and female _P. maculiventris_ was not significantly altered (Table 1). No explanation can be offered for the high and equal mortality observed in this part of the study. Weight of RC adult females was significantly lower than for SC females; however, adult male weight was not significantly affected.
Fig. 4 - Weight of *P. maculiventris* nymphs at the onset of each developmental stage when reared on *P. includens* larvae fed susceptible 'Davis' and resistant 'PI227687' greenhouse-grown soybean foliage.
Table 1 - Pre-imaginal development and mortality of *P. maculiventris* reared on *P. includens* larvae fed field-grown foliage of different soybean genotypes. 

<table>
<thead>
<tr>
<th>Soybean Genotype</th>
<th>Sex</th>
<th>Pre-imaginal developmental time (days)</th>
<th>Overall Survivorship</th>
<th>Weight (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>to 5th stadium</td>
<td>to imago</td>
<td>n</td>
</tr>
<tr>
<td>Davis'</td>
<td>♀</td>
<td>21</td>
<td>12.94 ± 0.22</td>
<td>21</td>
</tr>
<tr>
<td>'PI227687'</td>
<td>♀</td>
<td>20</td>
<td>13.61 ± 0.22 *</td>
<td>20</td>
</tr>
<tr>
<td>Davis'</td>
<td>♂</td>
<td>19</td>
<td>12.84 ± 0.17</td>
<td>19</td>
</tr>
<tr>
<td>'PI227687'</td>
<td>♂</td>
<td>23</td>
<td>13.07 ± 0.15</td>
<td>23</td>
</tr>
</tbody>
</table>

- foliage selected from ≥ 4th trifoliates from plant base and < 3rd trifoliates below terminals of field-grown plants.
- 'Davis', susceptible cultivar; 'PI227687', resistant genotype.
- Values followed by * and ** are significantly different, (P ≤ 0.05) and (P ≤ 0.01), respectively.
- Time from egg hatch.
- weights determined within 2 h subsequent to molt, prior to feeding.
**P. maculiventris Reproductive Parameters**

Mean longevity of both male and female RC adults tended to be greater than that for SC insects but not significantly so (Table 2). Pre-ovipositional period was unchanged for females in the RC cohort. Again, fecundity of RC females was numerically but not significantly higher.

Daily progeny production was delayed and extended somewhat for RC females (Fig. 5). This resulted in a reduced intrinsic rate of increase (r) and a slightly increased doubling time (DT) (Table 2).

**T. podisi Life History**

Pre-imaginal development time and adult emergence of both male and female T. podisi were unaffected, regardless of whether development occurred in eggs of RC or SC P. maculiventris (Table 3). These results are in contrast to our earlier findings (Orr et al. 1985a) where a 26.5% reduction in emergence of T. chloropus adults from eggs of N. viridula which had been reared on pods of the stink bug-resistant soybean genotype 'PI171444' was reported. However, in the present study the host of the egg parasitoid was a predator, one trophic level removed from that of the phytophagous pentatomid described above. This may have acted to ameliorate the quality of host eggs for T. podisi.

All reproductive parameters of T. podisi were significantly altered, however, when development occurred in eggs of RC stink bugs. Longevity of both male and female T. podisi in the absence of hosts was not significantly lower for parasitoids that developed in RC eggs.
Table 2 - Reproductive parameters of adult *P. maculiventris* reared on *P. includens* larvae fed field-grown foliage of different soybean genotypes. a/

<table>
<thead>
<tr>
<th>Soybean Genotype</th>
<th>Longevity (days)</th>
<th>Pre-ovipositional period (days)</th>
<th>Fecundity</th>
<th>DT (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>females</td>
<td>males</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>n ± SE</td>
<td>n ± SE</td>
<td>n ± SE</td>
<td>([8][8]⁻¹)</td>
</tr>
<tr>
<td>'Davis'</td>
<td>21 13.0 ± 1.9</td>
<td>19 12.3 ± 1.5</td>
<td>5.75 ± 0.281</td>
<td>21 210 ± 40.3</td>
</tr>
<tr>
<td>'PI227687'</td>
<td>20 17.6 ± 3.5</td>
<td>23 14.1 ± 2.9</td>
<td>5.42 ± 0.312</td>
<td>20 250 ± 71.6</td>
</tr>
</tbody>
</table>

a/ Foliage selected from ≥ 4th trifoliate from plant base and < 3rd trifoliate below terminals of field-grown plants.
b/ 'Davis', susceptible cultivar; 'PI227687', resistant genotype.
Fig. 5 - Daily progeny production and survival of two *P. maculiventris* cohorts reared on *P. includens* larvae which had been fed either susceptible 'Davis' (■, ——) or resistant 'PI227867' (=, ——) field-grown soybean foliage.
Table 3 - Pre-imaginal development and adult emergence of *T. podisi* from eggs of *P. maculiventris* reared on *P. includens* larvae fed field-grown foliage of different soybean genotypes.

<table>
<thead>
<tr>
<th>Soybean Genotype</th>
<th>Developmental time (days)</th>
<th>Successful Emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>females</td>
<td>males</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>x ± SE</td>
</tr>
<tr>
<td>'Davis'</td>
<td>319</td>
<td>11.1 ± 0.87</td>
</tr>
<tr>
<td>'PI227687'</td>
<td>220</td>
<td>11.1 ± 0.72</td>
</tr>
</tbody>
</table>

*a/* Foliage selected from ≥ 4th trifoliates from plant base and < 3rd trifoliates below terminals of field-grown plants.

*b/* 'Davis', susceptible cultivar; 'PI227687', resistant genotype.
(Table 4). However, when allowed to oviposit ad libitum, the longevity of *T. podisi* females which emerged from RC eggs was significantly reduced.

