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Experimental inundative releases of different strains of the egg parasite Trichogramma in Brussels sprouts

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Abstract

The effectiveness of inundative releases of four strains of the egg parasite *Trichogramma* (Hymenoptera, Trichogrammatidae) to control five lepidopterous species infesting Brussels sprouts crops in the Netherlands was examined in small-scale field experiments in 1982-1985. Strains were selected on the basis of behavioural characteristics investigated in laboratory experiments, i.e. parasitization activity at low temperature and host-species preference. *Mamestra brassicae* (Noctuidae) was the most abundant host species. Its density usually averaged between 0.5 and 2.0 eggs/plant throughout most of the season (June-September). A very high peak density of 12 eggs/plant occurred in 1982. In other years the peak was below 2.5 eggs/plant.

Correspondence between the observed patterns of parasitism and behavioural characteristics of the strains was in general present. A strain of *T. evanescens* (no. 57), with a high activity at 12 °C, performed best against *M. brassicae*. However, even its highest rate of parasitism (52%) was not sufficiently effective. A strain of *T. maidis* (no. 11) performed best against *Pieris brassicae* and *P. rapae* (Pieridae), but parasitism remained low (<30%) and was generally limited to peak densities (<0.5 eggs plant) occurring in 1982 and 1985. *Plutella xylostella* (Yponomeutidae) was an abundant species in some years, but parasitism of its eggs was never observed. Egg densities of *Evergestis forficalis* (Pyralidae) remained low in all years. The relationship between parasitims and host density and the influence of the parasite-release rate are discussed. Low host densities may have been a limiting factor for effective parasitism.

Additional keywords: biological control, egg parasites, Brussels sprouts, *Mamestra brassicae, Pieris brassicae, Pieris rapae.*

Introduction

Species of the genus *Trichogramma* (Hymenoptera, Trichogrammatidae) are known as parasites of eggs of various species, especially Lepidoptera (Nagarkatti and Nagaraja, 1977). Due to the relative cheap mass rearing on factitious hosts, *Trichogramma* is more than any other natural enemy species suitable for the inundative release method of biological control (Stinner, 1977). Inundative releases of *Trichogramma* are being practized or tested against various pests in many countries (e.g. Ridway et al., 1981; Voronin and Grinberg, 1981). In western Europe, release programs to control the

European corn borer, *Ostrinia nubilalis*, are conducted on a commercial basis (Bigler, 1986; Hassan, 1981).

In 1980 a cooperative project was started by several Dutch research groups[1] and the Institute for Biological Pest Control in Darmstadt (FRG) to study the possibility of using inundative releases of *Trichogramma* for the control of lepidopterous pests in cabbage crops (Brussels sprouts) (Glas et al., 1981; Van Lenteren et al., 1982). Five Lepidoptera species usually infest cabbage crops in the Netherlands: *Mamestra brassicae, Pieris rapae, Pieris brassicae, Plutella xylostella* and *Evergestis forficalis.* From 5-10 insecticide sprays are generally applied per season to control these pests.

After two years of a 'trial and error' approach (Van Lenteren, 1980) to the experimental field release of *Trichogramma*, a research program aiming at the selection of an effective *Trichogramma* strain, by means of pre-introductory experiments in the laboratory, was initiated (Pak and Van Lenteren, 1984). To conduct this program, a collection of 60 strains of various species and origins was obtained (Pak en Van Heiningen, 1985). Criteria to evaluate candidate strains are based on characteristics of the searching and parasitizing behaviour of *Trichogramma.*

In this paper we evaluate the results from field experiments conducted from 1982 to 1985. Each year two strains were released into different plots in a Brussels sprouts field. The aim of the experimental releases was to compare the performance of the strains and to determine whether this performance corresponds to certain behavioural characteristics which had been investigated in the laboratory. Criteria thus tested are the parasitization activity at low temperature (Pak and Van Heiningen, 1985) and host-species selection (Pak, 1988).

Material and methods

Releases. Experiments were conducted in different fields of Brussels sprouts (*Brassica oleracea* c.v. Rampart) near Wageningen. Uniform plots (35-100 m^2) were laid out in the field (0.25-0.5 ha). Plots were surrounded by 2 rows of plants and separated by uncultivated margins (ca. 1 m). Standard cultural practices were carried out, but no pesticides were applied. Temperature recordings (1.5 m above ground level) were obtained from a nearby weather station. Details of the experimental design are given by Van Alebeek et al. (1986) and Van der Schaaf et al. (1984).

