STRATEGIES FOR FIELD USE OF BACULOVIRUSES

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I. INTRODUCTION

In recent years, there has been increased awareness in maintaining the quality of the environment. This has led to the development and use of microbial agents as alternatives to chemicals for controlling noxious insect populations. The insect pathogens in the family Baculoviridae, by virtue of their specificity, virulence, and safety for nontarget species, have become logical candidates in this regard, and several have been registered with the United States Environmental Protection Agency (EPA) for use in the United States (Martignoni, 1978; Lewis et al., 1979; Ignoffo and Couch, 1981). In fact, these viruses, as well as members of the Reoviridae, have been in general use for some time, in one form or another, throughout the world (Bedford, 1981; Cunningham and Entwistle, 1981; Katagiri, 1981; Falcon, 1982; Huber, 1982).

Of the baculovirus products registered for use in the United States, only one, Elcar, *Heliothis* nucleopolyhedrosis virus (NPV), is in commercial production and in general use. The others, Gypchek, the gypsy moth, *Lymantria dispar*, NPV product, and TM-Biocontrol-1, the Douglas-fir tussock moth, *Orgyia pseudotsugata*, NPV product, are registered for use under the auspices of the USDA Forest Service (FS), although

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at present neither is in commercial production nor in general use. Another FS product, Neochek-S, the European pine sawfly, *Neodiprion sertifer* (NPV), has only recently been registered for use in the United States (Podgwaite et al., 1983). This virus is commercially produced and has been used in Europe for some time (Cunningham and Entwistle, 1981).

The development of virus products and control strategies for their use, has been patterned after conventional pesticide use and technology, i.e., broadcast application, usually from aircraft, timed to coincide with the most susceptible stage of the insect, and in response to threatened damage from an insect population that has already reached the economic threshold. Although this may be the most desired approach with many pests, with few exceptions (most notably the sawfly viruses), viral insecticides have provided less than expected results when used as substitutes for chemical pesticides.

The following discussion is focused on past, present, and future strategies for baculovirus use, with examples of conventional and novel application tactics, and the conditions under which these strategies and tactics have been successful, fallen short, or are likely to emerge as important elements in future pest management systems.

II. STRATEGIES FOR USE OF BACULOVIRUSES

Strategies for use of baculoviruses are indicated by the pest-virus interaction and by the nature of the resource being protected. Overall objectives may differ, but efficacy is usually defined in terms of population reduction or foliage protection, or both. For example, a Christmas tree grower can tolerate little defoliation before his crop becomes unmarketable and severe economic loss occurs. Thus, his approach in the use of a viral insecticide and how he measures efficacy will differ from that of the manager of a hardwood timber stand, who, though suffering some loss due to reduced tree growth during periods of defoliation, generally is more tolerant of pest populations, since it takes 2-3 years of heavy defoliation to cause tree mortality and the associated severe economic loss. For the manager of a spruce-fir forest, the situation is quite different, since his resource does not refoliate and extensive mortality follows heavy defoliation. His objectives, strategies, and tactics will reflect the high risk of tree mortality. Scenarios could be similar for agricultural pests, but the point remains the same: strategies for virus use are largely dictated by the economics of the situation, and perhaps secondarily by the nature of the particular virus-insect-host plant system being manipulated.

A. DIRECT CONTROL OF OUTBREAK POPULATIONS

Most control attempts using baculoviruses are made when the target pest has approached the economic threshold or is in the outbreak phase and has already caused substantial losses in the previous generation. The purpose of introducing virus in such situations is to induce artificial epizootics to reduce the pest population below some economic threshold. To introduce effective amounts of virus to as many individuals of the target population as possible in the shortest time, broadcast application usually is chosen. This tactic takes advantage of the density of the host population in the rapid transmission of the disease and the initiation of a widespread epizootic.

There are problems associated with introducing viruses, the most important of which is their instability. Numerous studies have shown that baculoviruses lose most of their insecticidal activity within a few days, and sometimes hours, after application. This has been demonstrated for cabbage looper, *Trichoplusia ni*, NPV, imported cabbageworm, *Pieris rapae*, NPV, and large white butterfly, *Pieris brassicae*, granulosis virus on cabbage (David et al., 1968; Jaques, 1972), *Heliothis* NPV on several host plants (Bullock, 1967; Ignoffo et al., 1973, 1974; Ignoffo and Batzer, 1971), and for *Lymantria dispar* NPV on oak (Lewis and Yendol, 1981). This rapid loss of activity is most often ascribed to the virucidal action of uv irradiation (David, 1969; Bullock et al., 1970; Morris, 1971).

There are other factors that affect the stability of viruses, most notably moisture and leaf surface pH. The former may, through some undetermined process, enhance uv inactivation of baculoviruses (David, 1969; Jaques, 1967a). The latter may be particularly critical to the survival of *Heliothis* NPV on cotton, where the pH (9.0-9.9) has been shown to be high enough to affect the integrity of the polyhedral inclusion body (PIB) (Andrews and Sikorowski, 1973). The problem of virus instability has been addressed to some extent by adding uv screens to baculovirus formulations before application. Several of these adjuvants/extenders have been tested in the laboratory and in the field (Yendol and Hamlen, 1973; Bull, 1978; Couch and Ignoffo, 1981; Luttrell et al., 1982, 1983; Hostetter et al., 1982). These adjuvants, some of which have been commercially developed and marketed, afford varying degrees of protection, but rarely what is needed for the least efficacious baculoviruses to be cost effective, that is, the extension of maximum viral activity over the entire life of the target stage.

The problem of viral instability is compounded by the mechanisms of viral pathogenicity. Since baculoviruses must be ingested to kill, sufficient infectious material must be deposited before a susceptible insect and remain viable long enough for the insect to ingest a lethal dose. This is complicated by nonuniform hatch rates that lead to nonuniform susceptibility of the target pest. Also, the rate of foliage development and weather conditions at the time of application can be major factors which prevent sufficient foliar coverage. Further, as much as 70% of the biological activity of a virus preparation can be lost through drift or droplet evaporation before impact on the target foliage (Lewis and Etter, 1978). Thus, the application window for these agents is very small. Many physical and biological factors act in concert to make broadcast application a very complex, high-risk tactic, the results of which can be compromised by only minor errors in timing, dose rates, and estimates of insect and foliage development.

Incorporating antievaporants and gustatory stimulants into spray formulations may help prevent physical loss of virus and offset rapidly decreasing virus activity after the product has been deposited on target foliage. Luttrell et al. (1983) found that mortality of cotton bollworm, *H. zea*, in the field was increased significantly when Elcar was used with a high rate of the feeding stimulant Coax. Nonuniformity of insect and foliage development can be compensated for by staggered applications of virus during periods of early larval development (Wollam et al., 1978). This may increase efficacy, but it also increases cost.