Fecundity was reduced by ca. 11% for *T. podisi* females in the RC treatment (Table 4). Although mean daily progeny production values were generally lower for parasitoids in the RC treatment, the pattern of oviposition over the lifetime of parasitoids was not changed (Fig. 6). The resultant r value was lower and DT value higher for parasitoids which developed in RC eggs. Similar results were noted for *T. chloropus* when reared from eggs of *N. viridula* fed pods of resistant soybean; fecundity was reduced ca. 48%, whereas temporal patterns of progeny production remained the same (Orr et al. 1985a). The less dramatic results obtained in the present study might again be explained by possible amelioration of host quality due to the one-step move up the trophic system.

**DISCUSSION**

Our results demonstrate that antibiotic effects exerted by insect herbivore-resistant soybean can influence organisms at all levels of the trophic system examined in this study. Development of the predatory pentatomid was affected in a manner similar to that of its herbivore host. In studies conducted with both greenhouse and field-grown plants, pre-imaginal development time increased and adult female weight tended to decrease for RC pentatomids. However, while mortality was increased for RC bugs in the greenhouse study, it appeared to be high and equal for bugs in either treatment employing field-grown plants. Although
Table 4 - Reproductive parameters of T. podisi from eggs of P. maculiventris reared on P. includens larvae fed field-grown foliage of different soybean genotypes.

<table>
<thead>
<tr>
<th>Soybean Genotype</th>
<th>Longevity (days)</th>
<th>Fecundity</th>
<th>DT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>males</td>
<td>females</td>
<td></td>
</tr>
<tr>
<td></td>
<td>n x ± SE</td>
<td>n x ± SE</td>
<td>n x ± SE</td>
</tr>
<tr>
<td>'Davis'</td>
<td>22 35.3 ± 1.72</td>
<td>37 13.4 ± 0.38 *</td>
<td>96 41.0 ± 0.65</td>
</tr>
<tr>
<td>'PI227687'</td>
<td>11 34.5 ± 0.94</td>
<td>39 12.5 ± 0.32</td>
<td>98 39.0 ± 1.11</td>
</tr>
</tbody>
</table>

Foliage selected from ≥ 4th trifoliates from plant base and < 3rd trifoliates below terminals of field-grown plants. 'Davis', susceptible cultivar; 'PI227687', resistant genotype.

Honey-fed individuals in all cases.

Paired values in columns followed by * and ** are significantly different, (P ≤ 0.05) and (P ≤ 0.01), respectively (Students' t-test).
Fig. 6 - Daily progeny production and survival of two *T. podisi* cohorts when reared from eggs of *P. maculiventris* which had been reared on *P. includens* larvae fed either susceptible 'Davis' (■ ■ ■ ■) or resistant 'PI227687' (—you——) field-grown soybean foliage.
fecundity of the predator (*P. maculiventris*) was not altered by resistant soybean, progeny production over the lifetime of females was delayed and extended, thereby reducing the estimated intrinsic rate of increase.

Both pre-imaginal development time and adult emergence of the egg parasitoid (*T. podisi*) were unaffected. However, both the fecundity and resultant intrinsic rate of increase determined for *T. podisi* were reduced.

Price (1986) suggested that plant toxins, when passed up the trophic system, may act to defend beneficial insects against their own natural enemies, thus improving the 'extrinsic defense' of plants. It might be predicted that the reduced reproductive capacity of *T. podisi* in resistant soybean would afford *P. maculiventris* a certain degree of 'protection'. This would be particularly evident if the effects on *T. podisi* life history were cumulative in successive generations. Such a cumulative effect could easily result in large reductions of the reproductive capacity of a local population of parasitoids over a single season if the species were multivoltine, as is *T. podisi*.

Yeargan (1980) conservatively estimated that, based on thermal requirements, *T. podisi* was capable of producing five generations per year in Kentucky. Using the same thermal requirements and climatic data from southern Louisiana (Orr et al. 1985b), an estimate of 13 generations can be obtained for *T. podisi* in southern Louisiana. *P. maculiventris* is active in soybean in Louisiana from June through October, providing a possible source of eggs throughout much of the season (authors' unpublished data). Therefore, a cumulative effect on
reproductive capacity as described above could quite easily occur for *T. podisi* populations. This 'protection' afforded *P. maculiventris* would be greatest late in the season, coinciding with peak prey abundance and a concomitant peak abundance in *P. maculiventris* egg masses (Orr *et al.*, 1986).

*T. podisi* attacks the eggs of several phytophagous pentatomids in addition to *P. maculiventris* eggs in Louisiana (Orr *et al.*, 1986). It might be expected that *T. podisi* would experience effects in these other hosts similar to those reported by Orr *et al.* (1985a) when the pre-imaginal development of another scelionid parasitoid species (*T. chloropus*) occurred in eggs of the phytophagous *N. viridula* which had been reared on resistant soybean.

Foraging behavior in resistant soybean by the predator *P. maculiventris* also might be expected to change in response to reduced prey size. Bouton *et al.* (1986) reported more effective regulation of Mexican bean beetles, *Epilachna varivestis* Mulsant, by *P. maculiventris* in resistant than in susceptible soybean. These results were attributed partly to a stronger functional response of the predator due to smaller prey size in resistant soybean.