Each year two *Trichogramma* strains were introduced as pupae in three plots each, whereas no introductions were made in three control plots. The numbers of the strains refer to the collection maintained at the Department of Entomology in Wageningen (Pak and Van Heiningen, 1985). One strain of *T. maidis* released in 1982 (no. 8), was used in the FRG to control *O. nubilalis* in corn (Hassan et al., 1978), whereas the other strain (no. 11) was locally collected. In laboratory experiments, females of strain 11 showed a high acceptance of both *Pieris* and *Mamestra* eggs (Van Dijken et al., 1986) and a low parasitization activity at low temperature (12 °C) (Pak and Van Heiningen, 1985). Strain 11 was therefore tested together with *T. evanescens* (no. 57), an Egyptian strain with a high activity at 12 °C, in the experiments of 1983 and 1984. In 1985 the performance of strain 57 was compared to that of strain 82, which had shown a

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superior performance among several indigenous strains tested in cabbage fields in the FRG (Hassan and Rost, 1985).

The *Trichogramma* were massproduced on eggs of the Angoumois grain moth, *Sitotroga cerealella* (Gelechiidae), at the Institute for Biological Pest Control in Darmstadt. The releases were made using paper cards carrying *Sitotroga* eggs parasitized at three different dates (Hassan et al., 1978), which were placed inside plastic or gauze containers under a protecting cover between 5-40 cm above the ground, at 1-4 release points per plot (variable between years). About 200 000 paratized eggs ha^{-1} were introduced at intervals of 14 days in the first three years, whereas this number was about 450 000 in 1985.

Sampling. All plots were sampled weekly during the release period by inspecting a certain number of plants. In 1982 and 1983 fixed plants were sampled, which were located on concentric circles around the center of each plot. Randomly selected plants were sampled in the next two years, because in 1983 the sample plants remained smaller than the other plants in the plots. The number of plants that could be sampled per plot within a day was limited by the size of the plants and the number of observations. In 1982 and 1983 the number of sample plants was held constant throughout the season: 23 (out of 98) and 49 (out of 220) plants per plot, respectively. In 1984 the number of plants examined per plot of 225 plants was decreased at mid-season from 100 tot 40, in 1985 from 40 to 25.

For each sample plant the numbers of eggs and larvae of the different host species and the degree of caterpillar feeding-damage (Theunissen and Den Ouden, 1983) were recorded to evaluate the effectiveness in pest suppression and damage reduction of parasite releases. Percentage egg parasitism was determined as the fraction of parasitized black eggs from the total number of eggs in the samples recorded on the sample date (1983, 1985) or thereafter by marking sampled leaves which carried unparasitized eggs and checking these for parasitism a few days later (1982, 1984). In addition to the quantitative plant damage, in 1984 the qualitative damage of harvested sprouts was determined.

Results

Temperature conditions. Figure 1 shows the weekly mean temperature for each year from June through September. The monthly averages (1951-1980) are 14.9 °C (June), 16.4 °C (July), 16.5 °C (August) and 14.4 °C (September). Especially in June, mean daily temperatures below 15 °C occur frequently (Pak and Van Heiningen, 1985). Temperatures in mid-June were generally below average. July was relatively warm in 1982 and 1983, but cool in 1984. August was cool in 1985, September in 1984 and 1985. Overall, the weather was fine in 1982 and 1983, whereas it was cool in 1984 and 1985.

Host-egg densities. Different patterns of egg distribution occur among the host species. *M. brassica, P. brassica* and *E. forficalis* lay eggs in clusters, whereas *P. xylostella* and *P. rapae* lay single eggs. For each species, egg densities were determined as the mean number per plant. Extremely high densities occurred in 1982, whereas they remained relatively low in other years. *M. brassicae* was the most abundant species in all years. The sampling precision for the mean number of eggs per plant (Cochran,

