A TEMPERATURE-DEPENDENT CONTROL PROGRAM FOR THE OMNIVOROUS LEAF ROLLER *PLATYNOTA STULTANA* WALSINGHAM (LEPIDOPTERA, TORTRICIDAE) IN COMMERCIAL ROSE PRODUCTION

A Thesis

Presented to the Faculty of the Graduate School

of Cornell University for the Degree of

Doctor of Philosophy

by

Ingeborg Zenner-Polania

January, 1974

BIOGRAPHICAL SKETCH

The author was born Ingeborg Zenner on August 5, 1940 in Catrop-Rauxel, West-Germany. She received the degree of "Ingeniero Agronomo" from the College of Agriculture at the National University of Colombia at Palmira, in December 1965. In 1966 she started working in the Department of Entomology of the Colombian Agricultural Institute (ICA), where she was awarded a scholarship to enter the Graduate School of the National University-ICA. She received her M.S. degree with a major in Entomology in August 1971. She entered the Ph.D. program at Cornell in September 1971, receiving the Comstock fellowship for the first year's study and an additional scholarship from the Colombian Government.

She is a member of the Entomological Society of America, the "Sociedad Colombiana de Entomologia" (Colombian Society of Entomology), the "Asociacion Latinoamericana de Fitotencia" (Latin American Association of Agronomy) and the Cornell Chapter of the Society of Sigma Xi.

The author was married to Fabio Polania in 1969.

ACKNOWLEDGMENTS

This thesis has been made possible by the kind assistance of many persons in many different ways and I gratefully acknowledge their help.

I would like to acknowledge in particular: Dr. Robert G. Helgesen for his assistance and advice in the direction of the research and in the preparation of the thesis; Drs. J. W. Boodley and L. L. Pechuman for serving as committee members and offering constructive suggestions in the preparation of the thesis; Dr. J. G. Franclemont for identifying the specimens; Dr. C. F. Wilkinson for helping with the determination of the detoxication enzymes, and Mrs. Nancy Kuenzel for critically reading parts of the manuscript.

The author is particularly indepted to Roses, Incorporated and the Joseph H. Hill Memorial Foundation for financial aid, to the Colombian Agricultural Institute for giving her the opportunity to undertake graduate study and to Dr. John G. Seeley and the Department of Floriculture for advice and donation of plants.

Above all, I thank my husband, Fabio, for his constant help and encouragement.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

INTRODUCTION

The omnivorous leaf roller, Platynota stultana Walsingham (Lepidoptera: Tortricidae, Tortricinae) is probably the second most important arthropod pest of greenhouse roses. Although losses caused by the attack of this leaf roller have not been studied, its potential economic importance is considerable because it feeds on leaves, shoots and flower buds of roses. As expected from its common name, this insect has been observed on over 40 plant species including such greenhouse crops as roses, carnation, chrysanthemum, fuchsia, aster,and cyclamen (Smith et al. 1965), and such field crops as oranges (McGregor 1934), cotton and tomatoes (Nelson 1936) and grapes (Lynn 1969).

Lord Walsingham (1884) first described Platynota stultana from specimens collected in Sonora, Mexico. Several years later the omnivorous leaf roller was reported attacking various cultivated plants in California, including roses (Busck 1933). The wide range led to a number of synonymies of this species, both in scientific and common names. The synonymy can be summarized as follows:

Platynota chiquitana Barnes and Busck (Barnes and Busck 1920)

Platynota tinctana Woglum (not Walker) (Woglum 1920)

Sparganotis tinctana Essig (not Walker) (Essig 1926)

Sparganotis stultana (Walsingham) (Meyrick 1913)

Atkins et al. (1957) observed that the common names orange webWorm Platynota orangeworm, orange caliz worm, orange Platynota, carnation moth, leaf tier and cotton leaf roller were all used for P. stultana. To avoid confusion they suggested the name "omnivorous leaf roller", a designation which has been adopted by most authors.

Besides P. stultana the subfamily Tortricinae includes a number of other species which are of considerable economic importance. Among the polyphagous species which feed on a wide range of herbaceous dicotyledonous plants, and which compare in host plant diversity to P. stultana, are: Archips argyrospilus (Walker), the fruit-tree leaf roller; Argyrotaenia velutiana (Walker), the red-banded leaf roller; and Cnephasia longana (Haworth), the omnivorous leaf-tier (Powell 1964, Mackay 1962, Hough 1927, Glass & Chapman 1952, Cram & Tonks 1959). Other species like Choristoneura fumiferana (Clemens), the spruce budworm, and Acleris variana (Fernald), the black-headed budworm, are considered to be host specific conifer feeders and well known forest pests (Mackay 1962, Powell 1964, Macdonald & Webb 1963, Miller 1966).

P. stultana was first observed attacking roses in the Eastern United States in 1933 by F. F. Smith (Busck 1933). This eastward movement of the insect was probably a result of eastern florists' rose stocks sent to California for budding. There the stock roses became infested and the insects were taken with the budded stock, where they readily established in the favorable environment of the eastern greenhouses (Busck 1933). Today the omnivorous lead roller is a serious pest in almost all the leading states in rose production. It has been reported attacking roses in California, Arizona (Atkins et al. 1957), Pennsylvania, Virginia (Smith et al. 1965), New York (Ota 1969), Massachusetts (Bourne 1936), Illinois (Compton 1941) and Michigan (Wildon 1946). In the northern part of the Eastern United States the omnivorous leaf roller (henceforth referred to as OLR) has never been reported by the authors cited above as attacking outdoor roses.

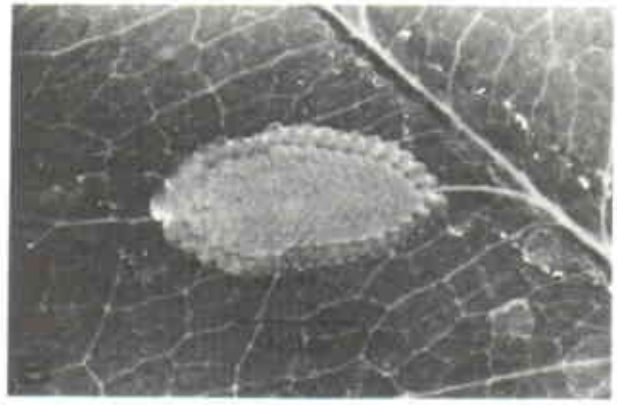
Nelson (1936) gives a description of the life history of the OLR, which he studied under laboratory conditions an roses. The adult is a relatively small moth with an alar expanse of 12 to 16 mm. The fore wings are dark brown, with the outer half a lighter, yellowish brown (Fig. 1A); this variation in color is more clearly marked in the male. The eggs are deposited during the night in an overlapping shingle fashion in flat clusters (Fig. 1B). Invividual eggs are flattened and oval in outline and are similar in color to rose leaves. The newly emerged larvae are from 1.4 to 1.8 mm in length, of yellowish white color, with the head and the prothoracic shield brown. As the larvae develop their color becomes darker, yellowish to brownish green; the head and the thoracic shield remain brown. One or two days before pupating the larva spins a cocoon within a rolled leaf. The pupae are yellowish brown to brown and their size varies from five to nine mm. Nelson (1936) indicates that the larvae undergo five instars, but Zenner-Polania & Helgesen (1973) concluded that the number of instars of the OLR is five for males and five or six for females; the frequency of the sixth instar in females being influenced by temperature.

Several authors have observed the total or partial life cycle of the OLR, rearing them either on natural or artificial food at 21.1, 23.9, 24.4, 26.7 and 32.2°C (Nelson 1936, Bohart 1942, Atkins et al. 1957 and AliNiazee et al. 1971). However, the developmental times of the different larval instars at various temperatures, and the relationship between developmental velocity and temperature has not been studied.

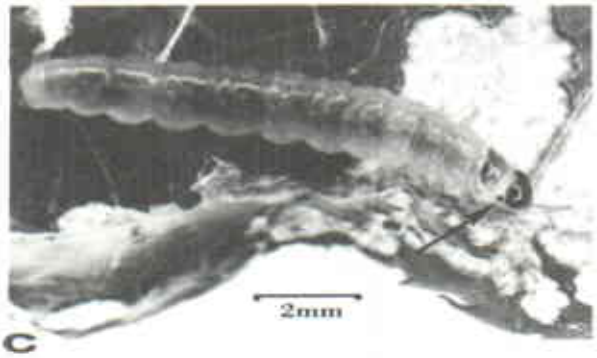
The chemical control of P. stultana on roses and other host plants has been the objective of several workers. Hall & Dunn (1958) obtained control with sprays containing Bacillus thuringiensis var. thuringiensis

Fig. 1. Life cycle of the OLR. A. Female. B. Egg mass. Note the overlapping of the eggs in a shingle fashion. C. Third instar larvae ready to molt. Note the eyespot immediately behind the head-capsule. D. Female (a) and male (b) pupa. Note the three and four ventral sutures posterior to the wing pads respectively. E. Exuvia. Exuviae can be observed protruding partially from the web for a long time after adult emergence. F. Female drying her wings after emergence.

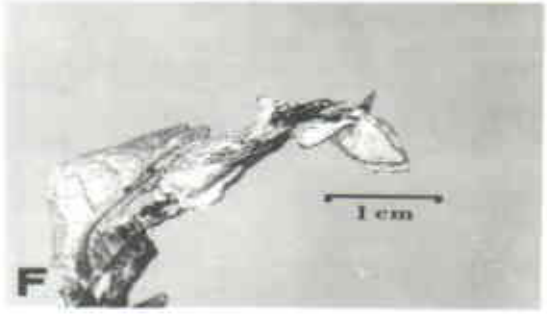
A



D



C



F

and Smith et al. (1965), while testing several materials, satisfactorily controlled adults and larvae of all instars with mexacarbate (Zectran(R)) and mexacarbate plus ronnel (Ronnel(R)). At that time mexacarbate was removed from the market and since a suitable replacement was needed, Ota (1969) studied the efficacy of different compounds against this pest. He determined that B. thuringiensis as well as trichlorfon (Dylox(R)) and Matacil(R) were as effective as mexacarbate, and that methomyl (Lannate(R)) and Azodrin(R) gave excellent control of this insect. Ota's (1969) studies were conducted in the laboratory and commercial greenhouses. In his laboratory tests the larvae were allowed to develop at least two weeks on the host plants so most of them were in the third and fourth instar at the time of the subsequent treatments. No indications were made of the larval instars against which the treatments were applied in the greenhouse. Naegele & Jefferson (1964) observed that this pest could not be consistently eliminated by carbaryl (Sevin(R)) or by naled (Dibrom(R)) fumigation. Six applications of dichlorvos (Vapona(R)) aerosol at weekly intervals, which will kill adults and young larvae of the first three instars are currently recommended. However, 10 or more applications are required to eliminate the pest (Smith 1969).

Other tortricid larvae can cause damage similar to P. stultana on roses (Smith et al. 1965), but are much easier to control (Atkins et al. 1957a). Therefore, the leaf roller complex that formerly occurred on greenhouse rose crops has been reduced primarily to this species, because it has survived the insecticide applications that eliminated other species (Smith et al. 1965). Several authors suggest that the OLR is very difficult to control because of the excellent protection given

the larvae by their webbed retreats, and because later instar larvae are not very susceptible to most insecticides (Nelson 1936, Naegele & Jefferson 1964, Smith et al. 1965, Lynn 1969 and Helgesen & Freeman 1971).

The ineffectiveness of the insecticides could be explained by a possible high activity of the midgut microsomal oxidase enzymes, which function in the detoxification of foreign compounds, particularly in late instars. Krieger et al. (1971) observed a much higher activity of these enzymes in polyphagous Lepidoptera species and since the OLR is polyphagous this concept could explain an inherent resistance to insecticides in late instar OLR.

Other factors which may explain the poor control of P. stultana might be the lack of effective methods for determining a) critical population levels (AliNiazee & Stafford 1971) and b) proper timing schedules. At the moment it seems that insecticides are applied as soon as the grower observed that the population of the OLR has reached a certain level he thinks is potentially threatening. No consideration is given to the stage of the insect, although it is well established that larvae from the third instar on are most difficult to control, and eggs and pupae are not affected by insecticidal applications. To efficiently control the OLR, the rose grower must know the population level at which control practices should begin, and the proper timing of the insecticide applications which must be directed against younger, more susceptible larval instars of the leaf roller. To date these two factors have not been investigated.

Therefore, the principle objectives of this study were to obtain the most effective and economic control program for the OLR by

ascertaining the population level at which insecticidal applications should begin and by determining the proper timing and frequency of these applications. To develop such a program the effect of temperature on the population dynamics of the OLR as well as its abundance and distribution at the prevailing greenhouse temperature had to be determined.

Moreover, to determine the best insecticides for OLR control the efficacy of certain insecticides had to be defined for this program. This included an analysis of: a) the toxicity of the materials, b) the residuality and c) the epoxidase activity of late instar larvae of the OLR.

MATERIALS AND METHODS

Role of temperature on the population dynamics of the OLR

Stock culture

The OLR used in this investigation was obtained from the stock culture of the N.Y. State Agricultural Experiment Station at Geneva, N.Y. and from a commercial rose house at Riverhead, N.Y. At the beginning of the experiments no independent culture was maintained, so that the progeny from the Geneva stock was used for the 10, 15 and 20°C treatments, and the progeny from the 20°C treatment for the 25°C and 24 day- 18°C night treatments. The progeny of the 25°C treatment were crossed with individuals from the natural population from Riverhead and an independent stock culture was established at 25°C, from which the insects for the other treatments were derived.

Rearing of the OLR on artificial diet

Since a large number of insects was necessary for this research a simple artificial diet was found to be advantageous. The use of the artificial diet was also the best way to observe individual larvae throughout the whole life cycle without disturbing them, whereas using a host plant permits the insect to roll and web leaves together, which makes direct observations impossible.

For rearing the OLR, AliNiazee *et al.* (1971) used the cabbage looper diet described by Ignoffo (1963) and modified by Henneberry & Kishaba (1966). Ignoffo's (1963) diet was based on the synthetic media developed for the pink bollworm by Vanderzant and Reiser (1956) and modified by Adkisson *et al.* (1960). AliNiazee *et al.* (1971) introduced a slight decrease in the quantity of wheat germ, which they replaced

by wheat bran producing a slightly coarser texture to the medium; on this diet "all the larval instars thrive well without any significant deleterious effects and reduction in the fecundity even after 10 generations".

The preparation of the diet for this study was facilitated by using the "Vanderzant-Adkisson Special Wheat Germ Diet for Insects(R)", and the "Vanderzant Modification Vitamin Mixture for Insect Diet(R)", both prepared by Nutritional Chemicals. This gave an excess of alphacel, ascorbic acid and Vitamin B_{12} and an addition of alpha tocopherol and inositol to the original diet, which did not interfere in the development and fecundity of the OLR. In Table 1 the weights of ingredients used in a formulation of 100 ml of artificial diet used in this study are given.

To prepare 945 ml of the diet in a 1000 ml blender 220 ml of distilled water was combined with 112.5 gr of wheat germ diet and 4.5 ml of potassium hydroxide (4M). Under continuous mixing 13.5 gr of alfalfa meal, 4.3 ml of methyl p-hydroxybenzoate (15% w/v in 95% alcohol), 3.75 ml of formaldehyde (37%), 4.5 ml of sorbic acid (38%) and 30 ml of vitamin mixture were added.