It seems noteworthy that, in every instance studied thus far, resistant soybean genotypes to some degree adversely affect the life histories of not only the insect herbivores which feed on these plants but also the associated beneficial insects which comprise the third trophic level (Yanes and Boethel 1983, Powell and Lambert 1984, Orr and Boethel 1985, Orr *et al.* 1985a, Kauffman and Flanders 1985). However, all trophic levels and their interactions must be considered to obtain an accurate picture of overall population effects. This study has
demonstrated that antibiosis can have an effect on organisms through four different trophic levels. It has shown also that the specific relationships between organisms on the various trophic levels are important in the determination of the final outcome of resistant-plant effects.

Obviously, it is impossible to weigh the absolute importance of mortality factors determined in this study without a complete field life table analysis. Such analyses have been conducted in the past for a number of pest insect species, such as the spruce budworm (Morris and Miller 1954). However, such analyses do not exist for predators or parasitoids (Price 1975). Nevertheless, due to the magnitude of the measured values (mortality, fecundity, development time) and changes noted in those values in this study, it would seem justifiable to make some statements concerning the possible interactions between them.

As suggested earlier, *P. maculiventris* may be 'protected' from some of the mortality resultant from egg parasitism. Total egg parasitism of this pentatomid by five indigenous species of parasitoids accounted for ca. 26% loss of eggs during 1983 and 1984 in Louisiana (Orr et al., 1986). Reductions in egg parasitism may well result in a substantial increase in predator survival. However, populations of *P. maculiventris* in resistant soybean may be faced with a possible 100% increase in nymphal mortality (ie. from ca. 24 to 50.0%, as indicated in this study), an increase in pre-imaginal development time, and delayed reproduction. Thus, the positive influences of reduced egg mortality shown in our study and increased foraging efficiency shown by Bouton et al. (1986) may act only to partially ameliorate the more direct negative effects resistant plants have on *P. maculiventris*. 
Gutierrez (1986) argued that the net effect (positive or negative) of resistant plants, when in combination with natural enemies, depends on whether herbivore populations are reduced to a greater extent than that of natural enemies. Determination of the final outcome of the interactions examined in this study and similar studies is difficult. As noted by Painter (1951) and subsequently others, the uniqueness of each system with regard to the effects of plant resistance on the biologies of the various organisms involved in biological control hinders a general understanding. Our study has further shown the complexity of these interactions by demonstrating effects through four trophic levels. To understand this complexity will require thorough life table analyses based on field research and/or population modelling to address those events difficult to observe directly in nature.
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CHAPTER II

Impact of Selected Soybean Insecticides

On Trissolcus basalis (Hymenoptera: Scelionidae), an Egg Parasitoid of Stink bugs (Hemiptera: Pentatomidae)

This chapter is written in the style of the Journal of Economic Entomology and has been submitted for publication in this journal.
Field studies were conducted to determine the influence of the primary insecticides applied to control Louisiana soybean insect pests on survival of a major biological control agent of stink bugs. Adult egg parasitoids, *Trissolcus basalis* (Wollaston), were little affected by permethrin field applications, while methyl parathion had an adverse but short-lived effect on parasitoid survival. High levels of adult parasitoid mortality were observed only within the first 6 h following methyl parathion application. Neither insecticide affected emergence of parasitoids from their host eggs, suggesting that stink bug eggs provided a barrier to insecticide penetration. However, parasitoids apparently contacted insecticide residues when chewing through host egg shells to emerge, resulting in some post-emergence mortality caused by methyl parathion. The degree of this mortality was affected by three factors: 1) parasitoid developmental stage at time of insecticide application, 2) position of parasitized egg masses in the soybean canopy, and 3) parasitoid gender. Overall, results of this study suggest a general compatibility between a major biological control agent of stink bugs, *T. basalis*, and insecticidal control of both stink bugs and lepidopterous pests in Louisiana soybean.
INTRODUCTION

The pod feeding Pentatomidae are one of three major pest guilds in the United States which together account for most of the insect damage to soybean (Kogan 1980). In Louisiana, soybean is damaged by several stink bug species, the most important of which is the southern green stink bug, *Nezara viridula* (L.) (Jensen & Newsom 1972).

Parasitoids of stink bug eggs have been found in a number of states and in every case were reported to be important natural enemies (Jones 1979, Yeargan 1979, Buschman & Whitcomb 1980, Orr et al. 1986). The egg parasitoid *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) is the dominant native parasitoid of *N. viridula* in Louisiana (Thomas 1972, Orr et al. 1986). *Trissolcus basalis* has been introduced into a number of different countries for the control of *N. viridula*. For example, highly successful results were obtained after release of this parasitoid species in Australia, New Zealand, and Hawaii (Caltagirone 1981). However, *T. basalis* and other native parasitoids species have failed to provide adequate control of stink bugs in the continental United States (Jones et al. 1983). Often, parasitoids may be limited in their effectiveness at the edges of a host's range due to greater sensitivity to environmental factors (Coppel & Mertins 1977). This may be the case with *T. basalis* in the United States, because the Gulf Coast and southeastern Atlantic states represent the northern limit of the distribution of both *N. viridula* and *T. basalis*. Differences have been demonstrated in both the biology (Powell & Shepard 1982) and ecological adaptability (Ratcliffe 1965) of *T. basalis* strains from different geographical locations. It may be possible to find and import strains
of scelionids such as \textit{T. basalis} to the United States which are more effective than the indigenous egg parasitoid guild. So indeed, the prospects for classical biological control of stink bugs, particularly \textit{N. viridula}, in the southeastern United States appear good (Jones et al. 1983, Orr et al. 1986).