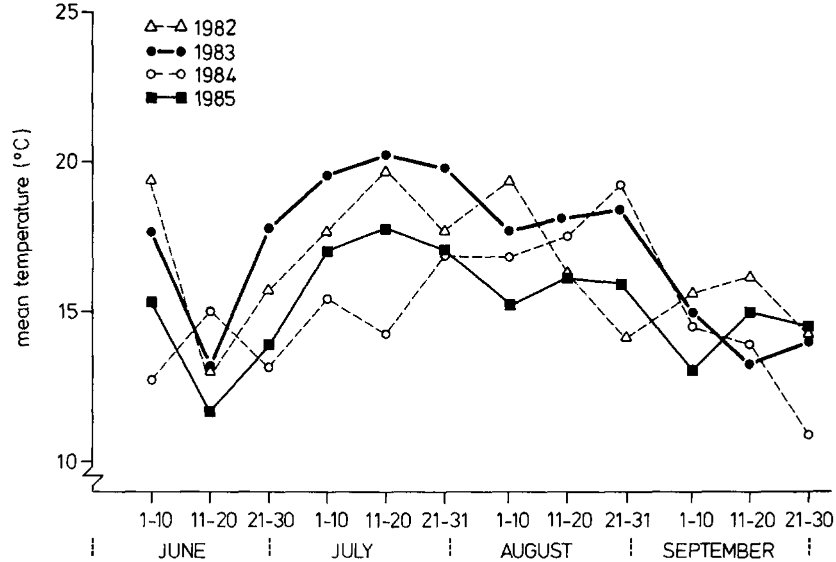

Fig. 1. Mean field temperature (°C), for periods of 10 days from June through September in 1982-1985.

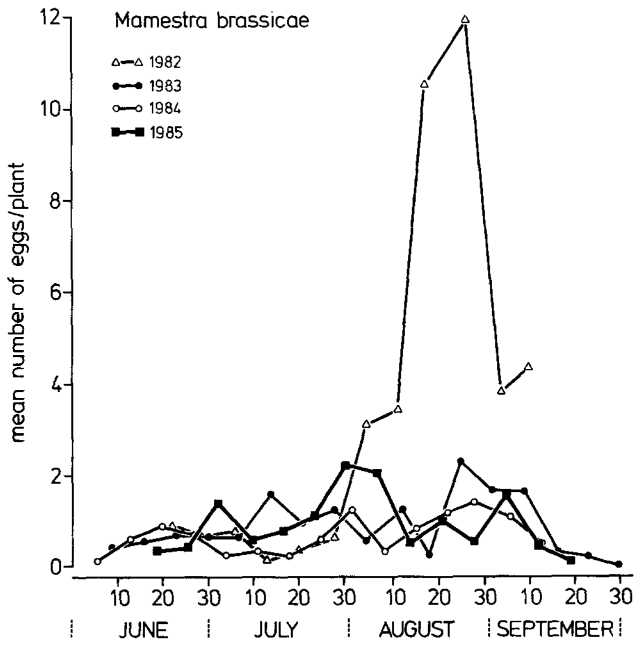

Fig. 2. Egg-population density of *M. brassicae* in 1982-1985. Numbers are averages for release and control plots.

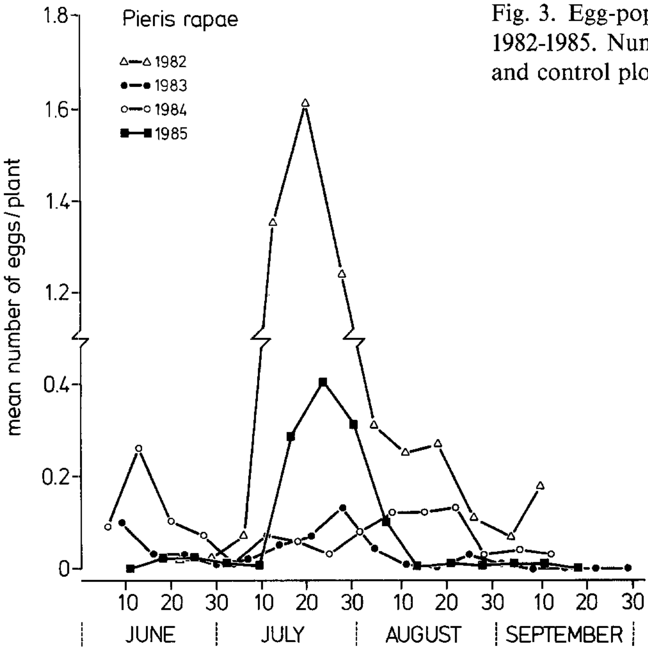

Fig. 3. Egg-population density of *P. rapae* in 1982-1985. Numbers are averages for release and control plots.

1977) was generally between 10 and 20% of the mean value at the 0.05 level of significance.

The abundance of *M. brassicae* eggs for each year is shown in Figure 2. Peak densities usually occurred in the second generation, at the end of August. A high peak density of 11.9 eggs/plant occurred in 1982. In subsequent years the peak was below 2.5 eggs/plant.

