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# MODELLING THE EPIZOOTIOLOGY OF *SPODOPTERA EXIGUA* NUCLEAR POLYHEDROSIS VIRUS IN A SPATIALLY DISTRIBUTED POPULATION OF *SPODOPTERA EXIGUA* IN GREENHOUSE CHRYSANTHEMUMS

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## Summary

An epizootiological simulation model was developed to study the feasibility of using Spodoptera exigua nuclear polyhedrosis virus for inoculative control of S. exigua in greenhouse chrysanthemum crops. In the model, eight developmental stages of the insect and three routes of infection are distinguished. S. exigua populations are made up of patches of caterpillars. Each patch originates from a single egg batch. Patches differ in the initial number of infected eggs. The epizootiology of SeMNPV in a patch depends strongly on the initial number of infected eggs. Therefore, a compound simulation approach is adopted, classifying patches according to initial number of infected eggs and time of initiation. The epizootiology of the virus in the whole population is obtained by summation over the different infection-age classes of patches.

Model results indicate that the presence of a stable polyhedra population is a crucial factor determining long-term control by inoculative spraying.

## 1. **Introduction**

Beet armyworm, Spodoptera exigua (Hübner), is a polyphagous pest of cultivated crops in tropical and subtropical regions (Brown & Dewhurst, 1975). After accidental introduction it became a serious pest in ornamental and vegetable crops in greenhouses in the Netherlands (Smits, 1987). Damage in chrysanthemum crops is mainly caused by late instar larvae feeding on the upper leaves and flowers. Resistance against insecticides (Poe et al., 1973; Cobb & Bass, 1975) makes chemical control very difficult, so that alternatives had to be found. Smits (1987) found that Beet armyworm can be controlled by inundative spraying of S. exigua multiply-embedded nuclear polyhedrosis virus (SeMNPV). In chrysanthemum crops little damage can be tolerated. Therefore, SeMNPV should be sprayed during the initial phase of exponential growth. A 100% control is rarely achieved, however. To prevent pest resurgence after spraying, the virus should maintain itself in the population and thereby reduce the net reproductive rate R (number of adult daughters per female) of the moth population below 1.

A simulation model was developed to study the long-term epizootiology of SeMNPV in S. exigua populations in glasshouse chrysanthemums and evaluate whether inoculative use of this virus may lead to effective control and lasting population regulation. The model is based on life-history and host-virus interaction data published in literature. Sensitivity analysis of the model increases the insight in the dynamics of the insect-virus system and pinpoints the main factors influencing its dynamics. This basic knowledge may be used to develop management strategies. In this paper we present the structure and some results of the model.

## 2. Description of the model

### 2.1 Structure

Age-structure. The model simulates the temporal dynamics of eight developmental stages of the insect: eggs, five larval stages (L1-L5), pupae and adult females. Males are ignored in the model, assuming that their number is sufficient to assure fertilization of the females. Numbers and development within each stage are represented using the fractional boxcar-train method (Goudriaan, 1986; Goudriaan & van Roermund, 1989), which allows for variable duration of development according to fluctuating temperature and individual variation. Mortality during development is calculated using a relative mortality rate which varies with temperature and developmental stage. Separate boxcars are used for infected individuals.

Infection-processes. Three routes of infection are distinguished:
(1) caterpillars consuming a sufficient amount of sprayed polyhedra
(2) caterpillars eating from a leaf contaminated by a deceased caterpillar (horizontal transmission)
(3) females laying infected eggs (vertical transmission)

Infection by sprayed polyhedra. It is assumed that sprayed polyhedra are distributed homogeneously over the leaf layers of the crop (Leaf area index=3). The rate of ingestion of polyhedra by caterpillars equals the product of the feeding rate and the density of polyhedra on the leaf surface. The feeding rate is instar dependent (Table 1). Each ingested polyhedron has the same chance (p) of causing a lethal infection.

Polyhedra are inactivated by UV-radiation at a constant relative rate, analogous to radioactive decay. A proportion of the polyhedra may be deposited at places sheltered from UV radiation. These sheltered polyhedra can remain active for several years (Jacques, 1985; Olofsson, 1988). In the model, unexposed polyhedra remain infectious throughout the simulated period of 150 days.