A major barrier to the establishment of exotic natural enemies through classical biological control programs is often the inability to integrate these enemies with existing chemical control practices (DeBach 1974). At present, the most widely employed means of soybean insect pest control in the United States is the application of conventional chemical pesticides (Newsom 1980). In Louisiana, the most important soybean insect pest complexes are the pod feeding pentatomids and the lepidopterous defoliators (Newsom et al. 1980). These pest complexes frequently occur simultaneously in the field, and therefore control measures implemented against one may impact the other (Newsom & Boethel 1987). Current management practices for stink bugs and lepidopterous pests in Louisiana soybean most commonly include the application of methyl parathion and permethrin, respectively (Tynes & Boethel 1987). This study was conducted to determine the influence of the primary insecticides applied to soybean in Louisiana on survival of \textit{T. basalis}, a major natural enemy of \textit{N. viridula}.

\textbf{MATERIALS AND METHODS}

\textit{Insect colony maintenance.} The host species used in this study was \textit{N. viridula}. Stink bug colonies were established and maintained with field-collected insects from St. Gabriel, Louisiana. Bugs were held in
37.9-liter terraria and provided a constant supply of fresh green beans, *Phaseolus vulgaris* (L.), shelled peanuts *Arachis hypogaea* L., and water. Colonies of *T. basalis* were established with parasitoids reared from *N. viridula* egg masses which were collected from soybean at St. Gabriel, Louisiana. Parasitoids used in all experiments were either $F_1$ or $F_2$ progeny of field-collected insects. All colonies were maintained at 27 ± 1°C, 75 ± 5% RH, and L:D 14:10 photoperiod (standard conditions).

**Insecticide application.** All studies were conducted during 1988 and 1987 at the St. Gabriel Research Station, St. Gabriel, Louisiana. In all experiments, insecticide was applied with a CO$_2$-pressurized backpack sprayer at 0.561 and 0.084 kg AI/hectare for methyl parathion (methyl parathion 4EC, Micro-Flo Co., Sparks, Georgia) and permethrin (Ambush 2E, ICI Americas Inc., Wilmington, Delaware), respectively. The spray boom was equipped with 8002 T-jet nozzle tips and was calibrated for an output of 224.5 liters water/hectare.

In addition to insecticide treatments, a plot was sprayed with Agmark© P-2 dye (Lan Products, Brownwood, Texas) to estimate the distribution of the insecticide sprays through the soybean canopy. Krome Kote deposit cards (Louisiana Cooperative Extension Service, Baton Rouge, Louisiana) were clipped horizontally to metal stakes within the dye plot to determine droplet density and Volume Mean Diameter (a measure of average droplet size) on upper and lower card surfaces in both the upper and lower 30 cm of the soybean canopy.

*T. basalis*: adult mortality. To examine insecticide impact on adult *T. basalis*, female parasitoids were exposed to soybean (cv. 'Centennial')
foliage at various times following insecticide application (see above) to small plots (1.8 by 15.2 m) along a field margin. All plots used had no prior insecticide applications. A survey conducted during 1986 at the study site revealed that 49 of 50 *N. viridula* egg masses collected throughout the canopy of a soybean field had been oviposited on lower surfaces of leaves (authors' unpublished data). Therefore, all parasitoids in these studies (both adult and pre-imaginal experiments) were placed on lower leaf surfaces based on the assumption that natural host searching by adult wasps would be concentrated there.

Approximately 12 h prior to the start of the experiment, honey was thinly streaked inside clear plastic cups (30 ml), and female parasitoids from a laboratory colony were aspirated in groups of five into each cup. Cups were taken to a laboratory near the field site and held at ca. 27 °C and ambient photoperiod (field lab conditions) until required for the experiment.

Parasitoids then were exposed to lower leaf surfaces in the upper 30 cm of the soybean canopy at varying times following insecticide application: 1, 3, 6, 12, and 24 h (48 h in 1986 only). Each group of five parasitoids was anesthetized with CO₂ just prior to being placed in an individual field clip cage. Ten cages were used for each treatment at each time period. Clip cages provided a circular arena (1.5 mm deep by 27 mm diam.) bounded by a leaf surface on one side and fine screen (30 mesh/cm) on the other. A different set of leaves was used for each time period. Parasitoids were exposed to foliage for ca. 1 h, then transferred to clear plastic bags (50.8 by 20.3 by 7.6 cm) and held at field lab conditions until time permitted further processing.
Within 8 h, parasitoids (5 per dish) were aspirated into petri dishes (100 by 15 mm) that contained a 7 cm disc of moistened filter paper. Honey spread in a thin layer on petri dish lids served as a food source. Parasitoids were maintained at standard conditions until 48 h had elapsed since their field exposure, at which time mortality was assessed. The experiment with adult parasitoids was repeated three times: October 1, 1986 (with methyl parathion only, soybean growth stage = R6); August 5 (soybean growth stage = R2) and August 17 (soybean growth stage = R3), 1987.

*T. basalis: pre-imaginal mortality.* A second experiment examined insecticide impact on parasitoids developing within host eggs. Parasitoids in larval or pupal stages within their host eggs were placed at different canopy levels in small marked plots (3.7 by 15.2 m) along a soybean (cv. 'Centennial') field margin. Plots then were treated with insecticides as described previously. None of the plots used had been treated previously with insecticide. As in the adult experiment, all egg masses were placed on the undersurfaces of leaves to mimic natural stink bug egg-laying behavior.