Depending on the particular baculovirus used, it may be as many as 7-14 days after application before mortality is significant. During this time the insect may continue to defoliate, causing damage and loss that must be an accepted part of any direct control strategy. Again, timing of application is critically important so that the target is reached at as early a life stage as possible to minimize defoliation before peak insect kill.

Environmental acceptability is a major reason why microbials have reached at least an introductory level of prominence in pest management strategies. They have been introduced to the pest management arena after several decades of indiscriminant use of chemical pesticides, the results of which have rendered well over 200 insect pest species resistant to these chemicals (FAO, 1970). However, there is some evidence that insect populations develop resistance to baculoviruses (see Briese and Podgwaite, this volume). Since the use of baculoviruses in control programs is a relatively recent development, neither enough time has passed nor enough data been made available to determine whether insect resistance is evolving in areas that have been treated repeatedly with these agents. Nevertheless, users should be aware of the possibility of resistance and be advised that any strategy involving treatments on successive insect generations is likely to result in a certain degree of resistance.

A common argument against the use of chemical pesticides is the resurgence of target pests that often is seen in the year following application (Falcon, 1973). This necessitates repeated applications of pesticides in succeeding generations. Similarly, the use of baculoviruses may not be prudent in situations where natural population collapse is imminent, either from starvation or disease. Since the least efficaceous viruses, used at dosages that are economically competitive with chemicals, generally reduce populations by 50-90% (Lewis, 1981; Ignoffo and Couch, 1981), it should be recognized that population rebound is likely when baculoviruses are used as direct control agents, particularly at high population densities. As with chemicals, yearly applications of baculovirus products may be necessary to afford desired control and crop protection.

Finally, baculovirus products are expensive to produce and to use. However, added cost often can be rationalized on the basis of safety and specificity relative to chemicals. Unfortunately, specificity is one reason why more baculoviruses are not available for use. Commercial producers are understandably interested in developing products that satisfy a broad market, as opposed to investing substantive amounts on products that will be used against one insect and perhaps only sporadically. The following is a brief account of the status of various baculoviruses as direct control agents.

1. *Heliothis zea* NPV (Elcar)

This virus, researched intensively for over a decade before its registration with EPA in 1975, has been in operational use on a fairly wide scale since 1979. Ignoffo and Couch (1981) reported that 150-200 field tests were conducted with *H. zea* NPV between 1960 and 1980; about 90% of these were on cotton and corn. Although results have varied, generally this NPV has been as effective as insecticide on cotton when used at rates above ca. 5×10^{10} PIB/0.4 ha. At high infestation levels of *H. zea* on corn, control has been less than that obtained with standard insecticides. However, at light to moderate infestations, results have been somewhat better. Similarly, tests on soybean and sorghum have provided reasonable control--90-96% and 88% population reduction, respectively.

Desired levels of control of tobacco budworm, *H. virescens*, on tobacco and *H. zea* on tomato have not been demonstrated.

Bohmfalk (1982) reported that since 1976 when Elcar was commercialized by Sandoz, Inc., there has been a mixed response to the product, which has been reflected in sales. As a partial explanation he noted that most cotton producers in the United States are resistant to change and have grown accustomed to seeing dead bollworms immediately after treating their fields with chemical insecticides. Since no such response is seen immediately following treatment with Elcar, many growers have decided that this product is not effective. He also cited competition with chemicals (particularly pyrethrins), formulation and application problems, and the lack of sophistication of the user in recognizing differences between pests and beneficial insects as other roadblocks to the success of Elcar. He concluded that the industry is experiencing difficulties in introducing this product into general use despite concentrated research and development efforts.

2. *Lymantria dispar NPV (Gypchek)*

A widespread outbreak of gypsy moth throughout the Northeastern United States in the 1970's led to the intensification of ongoing research directed toward the registration of a gypsy moth NPV product. Before this, direct-broadcast spray tests had provided limited control or unacceptable results primarily due to problems with formulation and differences in susceptibility among gypsy moth populations (Rollinson et al., 1965; Magnoler, 1968). From 1972 to 1978, the year that Gypchek was registered, there were several field tests on variations in virus product, application hardware, dose rates, timing, and formulation. In 1972 a ground mistblower test at 1×10^{13} PIB/0.4 ha provided a 90% reduction in egg masses compared with a 65% increase in untreated plots (Yendol et al., 1977). In 1974, an aerial test at the rate of 1×10^{12} PIB/0.4 ha resulted in no significant differences between numbers of pretreatment and posttreatment egg masses in treated plots (Yendol et al., 1977). Results of single and double applications of NPV at 2.5×10^{12} PIB/ha in 1975 were compromised by natural NPV epizootics in both treated and control plots. However, second year evaluation of the test indicated the NPV application did not improve the population quality of the next generation as measured by no increase in egg mass size, reduced larval emergence, and prolonged incidence of virus in the treated population (Wollam et al., 1978). Field tests with lower dosages in 1976 and tests of different nozzling systems in 1977 resulted in acceptable foliage protection (<55% defoliation) and population reduction (57-87%). However, a 1978 test of new formulations was again compromised by a natural population collapse (Lewis and Yendol, 1981). In 1981, results of further tests with Gypchek in 4L and Protec formulation, although promising, were inconclusive (Lewis and Podgwaite, 1982, unpublished).

Lewis (1981) concluded that the cost benefit in using Gypchek is positive if environmental considerations are paramount, if damage to other naturally occurring biotypes must be minimized, if gypsy moth is the primary insect in the treatment area, and if careful timing and application are not serious constraints. He added that the cost benefit is negative if immediate pest knockdown and long residual pesticide activity are required. Unfortunately, the conditions for achieving a positive cost benefit often are not realized. Environmental considerations are rarely as important to users as protecting their investment, and "environmental conciousness" suddenly becomes secondary under the threat of economic loss. Further, it is rare when careful timing and application are not constraints when using microbials. Disconcertingly, 5 years after registration, Gypchek is not in commercial production.

3. *Orgyia pseudotsugata NPV (TM-Biocontrol-1)*

This virus was registered with EPA by the FS in 1976 (Martignoni, 1978). Extensive field tests have shown it is an effective direct-control agent (Stelzer and Neisess, 1978). In a small-scale aerial test in 1973, dosages of 2.5×10^{11} and 2.5×10^{12} PIB/ha in a formulation of Shade and molasses resulted in reductions of about 97 and 98%, respectively, in treated tussock moth populations 35 days after treatment. Control populations were reduced by 47% by a natural virus epizootic. Average defoliation was 25% in treated plots compared with 64% in the controls.