In 550 ml of distilled water 22.5 gr of agar were dissolved and added to the previous mixture. Finally 0.125 gr of aureomycin were added and the diet blend together until a homogeneous color was obtained. Still warm it was poured into plastic Petri dishes and after it had cooled it was stored in a refrigerator at $\pm$ 7°C.

Experimental design

Controlled laboratory conditions

Temperature.-To measure the relationship between temperature and

Table 1. Weights of ingredients for 100 ml of artificial diet, modified after Henneberry & Kishaba (1966) and AliNiazee et al. (1971)

Basic diet		Vitamin Mixture	
Ingredient	mg	Ingredient	mg
Special Wheat Germ Diet for Insects: Vanderzant-Adkisson	11.77	Vanderzant Modified Vitamin Mixture for Insect Diet	633.706
Composition of above:	mg	Composition of above:	mg
Wheat Germ	2.85	Alpha Tocopherol	15.23
Casein, Vitamin free	3.32	Ascorbic Acid	514.00
D Sucrose	3.32	Biotin	0.038
Salt Mixture	0.95	Calcium Pantothenate	1.90
Alphacel	1.33	Choline Chloride	95.00
Agar	2.37	Inositol	0.038
Alfalfa Meal	1.43	Niacinamide	1.90
Water	81.00	Pyridoxine HCl	0.45
Potassium Hydroxide	0.10	Riboflavin	0.90
Methyl p-hydroxy benzoate	0.13	Thiamin HCl	0.45
Sorbic Acid	0.05	Vitamin B_{12} Trituration in Mannitol	3.80
Formaldehyde	0.04		
Aureomycin	0.013		

age-specific developmental rate of P. stultana, the different stages were observed and reared in refrigerator-type chambers at constant temperatures of 10, 15, 20, 25, 30 and 35°C (± .5°C). Additional insects were also reared at alternating temperatures of 24-15.5°C day-night, 24-18°C day-night and 29.5-18°C day-night (± .5°C), with the cool period being 14 hours, so that the variability in the rate of development could be compared to that at constant temperatures. The change of temperature was affected manually at the end of each temperature period. These alternating temperatures and the length of the night temperature were chosen, since they represent the range of greenhouse temperatures recommended for rose culture (Mastalerz 1969, Laurie et al. 1969). A photoperiod (fluorescent light) of 16 hours was maintained in all chambers. No exact humidity regime was maintained and the relative humidity in the chambers fluctuated at the constant temperature treatments from 50 per cent day to 70 per cent night and at the alternating temperatures from 60 per cent day to 80 per cent night.

Larval and pupal development.-In each chamber 51 to 65 larvae were reared individually in 60 x 15 mm plastic Petri dishes. These larvae were obtained from egg masses deposited at the beginning of the oviposition period. Only recently emerged larvae, corresponding to those which emerged during the first 15 minutes after initiation of egg eclosion were used. At the 24-18°C alternating temperature treatment this was not possible and many larvae came from egg masses deposited at the middle and the end of the oviposition period or had emerged after the 15 minute period. The larvae were transferred with a camel-hair brush to a piece of diet.

Initially observations were made every four hours. However, after

several observations, the moment of molting could be predicted with an accuracy of half an hour, because the larval eyespot of the next instar is visible for a certain time before the molting process occurs (Fig. 1C). Therefore, observations were made whenever necessary (i.e. at almost the exact moment of molting).

The individual larva was always provided with fresh diet, but the old parts of the diet were left in the Petri dish, since those pieces represented the "web" for the larva. As soon as the pupa was formed most of the old diet was removed to give the emerging adult enough space to emerge and dry the wings. For each age class of every individual the developmental time in days and the mortality were recorded. The sex of the pupae was differentiated by size and by morphological differences observed for other tortricids by George (1965) and Roelofs & Feng (1967): male pupae have four ventral suture posterior to the wing pads while females have only three (Fig. 1D).

Fecundity and Fertility.- Pairs of adults obtained at each temperature treatment were then confined to a 13 x 33 mm plastic bag, the "oviposition cage", which was put in the chamber at the same temperature at which the larvae and pupae had been reared. Cotton impregnated with a 10% sugar solution served as food for the adults. The use of plastic bags was recommended by Prof. W. L. Roelofs[1/], who had used them successfully for his work with the OLR. Females normally lay eggs on smooth surfaces, including the sides of plastic bags. The collection of the egg masses was done by cutting out the part of the plastic bag with the egg mass. Mortality and fecundity of the moths were recorded

---

[1/] N.Y. State Agricultural Experiment Station, Geneva, N.Y.

daily. The eggs laid by each female were put on moist filter paper in a plastic Petri dish in the chamber at the respective temperature. As soon as traces of the head-capsules were visible, the total number of eggs per egg mass was counted under a microscope distinguishing between fertile and non-fertile eggs. The latter do not show the head-capsule and maintain their uniform green color. Each day the moths were transferred to a new plastic bag and given a fresh cotton ball impregnated with sugar solution. Whenever it was possible the eggs laid by the female at one temperature were used for the observations at the same temperature treatment. For the treatments where no fertile females or no females at all were obtained (i.e. 10, 15 and 35°C) eggs laid at 25°C were used. Each egg mass was observed individually. The incubation time in days was recorded from the moment of oviposition to the moment the first larva emerged. Since most eggs from a single egg mass hatch almost simultaneously, requiring a maximum of 15 minutes (Atkins et al. 1957), the number of larvae emerged during this period, the number of non-viable eggs and unhatched viable eggs, and the number of larvae emerged later were recorded for all egg masses.

Commercial greenhouse conditions

In the greenhouse the developmental studies were carried out on roses. Egg masses ready to hatch were placed on the leaflets, and the developmental time and mortality were recorded for the total larval, pupal and egg stage. No data on the duration of the different instars were taken. A total of 50 larvae and 30 pupae were observed and the fecundity and fertility of the resulting females were recorded. The mean fluctuating temperature at which each stage had developed was measured with a Belfort hygrothermograph.

Analysis

For the constant temperature treatments the regression equation of the relationship between developmental velocity and temperature, the thermal constant (K) and the threshold temperature (t) were determined for all developmental stages of the males and females. Wigglesworth (1967) reviewing the effect of temperature on the life cycle of insects concluded, that for most lepidopterous larvae and pupae the velocity-temperature relationship is linear over a certain range of normal temperatures, but departs at its upper and lower levels. The linear section of the curve is conventionally used to determine the regression equation, K and t. The threshold temperature (t) can be defined as the temperature at which this regression line intersects the x-axis (Wigglesworth 1967). K, in terms of degree-days of required heat above t, is by definition

$$K = D\ (T - t),$$

where D is the number of days spent in that particular stage at temperature T. Developmental velocity (V), in terms of per cent development per day, is expressed as $V = 100/D$. Substitution gives the regression equation:

$$V = 100\ (T - t)/K;$$

hence $K = 100/b$, where b is the slope of the regression line (Morris & Fulton 1970).

The development of the different stages of the OLR at constant and alternating temperatures was compared on the basis of equivalent temperatures. The equivalent temperature (= mean fluctuating temperature) was calculated taking into account the number of hours per day each temperature was used; this gave a mean fluctuating temperature of 19,

20.5 and 23°C for the 24-15.5, 24-18 and 29.5-18°C day-night fluctuating temperatures respectively.

To determine the percentage of increase or decrease in the rate of development at the mean fluctuating temperature over the mean constant temperature the following formula suggested by Hagstrum and Hagstrum (1970) was used:

$$\% \text{ increase} = \frac{\text{Increase in rate of development at mean fluctuating temperature above that of mean constant temperature}}{\text{time required for development at mean constant temperature}}$$

Determination of injury levels as they relate to insecticide applications

The population level of a pest at which control measurements should begin has been referred to as the "Economic Threshold". Insecticidal applications at this level will theoretically prevent the insect population from reaching the "Economic Injury Level", which by definition is "the lowest population density that will cause economic damage" (Stern et al. 1959). Chant (1966) indicates that these threshold levels are difficult to determine because of the many factors involved and because the threshold levels will change constantly with the changing economic and environmental conditions.

It is beyond the scope of this thesis to determine the Economic Threshold and the Economic Injury Level in all its aspects. Therefore, the population level for insecticidal applications was determined only taking into account the damage caused by the OLR larvae and the general behavior of the pest population in the greenhouse. The economic aspects involved in ascertaining these levels, such as operation cost, cost of control versus losses, etc., have not been considered.

Damage caused by the OLR larvae

Presently no official market grades and standards for cut hybrid

tea roses have been accepted by the industry. But all tentative grades and standards, besides the general characteristics of flower and stem, specify that the flower, stem and foliage should be free from damage. Damage in this case has been defined as caused by several agents, including insects and dirt or other foreign materials. The recommended tolerance is that no more than five per cent, by count, of any lot shall fail to meet specifications for the grade (University of Illinois 1968, Laurie et al. 1969, Rathmell 1969). If only insect damage is taken into account this means that when bunched or boxed no more than five per cent of the roses should show insect attack.

The damage caused by the OLR larvae was divided into that produced by the first and second instar larvae and that by the remaining instars. To obtain these data 100 first instar larvae were followed in their development on roses to determine the site and nature of their damage. To ascertain the amount of damage caused by the later instars all webs found on 24 plants were analyzed and grouped according to their distribution on shoots, flower buds, leaves and stems.

Larval dispersal and mortality

Evaluation of dispersal and mortality of the first instar larvae was made by observing the development and eclosion of 35 egg masses (mean number of eggs per egg mass = 98), then counting the established first instar larvae and measuring the distance they can travel with the help of the silk threads they produce and the air movement. To get a complete picture of mortality and dispersal one hundred first instar larvae were observed up to the moment they formed a web and then until adult emergence.

All greenhouse observations on the pest population were made on

three benches (3.4 x 8.4 feet) of four year old "Red American Beauty Roses" located in the Cornell insectary.

The laboratory studies on mortality, fertility and the life cycle at the different temperatures combined with the greenhouse studies have been used to predict the population growth of the OLR.

Efficacy of insecticides against the OLR

Activity of detoxification enzymes

A high activity of the microsomal oxidase enzymes, which as indicated in the introduction could be partly responsible for the ineffectiveness of insecticides against later instars was suspected for the OLR. Krieger et al. (1971) indicate that polyphagous lepidopterous species (those which feed on more than 11 plant families) show a high midgut microsomal oxidase activity. From the OLR's host plant list presented by Atkins et al. (1957), those plants reported by several authors and personally observed in the greenhouse as a host plant, were grouped into their respective plant family in Table 2. It was found that at least 14 plant families contain host plants of P. stultana, indicating that the OLR is a highly polyphagous species, which theoretically should show a high microsomal oxidase enzyme activity.

The microsomal oxidase activity in the midgut of the OLR was estimated in terms of the rate at which aldrin is epoxidized to dieldrin, and the assay method used by Krieger et al. (1971) was followed. The midgut of 65 last instar larvae, reared in the laboratory were cleared of the gut content and homogenized in a homogenizing tube with teflon pestle in ice-cold 0.15 M KCl. Samples of the homogenate (0.5 ml) were added to a mixture of tris-HCl buffer, glucose-6-phosphate, nicotinamide adenine dinucleotide phosphate, glucose-6-phosphate

Table 2. Host plant families and their plant species attacked by *P. stultana*

Plant family	Plant species	Source
Rosaceae	rose	Busck 1933, present
Leguminosae	beans, alfalfa	Atkins *et al.* 1957, present
Malvaceae	cotton	Atkins *et al.* 1957
Rutaceae	citrus	McGregor 1934
Lauraceae	avocado	Atkins *et al.* 1957
Vitaceae	grape	Lynn 1969
Celasteraceae	*Eunonymus*	Campbell 1971
Caryophyllaceae	carnation	Smith *et al.* 1965
Compositae	aster, chrysanthemum	Smith *et al.* 1965, present
Primulaceae	cyclamen	Smith *et al.* 1965, present
Geraniaceae	geranium	Atkins *et al.* 1957
Solanaceae	tomato, potato	Nelson 1936, present
Cucurbitaceae	melon	Atkins *et al.* 1957
Annonaceae	cherimoya	Atkins *et al.* 1957

dehydrogenase and KCl. After addition of aldrin in ethanol, the mixture was incubated for 30 minutes at 30°C, after which the enzymatic reaction was terminated by adding acetone. The chlorohydrocarbons were then extracted quantitatively into petroleum ether, and the dieldrin production was measured by electron-capture gas chromatography. The protein content of the homogenate was estimated by the Biuret method (Krieger et al. 1971, Krieger & Wilkinson 1969, Krieger & Wilkinson 1970, Fincham 1954).

Toxicity

Experimental design

In the greenhouse individually potted roses (five gallon pots) of the variety "Red American Beauty" were artificially infested with egg masses about to hatch obtained from the laboratory stock culture.

Before the insecticidal applications were initiated, the insects were allowed to develop through several generations to obtain an uniform infestation and a natural overlap of generations under greenhouse conditions. At the time of the first application all stages of the insect were present in approximately the same proportion.

Two trials with 45 and 36 potted roses each, with an average of four branches per plant were arranged in a randomized block design with three replications of five and four treatments respectively. Each replicate consisted of nine branches on three rose bushes. The average number of five-leaflet leaves per branch for the first experiment was 22.6 $\pm$ 8.0 and for the second test 25.8 $\pm$ 6.9.

All liquid insecticides were applied with a one gallon hand sprayer and the plants sprayed to the point of run off. To all insecticidal mixture, except mexacarbate, 1.5 cc of Ortho Chevron Spreader was added

per gallon. The granular material was scattered on the soil surface, worked in and finally watered in.

The number and frequency of the insecticide applications were determined by a computer program (see last part of this section).

Description of the insecticides

The efficacy of the following insecticides was evaluated in this experiment:

Aldicarb (Temik(R)). A carbamate with systemic insecticide-acaricide nematicide action; stomach poison; LD_{50}* = 0.93 mg/kg; known to control several lepidopterous larvae. Several rose growers claim to obtain good results against the OLR with this insecticide, therefore it was included to determine whether it is really effective against this pest.

Mexacarbate (Zectran(R)). A carbamate with systemic insecticide action; contact and stomach poison; LD_{50} = 15 mg/kg (Thomson 1972). This insecticide gave excellent results against P. stultana in several tests conducted by Smith et al. (1965).

Bacillus thuringiensis (Thuricide(R)). A bacteria which forms protein crystals at the time of sporulation, which are highly toxic for certain insects, especially Lepidoptera. The sporulated bacillus when ingested produces a paralysis of the gut and the insect dies in from two to four days (Steinhaus 1965); non-toxic to mammals. This material is of known effect against the OLR (Ota 1969).

Trichlorfon (Dylox(R)). An organic phosphate with systemic action; stomach poison; LD_{50} = 450 mg/kg (Thomson 1972); recommended for the use on ornamentals against several lepidopterous larvae (Chemagro 1973).

---

* all LD_{50} are acute oral dosages for rats

The soluble powder formulation of this insecticide controlled the OLR (Ota 1969) and here the emulsion was used to determine whether there is a difference between the two formulations.

Orthene$^{(R)}$ (O,S-dimethyl N-acetyl phosphoramido thioate). An organic phosphate with systemic insecticide-acaride action; stomach poison; LD_{50} = 945 mg/kg; reported to give good control of several lepidopterous larvae (Chevron Chem. Co. 1971). This insecticide has not previously been tested against the OLR.

Carbaryl plus molasses (Sevimol$^{(R)}$). A carbamate with stomach and contact action; LD_{50} = 307 mg/kg. Carbaryl alone has been reported as not very effective against the OLR. This material was included to determine the effect of the mixture.