Egg masses (ca. 50-100 eggs each) were exposed individually to 1-3 female *T. basalis* for ca. 8 h to obtain pre-imaginal *T. basalis* for field exposure. Egg masses were parasitized either 2 d or 8 d prior to field exposure so that parasitoids would be in the larval or pupal stage, respectively, when exposed to the insecticides. Telenomine eggs typically will hatch within 24 h of oviposition (Johnson 1984), and pupae can be seen through egg choria 8 d following oviposition. Within 2 d of parasitization, egg masses were divided into experimental egg
masses of five eggs each (in a single row) and glued (Elmers' Glue-All®, Borden Inc., Columbus, OH) to individual labelled index card strips (5 by 1 cm). Egg strips then were maintained at standard conditions until required for field exposure. On the morning of the experiment, egg strips were stapled to the undersurface of soybean leaves either in the upper or lower 30 cm of the soybean canopy. In each of the plots, egg strips were placed in groups which contained parasitoids in both the larval and pupal stages within egg masses at both upper and lower canopy positions. A total of 20 groups of egg strips were placed in each of three plots (methyl parathion, permethrin, control).

After all egg strips had been placed in the field, insecticides were applied as described previously. Egg masses (5 per dish) were left in the field for ca. 1.5 h, then collected, returned to the laboratory, and placed into petri dishes (100 by 15 mm, five egg strips per dish) that contained a 7 cm disc of moistened filter paper. Egg strips were maintained at standard conditions until 1 d prior to expected parasitoid emergence (Orr et al. 1985) at which time strips were transferred individually to clear plastic cups (30 ml). Survival at 48 h after emergence was recorded for parasitoids from each egg mass. Any eggs which remained intact were dissected to determine their contents so that percent adult emergence could be calculated. Eggs were subjected to predation while in the field mainly from grasshoppers which were apparently attracted to the white index card strips and their associated survey tape position markers. Therefore, only eggs which remained completely intact and contained unemerged adult parasitoids were used in emergence calculations. The number of 'failed' eggs (ie. those which did not contain recognizable remains of parasitoids) was not
significantly different between treatments ($F=0.43, P=0.652$, df=2) and was not included in determinations of pre-imaginal mortality. The pre-imaginal experiment was repeated twice: July 30 (soybean growth stage = R2) and August 27 (soybean growth stage = R5), 1987.

Data analysis. The data for adult survival were analyzed using a Chi-square test of significance. A split plot design was used in the test for insecticide effects on pre-imaginal parasitoids. Main plots were chemical treatment, sub-plots were soybean canopy position, and sub-sub-plots were parasitoid developmental stage. Data for survival of emerged parasitoids in the pre-imaginal experiment were analyzed using a general linear models procedure and significant means separated using Duncan's (1955) multiple range test (SAS Institute 1985). Percent emergence data in the pre-imaginal experiment were compared using a Chi-square test of significance. Sex differences in the pre-imaginal experiment were analyzed using 95% confidence intervals.

RESULTS AND DISCUSSION

Insecticide coverage in this study, as determined with agricultural dye and spray cards, varied according to leaf surface and canopy position. Results indicate that spray droplets deposited on the lower surfaces of leaves had at least a 10-fold lower density and a 9-fold smaller size than those on the upper surfaces of leaves (Table 1). In addition, the lower surfaces of leaves in the lower portion of the canopy received considerably less insecticide than did lower leaf surfaces in the upper portion of the canopy based on both droplet
Table 1 - Insecticide penetration through a soybean canopy. Soybean growth stage R2; July 30, 1987; St. Gabriel, Louisiana.

<table>
<thead>
<tr>
<th>Canopy position</th>
<th>Card surface</th>
<th>VMD (μm)</th>
<th>Drops per cm² (no.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>upper</td>
<td>upper</td>
<td>772.7 ± 59.5</td>
<td>158.3 ± 24.3</td>
</tr>
<tr>
<td></td>
<td>lower</td>
<td>81.8 ± 92.3</td>
<td>4.6 ± 1.5</td>
</tr>
<tr>
<td>lower</td>
<td>upper</td>
<td>263.8 ± 55.0</td>
<td>10.5 ± 3.3</td>
</tr>
<tr>
<td></td>
<td>lower</td>
<td>&lt; 1</td>
<td>&lt; 1</td>
</tr>
</tbody>
</table>

a/ Upper 30 cm or lower 30 cm of soybean canopy
b/ 10 replications; kromotreated double-sided spray cards on metal stakes
c/ 'Volume Mean Diameter' of spray droplets
density and Volume Mean Diameter (Table 1). Stink bug egg masses and adult parasitoids were placed only on lower leaf surfaces in this experiment to mimic natural host placement and parasitoid searching behavior. Based on the results of this test, it would appear that the natural placement of egg masses offers a fortuitous refugium from insecticide applications.

In separate studies at St. Gabriel, N. viridula mortality due to methyl parathion applied with similar methodology to the present study was 92% in 1986 (Layton & Boethel 1987), and ranged from 95 to 98% in 1987 (Layton & Boethel unpublished data). In further studies at St. Gabriel, mortality of soybean looper, Pseudoplusia includens (Walker), and velvetbean caterpillar, Anticarsia gemmatalis Hübner, due to permethrin applied at 0.112 kg AI/hectare, was 95 and 100% respectively in 1986 (Layton & Boethel 1987). Soybean looper mortality in 1987 was 88% (Layton & Boethel 1988).

Methyl parathion had an adverse, but short lived, effect on T. basalis survival each time the adult experiment was repeated. In 1986, survival of adult T. basalis was 0% for the first 3 h following application of methyl parathion, but rose steadily to reach 98% only 12 h after treatment (Fig. 1). Survival of adult parasitoids from plots treated with methyl parathion in 1987 ranged from 12.8 to 47.7% just after spray application, but declined to 0% at 6 or 3 h after application, in the first and second repetitions respectively. This effect was not observed in 1986. In 1986, the experiment was conducted on a day with minimal cloud cover while both repetitions in 1987 were conducted on heavily overcast days. The decrease in survival of parasitoids in 1987 coincided with an observed break in the clouds and a
Fig. 1 - Influence of permethrin and methyl parathion on survival of adult female *T. basalis* exposed to soybean foliage at different times following spray application: (A) October 1, 1986 (48 h; soybean growth stage = R6); (B) August 5, 1987 (24 h; soybean growth stage = R2); (C) August 17, 1987 (24 h; soybean growth stage = R3).
concomitant increase in ambient temperature. Organophosphorous insecticides typically have positive temperature coefficients (Camp et al. 1969) and in the field may display increased activity due to increased volatilization at higher temperatures (Spencer et al. 1973). Although high parasitoid mortality occurred within 6 h of methyl parathion application in all three repetitions of this experiment, very little or no T. basalis mortality occurred 12 h following application, and no mortality was observed 24 h post-application (Fig. 1).

