THE FALL ARMYWORM: STATUS AND EXPECTATIONS OF BIOLOGICAL CONTROL WITH PARASITOIDS AND PREDATORS

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ABSTRACT

Biological control of the fall armyworm, Spodoptera frugiperda (J. E. Smith), in areas of overwintering and throughout its annual geographic distribution, is a highly desirable alternative to conventional reductionist methods. Fragmented efforts to advance biocontrol strategies against the fall armyworm have not to date effectively enhanced what nature has provided. This review assesses the impact of endemic parasitoids and predators as regulators of fall armyworm populations and identifies areas of research and development that must be addressed before significant advances can be made in importation and augmentation strategies.

RESUMEN

El control biológico del gusano cogollero, Spodoptera frugiperda (J. E. Smith), en áreas donde invernan y toda su distribución anual, es una alternativa altamente deseable a los métodos reduccionistas tradicionales. Esfuerzos fragmentados para promover estrategias de control biológico contra el gusano cogollero, hasta la fecha, no han efec- tivamente mejorado lo que la naturaleza ha proveido. Esta revisión evalúa el impacto de parasitoides y depredadores endémicos como reguladores de poblaciones del gusano.
cogollos, e identifica áreas de investigación y desarrollo que deben ser tomadas en cuenta antes que avances significativos se puedan hacer en las estrategias de su importación y aumento.

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Following the first appearance each year of larvae of the fall armyworm (FAW), Spodoptera frugiperda (J. E. Smith), in whorl-stage corn during the spring (April in Tifton, GA), we typically wait in anticipation to see whether its populations will be regulated by biotic and abiotic mechanisms or whether another 1977 is in store during which attributable crop losses and cost of control exceeded $300,000,000 in the continental United States. Unfortunately, our ability to predict seasonal outcomes is limited to that of the occasional end-of-the-season prognosticator who offers an "I told you so" to a prediction not recalled by others.

Anyone having collected and observed FAW larvae from whorl-stage corn is readily aware that there exists an abundance of natural control agents which take a substantial toll on their numbers (Ashley 1979), and yet our ability to positively influence their performance by any means of augmentation, conservation, manipulation, etc., in the continental U.S. has been to date essentially nonexistent. Are we then bound to accept only what endemic natural agents can provide in the management of the FAW and other lepidopterous pests of annual cropping systems, or can we improve on and supplement the given systems to the benefit of integrated pest management? We believe that better systems can be developed which can substantially enhance the ability to effectively manage the FAW, but that currently limited resources and personnel will impede rapid advancement.

Certain known or suspected factors concerning the FAW serve as a base from which research approaches to biocontrol of the FAW can proceed.

1) The contribution of FAW overwintering areas to the seasonal population dynamics in the eastern U. S. is unknown.
2) Whorl-stage corn is likely the primary host that contributes most significantly to the early-season population dynamics.
3) Because of the general absence of insecticides in whorl-stage corn, conservation of natural control agents is enhanced.
4) Among biotic agents, parasitoids appear to cause the highest mortality among FAW larvae on host plants.
5) The requisites for the successful colonization of exotic natural enemies in temporary agroecosystems is essentially unknown.
6) Neither the research base nor the associated rearing technology are currently available to permit the consistent and/or economical production of parasitoids or predators of the FAW needed for large-scale augmentation.

This presentation will focus primarily on importation, colonization, and augmentation strategies of parasitoids and predators. For the first author's thoughts on conservation and manipulation of entomophagous agents in the southeastern U.S., the reader is referred to Gross (1986).
IMPORTATION AND COLONIZATION