Methomyl (Lannate$^{(R)}$). A carbamate with systemic insecticide-acaricide action; contact and stomach poison; LD_{50} = 17 mg/kg; recommended against lepidopterous larvae (Thomson 1972, Kenaga & Allison 1969). This insecticide was found to give the best control of the OLR in Ota's (1969) experiments. Although not labelled for greenhouse use it was included as a standard measure for other materials.

Treatments, formulation, concentration and dosage of these insecticides are indicated in Table 3.

Evaluation of the materials.

The effectiveness of the materials was evaluated by making counts one day before and four days after the insecticide applications on the same marked three branches per rose bush. Four days after was chosen primarily because B. thuringiensis needs from two to four days to kill the affected larvae. The first count one day before the application was necessary to obtain an overall view of the insect population, the

Table 3. Treatments, formulation, concentration and dosage used against the OLR

Treatment	Formulation & concentration	Dosage lb. active ingredient /100	Dosage actual /100	Dosage ingredient /1
			gallons of water	
Experiment 1				
1. Bacillus thuringiensis	7.2 BIU/lb. liquid	4 BIU	1 quart	2 tsp
2. aldicarb [a]	10 G	-	40 oz./ 1000 sq. ft.	1/2 tsp /pot
3. mexacarbate	2 E	0.5	1 quart	2 tsp
4. trichlorfon	4 E	0.5	1 quart	2 tsp
5. Check	-	-	-	-
Experiment 2				
1. Orthene	75 SP	1.0	1.33 quart	4 tsp
2. Sevimol (R)	4 E	1.0	1 quart	2 tsp
3. methomyl	90 SP	0.25	0.3 quart	1 tsp
4. Check	-	-	-	-

[a] one application

others were needed to obtain data on a possible residual effect of the materials and up to which instar the insecticide controls the larvae. To obtain these data the following observations were made:

Number of egg masses per branch. The presence or absence of an egg mass on a particular branch gives a good indication of the future number of first instar larvae on that or other branches, which should be present if no insecticide would have been applied or if the insecticide would not have acted against this stadium.

Number of first and second instar larvae per branch. These two stadia can be easily differentiated by their damage and they are visible under a magnifying glass, without being disturbed.

Number of webs per branch (corresponsing to the third, fourth and last instar and to the pupae). If not disturbed these larval instars normally stay within the web initiated and pupate there. Previous counts of 100 webs indicated that 98 were occupied by either larvae or pupae; this gives a high accuracy when taking a web as an index of the presence of a larva or pupa. AliNiazee et al. (1970) also judged the effectiveness of insecticides by the number of webs obtained in an one-hour search. By this method the existing OLR population in any given field was effectively determined by the same authors.

Number of exuviae per branch. This indicated the number of adults emerged and also shows the number of later instars killed by the respective insecticide if there is no adult emergence after a certain period of time. All exuviae found during a count were removed to avoid possible confusion.

After all applications had been made, the webs which had been counted were opened and the number of live larvae, as well as the

number of pupae was counted.

Based on these counts the mortality for the two larval groups was calculated and the data on effectiveness of the insecticides against the different instars obtained.

Since several applications had been planned, this type of evaluation instead of that used by other authors was chosen after considering that the 10 minute search of larvae on the treated host plants used by Ota (1969) was not convenient for this experiment. Also by this means the the webs are destroyed, the larvae migrate, initiate another web and are therefore more exposed to a possible residual effect of the insecticide. The method of counting the number of pupae, number of vacant webs and number of dead and living larvae used by Smith et al. (1965) would have been convenient, if only one insecticidal application had been planned.

After analyzing the data obtained by these two tests a final trial was set up with the three insecticides which had given the best control. The insecticides selected were: Orthene$^{(R)}$, mexacarbate and trichlorfon; their formulation, concentration and dosage used is the same as that given in Table 2. The selection of these materials was based on their effectiveness and residual activity shown against the OLR larvae, their non-phytotoxicity and the general appearance of rose plants following applications.

The same randomized block design with three replications and four treatments (36 potted roses) was used as in the other tests. The average number of five-leaflet leaves per branch for this experiment was 23.5 ± 7.3. Another timing schedule for the applications was programmed, based on the data of the previous tests. The same observations as for the first two trials were made to evaluate the effectiveness of the

insecticides, but counts were only made one day before the first application and four days after the last application, since data regarding residuality and age-specific kill of these materials had already been determined.

Residuality

Since during the progress of the two control experiments it was observed that the insecticides had a certain residual activity, two residuality tests, one on roses and the other on beans were set up to determine this aspect of the insecticide.

Table 4 shows the insecticide treatments used.

Residuality on roses.

In this test the WP of Bacillus thuringiensis was included to see whether there is a difference in activity and/or residuality between the two formulations. Two dosages of both mexacarbate and trichlorfon were applied to determine if the lower ones are as effective as the higher ones, the latter having been used in the first control experiment.

The materials were applied on five year old "Red American Beauty" roses on a bench space of 3.4 x 4.2 feet. Several generations of the OLR had developed on the roses. At the time of the applications all stages of the insect were present in approximately the same proportions. The same counts as for the insecticide experiments were made on 20 marked branches per treatment. The mean number of five-leaflet leaves per branch for the whole experiment was 28.7 $\pm$ 5.4. The counts were made one day before and 5, 10, 15 and 20 days after the insecticidal applications.

Residuality on beans.

In this test all insecticides were included which previously had

Table 4. Treatments, formulation, concentration and dosage used to determine residual activity against the OLR on roses and beans

Treatment	Formulation & concentration	Dosage lb. active ingredient /100	actual ingredient /100 gallons of water	/1
On Roses				
1. *B. thuringiensis*	7.2 BIU/lb. liquid	4 BIU	1 quart	2 tsp
2. *B. thuringiensis*	7.2 BIU/lb. WP	4 BIU	0.55	2.6 gr
3. trichlorfon	4 E	1.0	1 quart	2 tsp
4. trichlorfon	4 E	0.5	1/2 quart	1 tsp
5. mexacarbate	2 E	0.5	1 quart	2 tsp
6. mexacarbate	2 E	0.25	1/2 quart	1 tsp
On Beans				
1. Orthene (R)	75 SP	1.00	1.33 quart	4 tsp
2. mexacarbate	2 E	0.5	1 quart	2 tsp
3. Sevimol (R)	4 E	1.00	1 quart	2 tsp
4. *B. thuringiensis*	7.2 BIU/lb. liquid	4 BIU	1 quart	2 tsp
5. trichlorfon	4 E	1.00	1 quart	2 tsp
6. methomyl	90 SP	0.25	0.3 quart	1 tsp

been tested on roses for their effectiveness, with the exception of aldicarb. Two pots per treatment with five bean plants each were used. All insecticides were applied on day 0 and egg masses about to hatch were placed on two OLR free pots on day 0, 2, 4, 8, 16 and 20. Counts were made the day following introduction of the egg masses and from then on every two days up to the moment the number of established larvae remained constant.

Timing of insecticide applications

The most efficient control of any pest by insecticides is contingent upon the proper timing schedule of the applications. A timing schedule is determined by the population dynamics of the insect species, by the susceptibility of the different stages and instars to the insecticide and by the residual activity of the insecticide. Its effectiveness is based upon the idea that the insecticide application will kill a portion of the insect population, leaving the rest unharmed and able to follow the life cycle. The next application will kill the newly developed portion and after a certain number of applications the whole population will theoretically be eliminated.

For the first two insecticidal tests a tentative schedule of applications was computed based on the degree-days required for the development of the OLR, the adult longevity and the age-specific fecundity. In addition the following assumptions were made:

a) The number of insects in all age classes is approximately equal at the time of the first insecticidal application.

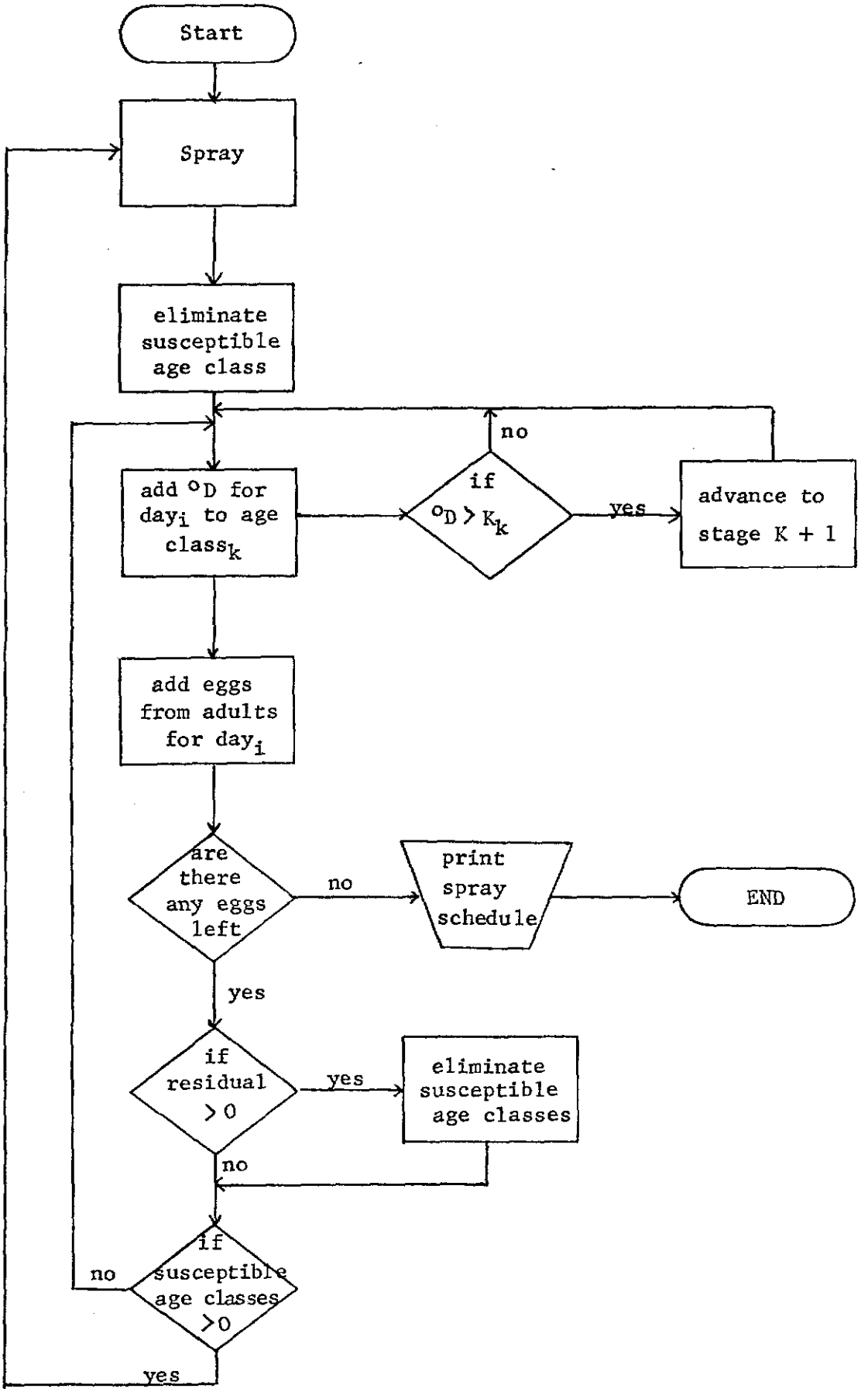
b) The insecticides have a 100 per cent effectivness against the first and second instar larvae, but no effect against the later instar larvae.

c) The insecticides do not have any residual activity.

The last two assumptions were changed when the timing schedule for the final test was programmed, since the first two insecticidal tests and the evaluation of the residuality of the insecticides had indicated that the materials to be used were also effective against third instar larvae and did show a certain residual activity

The flow chart of the program used to obtain the timing schedules is presented in Fig. 2.

Fig. 2. Flow chart used to obtain the temperature-dependent spray program.


Start
Spray
eliminate susceptible age class
add °D for day$_i$ to age class$_k$
if °D > K$_k$
no
yes
advance to stage K + 1
add eggs from adults for day$_i$
are there any eggs left
no
print spray schedule
END
yes
if residual > 0
yes
eliminate susceptible age classes
no
if susceptible age classes >0
no
yes

RESULTS

Role of temperature on the population dynamics of the OLR

Eggs

Table 5 presents the effect of constant and alternating temperatures on the egg development and survival of the OLR under both laboratory and greenhouse conditions. The incubation period was the time elapsed between the oviposition, which occurred at all temperatures two to three house after the beginning of the night period, and the moment the first larva emerged. Eggs never hatched during the night period and the time of the day was almost constant for each temperature treatment.

The incubation period decreased form 28 to 4 days as the temperature increased from 15 to 35°C. The egg masses laid and incubated in the greenhouse at a mean fluctuating temperature of 21.1°C developed only slightly faster than those at the mean fluctuating temperature of 20.5°C in the laboratory.

No hatch was recorded for the egg masses incubated at 10°C, but up to the highest temperature an apparently normal hatch was observed.

Most viable eggs of an egg mass hatched during a period of 15 minutes after the beginning of eclosion, and the "per cent of total hatch" in Table 5 represents the larvae emerged during this period. While at 20, 25 and 30°C constant temperatures the larvae emerged during this period represented over 75 per cent, at the extreme temperatures (15 and 35°C) only 59 and 64 per cent emerged respectively. The

Table 5. Effect of temperature on the egg development and survival of the OLR.

Temp. °C	No. of eggs incubated	Incubation period (days) Mean	SD	% of total hatch Mean	SD	% non-viable eggs Mean	SD	% unhatched viable eggs Mean	SD	% hatch (total) Mean	SD
Laboratory											
10[a]	5857	No development									
15[a]	4214	28.0	± 2.1	58.8	± 16.6	8.2	± 6.7	16.7	± 13.4	75.2	± 14.4
20	6538	12.0	± 0.5	85.3	± 11.2	3.8	± 7.5	5.6	± 7.7	90.4	± 10.4
25	6731	6.7	± 0.2	78.4	± 20.9	6.9	± 11.3	7.7	± 9.1	85.3	± 16.4
30	5656	4.8	± 0.3	75.1	± 21.4	5.9	± 12.3	7.5	± 11.7	86.2	± 17.7
35[a]	9430	4.3	± 0.1	63.9	± 18.1	2.0	± 3.5	11.1	± 10.5	86.7	± 12.4
19[b]	11997	12.3	± 0.4	89.7	± 10.9	0.8	± 1.8	3.3	± 3.7	95.7	± 4.1
20.5[b]	4212	10.0	± 0.5	69.9	± 24.7	9.5	± 11.4	5.8	± 6.9	85.	± 12.4
23[b]	11199	8.8	± 0.4	86.8	± 15.6	1.5	± 5.3	4.0	± 6.5	94.4	± 8.9
Greenhouse											
21.1[b]	2240	9.8	± 0.5	-		-		-		86.3	± 8.1

[a] eggs laid at 25°C

[b] mean fluctuating temperature

highest percentage of emergence was obtained at 20°C. (85 per cent). Regarding the alternating temperature treatments, at the mean fluctuating temperature of 19 and 23°C, over 80 percent larval emergence was obtained, which was similar to the 20°C constant temperature treatment. However, at the mean fluctuating temperature of 20.5°C a comparatively low percent (70) of the total number of eggs per egg mass hatched during the 15 minute period, which was approximately 15 per cent less than that obtained for the corresponding constant temperature.