Permethrin had only a minor impact on adult T. basalis in this study. The maximum recorded parasitoid mortality due to permethrin was 11 % immediately following application (Fig. 1). However, mortality was at or near 0% at 6 h after application. These results are surprising because permethrin has been demonstrated to have a relatively long residual impact on some pest insect populations (Southwick et al. 1986). Also, several parasitoids including another scelionid, Telenomus remus Nixon, have been shown in laboratory tests to be relatively susceptible as adults to certain pyrethroid materials, including permethrin (Waddill 1978).

Neither insecticide used in this study affected significantly (Repetition I: $\chi^2 = 3.4$, $P \geq 0.05$, df=2; Repetition II: $\chi^2 = 1.2$, $P \geq 0.05$, df=2) the percentage of parasitoids able to develop in and emerge from their host eggs, indicating that these chemicals did not affect survival of developing parasitoids within host eggs. However, some mortality of parasitoids was observed following their emergence from eggs exposed to methyl parathion, indicating that chemical residues may have been on eggs but did not enter them (Table 2). This suggests that stink bug eggs provided a barrier to insecticide penetration.
Table 2 - Survival of adult *T. basalis* 48 h after emergence from parasitized eggs of *N. viridula* exposed to selected insecticide treatments in soybeans.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Treatment</th>
<th>Repetition I</th>
<th>Repetition II</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>% Survival (x ± SE)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Repetition I</td>
<td>Repetition II</td>
</tr>
<tr>
<td>Insecticide</td>
<td>Methyl parathion</td>
<td>75.2 ± 4.5 a</td>
<td>33.9 ± 5.3 a</td>
</tr>
<tr>
<td></td>
<td>Permethrin</td>
<td>100.0 ± 0.0 b</td>
<td>98.9 ± 0.9 b</td>
</tr>
<tr>
<td></td>
<td>Control</td>
<td>100.0 ± 0.0 b</td>
<td>99.5 ± 0.5 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F(P)=120.5(0.0001) df=2</td>
<td>F(P)=157.9(0.0001) df=2</td>
</tr>
<tr>
<td>Canopy position</td>
<td>Upper</td>
<td>83.3 ± 3.4 *</td>
<td>72.8 ± 5.0 *</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>99.2 ± 0.4</td>
<td>83.2 ± 3.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F(P)=125.4(0.0001) df=1</td>
<td>F(P)=14.9(0.0005) df=1</td>
</tr>
<tr>
<td>Developmental stage</td>
<td>Pupal</td>
<td>90.2 ± 2.8 *</td>
<td>75.4 ± 4.2 *</td>
</tr>
<tr>
<td></td>
<td>Larval</td>
<td>93.9 ± 1.8</td>
<td>82.9 ± 3.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F(P)=72.7(0.0001) df=1</td>
<td>F(P)=6.9(0.01) df=1</td>
</tr>
<tr>
<td>Parasitoid Sex</td>
<td>Female</td>
<td>94.4 ± 1.5 *</td>
<td>82.5 ± 2.7 *</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>84.3 ± 2.8</td>
<td>68.6 ± 4.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F(P)=29.6(0.0001) df=1</td>
<td>F(P)=32.8(0.0001) df=1</td>
</tr>
</tbody>
</table>

a/ Survival recorded 48 h after insecticide application; values followed by the same letter did not differ significantly (Duncans [1955] multiple range test; P≤0.05); values followed by asterisk are significantly different (general linear model analysis); F(P) = F-value(probability level) from general linear model analysis, df = degrees of freedom.

b/ Upper 30 cm or lower 30 cm of soybean canopy.

c/ Parasitoid developmental stage at time of insecticide application.
Survival of parasitoids which did emerge from their host eggs was reduced significantly only by methyl parathion (Table 2). Three factors, each discussed separately below, were found to have a significant impact on survival of *T. basalis* in methyl parathion-treated plots.

Parasitoids that emerged from stink bug egg masses that were placed in the upper portion of the canopy had significantly lower survival than those emerging from masses placed in the lower part of the canopy (Table 2). This can be explained by the distribution of insecticide coverage through the soybean canopy. Spray droplet density and size were greater in the upper portion of the canopy (Table 1). Therefore, parasitoids emerging from eggs in the upper canopy would have a greater chance of encountering pesticide residues on egg choria while chewing through them to emerge, resulting in greater mortality.

Developmental stage also has been shown to affect the relative susceptibility of organisms to pesticides (Matsumura 1985). Initial examination of data from the present study indicated that stage of parasitoid development when exposed to methyl parathion significantly affected their survival (Table 2). However, the lack of significant reductions in emergence in response to insecticide demonstrated that the primary impact of the insecticide was on adult survival following emergence and contact with insecticide rather than on development of parasitoids within eggs. Thus, developmental stage of parasitoids at the time of insecticide application appears to be important in that it determines the time allowed for pesticide degradation prior to emergence of parasitoids. Therefore, parasitoids in an early stage of development within host eggs when hosts are exposed to methyl parathion will emerge
from host eggs when residue concentrations are low and experience reduced mortality (Table 2).