Horizontal transmission. The eggs are laid on the lower leaves of the hostplant. After emergence first instar larvae migrate vertically to the top leaves. From the third larval stage, larvae show horizontal dispersal. Finally, an area of 1 $m^2$ is infested (Smits & Vlak, 1988). The sizes of the dispersive ranges (i.e. all the leaves that can be visited during an instar) are listed in Table 1. In the model, polyhedra spread over one leaf after disintegration of an infected larva. The relative infection rate due to horizontal transmission is determined by the frequency of visits of caterpillars to such contaminated leaves. One visit is sufficient to cause a lethal infection.

Vertical transmission. Some of the infected fifth instar larvae develop into females that lay eggs that are virus infected. Eggs infected by such vertical transmission are supposed to be randomly (Poisson) distributed over the infected females' egg batches. The initial number of infected eggs in an egg batch has a strong curvilinear effect on the number of adult females that will emerge from it (Fig 1C). Therefore, constructing a 'homogeneous' model with an average number of initially infected eggs per patch would result in erroneous results. Instead, the compound simulation approach is adopted (Fransz, 1974; Rabbinge et al., 1984; Sabelis & Laane, 1986; Ward et al., 1989). Clusters are divided over classes, taking initial number of infected eggs and time since egglaying (= time of start of a cluster) as stratification criteria. The model is not valid at high densities because interactions between patches are neglected. As damage tolerance in chrysanthemum is very low, we are only interested in the low density situations which are correctly represented by the model.

### 2.2 Parameters

Temperature dependent development rates are calculated by linear interpolation using experimental data from Fye & McAda (1972). The sex ratio is 1:1 (Smits, 1986). Mortality during egg development totals to 10% at optimal temperatures (20-30°C) and increases to 40 % at 15°C and further to 90% at 8°C (Poe et al., 1973). Mortality during larval development is 15% (Fye & McAda, 1972). Mortality in the pupal stage is 15% at 20-30°C and 40% at 33°C (Fye & McAda, 1972). Eggs are laid 5.1 [Picture] 1.9 days after adult emergence, irrespective of temperature (Fye & McAda, 1972). Fecundity is [Picture] 500 eggs per female (Fye & McAda, 1972). The eggs are laid in batches of 25-50 (Smits et al., 1986). In the model, the number of eggs per batch is set to 35 eggs. Instar specific rates of leaf consumption are given in Table 1. To estimate the instar-specific infection chance per ingested polyhedron, p, the exponential model proposed by Hughes et al. (1984) is fitted to the experimental data of Smits & Vlak (1988). The estimated values of p are given in Table 1.

Table 1: Consumption rate[1] (C, cm$^2$.day$^{-1}$), infection chance per ingested SeMNPV polyhedron (p, $\#^{-1}$), product of C and p, indicating the susceptibility to virus spray, number of leaves visited per day (L$_v$, #.day$^{-1}$) and the number of leaves in the dispersive range (L$_r$, #) for five larval instars of *Spodoptera exigua*.

| Instar | C | p | C * p | $L_v$ | $L_r$ |
|---|---|---|---|---|---|
| L1 | 0.024 | .14 | .030 | 1 | 50 |
| L2 | 0.22 | .26 | .057 | 1 | 5 |
| L3 | 1.8 | .014 | .025 | 1 | 320 |
| L4 | 7.3 | .0038 | .028 | 3 | 320 |
| L5 | 14 | .000056 | .00078 | 5 | 320 |

[1] from Smits (1987).

Due to inactivation of polyhedra exposed to UV radiation, the proportion of infected caterpillars feeding on an infected medium, reduced from 66% to 33% in 1 to 3 days (MacCollom & Reed, 1971; Podgwaite et al., 1979; Jacques, 1985). Assuming an exponential decay of infective polyhedra and using the exponential infection model, these data yield estimates of the relative infection rate of 1 to .33 day$^{-1}$. In the model a relative infection rate of 0.7 day$^{-1}$ is assumed, corresponding to a halflife of 1 day. No data from greenhouse environments, which have low UV levels, are available.

The incubation period (time elapsed between infection and death) decreases with temperature. Infected larvae disintegrate in 4 days at 30°C and in 8 days at 20°C. The instar-dependent numbers of leaves visited per day are given in Table 1. The fraction infected L5 larvae developing into infected females is rather arbitrarily set to 50%. Smits (1987) observed a percentage of infected eggs in broods of infected females of 10-28%. This proportion is set to 15% in the model. No differences in fecundity, mortality or egg hatchability could be shown between healthy and infected females (Smits, 1987).