Volumes have been written on the merits of importing new species of parasitoids and predators to assist and/or even replace endemic natural agents in the management of target species. Yet the statement by DeBach (1964) that “the possibility of importing natural control agents has been vigorously explored for only a relatively few species, and it is doubtful that the last or perhaps best natural enemy has been imported even in those projects most assiduously attacked by the biological method” is as appropriate today as it was 21 years ago. This statement is particularly true for efforts involving the FAW. Clausen (1956) reported the unsuccessful attempt in 1944 to establish the parasitoid Archytas incertus (Maeq.) (Tachinidae) from Argentina by introducing ca. 700 specimens near the Everglades Experiment Station, FL. This importation also included several thousand adults of the carabid, Calosoma argentinense Csiki, which also failed to establish. More recent efforts by Waddill and Whitcomb (1982) to establish Telenomus remus Hixon, a scelionid egg parasitoid of Spodoptera, were unsuccessful in south Florida despite the release of ca. 663,500 individuals over 2 years. T. remus is indigenous to Sarawak and New Guinea and has been successfully established on FAW in Barbados and Montserrat. Ashley et al. (1982) also were unsuccessful in establishing Eiphasoma vitticole Cresson, an ichneumonid parasite from Bolivia, in south Florida following the release of ca. 1,000 pairs over 4 months in 1980. Towne (1971) considered as favorable the opportunities for colonizing exotic Ichneumonidae on endemic insect pests but saw limited potential for host population regulation with the Ichneumonidae because their rates of parasitization were seldom high and they move about freely leaving many hosts unparasitized. Ophion flavidus Brule is an endemic ichneumonid parasitoid of the FAW which is aptly described by the above statement (personal observation). Pair and Waddill (unpublished) tried unsuccessfully during 1983-84 to establish Microplitis rufiventris Kok. (Bracidae) from Egypt on FAW in volunteer corn at Homestead, FL, by releasing ca. 3,000 individuals, and on FAW in corn in Tift County, GA, (July 1984) by releasing 940 mated females. An additional 512 mated females were also released in alfalfa at Tift County, GA, in August 1984 against FAW, beet armyworm, S. exigua (Hubner), corn earworm, Heliothis zea (Boddie), and the yellow-striped armyworm, S. ornithogalli (Guenee), without successful colonization. Ashley et al. (unpublished) failed to recover Microplitis manilae Ashm. and Microplitis spp. (Australia) following releases against FAW near Homestead, FL in 1982.

The debate is ongoing among biocontrol (BC) theorists over the factors which increase the probability of successful establishment by exotic biocontrol agents. Ehler (1982) found that “after almost 100 years of practice in classical BC, an adequate theoretical framework for assaying multiple-species introductions is generally lacking.” Strategies regarding single-species introductions against insect pests of annual row crops are even less clear. Beirne (1962) reported that of the BC successes, over one-half of those listed by Sweetman (1958) were oceanic or subtropical ecological islands. DeBach (1971) countered that no such correlation existed between BC success and geographical location, but that the number of successes attained would be proportional to the amount of research and importation work carried out. More recently, Hall and Ehler (1979) used data from Clausen (1978) in which exotic insect introduction data from 1890 were summarized again to affirm that, indeed, establishment of natural enemies was higher on islands than on continents. These findings may later be relevant as primary sources of migrant FAW are identified (Pashley et al. 1985).

Hall and Ehler (1979) also affirmed that the rate of establishment of natural enemies was significantly higher in stable environments (forests and rangelands) than in unstable
habitats (vegetable and field crops), but that establishment in intermediate habitats (orchards or other perennial systems) did not differ significantly from that of annual cropping systems. Data available to date, however, suggest that colonization of exotic natural enemies on insect pests of annual crops will not proceed with the comparative ease of that found for coccids and other Homoptera attacking intermediate habitats wherein colony populations build over a long period of the year in finite locations. Nevertheless, the higher degree of difficulty is no longer cause for delaying the advancement of this important strategy for improving our ability to manage the FAW.

Also unsettled are the methods by which natural enemies for introduction into foreign habitats should be selected; and because the predominant research efforts have been concentrated in the semi-permanent to permanent habitats, many of the standards in methodology adopted for these systems are likely inappropriate for use in annual cropping systems. Flanders (1959) appropriately noted that dominant entomophagous insects obtained from native habitats in which their host(s) exist at low population densities are likely to be the most effective, particularly if they are host specific.