Table 5 also shows the percentage of a) non-viable eggs, b) unhatched viable eggs, and c) the total hatch. The "non-viable" eggs stayed green and no change of color was observed, while these which were viable first turned yellowish-green and then one to two days before the emergence of the larvae turned dark brown This color was caused by the head-capsules and thoracic shields being visible through the chorion. The percentage of unhatched viable eggs at 15 and 35°C (16.7 and 11.1 per cent respectively) was much higher than that at the other temperatures. The total percentage of eggs hatched at 15°C was considerably lower than that at all other temperatures showed a higher total percent hatch than the constant temperature treatments.

The standard deviations of the various percentages in Table 5 can be considered relatively high, indicating a high variability between the viability of the eggs within each egg mass and between the egg masses.

When the duration of the incubation period at each temperature

was plotted against temperature a line in the form of a hyperbola was obtained (Fig. 3). When the developmental velocity (%/day, see Table 1-A Appendix) was plotted against temperature, a relatively straight line between 15 and 30°C can be observed. This velocity line departed at its upper limit (30°C) and at its lower limit (15°C) and was straight only over the normal range of temperature.

To estimate the rate of development at temperatures other than those studied, the temperature summation formula was used. To determine t, the regression equation for the velocity line was calculated:

$$V = 1.1678\ T - 14.3764,$$

which gave a threshold temperature for the egg development of 12.31°C and a thermal constant of 85.6 degree-days. This K calculated from the regression equation based on the egg developmental rates at different constant temperatures was considered equal to K = 87.8°C, obtained for the 28 egg masses observed in the greenhouse at 21.1°C mean fluctuating temperature.

Comparing the egg development at the mean fluctuating temperature with that at the corresponding constant temperature, the mean fluctuating temperatures of 19 and 20°C accelerated development, while at the 23°C mean fluctuating temperature a retardation was observed. The percentage increase was 7.4 and 5.1 per cent for the 19 and 20.5°C mean fluctuating temperatures respectively and the decrease was 9.9 per cent at the 23°C mean fluctuating temperature.

Larvae

Results on the developmental time for the larvae at the various temperature treatments are shown in Tables 6, 7 and 8 for males and type

Fig. 3. Relationship between temperature and developmental rate (solid line) and developmental time (dotted line) of the egg stage of the OLR. Data recorded by Atkins et al. (1957) (A) and Nelson (1936) (N) are superimposed on the developmental time curve.

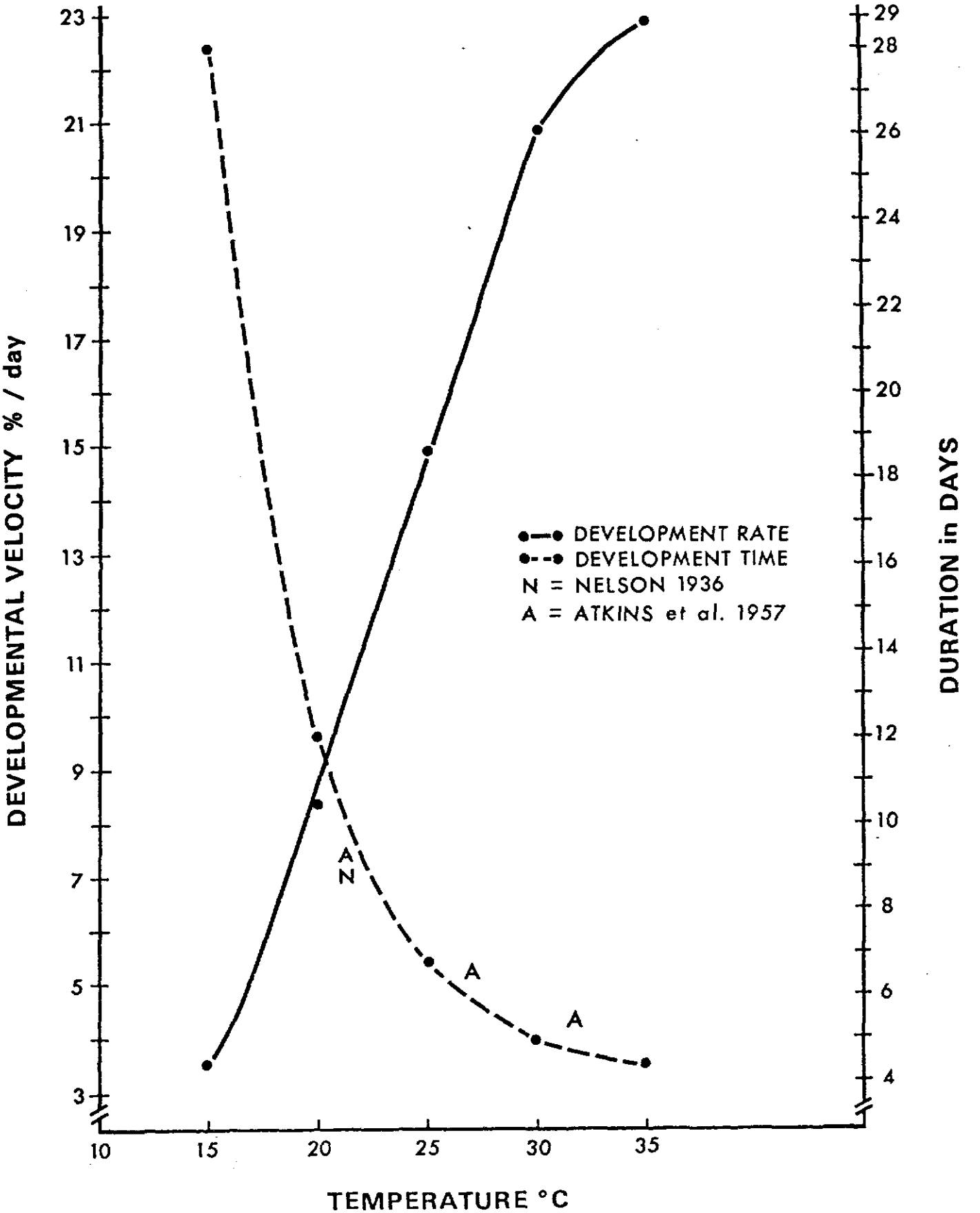

DEVELOPMENTAL VELOCITY % / day
DURATION in DAYS
TEMPERATURE °C
DEVELOPMENT RATE
DEVELOPMENT TIME
N = NELSON 1936
A = ATKINS et al. 1957
N
A
A
23
21
19
17
15
13
11
9
7
5
3
29
28
26
24
22
20
18
16
14
12
10
8
6
4
10
15
20
25
30
35

Table 6. Effect of various temperatures on the developmental time in days of the larval stadia of the male OLR reared on artificial diet.

Temperature	Instars					Total larval stage	
	1st	2nd	3rd	4th	5th	Mean	SD
15 (N = 18)[a]	13.2 ± 2.0	10.0 ± 1.1	11.8 ± 0.9	12.8 ± 0.8	24.7 ± 1.5	72.7	± 4.7
20 (N = 23)	7.7 ± 1.4	5.4 ± 0.5	4.7 ± 0.4	5.3 ± 0.4	8.7 ± 0.5	32.0	± 2.2
25 (N = 31)	4.1 ± 0.4	2.8 ± 0.3	2.6 ± 0.4	2.6 ± 0.2	4.5 ± 0.4	16.8	± 0.9
30 (N = 41)	3.3 ± 0.3	2.1 ± 0.2	2.0 ± 0.1	2.2 ± 0.2	3.3 ± 0.5	13.1	± 0.8
35 (N = 29)	3.0 ± 0.2	2.1 ± 0.2	1.8 ± 0.2	2.1 ± 0.3	3.5 ± 0.5	12.7	± 1.0
19[b] (N = 23)	8.2 ± 1.7	5.5 ± 0.5	4.5 ± 0.6	5.0 ± 0.4	8.2 ± 0.5	31.6	± 2.0
20.5[b] (N = 29)	6.4 ± 0.6	4.8 ± 0.6	4.0 ± 0.4	4.2 ± 0.5	6.6 ± 0.4	26.1	± 1.7
23[b] (N = 25)	6.4 ± 1.9	4.0 ± 0.5	3.4 ± 0.3	3.6 ± 0.4	6.3 ± 0.5	23.9	± 2.5

[a] N = No. of larvae observed

[b] mean fluctuating temperature

Table 7. Effect of various temperature treatments on the developmental time in days of the stadia of the type A female larvae of the OLR reared on artificial diet

Temperature °C	Instars					Total larval stage
	1st	2nd	3rd	4th	5th	
	Mean SD	Mean SD	Mean SD	Mean SD	Mean SD	Mean SD
20 (N = 14)[a]	7.6 ± 1.0	5.4 ± 0.5	5.2 ± 0.4	6.3 ± 0.4	8.7 ± 0.4	33.3 ± 1.3
25 (N = 21)	4.2 ± 0.4	3 1 ± 0.2	2.9 ± 0.1	3.0 ± 0.3	4.8 ± 0.4	18.3 ± 0.7
30 (N = 14)	3.1 ± 0.3	2.2 ± 0.3	2.1 ± 0.1	2.4 ± 0.3	3.8 ± 0.4	13.7 ± 0.8
35 (N = 22)	2.9 ± 0.2	2.1 ± 0.3	2.0 ± 0.3	2.4 ± 0.4	3.8 ± 0.3	13.4 ± 0.9
19[b] (N = 32)	8.8 ± 1.9	5.6 ± 1.1	5.0 ± 0.4	5.6 ± 0.5	8.8 ± 0.4	34.1 ± 2.4
20.5[b] (N = 15)	6,0 ± 0.6	4.5 ± 0.4	4.1 ± 0.2	4.9 ± 0.3	7.0 ± 0.4	26.6 ± 1.3
23[b] (N = 25)	6.2 ± 2.0	4.0 ± 0.6	3.7 ± 0.3	3.9 ± 0.3	7.0 ± 0.6	25.1 ± 2.8

[a] N = No. of larvae observed

[b] mean fluctuating temperature

Table 8. Effect of various temperatures on the developmental time in days of the stadia of the type B female larvae of the OLR reared on artificial diet.

Temperature °C	Instars												Total larval stage	
	1st		2nd		3rd		4th		5th		6th			
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
15 (N = 11)[a]	12.3	± 2.4	11.7	± 1.6	12.2	± 0.8	12.8	± 1.5	13.5	± 0.7	29.0	± 4.0	91.7	± 7.8
20 (N = 10)	8.6	± 1.7	5.8	± 0.9	5.0	± 0.4	4.5	± 0.4	5.6	± 0.7	8.3	± 1.1	38.1	± 2.6
25 (N = 4)	5.5	± 0.6	3.2	± 0.4	2.8	± 0.1	2.4	± 0.4	3.0	± 0.2	5.0	± 0.3	21.9	± 1.9
30 (N = 8)	3.6	± 0.9	2.2	± 0.4	2.3	± 0.3	2.1	± 0.3	2.1	± 0.3	3.3	± 0.5	15.0	± 0.5
35 (N = 8)	3.3	± 0.3	2.2	± 0.3	2.1	± 0.1	2.2	± 0.3	2.8	± 0.2	3.7	± 0.3	16.5	± 0.9
19[b] (N = 4)	13.4	± 0.5	4.8	± 0.2	4.1	± 0.2	4.2	± 0.4	3.5	± 0.0	8.0	± 0.0	37.5	± 1.4
20.5[b] (N = 5)	7.3	± 1.5	5.1	± 0.2	4.1	± 0.4	3.9	± 0.1	4.1	± 0.1	7.7	± 1.4	32.4	± 3.3
23[b] (N = 5)	9.7	± 1.4	3.8	± 0.0	3.4	± 0.5	2.9	± 0.1	4.6	± 0.5	7.1	± 0.4	31.7	± 1.7

[a] N = No. of larvae observed

[b] mean fluctuating temperature

A and B females respectively. The division into these female types was necessary, because with the exception of the 15°C treatment both female forms occurred simultaneously. The division was used in the way suggested by Zenner-Polania & Helgesen (1973): females with five instars = type A, and females with six instars = type B.

The data in the three tables show that the influence of temperature on the developmental time of all larval instars of the OLR is clearly marked: the developmental time decreased as the temperature increased. The total larval stage of the males for example decreased from 14 days at 15°C to 13 days at 35°C. In general the time spent in the first and last larval instar was longer than that spent in any other stadium, which was relatively similar in duration for both males and females within each temperature treatment. The prepupal stage was not exactly recorded, but it was observed that it varied from five to six days at 20 to one one day at 35°C.

Males spent a shorter time in the larval stage than both female types. At 20°C the difference in duration of the total larval stage was one day between males and type A females, and five days between type A and type B females. As the temperature increased, however, the difference in the duration of the total larval period between the three types decreased.

Comparing the two female larval types the first three stadia were of similar duration for the respective temperature treatments. The difference in the total larval development time between the two types was produced by the extra instar of the type B larvae, which apparently was the fifth instar. At the 15°C treatment no type A females were

observed. Some larvae (13.7 per cent) molted to a seventh stadium, but died before pupating after more than 45 days in this instar.

For all larvae observed in the greenhouse an average developmental time of 28.7 $\pm$ 2.1 days was recorded at a mean fluctuating temperature of 20°C.

The variability of the developmental times at the different temperatures was very low and seldom was the standard error found to be higher than 10 per cent of the mean; an accuracy level accepted as satisfactory by Southwood (1971) for life table studies.

Larval mortality at the different instars and temperatures are given in Table 9. None of the larvae in the 10°C chamber established a feeding site and a 100 per cent mortality was observed in the first instar. For the other temperature treatments mortality was highest for the first and second instar in general and 100 per cent survival was observed for the fourth and fifth instar larvae. Only at the extreme temperatures was a mortality of the last instar larvae noted. This was especially high at 15°C and comprised all seven-instar and most six-instar larvae, which as suggested by Zenner-Polania & Helgesen (1973) would have been females.

Regarding total larval mortality, high percentages were observed for the 20°C constant temperature and the 23°C mean fluctuating temperature as compared with the other temperature treatments (excluding the 15°C treatment, where mortality was considered to be very high). In the greenhouse a very high larval mortality was observed, which was mainly caused by the death of 50 per cent of the first instar larvae; once established survival was very high and only two out of fifty larvae observed in the greenhouse died.

For all instars of both sexes the developmental velocity (per cent/

Table 9. Larval mortality of the OLR at various temperatures

Temperature °C	Percentage Larval instars 1st	2nd	3rd	4th	5th	6th	7th	Total larval mortality
Laboratory								
10	100.0							100.0
15	13.7	5.8	1.9	0	0	5.8	13.7[a]	41.1
20	3.8	5.7	0	0	0	0		9.6
25	1.6	1.6	0	0	0	0		3.3
30	3.0	0	0	0	0	0		3.0
35	1.6	0	0	0	0	1.6		3.3
19[b]	1.6	1.6	0	0	0	0		3.2
20.5[b]	2.0	0	0	0	0	0		2.0
23[b]	3.2	4.9	0	0	0	0		8.1
Greenhouse								
20[b]	50.0	4.0	0	0	0	0		54.0

[a] only at 15°C were several larvae observed to enter a seventh instar

[b] mean fluctuating temperature

day, Table 1A-Appendix) was plotted against the temperature. A relative straight line was obtained for all instars of the females type A between 20 and 30°C and for all instars of the males and type females between 15 and 30°C (Figs. 4, 5 and 6).