P. rapae was the second abundant species, but was much less abundant than *M. brassicae* (Fig. 3). In 1983 and 1984, the *P. rapae* egg density varied between 0 and 0.2 eggs/plant throughout the season. However, peak densities were obeserved at the end of July in 1982 and 1985 (1.6 and 0.4 eggs/plant, respectively).

In 1983, 1984 and 1985, only a few *P. brassicae* egg clusters were found. Egg densities never exceeded 0.15 eggs/plant (Fig. 4). Contrary to this, an extreme peak density occurred in August 1982 (6.1 eggs/plant).

P. xylostella eggs were only found in 1983. Since larvae of this species were always found, eggs of this species were probably overlooked, due to their small size and greyish colour. *E. forficalis* egg densities were very low in all years.

Parasitism of Mamestra brassicae. In 1982 the first parasitized *M. brassicae* eggs were found in the beginning of August (Fig. 5). In June and July the egg density had been low, less than 3 clusters per 100 plants (Fig. 2). Except for the first sample date, the maximum temperature averaged over 20 °C during this period. Table 1 shows that the mean seasonal parasitism was higher for strain 11 than for strain 8 (46.8 vs. 22.2%, respectively).

In 1983 parasitism started to increase at the end of June for both treatments, just after closing of the leaf canopy (Fig. 5). At the same time the first parasitized eggs

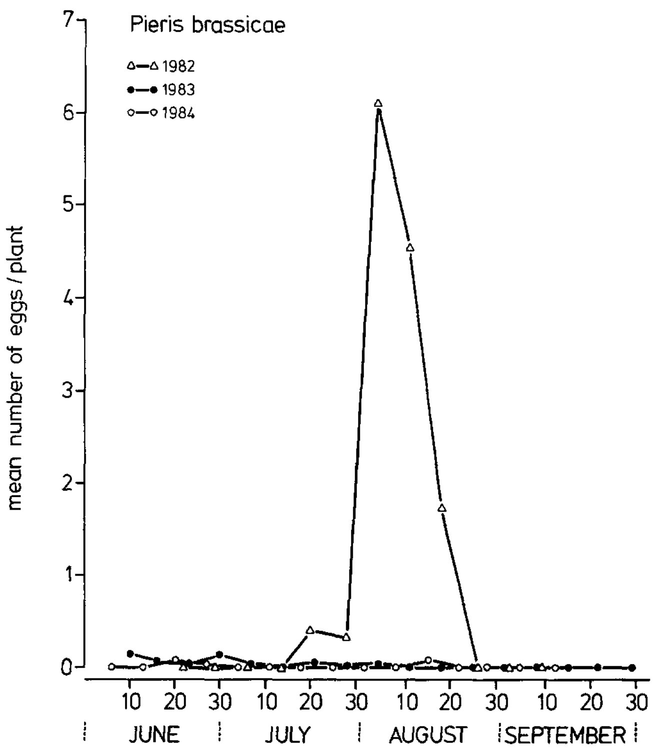

Fig. 4. Egg-population density of *P. brassicae* in 1982-1984. Numbers are averages for release and control plots.

were found in the control plots, which indicated that parasites had migrated from release plots into control plots across distances of up to about 20 m. Mean seasonal

Table 1. Percentage seasonal parasitism[1] of *M. brassicae* eggs for release and control plots (means for 3 plots) in four years of experimental releases of *Trichogramma* spp. strains in Brussels sprouts.

Year	Release plots				Control plots
	strain no.	parasitism (%)	strain no.	parasitism (%)	parasitism (%)
1982	8	22.2 b	11	46.8 a	0 c
1983	57	41.6 a	11	35.8 a	34.2 a
1984	57	23.9 a	11	12.1 b	4.2 b
1985	57	52.4 a	82	37.3 a,b	22.2 b

[1] % parasitism = 100 (number of parasitized eggs)/(number of unparasitized + parasitized eggs). Means per row followed by the same letter are not significantly different ($P < 0.05$, Fisher's exact test).