Beirne (1962) pointed out that non-host specific natural enemies are likely to be used with increasing frequency in future attempts at permanent biological control because they are easier to colonize and can survive the temporary absence or scarcity of crop pests by attacking other hosts. Barra (1959) agreed, suggesting that host-specific natural enemies have not been used effectively against the wide spectrum of opportunistic, vagile pests that attack hosts temporarily occupying disturbed or unstable crops such as annual row crops. These statements are particularly true for the dominant endemic parasitoids of the FAW in the southern U. S. including the tachinid Archytas marmoratus (Townsend), the braconids Cotesia marginiventris (Cresson), Chelonus insularis (Cresson), and the ichneumonid Campoletis spp., which are all polyphagous.

Reproductive Strategies

The viewing of natural enemies as r (reproductive rate) and K (carrying capacity) strategists (MacArthur and Wilson 1967) may also assist in selecting those which may complement others in the endemic guild. Species known as r strategists tend to occupy unpredictable environments, have high capacity for population increase (high r values), and are poor competitors; K strategists, on the other hand, tend to exist in more constant environments, have relatively low capacity for population increase, and are good competitors (Force 1974). While realizing that r and K selection is a relative concept and that most parasitoid guilds will usually develop a continuum of r to K strategists, if we examine the early season parasitoid guild of the FAW in Georgia, we find that the parasitoids A. marmoratus, C. marginiventris, and Campeolitias spp. are typically the earliest attackers of FAW larvae in whorl-stage corn when densities are relatively low. These species and others which perform in typical fashion are probably capable, when available in adequate numbers, of preventing pest population buildup, which should be the goal of biocontrol strategists, rather than seeking to take corrective action. C. insularis, an egg-larval parasitoid of the FAW, although occasionally present when host densities are low, is more highly efficient and more highly visible during mid- and late summer when FAW populations expand and hosts are abundant. Similar findings were reported by Miller (1980) for C. insularis parasitizing Spodoptera praefera (Grote) in alfalfa. Mitchell et al. (1984) reported that C. insularis were consistently high performers where distributions of FAW hosts were more uniform. Responses by Chelonus inanitus (L.) to populations of Spodoptera littoralis (Boisd.) in Israel were also highly density dependent (Rechav 1975). Whether through less efficient foraging
or otherwise, *C. insularis* apparently does not prevent host population buildups but rather tends to suppress and/or regulate populations at relatively high host densities. These statements and prior stated criteria suggest that *C. insularis* is the more low r-selected strategist (Miller 1977) compared to the higher r-selected *A. marmoratus* (Hughes 1975), *C. marginiventris*, and *Campoletis* spp. However, *C. insularis* would be the most obvious parasitoid available to collectors at peak or near-peak FAW populations, despite its apparent limited role in preventing outbreaks.

Recent studies by Pair et al. (1986), for example, showed that *A. marmoratus* was the primary parasitoid attacking medium and large FAW larvae in whorl-stage corn throughout most southern states during the spring of 1981-83 (Table 1). However, in areas of overwintering where FAW larval populations are more abundant and uniformly distributed, *C. insularis* was the dominant parasitoid in all larval-size categories (Table 2). Also, when we examine the frequency distribution of parasitism among larval sizes at all geographic locations studied, large larvae, without exception, are least parasitized (Table 3). Thus, the best opportunity for colonization of exotic parasitoids exists for those insect species utilizing large larvae in areas other than where overwintering occurs due to the low frequency of competition that occurs therein. Equal or greater opportunities may also exist for colonization of exotic parasitoids of the prepupae and pupal stages of the FAW. Pair and Gross (1984) found only the ichneumonid parasitoid *Diapetanomphora introita* (Cresson) to attack pupae of the FAW in Georgia. Clearly, more efforts are needed to explore the role of species which employ similar strategies. As suggested by Force (1974), natural enemies selected for importation are generally the most conspicuous within the endemic community and are usually *K* strategists. The intent here is certainly not to diminish the importance of a parasitoid such as *C. insularis* because it likely plays a vital role in regulating the seasonal dynamics of the FAW; but it would not likely be the best parasitoid to select for augmentation if the objective was to prevent early season buildup.