In a large-scale pilot test in 1974 (plots ca. 80-500 ha), a dose rate of 2.5×10^{11} PIB/ha resulted in a 90% reduction on treated plots. No survival to the pupal stage was noted in any of the virus-treated areas. Defoliation was 20% in treated areas and averaged 60% in control plots.

Like Gypchek, TM-Biocontrol-1 is not commercially available and there appears to be little interest in its development. One can only speculate that the primary reasons are cost, specificity, extended time between tussock moth outbreaks and, as with cotton growers and Elcar, the resistance of timber managers to use other than relatively inexpensive chemical controls.

4. *Neodiprion sertifer NPV (Neochek-S) and Other Sawfly Viruses*

Sawfly baculoviruses are the most efficacious of the insect viruses, and some can be substituted for chemicals in direct control strategies. They also are inexpensive to produce with costs ranging from $0.75 to $2.00/ha equivalent compared with $10 to $125/ha equivalent for lepidopteran baculoviruses (Cunningham and Entwistle, 1981). Many have the distinct advantage of being amenable to spot innoculation since virus is spread rapidly within and between sawfly colonies (Bird, 1961).

Of the sawfly baculoviruses, the NPV of *N. sertifer* has been the most widely used; at least 10,000 ha in 12 countries have been treated since the early 1950's (Cunningham and Entwistle, 1981). Podgwaite et al. (1983) found that Neochek-S at a dose rate of 2.5×10^9 PIB/ha provided acceptable control (>90% reduction) and foliage protection (ca. 94%) in moderate to dense populations of *N. sertifer*. This product is in production by the FS and, currently, ca. 12,000 ha equivalents--a 5-year supply at the current demand--are available for use.

Lecontvirus, the Canadian redheaded pine sawfly, *N. lecontei*, NPV product, is in the final stages of development and should soon be registered for use in the United States and Canada. For acceptable direct control of redheaded pine sawfly, Cunningham and Entwistle (1981) recommended a dose rate of 5.0×10^9 PIB/ha. They also reported that the NPVs of Swaine's jack pine sawfly, *N. swainei*, the Virginia pine sawfly, *N. pratti pratti*, the loblolly pine sawfly, *N. taedea linearis*, and the European spruce sawfly, *Gilpinia hercyniae*, are efficient alternatives to chemical insecticides, although more data must be accumulated before their registration as commercial insecticides. This may well be moot as economic losses caused by these pests are insigificant relative to losses caused by the major agricultural and forest pests (NAS, 1975). Limited markets do not encourage commercialization, so if the production of these NPVs is not subsidized by interested governments, it is likely that they will not be made available.

5. *Other Baculoviruses*

In addition to the baculoviruses already discussed, several others have been tested and at least developed partially as direct control agents (see review by Stairs, 1971). A few of these have shown considerable promise and are potential candidates for commercialization.

A granulosis virus (GV) of the codling moth, *Cydia pomonella*, has been tested extensively in apple orchards in the United States, Canada, Australia, and Europe (Huber, 1982). In European trials, dosages between 0.5 and 1 × 10^{14} PIB/ha resulted in reduction of 75 to 95% in unmarketable apples. In Australia, weekly applications at 1 × 10^{14} PIB/ha provided 98% protection against deep entries and unmarketable fruit (Morris, 1972). Huber (1982) reported that an added advantage of using this virus is that the natural enemies of other orchard pests, especially mites, aphids, and leaf hoppers, are unaffected and remain to exert control over their hosts.

Sandoz, Inc. has produced a NPV product (SAN 406) that has been used in certain of the tests mentioned. Falcon (1982) reported that this product was as effective as commonly used chemical insecticides in controlling codling moth in two commercial fruit orchards. Since codling moth is the key pest on crops on which it occurs, the results bode well for the eventual registration and commercialization of its baculovirus.

The NPVs of the alphalpha looper, *Autographa californica*, and the cabbage looper, *T. ni*, have been produced by Sandoz, Inc. as experimental preparations SAN 404 and SAN 405, respectively (Falcon, 1982). The development of the former has been of particular interest because of its wide host range, e.g., *T. ni*; beet armyworm, *Spodoptera exigua*; saltmarsh caterpillar, *Estigmene acrea*; *H. zea*; cotton leafperforator, *Bacculatrix thurberiella*; and diamond back moth, *Plutella xylostella* (Vail and Jay, 1973). In field studies, Falcon (1982) found that SAN 404 was effective in controling *T. ni*, but that it did not infect populations of *S. exigua* or *E. acrea*. Both products were more effective than *Bacillius thuringiensis* (*B.t.*) for controlling *H. zea* on cotton; one application of either provided acceptable control.

B. COLONIZATION FOR LONG-TERM CONTROL

Colonization of a biological control agent is most often thought of in the classical sense, i.e., the entomogenous parasite is introduced into a susceptible population, actively searches for primary and alternate hosts, gradually becomes established in close association with the primary host population, and causes some numerical responses in that population.

Since baculoviruses do not search out their hosts, the success of colonization depends heavily on both the biology and behavior of the host and on environmental factors that enhance viral persistence and transmission within and between insect generations. Because predisposing conditions to the successful use of this strategy are rare, it is not surprising that there have been relatively few cases where a single introduction of a baculovirus has resulted in acceptable control in any year other than the one in which it was introduced.

One such case involved *G. hercyniae* NPV, which was accidentally introduced, probably through contaminated parasites that had been imported from Europe to mitigate sawfly populations in North America (Balch and Bird, 1944). The effects of a single introduction (a few treated trees) of the virus in Ontario were followed over a 10-year period. Epizootics occurred each year and sawfly populations were held below the economic threshold (Bird and Burk, 1961). As a result of this and earlier introductions and parasites, *G. hercyniae* has remained enzootic in Eastern North America since the 1950's. Originally attributed to transovum transmission (Bird, 1953; Neilson and Elgee, 1968), the successful colonization of this virus is now thought to be due largely to overwintering persistence on foliage (Entwistle and Adams, 1977) and perhaps dispersal by birds (Entwistle et al., 1977a,b, 1978) which ultimately leads to infection of newly emerged larvae in the succeeding generation.

Introductions of *N. sertifer*, *N. lecontei*, and *N. swainei* NPVs can be expected to exert at least some degree of control in succeeding generations as these viruses persist and spread rapidly in the ecosystems of their respective hosts (Bird, 1961; Smirnoff et al., 1962). Thus, colonization strategies with NPVs of these species certainly merit consideration. Introductions can be single or multiple point, and should be precalculated to account for degree and rate of NPV dispersal (Cunningham and Entwistle 1981).