The developmental rate for the total larval stage of male and both female larval types, for all larval types together and the developmental time for all larval types together, were also plotted against temperature (Fig. 7). With the exception of the type B larvae the straight parts of the velocity lines were parallel between 20 and 30°C.

The regression equations of the developmental velocity for all instars of both sexes were calculated. The threshold temperature (t) and the thermal constant (K) in terms of degree-days were obtained as shown in Table 10.

The threshold temperature (t) showed a rising trend as the larval development advanced, t was at least 2°C higher during the last instar than at the first instar for male and type B larvae. Type A larvae showed a more constant t for the first four instars (13°C), but it declined abruptly at the fifth instar. With the exception of the fifth instar, type A larvae always had a higher t than male and type B larvae (Table 10).

The thermal constant was highest for the first and last instar for all larval types. The degree-day requirements were similar for the other instars of male and type A larvae and higher for the type B larvae excepting its fourth instar. Comparing the last instars of type A and male larvae, the former had a much higher heat requirement than the latter.

For the total larval stage the threshold temperature was a little

Fig. 4. Relationship between temperature and developmental rate of the different instars of the male OLR larvae. Roman numerals indicate larval instars.

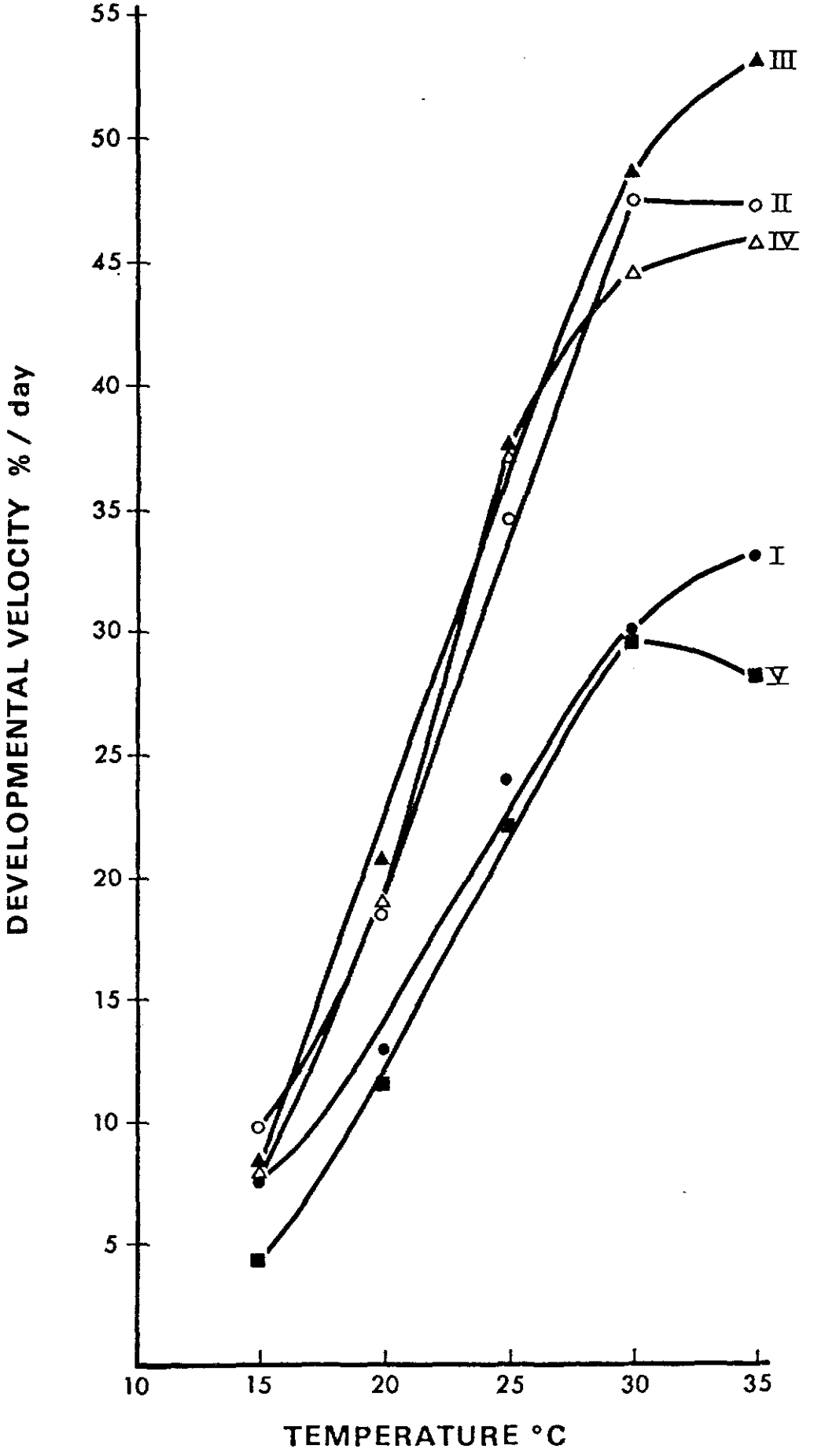

DEVELOPMENTAL VELOCITY % / day
TEMPERATURE °C
55
50
45
40
35
30
25
20
15
10
5
10
15
20
25
30
35
III
II
IV
I
V

Fig. 5. Relationship between temperature and developmental rate of the different instars of the type A female of the OLR larvae. Roman numerals indicate larvae instars.

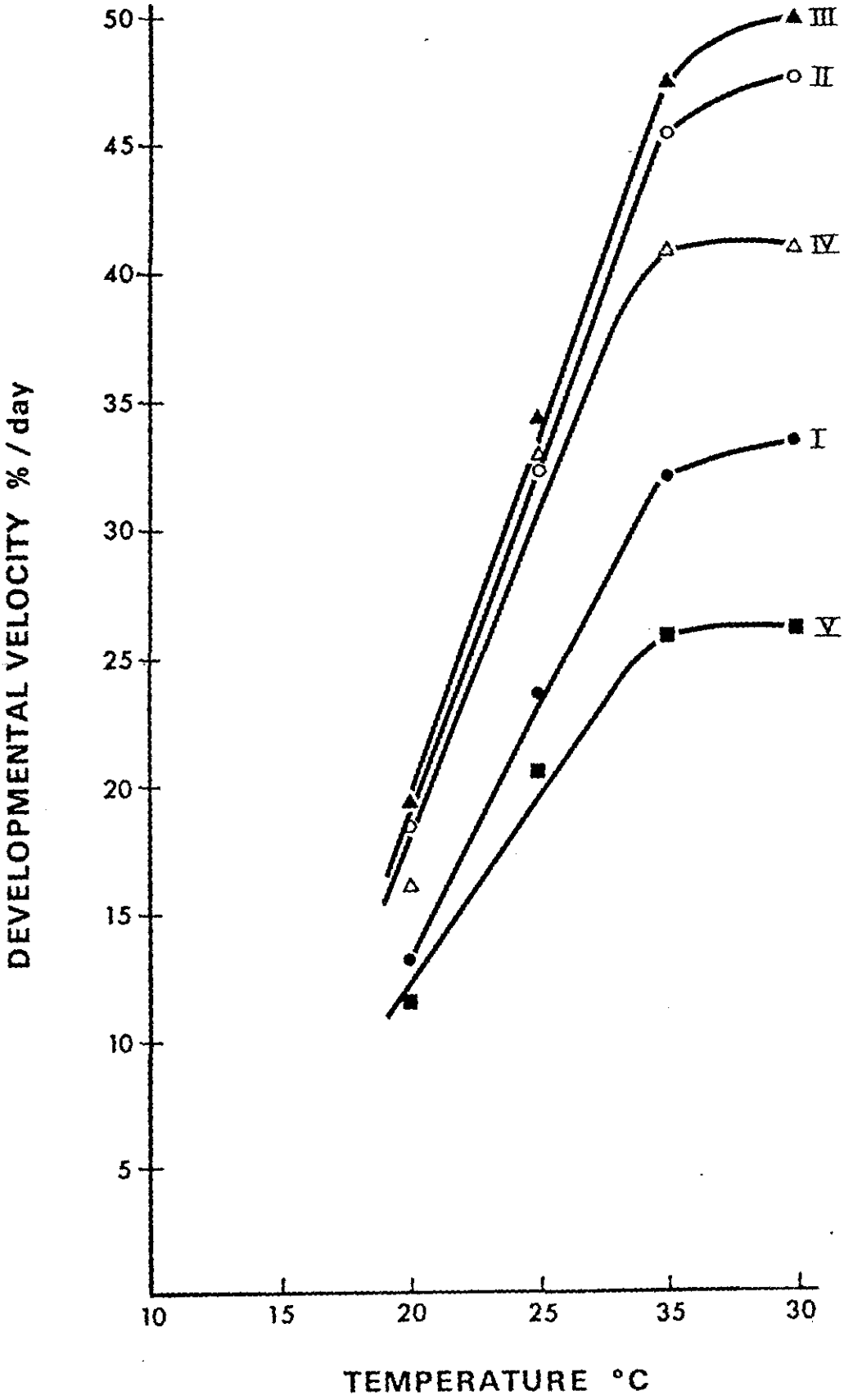

DEVELOPMENTAL VELOCITY % / day
50
45
40
35
30
25
20
15
10
5
10
15
20
25
35
30
TEMPERATURE °C
III
II
IV
I
V

Fig. 6. Relationship between temperature and developmental rate of the different instars of the type B female OLR larvae. Roman numerals indicate larval in tars.

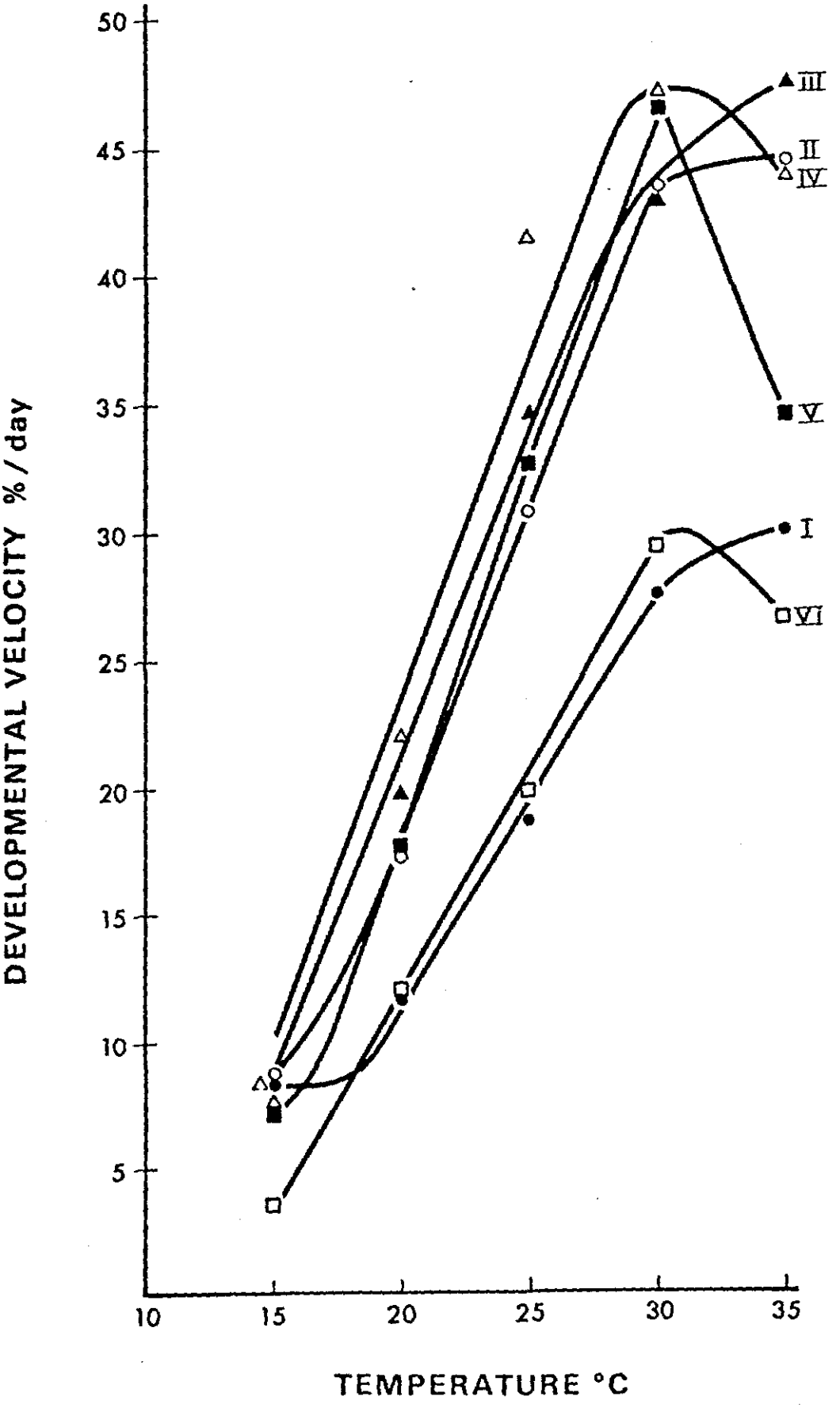

DEVELOPMENTAL VELOCITY %/day
50
45
40
35
30
25
20
15
10
5
10
15
20
25
30
35
TEMPERATURE °C
III
II
IV
V
I
VI

Fig. 7. Relationship between temperature and developmental rate (solid line) of the larval stage of males, type A females, type B females, and both sexes combined. Developmental times reported by other authors are superimposed on the developmental time curve for all larvae (dotted line).