Pschorn-Walcher (1977) suggested that r-selected species, which are good colonizers, are able to penetrate into and adapt to new environments, should be given high priority in any introduction program because they have a chance to demonstrate their full poten-

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**TABLE 1. Parasitism of Fall Armyworm Larvae by Indicated Parasitoids in Seven Atlantic And/or Gulf Coastal States and Northeastern Mexico During the Springs of 1981-83.**

<table>
<thead>
<tr>
<th></th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
</tr>
</thead>
<tbody>
<tr>
<td>CS</td>
<td>33.1</td>
<td>AM 37.1</td>
<td>AM 57.6</td>
</tr>
<tr>
<td>CM</td>
<td>30.5</td>
<td>CM 11.4</td>
<td>OF 26.4</td>
</tr>
<tr>
<td>RL</td>
<td>8.0</td>
<td>RL  9.4</td>
<td>LA  5.8</td>
</tr>
<tr>
<td>CI</td>
<td>6.1</td>
<td>CI  3.7</td>
<td>CS  0.9</td>
</tr>
</tbody>
</table>

Pair et al. 1986.

*Excludes data from south Florida.

CS — *Campoletis sonorana*

CM — *Cotesia marginiventris*

RL — *Rogas lophyrae*

CI — *Chelonus insularis*

AM — *Arcylygus marmoratus*

OF — *Opion flavus*

LA — *Lenopsis arachipica*

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TABLE 2. Parasitism of fall armyworm larvae by indicated parasitoids in south Florida during the springs of 1981-83.

<table>
<thead>
<tr>
<th></th>
<th>FAW parasitism</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Contributed by indicated species</td>
</tr>
<tr>
<td>Small</td>
<td>CI — 67.1</td>
</tr>
<tr>
<td></td>
<td>CM — 22.5</td>
</tr>
<tr>
<td></td>
<td>TD —  6.6</td>
</tr>
<tr>
<td>Medium</td>
<td>CI — 59.6</td>
</tr>
<tr>
<td></td>
<td>MA —  8.2</td>
</tr>
<tr>
<td></td>
<td>TD —  7.9</td>
</tr>
<tr>
<td>Large</td>
<td>CI — 56.1</td>
</tr>
<tr>
<td></td>
<td>AM — 16.8</td>
</tr>
<tr>
<td></td>
<td>OF —  7.5</td>
</tr>
</tbody>
</table>

1Pai et al. 1986.

CI = Chelonus insulatus
CM = Cotesia marginiventris
TD = Tetreesoge n.v.
MA = Metanesia autographa
AM = Archytas nemorumata
OF = Opissa floridan

TABLE 3. Parasitism of indicated sizes of fall armyworm larvae at three geographic regions in the southern U. S. (and NE Mexico) during the springs of 1981-83.

<table>
<thead>
<tr>
<th>Larval size</th>
<th>Coastal States</th>
<th>South Florida</th>
<th>SW Texas-NE Mexico</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>22.7</td>
<td>38.3</td>
<td>28.1</td>
</tr>
<tr>
<td>Medium</td>
<td>14.8</td>
<td>29.6</td>
<td>23.8</td>
</tr>
<tr>
<td>Large</td>
<td>12.1</td>
<td>14.8</td>
<td>17.6</td>
</tr>
</tbody>
</table>

1Pai et al. 1986.

tial before vying for position with the more competitive K-selected natural enemies. In contrast to the herbivores, which are the true r-strategists, their predators and parasitoids are generally slower to colonize vacant habitats. There is no selective pressure for them to colonize early as they would encounter a shortage of host/prey (Price and Waldbauer 1975). The difference in colonizing ability of the herbivores and their predators and parasitoids, coupled with differences in reproductive rates, frequently leads to pest outbreaks early in the season or after the application of insecticides. High r strategists do not generally depend on population density, and therefore are the ideal candidates for importation and colonization, and for augmentation when prevention of host population buildup is the ultimate goal. As suggested by Ehler and Miller (1978), r-selected pests may well be controlled by r-selected natural enemies.