There have been successful colonizations of the GV of the rhinoceros beetle, *Orcytes rhinocerus*, a serious pest of palm in the South Pacific Islands. In Western Samoa, virus introduced into log heaps established in *O. rhinoceros* populations and spread throughout the islands (Marschall, 1970). On Wallis Island, the virus spread over the entire island 2 months after its introduction into artificial log heaps (Hammes, 1971). As a result, palm damage dropped by 70-90%. Similar releases of the virus in Fiji, Tongatapu, American Samoa, the Takelau Islands, and Mauritius, either in log or manure heaps or as infected beetles, have resulted in the gradual spread of the virus and, generally, a significant decline in palm damage throughout the area (Bedford, 1981).

It should be noted that in what are considered major colonization successes, i.e., with sawfly and *Orcytes* baculoviruses, mechanisms of pathogenicity and host behavior have played major roles. These viruses are replicated in the midgut epithelium and are shed in the feces, providing for rapid horizontal transmission. Further, they are transmitted at mating, in *O. rhinoceros* GV by consumption of feces in contaminated breeding sites (Zelazny, 1976), and in sawfly NPVs by contamination of foliage during oviposition. Finally, since most sawfly species oviposit on coniferous hosts, persistent

NPV is readily available on needles consumed by emerging larvae in the succeeding generation. Viruses of pests of deciduous trees and most agricultural pests are lost to the soil with leaffall and through tilling, and are not readily available to insects of the following generation. Most of these virus do not replicate in the gut and are not dispersed in feces, so their effective colonization is much more difficult to achieve.

C. AUGMENTING NATURALLY OCCURRING BACULOVIRUS MORTALITY

Augmentation strategies may be particularly applicable in row crops where naturally occurring or introduced viruses can be returned to plant surfaces from the soil through cultivation or by other means. There is evidence that viruses in soil naturally contaminate leaves of low-growing crops through wind or rain splash (Jaques, 1967b; Tanada and Omi, 1974). Ignoffo (1978) suggested that epizootics could be created in field pest populations by blowing residual NPV from soil onto plants. For this to be reasonably effective, growers would need to know with some certainty the types, amounts, and distributions of viruses in their field. Thus, this tactic perhaps would best be implemented as a supplement to other control methods.

Ruzicka (1924) demonstrated efficacy of the nun moth, *Lymantria monacha*, NPV by blowing naturally contaminated litter into tree crowns with trench mortars. This apparently resulted in a virus epizootic. There is considerable evidence that forest insect viruses persist in soil and litter for extended periods (Podgwaite et al., 1979; Thompson and Scott, 1979; Mohamed et al., 1982; Kaupp, 1983). It is possible that epizootics could be initiated, or at least naturally occurring mortality could be increased, if technology were available to easily distribute contaminated litter from the forest floor to the forest canopy.

Parasitic and predacious insects are effective mechanical vectors of baculoviruses (Thompson and Steinhaus, 1950; Smirnoff, 1959; Raimo et al., 1977), and have been implicated in the natural transmission of these agents in the field (Smith et al., 1956; Bird, 1961; Reardon and Podgwaite, 1976; Levin et al., 1983). Similarly, birds feed on insects that have been infected with or killed by viruses (Hostetter and Biever, 1970; Entwistle et al., 1977a), and passively transport baculoviruses within their home range. The best documented case is that of *G. hercynia*, whose baculovirus has been carried up to 6 km from NPV-contaminated areas by birds, and whose dynamics appears to be partly regulated by this activity (Entwistle et al., 1977b). Small mammals also may feed on infected insects and foodstuffs and distribute infectious NPV in the environment (Lautenschlager and Podgwaite, 1977, 1979; Lautenschlager et al., 1980).

Certain mechanical vectors, particularly parasites, have been released or managed in direct control or colonization strategies, but rarely increase baculovirus mortality (Mohamed et al., 1981; Raimo and Reardon, 1981). This concept merits consideration but has not been exploited.

D. *INDUCING BACULOVIRAL EPIZOOTICS*

Both naturally occurring and artificially induced epizootics ensue most often after the pest insect has caused considerable economic loss. In most cases, this is a result of insufficient viral inoculum in the ecosystem during the initial susceptible stages of the pest or a distribution of virus such that it is unavailable for consumption and subsequent transmission of disease. Thus, it may be advisable to introduce virus earlier in the insects' life cycle, or perhaps in the preceding generation, to induce epizootics earlier than they normally would occur. Stairs (1965) introduced NPV into virus-free populations of the forest tent caterpillar *Malacasoma disstria* and initiated carryover and slowly developing epizootics in the next generation. Jaques (1977) found that an early single application of *T. ni* NPV and *P. rapae* GV was as effective in reducing cabbage loss as a series of viral applications. Podgwaite et al. (1981) introduced gypsy moth NPV into areas supporting sparse, enlarging gypsy moth populations (<175 egg masses/ha) by treating egg masses. This resulted in a 20% incidence of polyhedrosis in 4th-6th stage larvae in the year of treatment, followed by an NPV epizootic in the succeeding generation.

Early introduction of baculoviruses has not been widely tested, but lack of implementation probably lies in this strategy being recognized as a preventive measure. Often it is difficult to convince resource managers, farmers, and foresters to treat what at first glance are insignificant insect populations. This speaks to our collective inability, in the vast majority of cases, to forecast pest numbers with the degree of precision necessary to evoke such decisions.

E. INTEGRATED PEST MANAGEMENT

As emphasized earlier, most baculoviruses cannot be substituted for chemical pesticides with the expectation that they will provide the same quickness of kill and degree of population reduction. Thus, most are best suited for integration into a pest management scheme whose overall strategy is to take advantage of a variety of complementary control tactics, the combined effects of which bring pest populations below the economic threshold.

Although antagonisms do exist, baculoviruses generally are compatible with chemical pesticides, either as mixtures or when used sequentially (see reviews by Benz, 1971; Jaques and Morris, 1981). Falcon (1973) reported that cotton yields were not significantly different between plots that had received one application of Azodrin and then five applications of *H. zea* NPV and those that had received four applications of the chemical alone. Mohamed et al. (1983) tested Elcar in combination with eight chemical pesticides against *H. virescens*. Synergistic responses were found with several combinations, but differences were seldom in excess of 15% of calculated expected mortality. Since dosages used in the test were greater than normal field dosages, the authors concluded that at least with these chemical-NPV combinations, *H. virescens* control would not be altered significantly in the field. Jaques (1977) demonstrated increased efficacy when *T. ni* NPV and *A. californica* NPV were mixed with chemicals for control of cabbage looper and imported cabbage worm on late cabbage. Morris (1977) concluded that NPV plus a low dose of Sumithion was effective in suppressing spruce budworm populations for 3 years after treatment; there were no concomitant deleterious effects on the incidence of budworm parasites.