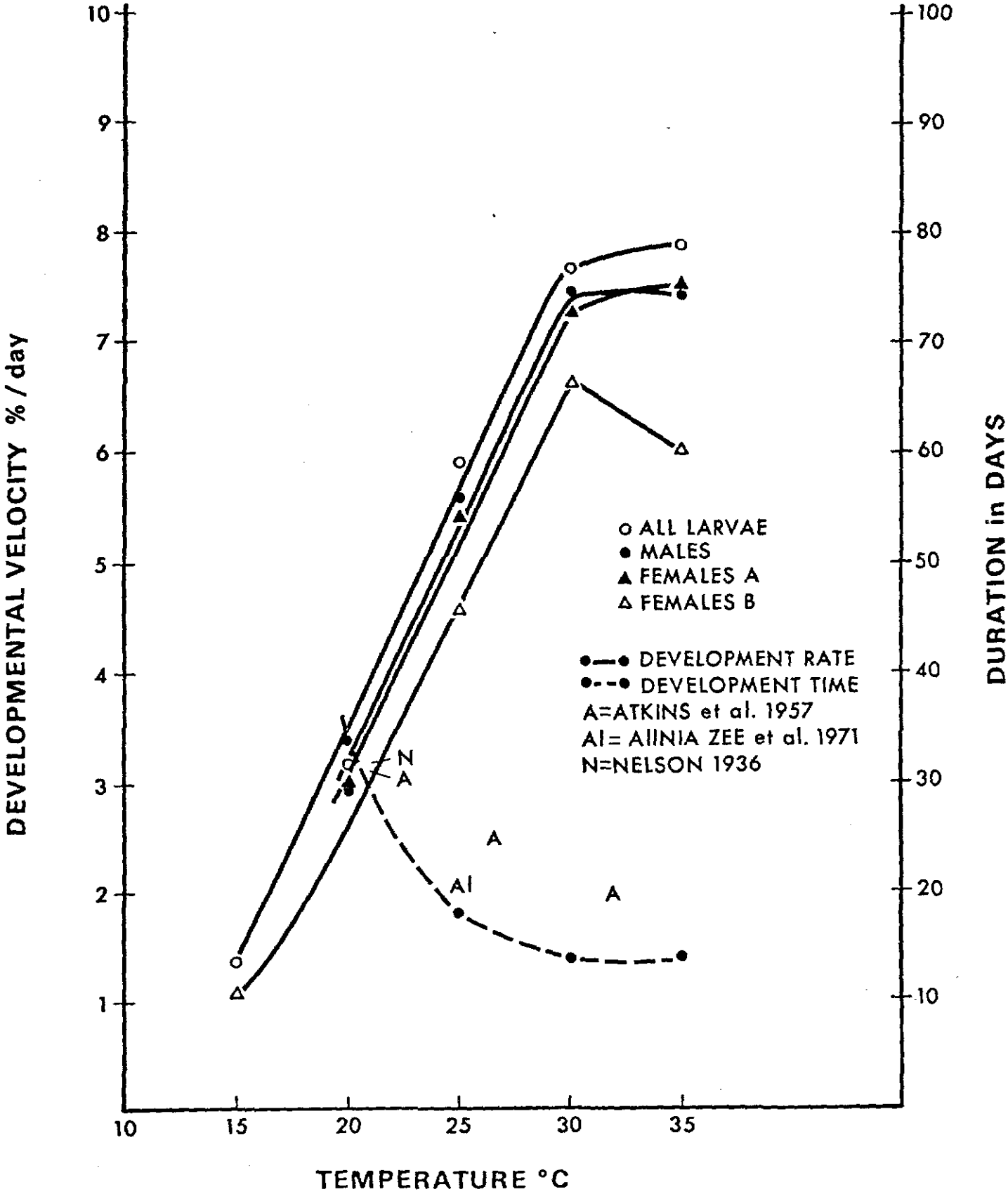

DEVELOPMENTAL VELOCITY % / day
DURATION in DAYS
TEMPERATURE °C
10
9
8
7
6
5
4
3
2
1
100
90
80
70
60
50
40
30
20
10
10
15
20
25
30
35
o ALL LARVAE
● MALES
▲ FEMALES A
△ FEMALES B
●—● DEVELOPMENT RATE
●--● DEVELOPMENT TIME
A=ATKINS et al. 1957
Al= AlINIA ZEE et al. 1971
N=NELSON 1936
N
A
A
Al
A

Table 10. Threshold temperature of development (t) and thermal constant (K) in terms of degree-days based on the regression equation of developmental velocity of the larval stage of the OLR

Larval	Type	Regression equation	Threshold temperature (t) °C	Thermal constant (K) °D
1st	♂♂	V = 1.5776 T - 16.8134	10.6	63.3
	♀♀ A	V = 1.9003 T - 24.6701	12.9	52.6
	♀♀ B	V = 1.3207 T - 13.1890	10.0	75.7
2nd	♂♂	V = 2.5435 T - 29.6923	11.6	39.3
	♀♀ A	V = 2.7061 T - 35.6766	13.1	36.9
	♀♀ B	V = 2.3766 T - 28.4035	11.9	42.0
3rd	♂♂	V = 2.7607 T - 33.1283	12.0	36.2
	♀♀ A	V = 2.8192 T - 36.9321	13.1	35.4
	♀♀ B	V = 2.4091 T - 27.6896	11.4	41.5
4th	♂♂	V = 2.5993 T - 31.2598	12.0	38.4
	♀♀ A	V = 2.4880 T - 32.3206	13.0	40.1
	♀♀ B	V = 2.7648 T - 32.5305	11.7	36.1
5th	♂♂	V = 1.7754 T - 22.9670	12.9	56.9
	♀♀ A	V = 1.4205 T - 16.3200	11.4	70.3
	♀♀ B	V = 2.6646 T - 33.8031	12.6	37.5
6th	B	V = 1.7373 T - 22.8454	13.1	57.5
Total larval stage	♂♂	V = 0.4310 T - 5.1853	12.0	232.0
	♀♀ A	V = 0.4257 T - 5.4109	12.7	234.9
	♀♀ B	V = 0.3728 T - 4.6561	12.4	268.2
	both sexes	V = 0.4470 T - 5.8250	13.0	223.7

higher for type A larvae than for type B larvae; males showed the lowest t. The total heat requirements in terms of degree-days for males and females A was similar, and lower than for type B larvae.

For the calculations of K and t of the total larval stage of both sexes only the developmental rates at 20, 25 and 30°C were taken, since at 15°C no females type A were observed. This explained a t of 13°C, higher than that calculated for either type separately, and a K of 224°D, much lower than a mean value for the three larval types. The mean K for the total larval stage (including both sexes) under greenhouse conditions was 216.6°D at a mean fluctuating temperature of 20°C. This was considered similar to K = 224°D obtained from the regression equation based on the developmental rates of both sexes at different temperatures under laboratory conditions.

For all regression equations in Table 10 a regression coefficient higher than 0.9 was obtained and f was always significant at the 0.05 level.

When comparing the developmental rate at the mean fluctuating temperature of the different instars for the male and type A and B female larvae with the developmental rate at the corresponding constant temperatures obtained by interpolation from Figs. 3, 4 and 5 respectively (see Table 2A-Appendix) the same general trend as for the eggs was noted. The developmental rate at 19 and 20.5°C mean fluctuating temperature increased or was equal to that at the corresponding constant temperature, while that at 23°C mean fluctuating temperature decreased or was equal to that at the constant temperature. For the total larval stage (including all larval types) the percentages calculated were:

Mean fluctuating temperature °C	Increase over corresponding constant temperature (%)
19	0.5
20.5	1.0
23	- 1.0

Therefore the developmental rate of the total larval stage of the OLR was very similar at the mean fluctuating temperature as compared to that at the corresponding constant temperature within the range of the temperatures studied.

All larval instars survived well on the artificial diet, with no observable deleterious effects after several generations. However, when more than one larva was confined to a Petri dish and one pupated first, the other one occasionally fed on the pupa, although enough diet was available. When 20 larvae were reared together in a 100 x 15 mm Petri dish, never more than 13 adults were obtained, one third or more of the pupae were always eaten. Since male larvae pupated first an excess of females was always obtained.

Pupae

Table 11 shows the effect of temperature on the developmental time of the pupae. An increase in temperature from 15 to 35°C brought about a decrease in the developmental time from 32 to 5 days for male and type B female pupae. Type A female pupae developed in half the time at 35°C than at 20°C.

At all temperatures male pupae took longer for their development than female pupae. At the constant temperatures this difference in time between male and female pupal development decreased as the temperature increased (from almost two days between male and type A female pupae at

Table 11. Effect of temperature on the developmental time in days and the mortality of the pupae of the OLR.

Temperature °C	No. observed	Males Mean ± SD	No. observed	type A females Mean ± SD	No. observed	type B females Mean ± SD	Both sexes Mean ± SD	Per cent mortality Both sexes
Laboratory								
15	12	32.9 ± 2.4	-	-	2	32.5 ± 3.5	-	31.3
20	23	12.6 ± 0.8	14	10.8 ± 0.5	10	11.6 ± 0.9	11.9 ± 1.0	0.0
25	31	7.0 ± 0.1	18	6.3 ± 0.4	4	6.2 ± 0.0	6.7 ± 0.4	5.0
30	40	4.9 ± 0.3	14	4.3 ± 0.3	8	4.3 ± 0.4	4.7 ± 0.4	1.5
35	25	5.1 ± 0.4	22	4.5 ± 0.5	4	5.0 ± 0.0	4.8 ± 0.8	11.6
19[a]	21	13.6 ± 0.6	32	12.2 ± 0.7	4	12.0 ± 0.1	12.7 ± 0.9	3.2
20.5[a]	29	10.7 ± 0.3	15	9.5 ± 0.4	5	9.6 ± 0.3	10.3 ± 0.6	0.0
23[a]	25	9.5 ± 0.5	25	8.5 ± 0.5	5	8.0 ± 0.6	8.9 ± 0.7	1.6
Greenhouse								
20.67[a]	30[b]						10.0 ± 0.6	0.0

[a] mean fluctuating temperature

[b] Total number of pupae observed (males and females)

20°C to half a day at 35°C), while for the alternating temperatures the difference in developmental time was always approximately one day. Both female types had a very similar pupal developmental time at all temperatures. The duration of the pupal stage in the greenhouse was very similar to that in the laboratory under equivalent temperature conditions.

The percentage mortality of the pupae is also presented in Table 11. This percentage was highest at the extreme temperatures of 15 and 35°C. No mortality was recorded for the 20°C constant and 20.5°C mean fluctuating temperature in the laboratory and at the 60.67°C mean fluctuating temperature in the greenhouse.

When the developmental velocity (%/day, see Table 1A-Appendix) was plotted against the temperature a straight line was obtained between 20 and 20°C for the three pupal types and the combination of all types (Fig. 8).

The regression equation, t and K were calculated and the following data obtained:

males: $V = 1.1316\ T - 14.0535$; $t = 12.4$; $K = 88.3$

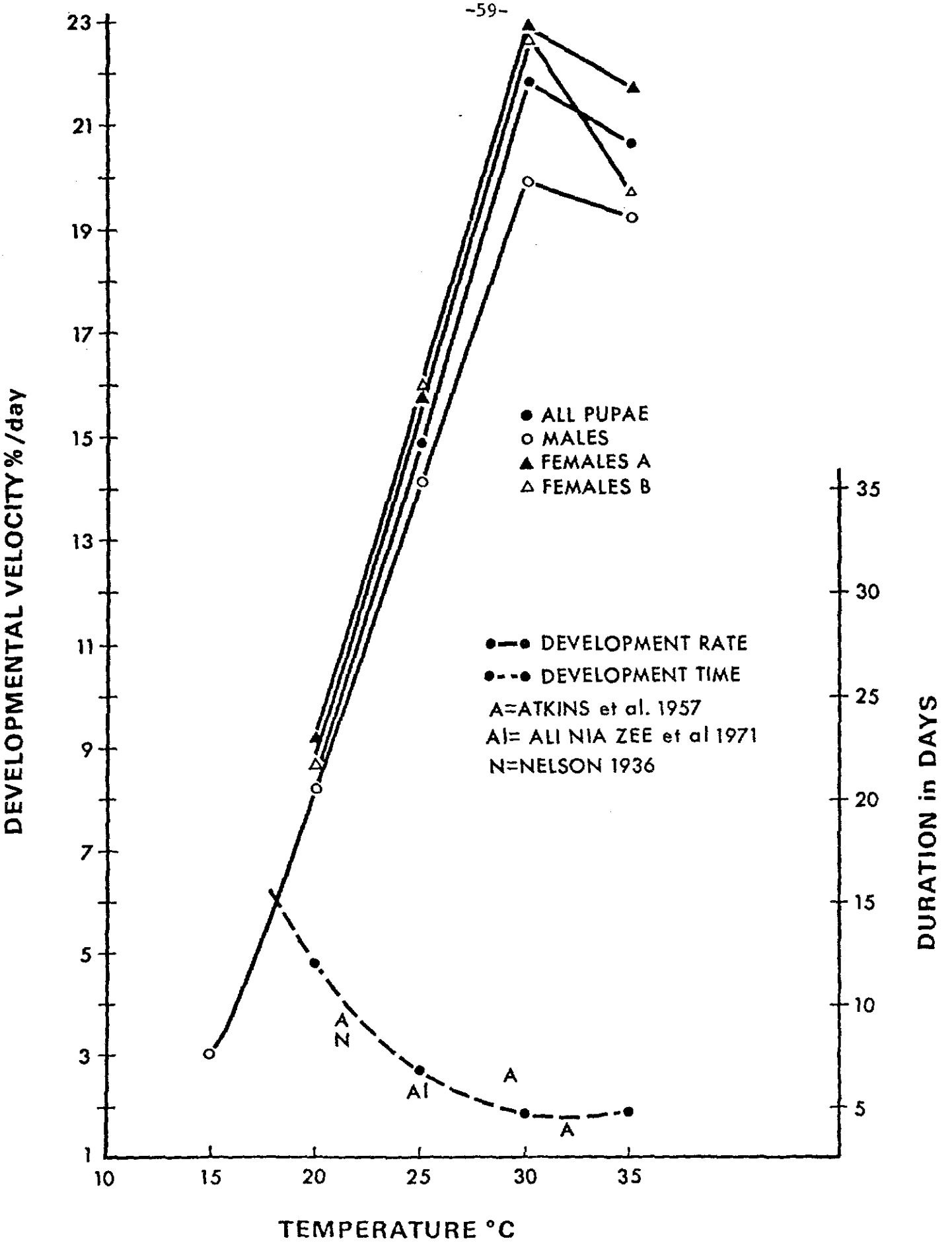
type A females: $V = 1.3747\ T - 18.4003$; $t = 13.3$; $K = 72.7$

type B females: $V = 1.4348\ T - 20.0444$; $t = 13.9$; $K = 69.6$

both sexes: $V = 1.2550\ T - 16.6550$; $t = 13.2$; $K = 79.6$

The threshold temperature was much lower for the males than for both female types and t for the two female types was very similar. K was higher for male pupae than for both female types, having the latter similar heat requirements. In the greenhouse the mean K for the pupae of both sexes together at a 20.67°C mean fluctuating temperature was 73.7°D.

Fig. 8. Relationship between temperature and developmental rate of the pupal stage of the male, type A and B female and all pupae (solid line). Developmental times reported by other authors are superimposed on the developmental time curve for all pupae (dotted line).


DEVELOPMENTAL VELOCITY %/day
DURATION in DAYS
TEMPERATURE °C
● ALL PUPAE
○ MALES
▲ FEMALES A
△ FEMALES B
●—● DEVELOPMENT RATE
●- -● DEVELOPMENT TIME
A=ATKINS et al. 1957
Al= ALI NIA ZEE et al 1971
N=NELSON 1936
N
Al
A
A
23
21
19
17
15
13
11
9
7
5
3
1
35
30
25
20
15
10
5
10
15
20
25
30
35

When the developmental rates at the mean fluctuating temperatures were compared with the interpolated rates from Fig. 8 at the corresponding constant temperatures (see Table 3A-Appendix), the same trend as for the egg and the larval development was observed: At the 19°C mean fluctuating temperature an increase in the developmental rate of the males and females A was obtained, while for the females B the rate was equal. At the 20.5°C mean fluctuating temperature for both sexes an increase and at the 23°C mean fluctuating temperature a decrease in the developmental rate over that at the corresponding constant temperatures was observed. Considering males and both female types together the general increase was 3.1 per cent, 3.9 per cent and -12.6 per cent at 19, 20.5 and 23°C mean fluctuating temperatures respectively over the corresponding constant temperatures.

Adults

Two to four hours before the adult emergence the pupa started a rotatory movement, destroyed the web and moved partially out of the retreat, leaving only the abdominal segments inside. After emergence the exuvia can be ovserved protruding from the web (Fig. 1E).

Adult emergence occurred only during the light period and the highest rate was observed from one to two hours after the lights came on in the chamber (early morning hours). Males emerged generally a little later than females. Both males and females needed at least 30 minutes after emergence for expanding and drying their wings before they were able to fly (Fig. 1F).

Table 12 shows the sex ratio and adult longevity in days of the OLR under laboratory conditions at various temperatures. At the intermediate temperatures of both constant and fluctuating temperature

Table 12. Sex ratio and adult longevity of the OLR at various temperatures under laboratory conditions.