PREDATORS

Reference thus far has been limited to parasitoids; however, were we to recall the frequency with which parasitism versus predation of FAW was witnessed in the field, predation would be declared the easy winner. However, our knowledge of the influence of predators on the seasonal dynamics of the FAW is almost totally lacking. Predators of insect herbivores of annual crops other than corn have been studied more extensively and are oftentimes reported to effectively regulate populations. For example, van den
Bosch (1975) reported that predators appeared to have advantages over highly host-specific natural enemies and that "it is no exaggeration to state that the noctuid's potential to cause massive damage to a million acres of San Joaquin Valley cotton is virtually nullified by the generalist predators." Similarly, Whitcomb (1974) reported that the population level of three lady beetles determined whether there was going to be a *Heliothis* *zea* outbreak in thousands of acres of cotton and cornfields in the U. S. No similar claims to date have been made for the FAW, although frequent reports of predation have been cited. Gross et al. (1985) reported the coccinellid *Coleomegilla maculata* (DeGeer) and the big-eyed bug, *Geocoris punctipes* (Say), as frequent diurnal predators of FAW eggs in south Georgia, while the earwigs *Labidura riparia* Pallas and *Dorni lineare* (Eschscholtz) joined *C. maculata* as nocturnal predators. They also demonstrated that aqueous larval homogenates of *H. zea* and *S. frugiperda* applied on whorl-stage corn caused the aggregation of adults of *C. maculata* and *G. punctipes*, and caused increased numbers of *C. maculata* egg masses to be oviposited in homogenate-treated plots. Predators of FAW eggs and larvae observed by Luginbill (1928) included *Podisus maculiventris* Say, *Orius insidiosus* (Say), *C. maculata*, *Nabis feras* L., *Vespaula carolina* L., *Solenopsis geminata* (Fab.), and *Pogonomyrnex herbatus* Smith. Painter (1955) recorded the ground beetle, *Onytyrgias famina* Sobir, from Guatemala as a predator of FAW larvae, while Young (1985) reported adults of another ground beetle, *Calosoma sayi* DeJean, as predators of FAW pupae in the laboratory. In a south Georgia sorghum field in August 1981, Pair et al. (unpublished) observed large numbers of *C. sayi* larvae preying on FAW pre-pupae and pupae. Huis (1981) reported that the earwig, *Dorni laevifrons* (Dohrn), preys on egg masses and the first three larval instars of the FAW. Pair and Gross (1984) frequently found larvae and adults of several species of carabids, and several late instars of the earwig, *L. riparia*, in FAW pupation cells containing macerated fragments of FAW pupae. Also, larvae of the elaterid *Conoderus* sp. appeared on occasion to attack FAW pupae. While the role of endemic predators in the management of FAW populations can only be surmised, based on findings with other lepidopteran pests of row crops, the opportunity to effectively expand the predator guild attacking the FAW appears limitless. However, appropriate caution must be taken to assure that exotic predators do not by preference prey on other primary endemic beneficial species.

Murdoch et al. (1985) suggested that conventional wisdom may be a poor guide to biological control, even in persistent ecosystems, and that local pest extinction rather than stable pest equilibrium may be the more appropriate goal, and that general predators can be good control agents in these and annual cropping systems. They referred to the use of predators to attempt local extinction of pests by the "lying-in-wait" strategy which requires a more or less continuous presence of the predators in local areas subject to pest infestation, combined with adequate attack on the pest when it reinvades or begins to increase.