Combinations of viruses, or combinations of viruses with other entomopathogens, especially (*B.t.*), have shown promise in reducing pest populations. Jaques (1977) found that either *T. ni* NPV or *A. californica* NPV in combination with formulations of *B.t.* generally increased crop protection over that resulting from the use of the viruses in combination without *B.t.* Sears et al. (1983) found that various combinations of *T. ni* NPV, *A. californica* NPV, and *B.t*, provided 90% marketable cabbage compared with 95% using either permethrin or methomyl. Bell and Romine (1980) reported adequate control of *H. virescens* on cotton with a combination of *B.t.* and *A. californica* NPV. However, Luttrell et al. (1982) found that combinations of *B.t.* with *H. zea* NPV and *A. californica* NPV against *H. zea* and *H. virescens* resulted in no greater mortality than that elicited by either virus alone. They concluded that the use of these combinations was not advantageous. Similarly, Johnson

(1982) found that combinations of *H. zea* NPV and *B.t.* on cotton, although suppressing pest populations by an average of 28% compared with control plots, were no more effective than either microbial used alone. Bell and Romine (1982) reported that a combination of *B.t.* and *A. californica* NPV resulted in a 95% reduction of *B. thurberiella* on cotton compared with untreated controls, but they speculated that the combination might not be cost effective when the cotton leafperforator is the only pest in the system.

Other integrated strategies have been tested. Campbell (1983) found that various combinations of gypsy moth NPV egg mass treatments, Disparlure, and mechanical methods were ineffective in reducing gypsy moth numbers in succeeding generations. However, parasite-NPV combinations have shown some promise for use in gypsy moth management systems. Raimo and Reardon (1981) found that the release of NPV-contaminated *Apanteles melanoscelus* females resulted in a 39% incidence of NPV in treated blocks compared with 22% in controls, while percentage parasitism was virtually the same in both treated and control blocks.

These examples, some positive, some not, reveal an increasing willingness toward integrating baculoviruses into pest management strategies through a variety of tactics.

III. APPLICATION TACTICS

Strategies discussed here can be implemented by a variety of tactics, some of which have been tested extensively. There is little question that direct control of outbreak populations is most often successful with broadcast application, either from aircraft or with ground spray equipment. Aerial application as it relates to viral control of forest pests is discussed in detail by Akesson and Yates (1978). Current aerial and ground technology (foggers, mistblowers, etc.) are assessed by Smith and Bouse (1981).

Other tactics have not been widely tested and are not in general use. Some of these have been suggested by Ignoffo (1978) and include (a) the release of both virus-infected and contaminated hosts (Evans and Allaway, 1983); (b) the release of contaminated parasitic and predacious insects; (c) the contamination, release, and management of birds and mammals, (d) the use of insect attractants to lure hosts to contaminated baits (Gard and Falcon, 1978); (e) the mechanical manipulation of the environment to make naturally occurring baculovirus more available for host consumption; (f) the induction of "latent" virus through the use of chemical stressors; and (g) the development of timed-release technology for distribution of virus.

The choice of tactical approaches for implementing control strategies that include the use of baculoviruses depends largely on the dynamics of the host-pest system to be managed, and the relative threat of economic damage. It may be possible to intercede with spot inoculation tactics early in the insects' developmental cycle, or in the preceding generation. However, waiting until pest numbers have reached the economic threshold almost certainly will require the use of broadcast application. What is critical to choice of tactics, and what is almost always lacking, is a clear understanding of host dynamics. Less clear is how introductions of baculoviruses affect the flux of succeeding generations, both quantitatively and qualitatively. If baculoviruses are to be fully exploited for more than knee-jerk responses to pest crises, these areas must be more fully understood.

IV. SUMMARY AND CONCLUSIONS

Pest managers appear to be at a crossroad in the collective development of baculoviruses as microbial insecticides. Although for several decades, baculoviruses have been recognized as potentially useful in controlling noxious pests, only few are available for use in pest management systems. The reasons for this are complex and interrelated but the primary reason involves efficacy. It is clear that if the marginally effective viruses, which are, ironically, pathogens of the most economically important insects, are to be seriously considered as alternatives to chemicals in any strategy that includes broadcast application, they must be formulated in such a manner as to extend or amplify their activity on foliage, or they must be manipulated genetically to enhance their virulence. Commercialization of baculovirus products has been hindered because these products are less marketable than chemicals, because of their specificity, and because of their unpredictability in the field. Specificity, of course, is a double-edged sword, cutting for the environmentalist but against the producer who would prefer a product that can be used against a broad spectrum of pests. That this has been recognized is evidenced by both the commercialization of *H. zea* NPV and increased interest in the development and commercialization of *A. californica* NPV, two "broad-spectrum" viruses which are effective against a variety of agricultural and forest pests. There is no logical argument against research on increasing the host range of the more specific baculoviruses through genetic manipulation. In the shorter term, methods research should focus intently on extending the activity of baculoviruses once applied to the host plant. This will be realized only through an intensive, systematic research and development program in the area of formulation and application.

The public at large, the users, generally equate the performance of microbials with that of chemicals--they expect equivalent results. The future of baculoviruses as pesticides may well lie in the collective abilities of scientists, educators, and producers to resolve this misconception by promoting the use of some baculoviruses as adjuncts to, rather than substitutes for, other pesticidal agents.

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REFERENCES

Akesson, N. B., and Yates, W. E. (1978). Aerial application technology: Aircraft and spray systems. *In* "The Douglas-Fir Tussock Moth: A Synthesis" (M. H. Brookes, R. W. Stark, and R. W. Campbell, eds.), pp. 160-164. U.S. Dept. Agric. Tech. Bull. 1585.

Andrews, G. L., and Sikorowski, P. P. (1973). Effects of cotton leaf surface on the nuclear-polyhedrosis virus of *Heliothis zea* and *Heliothis virescens* (Lepidoptera: Noctuidae). *J. Invertebr. Pathol. 22*, 290-291.

Balch, R. E., and Bird, F. T. (1944). A disease of the European spruce sawfly, *Gilpinia hercyniae* (Htg), and its place in natural control. *Sci. Agr. 25*, 65-80.

Bedford, G. O. (1981). Control of the rhinoceros beetle by baculovirus. *In* "Microbial Control of Pests and Plant Diseases 1970-1980" (H. D. Burges, ed.), pp. 409-426. Academic Press, London.

Bell, M. R., and Romine, C. L. (1980). Tobacco budworm field evaluation of microbial control in cotton using *Bacillus thuringiensis* and a nuclear polyhedrosis virus with a feeding adjuvant. *J. Econ. Entomol. 73*, 427-430.

Bell, M. R., and Romine, C. L. (1982). Cotton leafperforator (Lepidoptera: Lyonetidae): Effect of two microbial insecticides on field populations. *J. Econ. Entomol. 75*, 1140-1142.

