INTERACTIONS BETWEEN MICROBIAL AGENTS AND GYPSY MOTH PARASITES

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The parasite Cotesia melanoscelus attacks small gypsy moth larvae more successfully than large ones, and Bacillis thuringiensis retards the growth of caterpillars it does not kill. Together, both factors lead to higher parasitism by C. melanoscelus in areas sprayed with B. thuringiensis than elsewhere.

One of the major advantages of microbial agents over chemical insecticides is their specificity. They are usually benign to non-target organisms such as parasites and predators, and indeed many gypsy moth natural enemies are not harmed by treatments with microbial sprays. For instance, Dunbar et al. (1973) found that percent parasitism by a number of gypsy moth parasites was similar in check and Bacillus thuringiensis spray plots, and in another study the number of adult parasites caught in malaise traps during the year of treatment was usually the same in all plots (Reardon et al. 1979). However, in some cases parasite numbers were decreased by sprays. Reardon et al. (1979) and Andreadis et al. (1983) found that the pupal parasite, Brachymeria intermedia (Hymenoptera: Chalcididae), was not numerous in B. thuringiensis-treated areas. Ticehurst et al. (1982) showed that the tachinid parasites Compsilura concinnata and Blepharipa pratensis parasitized a lower percentage of gypsy moths in B. thuringiensis spray plots than in non-spray plots, and Kaya et al. (1974) noted that larvae of the predaceous beetle, Calosoma sycophanta, were less abundant in B. thuringiensis-treated as compared to untreated areas.

A decrease in parasite or predator populations in areas treated with a microbe does not necessarily mean that the agent has a direct effect on the natural enemy. Parasites and predators respond to host populations, which are generally different in treated and untreated plots. B. intermedia, for instance, seeks out high light intensities and so is usually most abundant in defoliated areas (Weseloh 1976b). Thus its numbers are often higher in check plots where most defoliation occurs. In field situations it is often not possible to tell whether the depressing effect of the agent is direct or indirect. Also, with one exception (to be detailed later), no laboratory studies have described the specific interactions between the most widely used microbial agent, Bacillus thuringiensis, and gypsy moth natural enemies.

A few workers have studied interactions between natural enemies and the gypsy moth nuclear polyhedrosis virus. Capinera and Barbosa (1975) showed that adults of the predaceous carabid beetle, Calosoma sycophanta, could pass viable virus polyhedral inclusion bodies through their gut without evident harm, and so may be a useful vector of this pathogen. Similarly, Raimo et al. (1977) demonstrated that the braconid, Cotesia (Apanteles) melanoscelus, could transmit virus from caterpillar to caterpillar when its ovipositor became contaminated, either artificially or from attacking diseased hosts. However, C. melanoscelus tends to avoid ovipositing in moribund hosts (Versoi and Yendol 1982), possibly restricting its usefulness as a vector.

Because such studies have not been extensive it is difficult to generalize about the impact microbial agents have on gypsy moth natural enemies. However, there is one interaction involving B. thuringiensis and the parasite, C. melanoscelus, that has received a substantial research investment.

In the early 1970's a number of field tests demonstrated that C. melanoscelus impact was enhanced in areas sprayed with B. thuringiensis. For example, in a 1972 spray test in Connecticut percent parasitism of field-collected caterpillars by C. melanoscelus averaged 1.0% in check plots and over 12 times higher (13.3%) in plots sprayed with Thuricide HPC or the experimental preparation IMC 90012 (Dunbar et al. 1973). The following year percent parasitism was 1.3, 7.0, and 20.6% respectively in check, Thuricide-16B, and Dipel WP plots. Also, an average of only 0.8 C. melanoscelus overwintering cocoons was located under each burlap band in check plots as compared to 4.7 in Thuricide and 8.1 in Dipel plots (Kaya, et al. 1974). Thus, the absolute number of parasite progeny as well as the proportion of hosts attacked increased in test plots. This is important because percent parasitism can be expected to increase in treated areas (assuming the disease has no direct effect on the parasite) even if parasites are not enhanced because low host numbers resulting from disease-induced mortality may result in a more favorable parasite:host ratio. Wollam and Yendol (1976) showed that this enhanced effect also occurred when 1000 mated female C. melanoscelus were released into plots which were also treated with Thuricide-16B. Counts of gypsy moth larvae under burlap bands as well as defoliation estimates were lower in plots receiving microbe and parasite than in plots receiving B. thuringiensis alone, C. melanoscelus alone or no treatments. This is the only study I know of where parasite releases

have been shown to actually reduce gypsy moth populations. It may be important that the effect occurred only when parasites were released in combination with B. thuringiensis.

The above reports show the potential which B. thuringiensis has for improving the effectiveness of C. melanoscelus. Because the combined effect was greater than the summed effect when either agent was present alone the phenomenon was a case of true synergism. Initially the causal mechanism was unknown. In early tests molasses was often used as an adjuvant in spray mixtures and may have attracted C. melanoscelus into the area. However, other parasites which should have responded to the molasses did not. Furthermore, I could not increase parasite activity by spraying from the ground with molasses. A clue to the mechanism involved occurred in the mid 1970's when I related C. melanoscleus parasitism rates to gypsy moth larval development (Weseloh 1976a). Percent parasitism by C. melanoscelus reached a peak when most hosts were in the second instar and declined thereafter, despite the fact that the parasite has two generations a year. First generation parasites emerge from overwintering cocoons when gypsy moth eggs are hatching and attack first instars. Their progeny develop without diapause and attack third and fourth instars. Clearly the first generation parasitized the most hosts in spite of the relatively large numbers of second generation adult parasites (as measured by sticky-panel catches) present when gypsy moths were fourth instars and larger. Results suggested that parasites did not successfully attack large caterpillars, and this was confirmed in laboratory tests. Because of the vigorous defensive movements and long hairs of older hosts, third and fourth instars were less frequently parasitized than were younger caterpillars (Weseloh 1976a).