**Numbers of Exotic Natural Enemies Released**

Beirne (1975) found that releases of large numbers of exotic natural enemies into new habitats increased the probability of establishment. Of 159 natural enemies introduced into Canada, species released in mean total numbers under 5,000, 10% became established; of species released at 5,000-31,200, 40% became established; and of species in which over 31,200 were released, 78% became established. These analyses also implied that the greater the number of releases per species the greater the possibility of establishment. About 90% of the forest species that were released more than 20 times
became established as compared with about 10% of those released less than 10 times each. Because some good colonizer likely established during the earliest of multiple releases, the estimates of numbers normally needed to insure successful establishment are probably inflated. Also from Beirne (1975), of the mean total 31,500 individuals for species introduced into forest environments, 23% became established; of a mean total 6,600 individuals for species introduced into orchard and ornamental shrub situations, 43% became established; and of a mean 33,000 individuals per species released into annual crops, 16% became established. Data of Beirne (1975), at least in part, provided support for MacKauer's (1972) view that although insectary propagation increased the total number of individuals available for release, it did not necessarily enhance the possibility of colonization. The relevance of these data from Canada to future attempts at colonization of natural enemies on FAW in the southern U.S. is unknown. Generalization, of course, serves only as a guide. Consider the exceptional case of Sailer (1981) who introduced 57 females and 130 males of the aphilid wasp, Prospaltella laborensis Howard, against the white fly, Dialeurodes citri (Ahmed), in Gainesville, FL, and achieved colonization. Evidence such as this suggests very strongly that factors responsible for the successful colonization of natural enemies in annual, perennial, and permanent habitats are poorly understood.

**Natural Enemy Release Strategies**

Of the innumerable factors that potentially influence successful colonization and/or successful performance of natural enemies following augmentation, none seem to receive less attention than the conditions surrounding the release itself. Typically, natural enemies are released from captivity into host-bearing habitats that encourage foraging. Unfortunately, unless care is taken to reorient released species, the primary tendency is not for foraging but rather for dispersal. Thus, following dispersal, the favorable opportunities provided by the release site are removed, immediately lowering the probability of successful colonization. Knippling (1977) noted that for highly mobile species, the dispersion of either or both the parasitoids and hosts was likely to preclude accurate measurement of the effect of parasitoid releases in areas consisting of several hundred or even several thousand acres. The dispersal tendency can be partially overridden by the pre-release provisioning of the appropriate kairomone(s) (Gross et al. 1975), pre-release host-parasitization experience (Gross et al. 1981), and/or by the provisioning of supplemental hosts within the target habitat (Knippling and McGuire 1968, Parker 1971, Parker and Pinell 1972, Gross 1981, and Gross et al. 1984). These techniques have been shown to be effective for increasing rates of retention and parasitization by *Trichogramma* spp. and would likely afford higher probability of establishment by other natural enemies. Lewis and Nordlund (1984) reviewed the role of semiochemicals in the performance of parasitoids of the FAW and discussed their implications for behavioral manipulation.