Benz, G. (1971). Synergism of micro-organism and chemical insecticides. *In* "Microbial Control of Insects and Mites" (H. D. Burges and N. W. Hussey, eds.), pp. 327-355. Academic Press, London.

Bird, F. T. (1953). The effect of metamorphosis on the multiplication of an insect virus. *Can. J. Zool. 31*, 300-303.

Bird, F. T. (1961). Transmission of some insect viruses with particular reference to ovarial transmission and its importance in the development of epizootics. *J. Invertebr. Pathol. 3*, 352-380.

Bird, F. T., and Burk, J. M. (1961). Artificially disseminated virus as a factor controlling the European spruce sawfly, *Diprion hercyniae* (Htg.) in the absence of introduced parasites. *Can. Entomol. 93*, 228-238.

Bohmfalk, G. T. (1982). Progress with the nuclear polyhedrosis virus of *Heliothis zea* by commercialization of Elcar. *Proc. 3rd Intern. Colloq. Invertebr. Pathol., Brighton, UK*, pp. 113-117.

Bull, D. L. (1978). Formulations of microbial insecticides: Microencapsulation and adjuvants. *Misc. Publ. Entomol. Soc. Amer. 10*, 11-20.

Bullock, H. R. (1967). Persistence of *Heliothis* nuclear-polyhedrosis virus on cotton foliage. *J. Invertebr. Pathol. 9*, 434-436.

Bullock, H. R., Hollingsworth, J. P., and Hartsack, A. W., Jr. (1970). Virulence of *Heliothis* nuclear polyhedrosis virus exposed to monochromatic ultraviolet irradiation. *J. Invertebr. Pathol. 16*, 419-422.

Campbell, R. W. (1983). Gypsy moth (Lepidoptera: Lymantriidae) control trials combining nucleopolyhedrosis virus, disparlure, and mechanical methods. *J. Econ. Entomol. 76*, 610-614.

Couch, T. L., and Ignoffo, C. M. (1981). Formulation of insect pathogens. *In* "Microbial Control of Pests and Plant Diseases 1970-1980" (H. D. Burges, ed.), pp. 622-634. Academic Press, London.

Cunningham, J. C., and Entwistle, P. F. (1981). Control of sawflies by baculovirus. *In* "Microbial Control of Pests and Plant Diseases 1970-1980" (H. D. Burges, ed.), pp. 379-407. Academic Press, London.

David, W. A. L. (1969). The effect of ultraviolet radiation of known wave-lengths on a granulosis virus of *Pieris brassicae*. *J. Invertebr. Pathol. 14*, 336-342.

David, W. A. L., Gardiner, B. O. C., and Woolner, M. (1968). The effects of sunlight on a purified granulosis virus of

Pieris brassicae applied to cabbage leaves. *J. Invertebr. Pathol. 11*, 496-501.

Entwistle, P. F., and Adams, P. H. W. (1977). Prolonged retention of infectivity in the nuclear polyhedrosis virus of *Gilpinia hercyniae* (Hymenoptera, Diprionidae) on foliage of spruce species. *J. Invertebr. Pathol. 29*, 392-394.

Entwistle, P. F., Adams, P. H. W., and Evans, H. F. (1977a). Epizootiology of a nuclear polyhedrosis virus in European spruce sawfly (*Gilpinia hercyniae*). The status of birds as dispersal agents during the larval season. *J. Invertebr. Pathol. 29*, 354-360.

Entwistle, P. F., Adams, P. H. W., and Evans, H. F. (1977b). Epizootiology of a nuclear polyhedrosis virus in European Spruce sawfly (*Gilpinia hercyniae*). Birds as dispersal agents of the virus during winter. *J. Invertebr. Pathol. 30*, 15-19.

Entwistle, P. F., Adams, P. H. W., and Evans, H. F. (1978). Epizootiology of a nuclear polyhedrosis virus in European Spruce sawfly (*Gilpinia hercyniae*): The rate of passage of infective virus through the gut of birds during cage tests. *J. Invertebr. Pathol. 31*, 307-312.

Evans, H. F., and Allaway, G. P. (1983). Dynamics of baculovirus growth and dispersal in *Mamestra brassicae* L. (Lepidoptera: Noctuidae) larval populations introduced into small cabbage plots. *Appl. Environ. Microbiol. 45*, 493-501.

Falcon, L. A. (1973). Biological factors that affect the success of microbial insecticides: development of integrated control. *Ann. New York Acad. Sci. 217*, 173-186.

Falcon, L. A. (1982). The baculoviruses of *Autographa, Trichoplusia, Spodoptera* and *Cydia*. *Proc. 3rd Intern. Colloq. Invertebr. Pathol., Brighton, UK*, pp. 125-128.

FAO. (1970). Pest resistance to pesticides in agriculture. Importance, recognition and countermeasure. Food and Agric. Organ., UN. Rome, Italy.

Gard, I. E., and Falcon, L. A. (1978). Autodissemination of entomopathogens: virus. *In* "Microbial Control of Insect Pests: Future Strategies in Pest Management Systems" (G. E. Allen, C. M. Ignoffo, and R. P. Jaques, eds.), pp. 46-51. NSF-USDA-U.FLA., Gainesville.

Hammes, C. (1971). Multiplication et introduction d'um virus d' *Oryctes rhinoceros* a l'ile Wallis. *C.R. Acad. Sci. (Paris) 273*, 1048-1050.

Hostetter, D. L., and Biever, K. D. (1970). The recovery of virulent nuclear polyhedrosis virus of the cabbage looper, *Trichoplusia ni*, from feces of birds. *J. Invertebr. Pathol. 15*, 173-176.

Hostetter, D. L., Smith, D. B., Pinnell, R. E., Ignoffo, C. M., and McKibben, G. H. (1982). Laboratory evaluation of adjuvants for use with *Baculovirus heliothis* virus. *J. Econ. Entomol. 75*, 1114-1119.

Huber, J. (1982). The baculoviruses of *Cydia pomonella* and other tortricids. *Proc. 3rd Intern. Colloq. Invertebr. Pathol., Brighton, UK*, pp. 119-124.

Ignoffo, C. M. (1978). Strategies to increase the use of entomopathogens. *J. Invertebr. Pathol. 31*, 1-3.

Ignoffo, C. M., and Batzer, O. F. (1971). Microencapsulation and ultraviolet protectants to increase sunlight stability of an insect virus. *J. Econ. Entomol. 64*, 850-853.

Ignoffo, C. M., and Couch, T. L. (1981). The nucleopolyhedrosis virus of *Heliothis* species as a microbial insecticide. *In* "Microbial Control of Pests and Plant Diseases 1970-1980" (H. D. Burges, ed.), pp. 329-362. Academic Press, London.