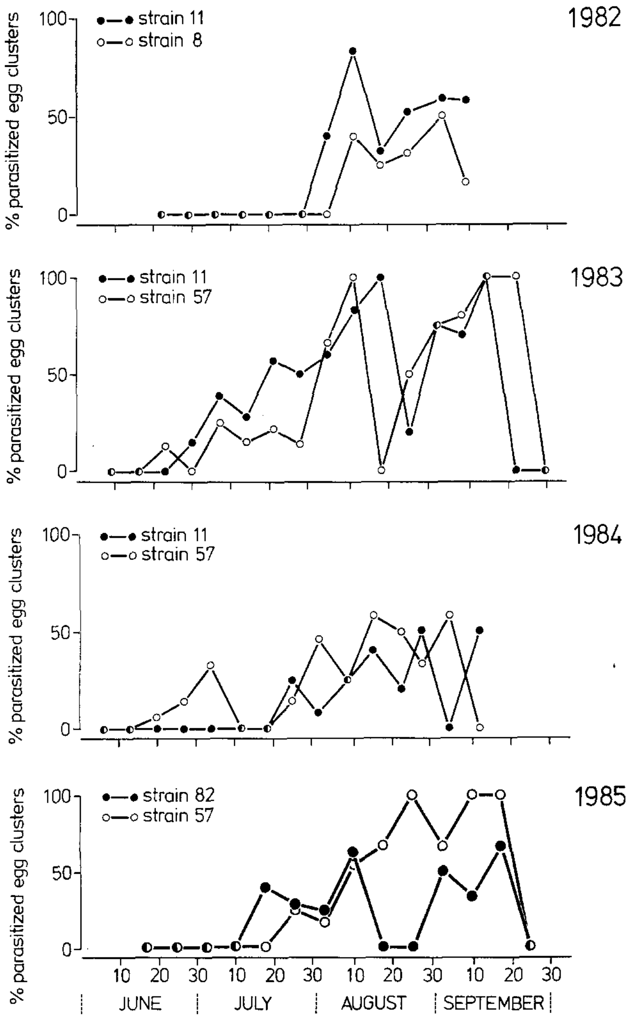

Fig. 5. Parasitism of *M. brassicae* egg clusters for different *Trichogramma* strains in 1982-1985.

parasitism was similar for the two strains and the control, averaging between 30 and 40% (Table 1).

In 1984 the mean temperature remained below 15 °C in June and July (Fig. 1). During this period parasitized *M. brassicae* eggs were only found in the plots treated with strain 57 (Fig. 5). Parasitism for both strains increased in the end of July, which coincided with the closing of the leaf canopy. Table 1 shows that egg parasitism was higher for strain 57 (23.9%) than for strain 11 (12.1%).

In 1985 the first parasitized eggs were found in the beginning of July, two weeks after the first parasite release. Parasitism remained low in July, but especially for strain 57 it increased considerably in August (Fig. 5). Seasonal parasitism was not siginificantly different between strain 57 and strain 82 (Table 1). Parasitism for strain 57 (52.4%) was higher in this year than in the previous years.

Parasitism of other host species. No parasitized *P. rapae* eggs were found in 1983 and parasitism was low in 1984 (1.6%). In 1982 parasitized eggs were found from the end of June through August (Fig. 6), which was a period of high egg density (Fig. 3). Seasonal parasitism for strain 11 and strain 8 was significantly different (28.2 vs. 16.5%, respectively, *P.* <0.05, Fishers's exact test), whereas there was no parasitism in the controls. In 1985 parasitism occurred in the period of peak density only. Seasonal parasitism was not different between strains 57 and 82, averaging 8.9%.

In 1983, 1984 and 1985, parasitism of *P. brassicae* eggs was not found. In 1982 parasitized *P. brassicae* eggs were found during a period of high egg density in August (Fig. 4). Mean seasonal cluster parasitism (i.e. percentage of egg clusters containing parasitized eggs) was significant (control 0%) but not different between the treatments (53 and 36% for strains 11 and 8, respectively; *P.* <0.05, Fishers's exact test).

Not a single parasitized *P. xylostella* egg was found in all four years. However, due tot their greyish colour, parasitized *P. xylostella* eggs probably are even more difficult to discover than unparasitized eggs. Parasitism of *Evergestis forficalis* clusters was only found incidentally.

Egg-cluster size. The probability that an egg in a cluster becomes parasitized depends on two conditions: (1) the probability of encounter with an egg cluster, (2) the probability of parasitism of eggs in the cluster given such an encounter. Both probabilities may be affected by the size of the cluster (Chesson, 1982). Fig. 7 shows that the mean size of *M. brassicae* egg clusters usually increased with the progression of the season. Cluster size did not correlate with the egg density.