The gender of organisms commonly influences the relative toxicity of pesticides, with females often being more tolerant than males (Matsumura 1985). Methyl parathion had a significantly greater impact on survival of male *T. basalis* than females in this study (Tables 2, 3). This differential mortality was not influenced by either canopy position or developmental stage (Table 3). Mortality of both sexes in the present study was recorded for an equivalent 48 h period following parasitoid emergence.

However, male *T. basalis* develop and emerge from host eggs 1-2 d prior to females (Powell & Shepard 1982). Thus, they would be exposed to higher concentrations of insecticides for a longer period of time than females. Intuitively, it may seem that the reduction in numbers of males in a treated field could have a very important influence on the subsequent parasitoid generation. Fewer available males might result in a reduction of the number of mated females in a local population thereby reducing the number of female progeny produced and lowering the reproductive potential of the population. However, the normal sex ratio of *T. basalis* is ca. 1:1 (Powell & Shepard 1982), and one male is capable of fertilizing many (up to 56) females (Wilson 1961). *N. viridula* egg masses in the field contain an average of 84 eggs/mass (Orr et al. 1986). Our results indicate that the lowest overall male survival in methyl parathion plots was 4.0% (Table 3). Therefore, from a mass of 84 parasitized eggs at least 2 males would be expected to survive. These 2 males could potentially fertilize all the females from that mass. Therefore, inherent reproductive behavior could reduce or
Table 3 - Comparative survival of male and female *T. basalis* 48 h after emergence from parasitized eggs of *N. viridula* exposed to methyl parathion applications in soybean.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Treatment</th>
<th>Survival (x ± SE)</th>
<th>95% Confidence interval of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>males</td>
<td>females</td>
</tr>
<tr>
<td>Repetition I</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insecticide</td>
<td>Methyl parathion</td>
<td>54.1 ± 7.0</td>
<td>81.9 ± 4.3</td>
</tr>
<tr>
<td>Canopy position</td>
<td>Upper</td>
<td>12.3 ± 6.3</td>
<td>56.4 ± 8.6</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>91.0 ± 5.4</td>
<td>99.0 ± 0.7</td>
</tr>
<tr>
<td>Developmental stage</td>
<td>Pupal</td>
<td>66.0 ± 10.1</td>
<td>72.3 ± 7.9</td>
</tr>
<tr>
<td></td>
<td>Larval</td>
<td>52.1 ± 9.8</td>
<td>89.3 ± 4.4</td>
</tr>
<tr>
<td>Repetition II</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insecticide</td>
<td>Methyl parathion</td>
<td>4.0 ± 2.8</td>
<td>44.2 ± 6.4</td>
</tr>
<tr>
<td>Canopy position</td>
<td>Upper</td>
<td>0 ± 0</td>
<td>15.9 ± 7.6</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>6.9 ± 4.9</td>
<td>61.9 ± 8.0</td>
</tr>
<tr>
<td>Developmental stage</td>
<td>Pupal</td>
<td>7.9 ± 5.6</td>
<td>33.9 ± 8.5</td>
</tr>
<tr>
<td></td>
<td>Larval</td>
<td>0 ± 0</td>
<td>55.6 ± 9.4</td>
</tr>
</tbody>
</table>

*a/* Survival recorded 48 h after insecticide application; data presented only for methyl parathion since little or no mortality was caused by permethrin

*b/* 95% CI for differences between means; asterisk indicates significant difference between sexes (P≤0.05)

*c/* Upper 30 cm or lower 30 cm of soybean canopy

*d/* Parasitoid developmental stage at time of insecticide application
eliminate the impact of higher male mortality on local T. basalis populations.

Overall, our results suggest a general compatibility between biological control of stink bugs and chemical control of both stink bugs and lepidopterous pests in Louisiana soybean. Under appropriate temperature and humidity conditions in the laboratory, peak emergence of stink bug egg parasitoids from host eggs occurs during the first half of photophase (Wilson 1961, Orr et al. 1985). In the field, peak emergence occurs in the morning, triggered by daylight and high humidity accompanying morning dews (D.B.O. personal observation). Insecticides are commonly applied in the morning when weather conditions are most stable for optimum coverage. Based on results presented here, egg parasitoids in permethrin-treated fields should be little affected by application of this insecticide. However, egg parasitoids present in a field treated with methyl parathion within 6 h of application will probably experience a high mortality rate. However, those that emerge from eggs or immigrate into fields 12 h or more after application of methyl parathion should not be affected. Also, parasitoids that are developing within stink bug eggs when insecticides are applied to fields will not be affected, and survival of those that emerge should increase as time after application increases. However, field data from previous years indicate that nymphal populations of stink bugs increase rapidly following methyl parathion and permethrin spray applications (M.B.L., D.J.B. unpublished data). This may reflect mortality of predators which attack N. viridula nymphs and eggs since T. basalis is apparently unaffected. These predators have also been shown to be of importance in natural control of stink bugs (Stam 1987, Yeargan 1979). Our results
suggest that future research efforts should be directed toward answering the question of whether predation of stink bugs is adversely affected by insecticidal applications to soybean.
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States strains of Trissolcus basalis, a parasitoid of the green

237-240.


SUMMARY

During the course of this research an examination was made of how two important integrated pest management tactics, namely host plant resistance and insecticidal control, interact in soybeans with components of a third important IPM tactic, biological control. Several important findings were realized from this research. These are enumerated below, by chapter:

CHAPTER I. Influence of Plant Antibiosis Through Four Trophic Levels.