## 3. Results

The interaction of the basic processes presented above can be studied on the level of the cluster and on that of the system as a whole. First some aspects of the behavior of separate clusters are presented.

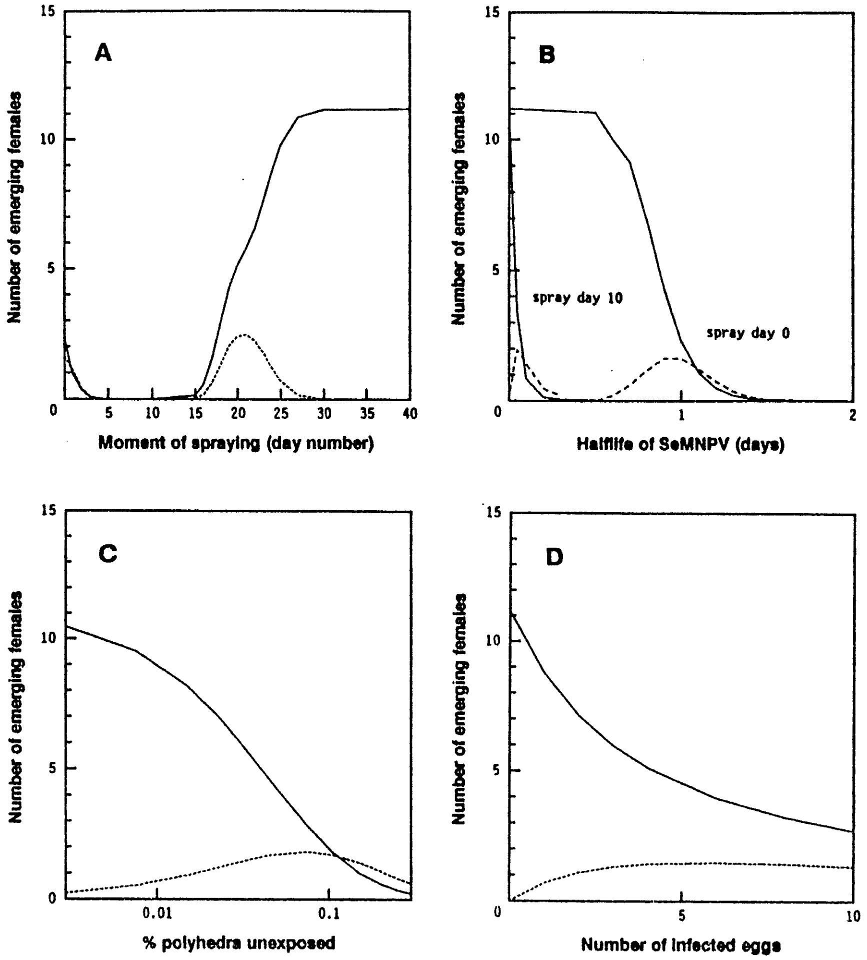

Figure 1: Analysis of cluster model. Figs A through D show the dependency of the number of healthy ( —— ) and infected ( -------- ) females emerging from a cluster on (A) the time between oviposition and spraying; (B) the halflife of sprayed polyhedra for two spraying moments (u = 0); (C) the fraction unexposed polyhedra, u, for zero or five initially infected eggs (spray on the day of oviposition); and (D) the number of initially infected eggs (vertical transmission; no spray); In all figures, temperature is 20°C and virus is sprayed at a dose of $10^8$ polyhedra/$m^2$.

### 3.1 Cluster behavior

The behavior of a cluster is characterized by the number of healthy and infected females that emerge from it. A large reduction (almost 100%) of moth numbers is accomplished when SeMNPV is sprayed in a 'window' of 10 days between day 5 and 15 after oviposition (Fig 1A). In this period, the more susceptible L1 to L4 instars are predominating (Table 1). The relation between mortality and the halflife of SeMNPV depends on the day of spraying (Fig 1B). When the spraying is well timed (day 10) a short halflife, approximately 0.5 day, still gives 100% control. When the virus is sprayed too early (day 0) a halflife of 1.5 days is needed to obtain complete control. For both days of spraying there is an 'optimum' halflife giving the greatest output of infected females. Shorter halflifes hamper the infection process. Longer halflifes give such a rapid horizontal infection that all caterpillars are infected and killed before the fifth stage. The effect of the unexposed polyhedra on the reduction of moth numbers is shown in Fig 1C. The number of emerging females strongly decreases as the proportion of unexposed polyhedra, u, increases. When u exceeds 0.1% ($10^5$ polyhedra/$m^2$) more infected than healthy females emerge. Fig 1D shows that the initial number of infected eggs has a major effect on the number of emerging females. At a vertical transmission level of 15% (ca. 5 infected eggs per cluster), the number of healthy females emerging from a cluster is halved, compared to the disease-free situation. At higher vertical transmission rates the reduction is even greater. The number of infected females that emerges from a cluster varies little with the level of vertical transmission. At all vertical transmission levels, the number of healthy females emerging from a cluster exceeds the number of infected ones with a factor two, also at vertical transmission levels of 30%, the highest value found experimentally. This result shows that vertical transmission alone is insufficient to obtain long-term control of S. exigua by inoculative spray of SeMNPV. Healthy patches will outgrow infected ones in number.