Percentages parasitism for different size classes of *M. brassicae* egg clusters are presented in Table 2. In some releases there was no effect of cluster size on parasitism, whereas in others parasitism was highest for the largest clusters. These observations suggest that under certain conditions large egg clusters have a higher probability of encounter than small clusters. The probability of parasitism for eggs in the cluster, however, decreased with increasing egg-cluster size (Table 3). This might have been due

Table 2. Parasitism of *M. brassicae* egg clusters of different sizes in three years of experimental releases of *Trichogramma* in Brussels sprouts.

Size class (eggs per cluster)	Percentage parasitism of egg clusters[1]											
	1982				1983				1984			
	strain 11		strain 8		strain 11		strain 57		strain 11		strain 57	
	n	%	n	%	n	%	n	%	n	%	n	%
2-10	9	11.1 a	10	10.0 a	47	40.4 a	35	28.5 a	44	6.8 a	58	15.6 a
11-30	41	39.0 ab	23	26.1 a	55	36.4 a	30	36.7 ab	37	10.8 a	51	45.1 b
>30	44	50.0 b	21	23.8 a	18	55.5 a	18	61.1 b	10	50.0 b	8	12.5 ab

[1] I.e. clusters with 1 or more parasitized eggs. Means within columns followed by the same letter are not significantly different by Fisher's exact test (*P* <0.05).

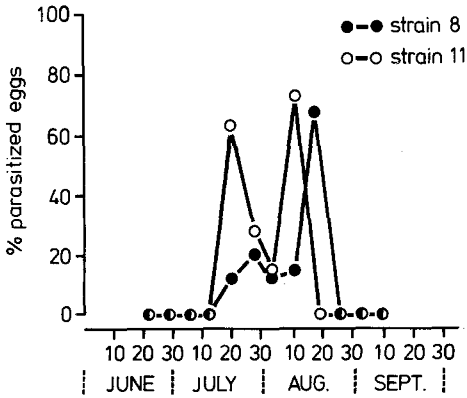

Fig. 6. Parasitism of *P. rapae* eggs for two *Trichogramma* strains in 1982.

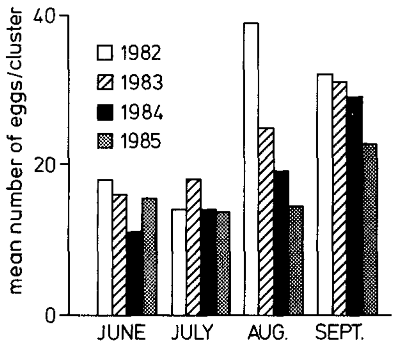

Fig. 7. *M. brassicae* egg-cluster size averaged per month in 1982-1985.

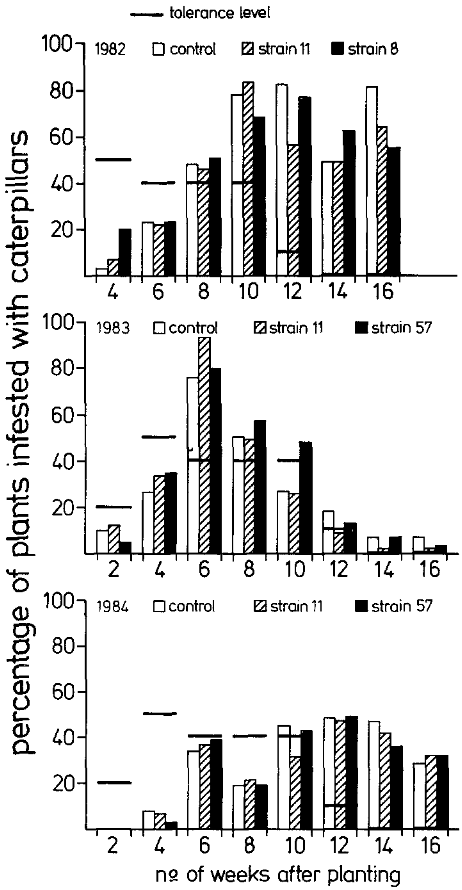

Fig. 8. Percentage of Brussels sprouts plants infested with caterpillars for different plant-growth stages in 1982, 1983 and 1984. Horizontal lines indicate tolerance levels.

Table 3. Percentage partly parasitized *M. brassicae* egg clusters of different sizes; data pooled for 1983 and 1984.

Size class (eggs per cluster)	n	% partly parasitized[1]
2-10	43	4.7 a
11-30	68	17.6 b
>30	40	45.0 c

[1] Percentage of total number (n) of clusters with parasitism; if followed by the same letter not significantly different by Fisher's exact test ($P < 0.05$).

to the limited egg complement of female wasps. However, it may also suggest that females leave egg clusters before parasitizing all eggs in the cluster.