Temperature	Sex ratio	Longevity in days					
°C	male : female	males		fertil females		non-fertilized females	
		Mean	SD	Mean	SD	Mean	SD
15	1 : 0.0	-		-		-	
20	1 : 1.0	9.9	± 3.6	12.0	± 4.2	10.9	± 3.8
25	1 : 0.6	17.7	± 3.9	16.2	± 3.7	14.4	± 2.3
30	1 : 0.5	7.3	± 2.0	9.3	± 2.9	8.3	± 2.0
35	1 : 1.0						
19[b]	1 : 1.6	19.2	± 4.6	19.7	± 3.6	18.9	± 2.9
20.5[b]	1 : 0.6	21.0	± 4.9	17.5	± 3.9	14.9	± 5.0
23[b]	1 : 1.2	17.4	± 4.7	16.1	± 3.4	12.6	± 3.3

[a] 81.6% of the females died either immediately after emergence or did not complete this process

[b] mean fluctuating temperature

treatments a high proportion of males to females was observed, while this ratio was reversed at the two extreme mean fluctuating temperatures and was 1:1 at the extreme constant temperature.

With the exception of the 20 and 30°C treatments where females lived longer than males, the latter always survived the females. Fertilized females had a longer lifespan at all temperatures than non-fertilized ones. This latter group was easily distinguished from the fertile females, since either few non-viable eggs were laid by them or they died with the abdomen turgid and of greenish color caused by the retained eggs. In general a longer life was observed for both sexes at the fluctuating temperatures than at the constant temperatures.

Mating occurred two to three hours after the dark period had started on the first or second day after the emergence of the females. Multiple mating was never observed for females but frequently for males, which fertilized up to four different females.

The females oviposited two to three hours after the night period had started on the second or third day after emergence. At the 25 and 30°C treatments most of the females started laying eggs on the second day after their emergence, while at the other temperatures most of the egg masses were laid at the third day of the female's life.

The oviposition record of the females at various temperatures is shown in Table 13. The variability of the mean number of eggs per female was very high at all temperatures. The highest number of eggs laid by a female was 1017 at 25°C, while the lowest was 81 eggs deposited at 20°C, and the average value was approximately 500 eggs per female. The number of egg masses per female varied from one to eighteen, with an average of seven.

Table 13. Oviposition record from day of emergence to death at various temperatures of fertilized females of the OLR under laboratory conditions.

Temperature °C	No. of females observed	Mean no. of eggs per female		Oviposition of 50% of the eggs after emergence	90%	Mean number of eggs per egg mass
		Mean	SD			
20	13	513.6	± 252.2	4	9	74.2
25	26	541.2	± 252.6	3	7	63.3
30	17	431.0	± 227.5	3	6	64.9
19[a]	28	636.1	± 181.2	4	10	57.4
20.5[a]	12	356.0	± 229.6	5	10	45.9
23[a]	20	698.0	± 163.3	4	9	60.9

[a]mean fluctuating temperature

Most females deposited 50 per cent or more of the eggs on the third to fifth day, and 90 per cent or more had been laid from the sixth to the tenth day after emergence. At the constant temperatures a higher mean number of eggs per egg mass was observed than at the fluctuating temperatures, although, excepting the 20.5°C mean fluctuating temperature, more eggs were laid per female at those latter treatments over a longer timespan.

In the greenhouse at a mean fluctuating temperature of 21°C fecundity was found to be approximately one third less than under laboratory conditions. The number of eggs per egg mass ranged from 43 to 309 with an average of 80 eggs per egg mass and an average of 160 eggs per female. Similar data were obtained, when the fecundity of 30 unfed mated females was determined in the laboratory at 20°C. These females laid a total of 5730 eggs and the number of eggs per egg mass ranged from 31 to 352, with an average of 84.6 eggs per egg mass and an average of 191 eggs per female.

Critical population level

Egg masses of the OLR were normally found on the older leaflets pertaining to the lower two thirds of the rose plant. Only four per cent of the egg masses observed were on the upper third of the plant. Contrary to Nelson's (1936) observation that egg masses are normally found on the underside of the leaflet, in the greenhouse 97 per cent of them were laid on the upper surface of the leaflets, two per cent on the stem and only one per cent on the upperside of the leaflets.

After their emergence the first instar larvae always moved to the young growth of the plant, where they established a feeding site. Older leaves were never found attacked by the first or second instar

larvae. When an egg mass was present on a particular rose plant all shoots and/or flower buds of this plant were subsequently attacked.

Damage caused by the OLR larvae

First and second instar larvae

The first instar larvae of the OLR established themselves first on the underside of the leaflet near the edge, feeding on the epidermis, which results in small transparent areas (Fig. 9A). After several days the larva had spun a cover over the initial feeding site, but could still be observed through the loosly webbed silken threads. Through the rest of the first and the total second larval instar the larva continued to feed on the lower epidermis of the leaflet, enlarging the transparent area. Some first instar larvae attacked the sepals of a flower bud instead of leaflets (Fig. 9B) or a shoot (Fig. 9C) and completed the whole larval and pupal stage feeding in and on the developing flower or shoot. Some second instar larvae started to roll the edge of a leaflet and stayed on that leaflet forming the web (Fig. 9D).

Later instar larvae

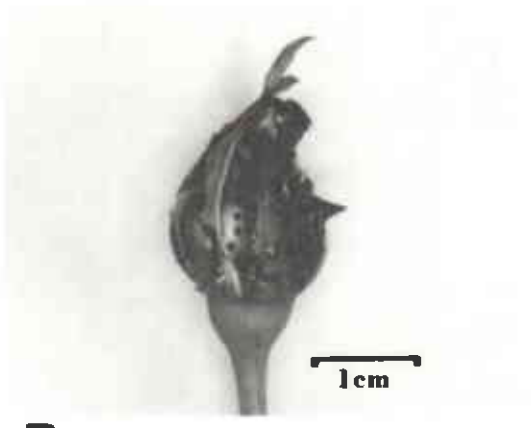
Immediately after molting to the third instar most larvae left the initial feeding site to establish themselves on older leaves, shoots, stems or flower buds and to form permanent webs.

The distribution of 168 webs on 24 rose bushes in the greenhouse is given in Table 14. At the time this observation was made a total of 21 shoots and 48 flower buds were present on these plants.

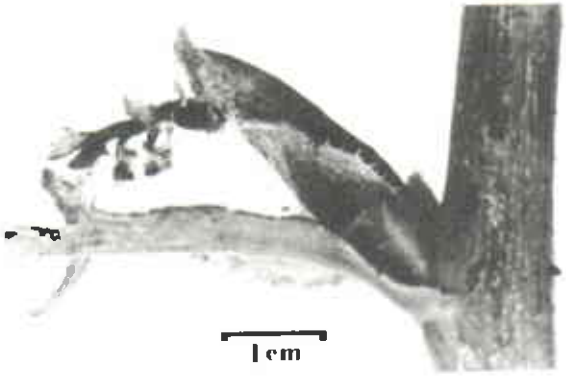
The webs formed on shoots consisted of the dead terminal part (cut off partially by the larva) webbed together with leaflets from the stem. The larva fed on the leaves surrounding the web and attached to

Fig. 9. Damage caused by the OLR larvae. A. Initial feeding site of the first instar larva. Note the transparent areas on the edge of the leaflet. B. Flower bud destroyed by several first instar larvae. Note the entrance holes and the attacked sepals. C. One first instar larva established on this shoot and destroyed it completely as its development advanced. D. Web formed with two leaflets by a young larva. E. Dead shoot forming part of the web of a fourth instar larva. Note the feeding damage to the surrounding leaflets. F. Several leaflets forming a web.

A

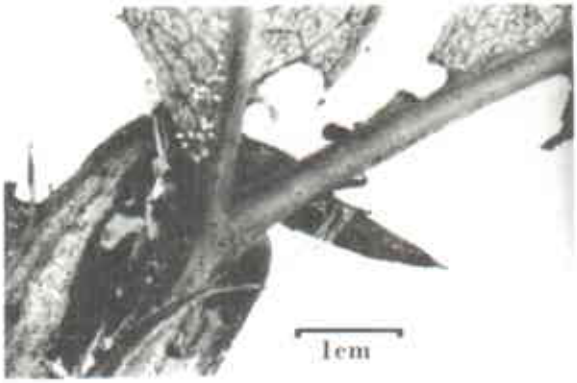


B



C

D



E

F

Table 14. Distribution of webs on shoots, flower buds, leaflets and stem of 24 rose bushes in the greenhouse.

Location of the web on the plant	Number of webs per location	Percentage of total number of webs
Shoot	10	6.00
Flower bud	32	19.00
Leaflet	124	73.80
Stem	2	1.20
Total	168	100.00

it (Fig. 9E). When the flower bud was attacked the web was formed with the bent over bud, the sepals and the next leaflet, and the larva fed either in the bud or on the leaflets. Many times the neck of the bud was fed on and broken off, but always formed part of the web. The most common webs were those formed with several leaflets tightly webbed together (Fig. 9F). In these webs often a dead leaflet rolled together and attached with silken threads to live leaflets served as a retreat. The larva was hidden and left this nest only to feed on the surrounding leaflets. As soon as part of the leaflet was eaten, it was incorporated into the web and the larva started feeding on another one. Some webs were formed by one older leaflet rolled together and the larva fed on that or other leaflets. Some last instar larvae left their original webs and formed new ones by rolling a part of a young leaflet, without feeding on it and pupated there. Some larvae acted as "stem borers" on young stems. The entrance hole was then covered by one leaflet tightly webbed around the stem. With the exception of the larvae mentioned above, the larvae pupated in the webs the third instar larvae had started. Only if disturbed did the larvae wriggle out of the webs and later start a new one. Generally one larva per web was observed, but occasionally third instar or older larvae used vacant webs from which the adult had already emerged.

Larval mortality and dispersal

For the 35 egg masses observed in the greenhouse (mean number of eggs per egg mass 98) a total of 91.6 per cent hatch was observed, corresponding to 3038 first instar larvae. Of this number, 1547 (50.1 per cent) survived and established a feeding site. The development of 100 of these larvae was followed: 95 molted to the third instar and

only five died during the first and second instar. No mortality occurred during the rest of the larval stage, all pupae survived and 95 exuviae were found attached to the webs, indicating normal adult emergence.

For the same 1547 established first instar larvae mentioned above the distance they had travelled from the egg mass was established and the data are shown in Table 15. Most first instar larvae established on the different branches of the same plant where the egg mass had been laid; approximately a third travelled to branches of plants at a distance of 12 inches. Sixty inches from the egg mass only 0.2 per cent of them were found.

Of the 100 first instar larvae observed further all molted to the second and third instar at the original feeding site. However, the young third instar larvae moved away and formed a web on the same plant (87 per cent), on a plant twelve inches away (11 per cent) or on a plant 24 inches distant (2 per cent). Later instars normally stayed and pupated within the web the third instar larvae had formed; only three per cent of them moved to another leaflet and pupated immediately.

Efficacy of insecticides

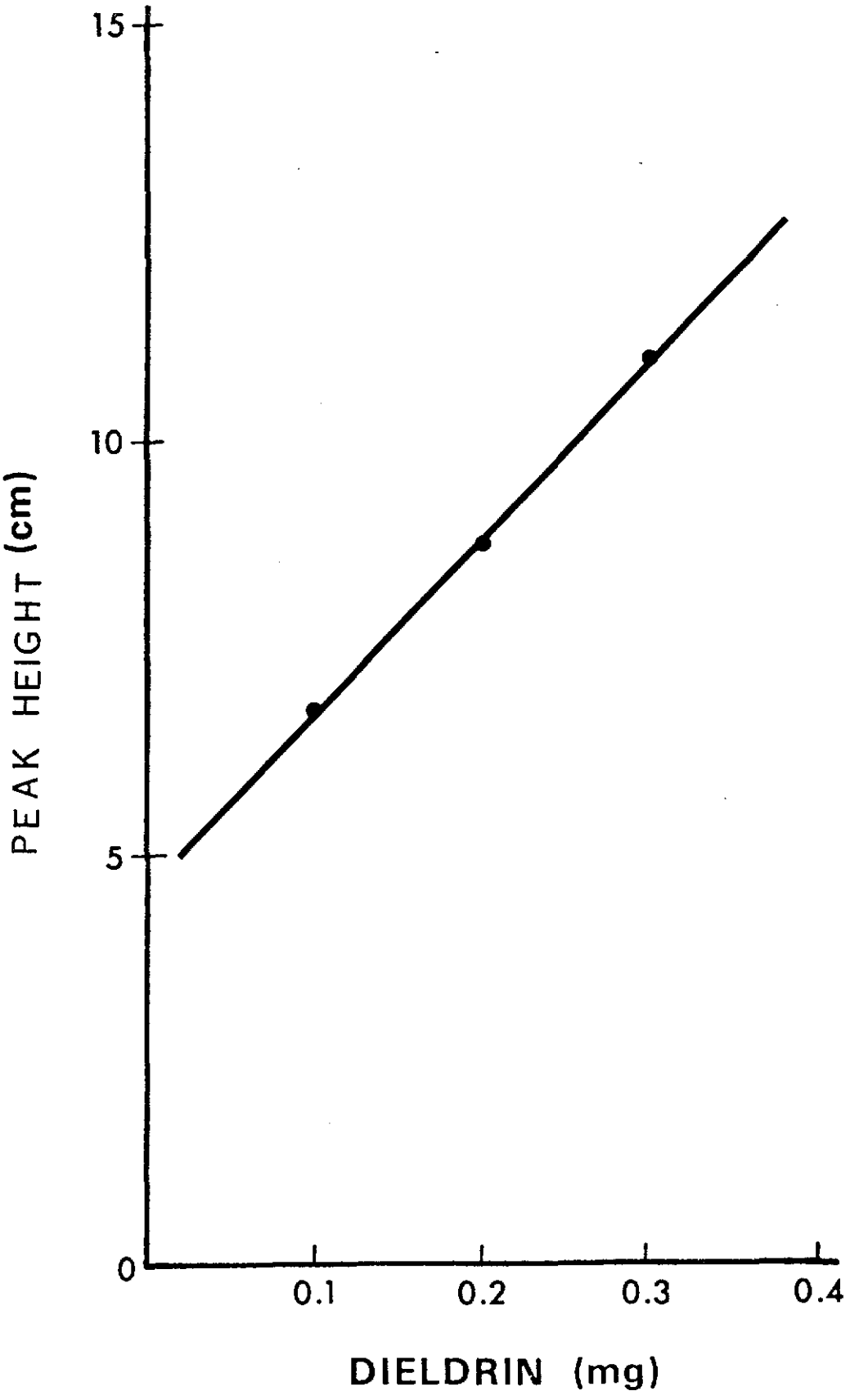
Detoxification enzymes

Using 1μl of the midgut preparation with the gas chromatographic analysis a mean peak height of 10.23 cm was obtained for the four replicates. Comparing this value with the dieldrin from the standard curve (Fig. 10), 1μl of the preparation corresponded to 0.271 mg of dieldrin. Since the original had to be diluted five times, 10 ml contained 13.55μg, which was equivalent to 35.5 nmoles of dieldrin. The protein content of the enzyme preparation per incubation was 3.75 mg. which gave an enzymatic activity of 9.47 nmoles per mg of protein for 30 minutes of

Table 15. Dispersal of the first instar larvae of the OLR (the distance in inches was measured from the plant on which the ggg mass was laid to the plant the larvae established the feeding site)

Distance from egg mass to feeding site (inches)	Number of larvae established at that distance	Per cent of total
0	703	45.4
12	503	32.5
24	246	15.9
36	75	4.8
48	16	1.0
60	4	0.2

Fig. 10. Standard curve of Dieldrin as determined by gas chromatographic analysis.