I did not relate these results to the parasite-B. thuringiensis interaction until Ticehurst et al. (1982) found that, in addition to the increased parasitism by C. melanoscelus which occurred in Dipel-treated plots (32.3%, as opposed to 4.4% in the check plots), Dipel caused a one-week lag in development of surviving gypsy moths as determined by the appearence of pupae and adult moths. A similar lag was documented by Andreadis et al. (1983). This lag was caused by the gut-paralyzing effect of the delta-endotoxin of B. thuringiensis, which causes caterpillars to stop feeding at least temporarily (Heimpel and Angus 1959). Ticehurst, et al. (1982) suggested that this retarded development might enable C. melanoscelus to attack the small hosts it can successfully attack for a longer time, thus improving its effectiveness.

Laboratory work was done to investigate this. Ahmad et al. (1978) showed that B. thuringiensis-related mortality of larvae parasitized with C. melanoscelus was similar to that of non-parasitized gypsy moths, and they also concluded that there was no evidence for a direct, toxic effect of B. thuringiensis on the parasite. Weseloh and Andreadis (1982) confirmed these results and also showed that surviving, B. thuringiensis-treated second instars were retarded in development about two days as compared to controls. When presented with untreated larvae of the same chronological age as larvae exposed to B. thuringiensis three days before, female parasites attacked both hosts equally. However, if B. thuringiensis exposure had occurred ten days previously, untreated hosts were attacked substantially less frequently than treated ones. Ten days after treatment 97% of the treated larvae were still third instars while only 60% of the healthy ones were, so the former were noticably smaller than the latter. More importantly, a significantly greater number of parasites were reared from treated larvae than from untreated ones. Thus retarded development caused by B. thuringiensis is a plausable mechanism for enhancing the effectiveness of C. melanoscelus.

To test this hypothesis, C. melanoscelus and gypsy moth larvae were sampled in a 1981 aerial spray test using Dipel 4-L (Weseloh et al. 1983). As in the other tests mentioned, C. melanoscelus parasitism was only 1.2% in check plots and 6 to 12 times higher (6.9-14.8%) in treatment plots. Also, numbers of parasite cocoons under burlap flaps averaged only 4.0 per flap in control areas and from 13.2-20.3 per flap in treated plots. Caterpillar numbers were greatest and caterpillars were largest in the check plots. On June 11, only 5.2% of larvae were still third instars in the check areas, whereas 22% to 49% were third instars or smaller in treatment plots. Simple and multiple linear regression analysis clearly showed that percent parasitism was more closely related to the average caterpillar size per plot than to caterpillar numbers. This last point is important because, together with the larger numbers of parasite cocoons in spray plots, it shows that the increased parasitization was not due soley to changes in parasite:host ratios. Along with laboratory experiments, the test proved that the rate of gypsy moth development is critical to the field effectiveness of C. melanoscelus.

The importance of retarded host growth in improving the efficiency of C. melanoscelus led me to explore other circumstances where caterpillar development could be influenced. For instance, it is conceivable that low B. thuringiensis doses, lower even than those which cause mortality, might still retard caterpillar development. Also, feeding deterrents, by temporarily stopping feeding, might also be effective. In their field test Ticehurst et al. (1982) used Dipel 4-L at one-half the usual rate, but this still caused substantial mortality and no lower concentrations have to my knowledge been tested. Accordingly, in 1981 and

1983 I sprayed individual apple trees with B. thuringiensis concentrations ranging from the usual dose of 0.84 BIU to 0.035 BIU per tree (Weseloh, manuscript submitted). Other trees were sprayed with the mitacide Plictran (tricyclohexylhydroxystannane), an antifeedant for gypsy moths (Meisner and Skatulla 1975). Plictran is registered for use on apples, and was applied at the recommended rate of 0.22 g/l active ingredient.

Larval numbers were reduced below controls for all B. thuringiensis rates of 0.21 BIU per tree or more, but only for the highest dose was defoliation reduced. Plictran did not decrease larval numbers, but it and all the B. thuringiensis concentrations significantly retarded caterpillar development. Attempts to monitor parasitism in these areas were not successful in 1981 because of extensive inter-tree movement of caterpillars and in 1983 because parasitism levels, in general, were very low. But the link between developmental rates of gypsy moths in the field and parasitism by C. melanoscelus has already been proved, so it is likely that if parasite activity could have been monitored it would have been increased by the treatments.

Interactions between B. thuringiensis and parasites is not restricted to C. melanoscelus. Wallner et al. (1983) found in a laboratory study that retarded development of gypsy moths caused by B. thuringiensis enhanced parasitism by an exotic braconid, Rogas lymantriae, although a higher proportion of males emerged from infected larvae than from healthy ones. Also, Hamel (1977) showed that percent parasitism by two parasites of the western spruce budworm, Choristoneura occidentalis, increased in areas sprayed with B. thuringiensis. The two parasites, Apanteles fumiferanae and Glypta fumiferanae, attacked pre-diapausing budworms before sprays were applied. Parasitized larvae did not eat as much as healthy ones, and so probably avoided ingesting lethal amounts of B. thuringiensis. This is a different mechanism than operates with the gypsy moth parasites, where it is parasitism occurring after spray application that is enhanced.

Natural enemies may frequently be enhanced by applications of microbial agents, although few studies have been reported. Clearly, this is an area of research that needs more emphasis. Chemical pesticides might have similar effects, but chemical pesticides usually lack the specificity of microbial agents and kill natural enemies along with the target pest. Looking for side effects of pathogens on hosts could be important because such side effects can profoundly influence the effectiveness of natural enemies.

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