Caterpillar densities. In 1982 the number of *M. brassicae* larvae/plant varied between 0 and 1.2 in the treated plots and between 0.1 and 2.3 in the control plots. In the second half of the season the number of larvae in the strain 11 plots was consistently lower than in the strain 8 or control plots. In 1983, 1984 and 1985 differences in larval densities of *M. brassicae* between treatments were not apparent. From June through September the density generally varied between 0.2 and 0.4 larvae/plant. For the other species no differences in larval densities between treatments were found in any year.

Theunissen and Den Ouden (1985) developed tolerance levels for the complex of caterpillars in Brussels sprouts (i.e. the percentage of plants that may be infested without occurrence of economic damage), relative to the growing stages of the plants. Tolerance drops sharply when sprout formation begins, 10-12 weeks after planting. Figure 8 shows that in 1982 and 1984 the tolerance level was exceeded in the second half of the season.

In 1982 and 1983 no differences in percentage of plants damaged by caterpillars were found between treatments. In both years leaf-area reduction averaged about 1%. Reductions of this magnitude probably do not result in yield losses for Brussels sprouts (Wit, 1982). The assessment of damage to sprouts at harvest in 1984 resulted in a similar percentage damage for treatments and control: 45% for strain 57, 47.5% for strain 11 and 57.2% for the control. This high figure for sprout damage compared to leaf damage shows that direct damage plays a very important role in Brussels sprouts crops.

Discussion

The present experiments were carried out to compare the performance of different *Trichogramma* strains in parasitizing several lepidopterous hosts species in Brussels sprouts. Behavioural differences between these strains have been investigated in laboratory experiments, e.g. the parasitization activity at low temperature (Pak and Van Heiningen, 1985) and the host-preference pattern (Pak et al., 1986; Pak, 1988; Van Dijken et al., 1986).

For mean temperatures below 15 °C in 1984, parasitism occurred in plots inundated with strain 57, whereas it was not apparent for strain 11. This corresponds to the respective parasitization activities of the two strains at 12 °C in the laboratory (Pak and van Heiningen, 1985). The overall seasonal performance of strain 57 was better than that of strain 11 in 1984, but not in 1983. The latter year was the warmest of all seasons, and temperature possibly was not so much a limiting factor for parasite activity in this year as it was in other years. Low rates of parasitism by *Trichogramma* in cabbage crops during periods of cool weather have been reported for other countries by Hassan and Rost (1985) and Parker (1970).

Parasitism for strain 57 was twice as high in 1985 as in 1984. This was probably due to the two-fold increase of parasite release, since weather conditions and host-egg densities were similar for these years. Strain 57 did not perform better than strain 82 (in 1985), which was the best performing strain in cabbage fields in the FRG (Hassan and Rost, 1985).

Host-species selection experiments in the laboratory indicated that *Trichogramma* generally prefer *Mamestra* eggs over *Pieris* eggs as a host (Pak and Van Lenteren, 1984). However, females of strains 11 and 82 accept *Pieris* eggs as readily as *Mamestra* eggs (Pak and De Jong, 1987; Pak, 1988; Van Dijken et al., 1986). In 1982 parasitism of *Pieris* eggs was higher for strain 11 than for strain 8. Since the two strains do not differ in parasitization activity at low temperature (Pak and Van Heiningen, 1985), the difference in field performance can be attributed to the difference in host preference. However, this does not explain why strain 11 was also more effective than strain 8 in parasitizing *M. brassicae* eggs. Parasitism of *P. rapae* eggs was not different between strain 57 and strain 82 in 1985, despite the difference in host preference between the two strains. Compared to 1982, parasitism during the peak density remained relatively low throughout the the season, which suggests that one or more unknown factors were limiting parasitism of *P. rapae* eggs in 1985.

Although the results are not always fully understood, they demonstrate that the determination of behavioural differences between strains in the laboratory may help to explain the relative performance of each strain in the field. Hence this shows the feasibility of using behavioural variations among strains as criteria in a pre-introductory selection program for candidate natural enemies. Nevertheless, it is obvious that we have not been able yet to select a strain of sufficient effectiveness as a control agent. Even for the best performing strain, the observed rates of parasitism of up to 50% appeared insufficient to suppress larval densities and to reduce sprout damage. Knipling and McGuire (1968) estimated that ca. 80% egg parasitism would be required for control of lepidopterous pests by *Trichogramma*. This figure is supported by field observations on different levels of parasitism by *Trichogramma*. For instance, in experiments to control *O. nubilalis*, egg parasitism of about 90% resulted in larval reductions between 83 and 90% (Hassan, 1982). Shcheptilnikova (1974) reported larval reductions varying from 80 to 88% in cabbage fields in which 87 to 98% of *M. brassicae* eggs had been parasitized by *Trichogramma*.