The site selected for attempted colonization of exotic natural enemies is of equal importance. Foremost in importance is the availability of hosts of the appropriate stage for parasitization. Most releases of exotic natural enemies against the FAW have logically been made in south Florida where abundant larval populations were available, particularly on volunteer whorl-stage corn. However, because of the total failure to date to achieve colonization of any exotic parasitoids introduced at this location, there is now reason to question the appropriateness of this geographic area for making inoculative releases. Unfortunately, these habitats are also typically occupied by several low selected endemic parasitoid species—the true competitors for eggs or early instar larvae.
[i.e., *C. insularis* and *C. marginiventris* (Rajapakse et al. 1986)] which force the newcomer to immediately compete for survival. A less hostile initial environment in north Florida or south Georgia might enhance the probability of successful colonization. Host density of FAW larvae in whorl stage corn at these locations could be increased through artificial infestation methods using the Bazooka-applicator method of Wiseman et al. (1980) wherein ca. 1,000 plants per man hour can be infested. The adaptation of a similar gravity-flow, tractor-mounted FAW larval applicator for use on larger acreage is certainly possible. Bierne (1980) suggested that accidentally-introduced exotic parasitoids can become permanent inhabitants of new areas more readily than deliberately introduced ones because the former are already colonized on their hosts when they arrive. As a logical alternative, he suggested that imported adult parasitoids be released in large cages that have been stocked with the target pest species, followed later by the distribution of parasitized hosts in the field. These strategies, if used in May or June in south Georgia, would provide the opportunity for introduced parasitoids (particularly of large larvae) to complete one generation essentially unimpeded before the appearance of large populations of FAW and their associated low r-selected endemic parasitoids during July. Also in question is how exotic natural enemies, which are inherently early colonizers (r-strategists) (capable of foraging at low host densities) likely respond to the high larval host densities of overwintering habitats. Do they stay and forage, or do they find this situation unacceptable and disperse in search of more favorable habitats? The answer obviously is not available; however, numbers of larvae parasitized by an endemic early-season colonizer, *A. marmoratus*, near Tifton, GA, are highest in early season and late season, but generally occur at very low levels during peak host densities (personal observation).

**Planning Importation and Colonization Strategies**

The primary current need is to identify, collect, and import polyphagous, early-season colonizers (r-strategists) that attack the egg stage, mid- to large larvae or pupae of the FAW in whorl-stage corn that are capable of overwintering throughout the geographical range of the host. Emphasis should also be placed on those species that have potential for mass production.

Most biocontrol strategists generally agree that a plan should be developed before attempting the introduction of exotic parasitoid species that could permanently alter the parasitoid guild. They also agree that adequate understanding of the behavior, ecology, and dynamics of candidate natural enemies should be well understood before importation and colonization within new ecosystems are attempted. Although the above proposal is the ideal situation, it has not been a requisite of prior successes, nor will it likely be a part of future successes (Ehler 1982). As efforts to establish new species of natural enemies on lepidopterous pests of row crops in the South increase (and they will as the Stoneville, MS, quarantine facility is joined by new quarantine facilities in Texas and North Carolina), primary emphasis should be placed on the keeping of precise records of information associated with the attempted colonization so that as time passes, a profile of conditions most conducive to successful colonization can be identified so that the opportunities offered by exotic natural enemies of insect pests can be fully exploited. Even if exotic natural agents from tropical regions may not survive overwintering in these areas, studies may allow strategists to develop an introduction profile that may assist in future releases.
AUGMENTATION

The ideal biological control agent would suppress populations of the FAW in areas of overwintering to the extent necessary to prevent dispersing populations from reaching economic levels throughout the geographic range. However, it is unreasonable to expect that any endemic or available exotic natural agent could regulate populations of a highly mobile pest species with access to a rapidly expanding enemy-reduced habitat at sub-economic levels without augmentation (Lewis and Nordlund 1980). The authors generally agree with Price (1981) that attempts at long-term regulation of pest species in agroeco-systems from an initial release of natural enemies is likely to be ineffective because of the many factors that interact to reduce their viability and efficiency.

With augmentation of the appropriate parasitoid species during periods of low host density, opportunities for effectively managing populations of the FAW in areas of overwintering or in areas of subsequent establishment appear promising. Knipling (1980) proposed that the production and release of 2,000 larval parasitoids per acre on 50,000 accumulative acres of FAW infestations in the overwintering area would serve an effective and desirable method of FAW suppression with rates of parasitization reaching 90%.