### 3.2 Population model

Fig. 2 shows examples of population dynamics at the system level. In the absence of virus, the number of moths grows exponentially. The upper curve represents the dynamics when introduced virus is inactivated completely (u = 0). The virus is sprayed when small larval stages are most abundant, such that a large reduction of moth numbers after the spray is achieved. However, during later generations moth numbers gradually grow at the same relative rate as in the absence of virus. The lowest curve shows the time course of the number of larvae when 1.5% of the sprayed polyhedra is not inactivated by UV radiation. Long-term population regulation is then achieved. These simulations with the population model confirm the conclusions drawn from studying the cluster model.

## 4. Discussion

Due to the high value of the crop, little feeding injury can be tolerated in Dutch glasshouse chrysanthemums and moth numbers must be controlled during the initial exponential growth phase. Inundative SeMNPV sprays give very good immediate control of S. exigua; Percentages kill of 95 to 100% are achieved (Smits, 1987). To accomplish also a long-term suppression of the pest population, the virus must give a lasting reduction of the net reproductive rate R of S. exigua below 1 and thereby maintain itself in the insect population.

At low moth densities, interactions between clusters are rare, such that, if there is complete inactivation of sprayed polyhedra, the virus can only propagate by vertical transmission. Under these conditions no long-term control can be achieved because healthy patches outgrow infected ones in number (Fig 1D). According to our simulations (Fig 2), long-term control is possible when the proportion of polyhedra, not exposed to UV radiation, is in the order of magnitude of 1.5%. Under these conditions the virus apparently maintains itself in the insect population, while the number of emerging females decreases to a total of less than 1 for all

15 clusters produced per female.

Obviously, virus persistence plays a major role in long-term inoculative control of moth numbers. Our simulations show that for short-term control, the moment of spraying and the halflife of polyhedra are important. Data on the inactivation of baculoviruses in glasshouses are, however, lacking. Therefore the present modelling results with regard to long-term control are speculative and experiments are needed to test our results. Attention should be given to the proportion of unexposed polyhedra and their distribution in the canopy.

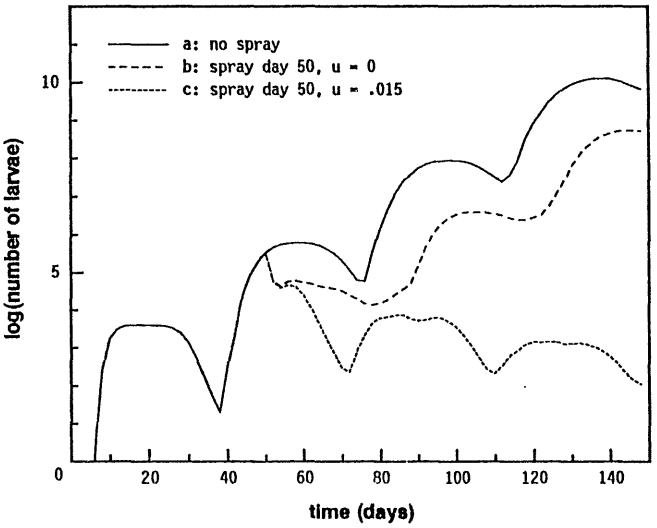

Figure 2: Analysis of population model: simulated total number of larvae over a period of 5 months (A) virus free; (B) sprayed with virus at day 50 without unexposed polyhedra (u = 0); (C) as (B) with 1.5% of the polyhedra not exposed to UV radiation (u = 0.015). Temperature: 20°C; Spray: $10^8$ polyhedra/m2; $t_{1/2}$ = 1 day.

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