Low host densities may limit parasitism by *Trichogramma* (e.g. Gross, 1981; Parker 1970; Kot 1964). However, some studies have shown that host-egg parasitism may be density independent (Pena and Waddill, 1983) or inversely density dependent (Hirose et al., 1976; Morrison et al., 1980). In the present study parasitism of *M. brassicae* did not appear related to egg density. In contrast, parasitism of *Pieris* eggs appeared to be limited to densities above 0.1 egg/plant. This is below the critical density for effective parasitism of *P. rapae* eggs (0.3-0.4 eggs/plant) found by Parker et al. (1971).

About 200 000 pupal parasites (females and males) were introduced every two weeks in the first three years. This figure is similar to or higher than the numbers used to control *O. nubilalis* in Europe (Bigler, 1986; Hassan, 1982). In 1985 the number of introduced parasites was doubled, which probably increased parasitism of *M. brassicae* eggs by strain 57 (see above). Percentages parasitism may be expected to increase with increasing numbers of released parasites (Knipling and McGuire, 1986; Kot, 1979). Since the positive relationship deaccelerates, the parasite release may have to be increased many-fold in order to achieve a substantial increase in host-egg parasitism (Houseweart et al., 1984; Smith et al., 1986).

This paper shows that certain behavioural characteristics of *Trichgramma* females influence the rate of host finding and parasitism. However, strains selected on the basis of these characteristics were not sufficient in parasitizing to be effective in the field.

To determine which qualities are required for a strain to be effective, further research is necessary, especially on aspects of searching behaviour. Certain behavioural 'inadequacies' may be overcome by releasing more parasites. Others, for example a tendency to disperse from a habitat with a low host density, may dominate and should be at best overcome by manipulation of parasite behaviour.

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Samenvatting

Experimentele inundatieve loslatingen van verschillende stammen van de eiparasiet Trichogramma in spruitkool

In spruitkool kan schade veroorzaakt worden door rupsen van vijf soorten Lepidoptera. Inundatieve biologische bestrijding met de eiparasiet *Trichogramma* (Hymenoptera, Trichogrammatidae) zou een alternatief kunnen zijn voor intensieve chemische bestrijding. In veldexperimenten (1982-1985) is de effectiviteit van vier *Trichogramma* spp. stammen vergeleken om de uitkomsten van laboratoriumonderzoek naar criteria voor de selectie van geschikte natuurlijke vijanden te evalueren. Selectiecriteria zijn gebaseerd op eigenschappen van het zoek- en parasiteringsgedrag van de parasieten, o.a. parasiteringsactiviteit bij lage temperatuur en gastheer-preferentie.

Mamestra brassicae (Noctuidae) was de talrijkste gastheersooort, met een gemiddelde dichtheid van 0,2-2,0 eieren/plant gedurende een groot deel van het seizoen (juni-september). Een extreem hoge piekdichtheid (12 eieren/plant) deed zich voor in 1982. In andere jaren was de piekdichtheid ongeveer 2,5 eieren/plant. Eieren van *M. brassicae* werden het meest geparasiteerd door stam 57 (*T. evanescens*), maar zelfs het hoogste gemiddelde seizoenspercentage parasitisme (52%) was niet voldoende voor een effectieve bestrijding. Een *T. maidis* stam (11) gaf de beste resultaten tegen *Pieris brassicae* en *P. rapae* (Pieridae), maar parasitisme was laag (<30%) en vrijwel beperkt tot piekdichtheden hoger dan 0,5 eieren/plant, die voorkwamen in 1982 en 1985. *Plutella xylostella* (Plutellidae) was soms talrijk, maar eiparasitisme leek niet voor te komen. De dichtheid van *Evergestis forficalis* (Pyralidae) was gering in alle jaren.

Relatief lage gastheerdichtheden kunnen een beperkende factor geweest zijn voor het optreden van een effectieve percentages eiparasitisme. De resultaten tonen aan dat er een overeenstemming is tussen selectiecriteria die in het laboratorium zijn onderzocht en de effectiviteit van geselecteerde stammen in het veld.

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