Ignoffo, C. M., Parker, F. D., Boening, O. P., Pinnell, R. E., and Hostetter, D. L. (1973). Field stability of the *Heliothis* nucleopolyhedrosis virus on corn silks. *Environ. Entomol. 2*, 302-303.

Ignoffo, C. M., Hostetter, D. L., and Pinnell, R. E. (1974). Stability of *Bacillus thuringiensis* and *Baculovirus heliothis* on soybean foliage. *J. Environ. Entomol. 3*, 117-119.

Jaques, R. P. (1967a). The persistence of the nuclear-polyhedrosis virus in the habitat of the host insect, *Trichoplusia ni*. I. Polyhedra deposited on foliage. *Can. Entomol. 99*, 785-794.

Jaques, R. P. (1967b). The persistence of a nuclear polyhedrosis virus in the habitat of the host insect, *Trichoplusia ni*. II. Polyhedra in soil. *Can. Entomol. 99*, 820-829.

Jaques, R. P. (1972). The inactivation of foliar deposits of viruses of *Trichoplusia ni* and *Pieris rapae* and tests on protectant activities. *Can. Entomol. 104*, 1985-1994.

Jaques, R. P. (1977). Field efficacy of viruses infectious to the cabbage looper and imported cabbageworm on late cabbage. *J. Econ. Entomol. 70*, 111-118.

Jaques, R. P., and Morris, O. N. (1981). Compatibility of pathogens with other methods of pest control and with different crops. *In* "Microbial Control of Pests and Plant Diseases 1970-1980" (H. D. Burges, ed.), pp. 695-715. Academic Press, London.

Johnson, D. R. (1982). Suppression of *Heliothis* spp. on cotton by using *Bacillus thuringiensis, Baculovirus heliothis*, and two feeding adjuvants. *J. Econ. Entomol. 75*, 207-210.

Katagiri, K. (1981). Pest control by cytoplasmic polyhedrosis viruses. *In* "Microbial Control of Pests and Plant Diseases 1970-1980" (H. D. Burges, ed.), pp. 433-440. Academic Press, London.

Kaupp, W. J. (1983). Persistence of *Neodiprion sertifer* (Hymenoptera: Diprionidae) nuclear polyhedrosis virus on *Pinus contorta* foliage. *Can. Entomol. 115*, 869-873.

Lautenschlager, R. A., and Podgwaite, J. D. (1977). Passage of infectious nuclear polyhedrosis virus through the alimentary tracts of two small mammal predators of gypsy moth, *Lymantria dispar*. *Environ. Entomol. 6*, 737-738.

Lautenschlager, R. A., and Podgwaite, J. D. (1979). Passage of nucleopolyhedrosis virus by avian and mammalian predators of the gypsy moth, *Lymantria dispar*. *Environ. Entomol. 8*, 210-214.

Lautenschlager, R. A., Podgwaite, J. D., and Watson, D. E. (1980). Natural occurrence of the nucleopolyhedrosis virus of the gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae) in wild birds and mammals. *Entomophaga 25*, 261-267.

Levin, D. B., Laing, J. E., Jaques, R. P., and Corrigan, J. E. (1983). Transmission of the granulosis virus of *Pieris rapae* (Lepidoptera: Pieridae) by the parasitoid *Apanteles glomeratus* (Hymenoptera: Braconidae). *Environ. Entomol. 12*, 166-170.

Lewis, F. B. (1981). Control of gypsy moth by a baculovirus. *In* "Microbial Control of Pests and Plant Diseases 1970-1980" (H. D. Burges, ed.), pp. 363-377. Academic Press, London.

Lewis, F. B., and Etter, D. O., Jr. (1978). Use of pathogens in forest pest management systems: Gypsy moth, *lymantria dispar* L. *In* "Microbial Control of Insect Pests: Future Strategies in Pest Management Systems" (G. E. Allen, C. M. Ignoffo, and R. P. Jaques, eds.), pp. 261-272. NSF-USDA. Univ. Florida, Gainesville.

Lewis, F. B., and Podgwaite, J. D. (1982). Unpublished data on Gypchek field tests. Center for Biological Control of Forest Insects and Diseases. Hamden, CT.

Lewis, F. B., and Yendol, W. G. (1981). Gypsy moth nucleopolyhedrosis virus: Efficacy. *In* "The Gypsy Moth: Research Toward Integrated Pest Management" (C. C. Doane and M. L. McManus, eds.), pp. 503-512. U.S. Dept. Agr. Tech. Bull. 1584.

Lewis, F. B., McManus, M. L., and Schneeberger, N. F. (1979). Guidelines for the use of Gypchek to control the gypsy moth. *USDA Forest Serv. Res. Paper NE-441*, pp. 9.

Luttrell, R. G., Young, S. Y., Yearian, W. C., and Horton, D. L. (1982). Evaluation of *Bacillus thuringiensis*-spray adjuvant-viral insecticide combinations against *Heliothis* spp. (Lepidoptera: Noctuidae). *Environ. Entomol. 11*, 783-787.

Luttrell, R. G., Yearian, W. C., and Young, S. Y. (1983). Effect of spray adjuvants on *Heliothis zea* (Lepidoptera:

Noctuidae) nuclear polyhedrosis virus efficacy. *J. Econ. Entomol. 76*, 162-167.

Magnoler, A. (1968). Laboratory and field experiments on the effectiveness of purified and nonpurified nuclear polyhedral virus of *Lymantria dispar* L. *Entomophaga 13*, 335-344.

Marschall, K. J. (1970). Introduction of a new virus disease of the coconut rhinoceros beetle in Western Samoa. *Nature (London) 225*, 288-289.

Martignoni, M. E. (1978). Production, activity and safety. *In* "The Douglas-Fir Tussock Moth: A Synthesis" (M. H. Brookes, R. W. Stark, and R. W. Campbell, eds.), pp. 140-147. U.S. Dept. Agr. Tech. Bull. 1585.

Mohamed, A. I., Young, S. Y., and Yearian, W. C. (1983). Effects of microbial agent-chemical pesticide mixtures on *Heliothis virescens* (F.) (Lepidoptera: Noctuidae). *Environ. Entomol. 12*, 478-481.

Mohamed, M. A., Coppel, H. C., Hall, D. J., and Podgwaite, J. D. (1981). Field release of virus-sprayed adult parasitoids of the European pine sawfly (Hymenoptera: Diprionidae) in Wisconsin. *Great Lakes Entomol. 14*, 171-175.

Mohamed, M. A., Coppel, H. C., and Podgwaite, J. D. (1982). Persistence in soil and on foliage of nucleopolyhedrosis virus of the European pine sawfly, *Neodiprion sertifer* (Hymenoptera: Diprionidae). *Environ. Entomol. 11*, 1116-1118.