1. Pre-imaginal development of the predatory pentatomid, *Podisus maculiventris* (Say), was affected by soybean antibiosis in a manner similar to that of its lepidopteran prey, *Pseudoplusia includens* (Walker). When reared on *P. includens* larvae which had been fed resistant soybean foliage (PI227687), the development time of *P. maculiventris* nymphs was increased, cumulative weight gain was reduced (on field-grown but not greenhouse-grown resistant foliage), and mortality was increased (on greenhouse-grown but not field-grown resistant foliage).

2) The pre-ovipositional period, fecundity, and longevity of *P. maculiventris* were unaffected when reared on *P. includens* larvae which had been fed resistant soybean foliage. However, progeny production by these predators was slightly delayed and extended.

3) Pre-imaginal development time and adult emergence of the egg parasitoid *Telenomus podisi* Ashmead were unaffected when allowed to develop in eggs of *P. maculiventris* reared on *P. includens* larvae...
which had been fed resistant soybean foliage. However, longevity of ovipositing parasitoid females and their progeny production were reduced. These results demonstrate an influence of plant antibiosis on the biology of insects through four trophic levels, thereby documenting a relationship heretofore undescribed.

CHAPTER II. Influence of Insecticidal Controls in Soybean on Trissolcus basalis (Hymenoptera: Scelionidae).

1) Field applications of permethrin had little effect on the survival of adult stink bug egg parasitoids, *Trissolcus basalis* (Wollaston). Although methyl parathion had an adverse impact on these parasitoids, high levels of adult mortality were observed only within the first 12 hours following spray application.

2) Neither insecticide reduced the percentage of parasitoids that developed in and emerged from their host eggs, suggesting that stink bug eggs provided a barrier to insecticide penetration. However, parasitoids apparently contacted insecticide residues when chewing through host egg shells to emerge, resulting in some 48 h post-emergence mortality caused by methyl parathion only.

3) The degree of post-emergent mortality was affected by three factors - 1) Parasitoid developmental stage at time of insecticide application: due to insecticide degradation, parasitoids emerging from host eggs closer to the time of insecticide application experienced greater post-emergence mortality than those emerging later, 2) position of parasitized egg masses in the soybean canopy: parasitoids emerging from eggs in the lower portion of the soybean
canopy escaped high mortality rates due to low insecticide penetration to the lower canopy, and 3) Parasitoid gender: male parasitoids had a lower survival rate than females, but high male mating capacity would preclude a reduction in the number of mated females.

It is generally considered that host plant resistance is compatible with biological control. The research documented here presents a somewhat contrary viewpoint.

These results have demonstrated that the high level of insect resistance in the form of chemical antibiosis displayed by a well-studied soybean genotype (PI227687) can adversely affect not only foliage-feeding pest insects, but their natural enemies as well. These effects can be seen in natural enemies with a wide range of life history strategies. This study has demonstrated plant influence on a predator and an egg parasitoid. Other work has shown that egg-larval and larval parasitoids may be affected in a similar, adverse manner. This work has shown additionally, that these adverse effects of plant antibiosis can be manifested in organisms at not only the second and third, but also the fourth trophic level.

It is important to note, however, that to date all experiments of this kind have been conducted in the laboratory. Ultimately, field studies will have to be conducted to determine the impact insect-resistant soybean will have on populations of the various insect members, both harmful and beneficial, of this agroecosystem.

Field research to date has been impeded by several factors. First is the lack of sufficient seed from resistant soybean genotypes to plant
large-scale field plots. Second, the mechanisms of resistance in soybean have been well-studied in only one genotype, the Plant Introduction 227687. This soybean genotype has very poor growth characteristics, i.e. procumbent growth habit, when compared with commercial susceptible cultivars. This makes sampling difficult and hinders comparisons of sampling data with that from plots of susceptible cultivars. These problems may be resolved with release of an acceptable insect-resistant commercial cultivar or in future studies by selection of an advanced breeding line which has both proven insect resistance and more acceptable growth characteristics. A third factor could be the very large task of monitoring representative insect species (including parasitoids and predators) in a field to get a full survey of plant effects.

The integration of chemical and biological controls in soybeans has long been a concern. However, the insecticidal controls most commonly employed in soybeans in Louisiana still are not compatible with the overall natural enemy complex. Although the research presented here has demonstrated compatibility of these chemicals with a major parasitoid of stink bugs, earlier studies indicated the predator complex is adversely affected. Perhaps a more thorough understanding of natural enemy field biology combined with more selective insecticides that are compatible with both the parasitoid and predator complexes found in soybeans, will be required.

Overcoming these hurdles will provide needed insight and understanding for the utilization and integration of insecticidal control, host plant resistance, and biological control. Only then will a truly integrated pest management system in soybeans be possible.
David Boyd Orr, youngest son of James and Peggy Orr, was born on September 26, 1958 in Burnaby, British Columbia, Canada. He graduated from Prince of Wales Secondary School, Vancouver, B.C. in June, 1976. He attended Vancouver Community College, Vancouver, B.C. from September, 1976 to May, 1977, and from January, 1979 to August, 1980. He then transferred to Simon Fraser University, Burnaby, B.C. from where he received his B.S. degree in Biological Sciences in June, 1983. In January, 1983, he began graduate study in the Department of Entomology at Louisiana State University where he received his M.S. in August, 1985. He is presently a candidate for the Doctor of Philosophy degree in the Department of Entomology at Louisiana State University.
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: David Boyd Orr

Major Field: Entomology

Title of Dissertation: Compatibility of Biological Control with Host Plant Resistance and Insecticidal Control in Soybeans

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Date of Examination:

April 20, 1938