Many natural agents of the FAW and other insect pests of annual crops have been reared in numbers adequate for laboratory, greenhouse, and screened cage studies; unfortunately, few are capable of being reared in numbers or at costs adequate to consider sustained augmentative releases. The notable exception, of course, is Trichogramma spp., which have been effectively and economically reared on unnatural hosts (Morrison et al. 1978) and aerially applied in the fashion of an insecticide (Jones et al. 1979). Trichogramma spp. have, however, only infrequently been cited as parasitoids of the FAW. Like Trichogramma, and as reported by King and Morrison (1984), without exception, parasitoids and predators being mass produced for control of arthropods are being reared on live hosts or host products. Near term advances in augmentation appear, therefore, to be limited to natural enemies that can be produced economically on unnatural hosts. C. insularis, for example, has been reared large scale on eggs/larvae of the meal moth, Ephesia kuehniella (Tardrew 1951, Bedford 1955). Starler and Ridgway (1977) listed only C. insularis as a parasitoid of armyworms among those natural enemies available for use in practical augmentation in the U.S. The larviporous Tachinidae (e.g., A. marmoratus) are particularly adaptable to large-scale rearing because in general maggots are deposited on substrates independent of the host, and alternatively can be mechanically extracted from fecund females and directly applied against host insects, thus eliminating the numerous chemically and physically mediated requisites of the host selection process (King et al. 1979, Hartley et al. 1977, Gross and Johnson 1985). Gross and Johnson (1985) initiated large-scale rearing of A. marmoratus on its natural host, the corn earworm, H. zea, and the FAW, and more recently on the greater wax moth, Galleria mellonella (L.), (unpublished) using the same methods. Laboratory-reared females of A. marmoratus (Gross and Young 1984) and mechanically-extracted maggots from fecund females (Gross et al. 1985) have both been employed against larval populations of the FAW in whorl-stage corn to effectively reduce the size of the subsequent host generation. The larviporous Tachinidae as primary attackers of late-instar host larvae offer more immediate opportunity for evaluation in augmentation strategies than other available groups and should also be considered for importation.

Studies of Strand and Vinson (1982a, b) suggest that the range of unnatural hosts available to parasitoid species may be extended by the application of host-recognition
kairomones from the natural host onto the unnatural host. Opportunities offered by this concept could greatly reduce the cost of parasitoid rearing and thus significantly advance augmentation strategies.

As might be expected, some resolvable problems have arisen from the production of natural enemies on unnatural hosts. Morrison and King (1977) suggested that reduced vigor of entomophages reared on unnatural hosts could occur due to inadequate nutrition, but offered that host suitability could be improved through improvements made in the diet of the host. Vigor of the tachinid Lixophaga diatraeae (Townsend) was improved when cereal diet fed the greater wax moth larvae was supplemented with wheat germ and the protein content increased (King et al. 1979).

As suggested by House (1977), to resort to a host insect to rear parasitoids in the laboratory is extravagant and parasitoid quality is hardly controllable. Unfortunately, biocontrol strategists have had little choice. Greany et al. (1984) provide a representative list of insect parasitoids that have been reared to adults on artificial media. Their compilation shows that endoparasitoids of eggs and pupae have been the best candidates for artificial rearing, but that hymenopterous larval endoparasitoids still have not been successfully reared to the adult stage on artificial media. Even with hymenopterous larval parasitoids reared on their natural hosts, sex ratios of progeny are typically skewed in favor of males, thus further limiting their near term use for augmentation. House (1977) suggested that the use of artificial diets or even a highly chemically defined synthetic one for the rearing of parasitoids without resorting to an insect host should not be ignored. Additionally complicating is the more recent find by Stoltz and Vinson (1979) and Stoltz (1982) that the host physiology may be altered by symbiotic viruses injected into the host at oviposition by hymenopterous parasitoids which likely influence successful parasitism.

Opportunities for augmentation of biocontrol agents against the FAW must be taken as they become available and as natural enemies are capable of being reared in numbers adequate for testing. Knipling (1977) suggested that until suitable parasitoids are increased by artificial means throughout a pest ecosystem by as much as 10 to 50 times above normal numbers during the early generation of the pest population cycles, the potential of the augmentation systems for managing insects will remain unknown.

REFERENCES CITED


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