Morris, D. S. (1972). A cooperative programme of research into the management of pome-fruit pests in southeastern Australia. III. Evaluation of nuclear granulosis virus for control of codling moth. *Abstr. 14th Intern. Congr. Entomol., Canberra*, p. 238.

Morris, O. N. (1971). The effect of sunlight, ultraviolet and gamma radiations and temperature on the infectivity of nuclear polyhedrosis virus. *J. Invertebr. Pathol. 18*, 292-294.

Morris, O. N. (1977). Long-term effects of aerial applications of virus-fenitrothion combinations against the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Entomol. 109*, 9-14.

NAS. (1975). "Pest Control: An Assessment of Present and Alternative Technologies," Vol. 4, p. 170. "Forest Pest Control" Nat. Acad. Sci., Washington, D.C.

Neilson, M. M., and Elgee, D. E. (1968). The method and role of vertical transmission of a nucleopolyhedrosis virus in the European spruce sawfly, *Diprion hercyniae*. *J. Invertebr. Pathol. 12*, 132-139.

Podgwaite, J. D., Shields, K. S., Zerillo, R. T., and Bruen, R. B. (1979). Environmental persistence of the nucleopolyhedrosis virus of the gypsy moth, *Lymantria dispar*. *Environ. Entomol. 8*, 528-536.

Podgwaite, J. D., Smith, H. R., and Zerillo, R. T. (1981). Feasibility of integrating nucleopolyhedrosis virus treatment of egg masses with small mammal management for control of the gypsy moth, *Lymantria dispar* . *Abstr. 14th Annu. Meet. Soc. Invertebr. Pathol., Bozeman, Montana,* pp. 41-42.

Podgwaite, J. D., Rush, P., Hall, D., and Walton, G. S. (1984). Efficacy of the *Neodiprion sertifer* (Hymenoptera: Diprionidae) nucleopolyhedrosis virus (baculovirus) product, Neochek-S. *J. Econ. Entomol.*, in press.

Raimo, B. J., and Reardon, R. C. (1981). Preliminary attempts to use parasites in combination with pathogens in an integrated control approach. *In* "The Gypsy Moth: Research Toward Integrated Pest Management" (C. C. Doane and M. L. McManus, eds.), pp. 408-413. U.S. Dept. Agr. Tech. Bull. 1584.

Raimo, B., Reardon, R. C., and Podgwaite, J. D. (1977). Vectoring gypsy moth nuclear polyhedrosis virus by *Apanteles melanocelus* (Hym.: Braconidae). *Entomophaga 22*, 207-215.

Reardon, R. A., and Podgwaite, J. D. (1976). Disease-parasitoid relationships in natural populations of *Lymantria dispar* (Lep.: Lymantriidae) in the northeastern United States. *Entomophaga 21*, 333-341.

Rollinson, W. D., Lewis, F. B., and Waters, W. E. (1965). The successful use of a nuclear polyhedrosis virus against the gypsy moth. *J. Invertebr. Pathol. 7*, 515-517.

Ruzicka, J. (1924). Die neusten Erfahrungen uber die Nonne in Bohmen. *Cent. Ges. Forsta. 50*, 33-68.

Sears, M. K., Jaques, R. P., and Laing, J. E. (1983). Utilization of action thresholds for microbial and chemical control of lepidopterous pests (Lepidoptera: Noctuidae, Pieridae) on cabbage. *J. Econ. Entomol. 76*, 368-374.

Smirnoff, W. A. (1959). Predators of *Neodiprion swainei* Midd. (Hymenoptera: Tenthredinidae) larval vectors of virus diseases. *Can. Entomol. 91*, 246-248.

Smirnoff, W. A., Fettes, J. J., and Haliburton, W. (1962). A virus disease of Swaine's jack pine sawfly, *Neodiprion swainei* Midd. sprayed from an aircraft. *Can. Entomol. 94*, 477-486.

Smith, D. B., and Bouse, L. F. (1981). Machinery and factors that affect the application of pathogens. *In* "Microbial Control of Pests and Plant Diseases 1970-1980" (H. D. Burges, ed.), pp. 635-653. Academic Press, London.

Smith, O. J., Hughes, K. M., Dunn, P. H., and Hall, I. M. (1956). A granulosis virus disease of the western grape leaf skeletonizer and its transmission. *Can. Entomol. 88*, 507-515.

Stairs, G. R. (1965). Artificial initiation of virus epizootics in forest tent caterpillar populations. *Can. Entomol. 97*, 1059-1062.

Stairs, G. R. (1971). Use of viruses for microbial control of insects. *In* "Microbial Control of Insects and Mites" (H. D. Burges and N. W. Hussey, eds.). Academic Press, London.

Stelzer, M. J., and Neisess, J. (1978). Field efficacy tests. *In* "The Douglas-Fir Tussock Moth: A Synthesis" (M. H. Brookes, R. W. Stark, and R. W. Campbell, eds.), pp. 149-152. U.S. Dept. Agr. Tech. Bull. 1585.

Tanada, Y., and Omi, E. M. (1974). Persistence of insect viruses in field populations of alfalfa insects. *J. Invertebr. Pathol. 23*, 360-365.

Thompson, C. G., and Scott, D. W. (1979). Production and persistence of the nuclear polyhedrosis virus of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae), in the forest ecosystem. *J. Invertebr. Pathol. 33*, 57-65.

Thompson, C. G., and Steinhaus, E. A. (1950). Further tests using a polyhedrosis virus to control the alfalfa caterpillar. *Hilgardia 19*, 411-414.

Vail, P. V., and Jay, D. L. (1973). Pathology of a nuclear polyhedrosis virus of the alfalfa looper in alternate hosts. *J. Invertebr. Pathol. 21*, 198-204.

Wollam, J. D., Yendol, W. G., and Lewis, F. B. (1978). Evaluation of aerially-applied nuclear polyhedrosis virus for suppression of the gypsy moth, *Lymantria dispar* L. U.S. Dept. Agr. Forest. Serv. Res. Paper NE-396. p. 8.

Yendol, W. G., and Hamlen, R. A. (1973). Ecology of entomogenous viruses and fungi. *Ann. N.Y. Acad. Sci. 217*, 18-30.

Yendol, W. G., Hedlund, R. C., and Lewis, F. B. (1977). Field investigations of a baculovirus of the gypsy moth, *Lymantria dispar* L. *J. Econ. Entomol. 70*, 598-602.

Zelazny, B. (1976). Transmission of a baculovirus in populations of *Orcytes rhinoceros*. *J. Invertebr. Pathol. 27*, 221-227.