15
10
5
0
PEAK HEIGHT (cm)
0.1
0.2
0.3
0.4
DIELDRIN (mg)

incubation period. Therefore, the activity of the midgut oxidase of P. stultana was 315 x 10^{-3} nmoles per mg protein per minute.

Temperature-dependent spray schedule

The three temperature-dependent spray schedules against the OLR are shown in Table 16. The first two timing schedules were meant for those insecticides which kill only the first two and first three larval instars respectively, but do not have a residual activity, while the third schedule should be used with insecticides which kill the first through the third instar and have a residual activity of four days. Changing residuality and/or larval instar killed, the timing schedule varied considerably. Using an insecticide with no residuality that kills the first three instars instead of one that only affects the first two instars, the number of applications at 20°C for example was reduced from six to four and the intervals between sprays increased from 11 to 16 days. This interval was increased to 20 days when planned for a material with a residual activity of 4 days, which kills up to the third larval instar.

Residual activity

In Table 17 the residual activity of the various insecticides tested against the first instar of the OLR on roses and beans is given. The residuality of the two formulations of B. thuringiensis on roses was observed to be equal. Although five days after the application no difference in residuality between the two dosages of both trichlorfon and mexacarbate were obtained, 10 and 15 days after the application the lower dosage showed respectively little or no activity.

On beans Orthene, Sevimol and methomyl were still 100 per cent effective against the first instar larvae eight days after the

Table 16. Temperature-dependent spray schedules against the OLR

Temperature °C		Day of spray					
	a	0	11	24	35	46	57
20	b	0	16	32	48	-	-
	c	0	20	40	60	-	-
	a	0	9	19	29	39	-
22	b	0	13	26	39	-	-
	c	0	19	36	-	-	-
	a	0	7	15	22	29	37
24	b	0	11	22	33	-	-
	c	0	16	31	-	-	-
	a	0	6	13	20	29	-
26	b	0	9	20	30	-	-
	c	0	13	29	-	-	-
	a	0	7	13	19	25	31
28	b	0	8	19	-	-	-
	c	0	16	-	-	-	-
	a	0	5	10	15	20	25
30	b	0	7	14	22	-	-
	c	0	13	24	-	-	-

a: Insecticide kills first and second instar larvae; no residual activity

b: Insecticide kills first, second and third instar larvae; no residual activity

c: Insecticide kills first, second and third instar larvae; residual activity of four days.

Table 17. Residual activity of the various insecticides against the first instar larvae of the OLR on roses and beans

Treatment	Per cent mortality of first instar larvae					
	Days after application					
On roses	5	10	15	20		
B. thuringiensis (liquid)	97.2	83.3	66.6	0		
B. thuringiensis (WP)	98.6	90.2	68.0	0		
trichlorfon (1.0)	100.0	75.0	35.0	0		
trichlorfon (0.5)	100.0	33.0	0	0		
mexacarbate (0.5)	100.0	66.6	0	0		
mexacarbate (0.25)	100.0	41.6	0	0		
	Days after application					
On beans	0	2	4	8	16[a]	20
Orthene	100.0	100.0	100.0	100.0	-	0
mexacarbate	100.0	100.0	62.50	36.2	-	0
Sevimol	100.0	100.0	100.0	100.0	-	0
B. thuringiensis (liquid)	100.0	81.2	83.7	56.2	-	0
trichlorfon	100.0	100.0	83.7	56.2	-	0
methomyl	10010	100.0	100.0	100.0	-	0

[a]The high temperature (40°C) at 16, 17 and 18 days after the application caused the non-establishment of any first instar larvae

insecticide application. The activity of B. thuringiensis, mexacarbate and trichlorfon was considerably lower on beans than on roses. On both host plants none of the materials showed a residual activity 20 days after the insecticide application.

Toxicity

Insecticide applications in the first two tests against the OLR were made on day 0, 8, 16 and 24, corresponding to the spray schedule for insecticides which kill the first two larval instars but have no residual activity at a mean temperature of 25°C. The efficacy of the insecticides used at this spray schedule is given in Table 18. The initial infestation, corresponding to the number of first and second instar larvae and the number of webs found one day before the first insecticidal application was considered quite uniform within each experiment. The second test showed a higher initial infestation than the first one. The total number of egg masses per treatment laid during the experiments was also uniform and no preference for oviposition on treated or untreated plants was observed. The total number of adults emerged during the experiments (indicated by the number of exuviae found) was low for those treatments which gave a final count of very few or no live individuals. The comparatively lower number of later instar larvae in the final count of the second experiment was caused by a one week long period with high day temperatures (40°C), which killed most of the first and second instar larvae.

A complete control of the OLR was obtained at this timing schedule with mexacarbate, trichlorfon, Orthene, Sevimol and methomyl, a good control with Bacillus thuringiensis and no control with aldicarb.

The effectiveness of the insecticides against the different larval

Table 18. Efficacy of four applications of various insecticides at eight day intervals against the OLR

Treatment	No. of 1st & 2nd instar larvae[a]	No. of webs[a]	Total No. of egg masses observed during the experiment[b]	Total No. of exuviae	No. of 1st & 2nd instar larvae[c]	No. of 3rd 4th & last instar larvae[c]	No. of pupae[c]
Experiment I							
B. thuringiensis	102	90	23	19	4	25	1
aldicarb	57	104	22	93	17	220	14
mexacarbate	79	115	19	23	0	0	0
trichlorfon	106	81	21	35	0	0	0
check	118	88	18	133	16	393	49
Experiment II							
Orthene	145	185	20	29	0	0	0
Sevimol	107	215	21	26	0	0	0
methomyl	100	197	23	16	0	0	0
check	91	199	25	74	31	126	20

[a] One day before the first insecticide application

[b] Comprises the interval between one day before the first and four days after the last insecticide application

[c] Four days after the last insecticide application

instars of the OLR is given in Table 19. Trichlorfon, Orthene, Sevimol and methomyl killed 100 per cent of the first three larval instars, while mexacarbate affected also the fourth instar. B. thuringiensis gave a high larval control up to the fourth instar, but never affected all larvae within an age class. Aldicarb gave a low per cent kill of the first and second instar larvae, and did not show any effectiveness against later instar larvae.

With the exceptions of methomyl, which produced necrotic borders on the new foliage, and Sevimol, which produced an overall clorotic aspect of the rose plant, the materials at the dosages used were not phytotoxic to rose plants.

In addition to the OLR control, mexacarbate and Orthene gave a good and excellent control respectively against spider mites.

For the last control experiment Orthene, mexacarbate and trichlorfon were selected, since they were considered the most promising materials against the OLR. All had given a complete control at the spray schedule previously used, killed first through third instar larvae and were not phytotoxic to the rose plant at the dosage employed.

Because of the above mentioned characteristics of the insecticides and an expected mean fluctuating temperature of 24°C the spray schedule of 0, 16 and 31 days was chosen from Table 16 for this test.

The efficacy of these insecticides at this timing schedule is given in Table 20. The initial infestation, corresponding to the number of first and second instar larvae and webs found one day before the first insecticide application was also uniform for this experiment. The total number of adults emerged (represented by the number of exuviae) was higher for trichlorfon than for mexacarbate and Orthene, indicating a

Table 19. Effectiveness of the insecticides against the different larval instars of the OLR (percentage mortality observed)

Treatment	Percentage mortality observed				
	Larval instar				
	1st	2nd	3rd	4th	last
B. thuringiensis	92.5 ± 6.5[a]	92.5 ± 6.5	92.5 ± 6.5	92.5 ± 6.5	68 ± 17
aldicarb	25.5 ± 24.5	25.5 ± 24.5	0	0	0
mexacarbate	100	100	100	100	92.5 ± 6.5
trichlorfon	100	100	100	92.5 ± 6.5	25.5 ± 24.5
Orthene	100	100	100	92.5 ± 6.5	68 ± 17
Sevimol	100	100	100	92.5 ± 6.5	68 ± 17
methomyl	100	100	100	92.5 ± 6.5	68 ± 17

[a] median ± 1/2 interval

Table 20. Efficacy of three applications at various insecticides at 16 day intervals against the OLR.

Treatment	No. of 1st & 2nd instar larvae[a]	No. of webs[a]	Total No. of exuviae observed[b]	No. of 1st & 2nd instar larvae[c]	No. of 3rd 4th & last instar larvae[c]	No. of pupae[c]
Orthene	84	162	23	0	0	0
mexacarbate	69	175	26	0	0	0
trichlorfon	70	159	38	0	0	0
Chec Check	79	183	93	46	237	29

[a]One day before the first insecticide application

[b]Comprises the interval between one day before and four days after the last insecticide application

[c]Four days after the last insecticide application

lower later instar kill with the former material. At this new timing schedule, which takes residual activity of the materials into account a complete control of the OLR was obtained. No live larvae or pupae were found four days after the last insecticide application on the treated plants, while in the check a very high infestation was observed. At the spray interval used Orthene was also effective against spider mites, while mexacarbate did not control this pest.

DISCUSSION AND CONCLUSIONS

Temperature and population ecology of the OLR

Since temperature is one of the most important abiotic environmental factors in the population ecology of insects, it is especially important to understand the relationship between temperature and an insect's population dynamics when designing pest management programs for insects.

Development of insects can only occur within the relatively narrow range of temperatures of approximately 0 to 50°C. However, no individual species is known which can thrive over this entire range, and the extremes of particular ranges vary considerably among different species. For Grylloblatta for example it was from -2.5 to 11.5°C, for Ptinus from 5 to 28°C, for Aedes from 14 to 36°C and for Thermobia from 12 to 50°C (Andrewartha & Birch 1961, Bursell 1964, Wigglesworth 1965). Platynota stultana was able to develop over a temperature range of 15 to 35°C. However, toward the extremes of this range survival and reproduction is adversely affected in most species. Therefore, a narrower range is included in this interval, known as the optimal range for development in which all parameters in the population dynamics of an insect are considered normal. For any particular species this optimal range is related to the prevailing temperatures in the environment where the animal has evolved. Organisms living in relatively uniform tropical temperatures will probably be acclimated and evolutionary adapted to a narrower range of temperatures than one that lives within the more highly fluctuating ranges of the temperate zones (Janzen 1967). Insects adapted to temperate zones have a favorable range that starts at a lower

limit (for example eggs of Smynthurus: 7 to 27°C) than that for animals from warmer zones (for example larvae of Haematobia: 15 to 26°C, larvae of Stomomyx: 23 to 30°C) (Andrewartha & Birch 1961, Wigglesworth 1965). For the egg and pupal stage of the OLR this range was from 18 to 25°C, for the larval stage from 18 to 30°C and for female fecundity and fertility from 18 to 25°C. This narrow range of optimal temperature for development and the high lower limit substantiates the subtropical origin of the OLR.

Within this favorable range of development there is a temperature for optimal growth, which was defined by Uvarov (1931) as that at which development occurs at the fastest rate with the highest survival. In a pest management program this optimal temperature can be interpreted as the temperature at which the intrinsic rate of increase, r_m, is highest, The optimal temperature for the egg and pupal development of the OLR was 20°C, while that for larval development was 25°C. The higher optimal temperature for larval development can be explained, because temperature increases metabolism. Eggs and pupae depend on their energy reserves, which at higher temperatures can become exhausted before development is complete, while the active feeding larval stage is able to replace these reserves. Furthermore, active larvae are able to raise the body temperature, while eggs and pupae have to increase their energy expenditure for heat production (Wigglesworth 1965). For adult longevity the optimal temperature of the OLR was around 25°C, and for both female fecundity and fertility 20°C.

Insects which have originated in temperate zones have a lower threshold temperature (t) than those originated in subtropical climates. Hypanthria cunea and Pseudaletia unipunctate (temperate) have a t around 10°C, while for Aedes aegypti (subtropical) this temperature is definitely

lethal (Morris & Fulton 1967, Guppy 1969, Krebs 1972). The theoretical t for the OLR was around 13°C, which indicates again its subtropical origin.

It is interesting that type B females always showed a lower t than type A females for larval development, excepting the fifth instar. Since the degree-day values obtained for the type B females were also much higher than those for the type A larvae, the former type can probably be considered as an adaption of P. stultana to lower temperatures, which probably do not occur in the subtropical habitat to which this insect is native. This explanation may be supported by Muller's (1942) hypothesis that temperature, which is regarded as a natural selective agent, may influence the gene pool directly and there may be an adaption of the gene pool to the temperature of the insect's habitat.

Although the threshold temperature for larval development was 13°C at 15°C a high larval mortality was observed and no fertile females were obtained, which indicates that on OLR population could not survive a prolonged period at the latter temperature. The high larval mortality at 15°C (41%) was caused by the extreme temperature, but the even higher mortality (54%) in the greenhouse could not be attributed to this environmental factor (Table 9). In the greenhouse first instar larvae are only able to establish a feeding site on the new growth of the rose plant, which a) provides them with better nutrition, and b) provides a more favorable physical condition than older leaves. The high first instar mortality (50%) in the greehhouse was therefore attributed to the passive dispersal (with the help of silken threads and air current) to inappropriate sites such as older leaves, soil surface, sidewalks, etc.

Insect pests that have originated in the tropical and subtropical zones lack the capacity to become dormant at a certain stage to survive exposures to temperatures below the range favorable for development,

while insects that are adapted to temperate zones overwinter by entering the state of diapause (Andrewartha & Birch 1961). The OLR is of sub-tropical origin, does not have a dormant stage and is therefore unable to survive our winters outdoors. To the commercial rose grower this means that infestations do not come from populations occurring outdoors, but from greenhouse or nursery sources.

Besides development there are other parameters such as sex ratio fecundity and fertility in the population dynamics of the OLR which can be influenced by temperature.

Although temperature has been reported to effect the sex ratio of some lepidopterous species (Wigglesworth 1967), for the OLR no significant influence of temperature on this parameter was observed.

Fecundity and fertility are affected adversely be extreme temperatures (Bursell 1964). For the OLR a normal reproduction was observed between 20 and 30°C, but even within this limited range a high variability was noted. The standard deviation of the number of eggs per female (Table 13) was always higher than 10% of the mean (from 23% 23°C mean fluctuating temperature up to 53% at 30°C, and 64% at the 20.5°C mean fluctuating temperature), which denoted a very high variation between the number of eggs laid per female within each temperature. The high variation at 30°C can be attributed to the extreme temperature, but in general it seems to be caused by some maternal influence on the progeny quality, which was specially marked at the 20.5°C mean fluctuating temperature treatment. Similar maternal influences have been observed for the spruce budworm, an other tortricid (Campbell 1962), and for the western tent caterpillar (Wellington 1965).

Kaae (1971) found that besides terperature, nutrition of both larvae and adults has a marked influence on the fecundity of the OLR. This

explains the much higher fecundity observed in the laboratory compared to that in the greenhouse, since the artificial diet provided better nutrition to the larvae than the host plant. Furthermore adults in the laboratory fed on sugar solution, while in the greenhouse no food was available to them.

Only the extreme temperatures used in this study (15 and 35°C) influenced fertility in that a much higher percentage of unhatched viable eggs was observed at these temperatures compared to the other treatments (Table 5). However, it was not possible to determine, whether the variability at the other temperature treatments and the variation in the percentage of non-viable eggs per egg mass and the percentage of total hatch was caused by an influence of temperature on the previous development of the females, by a lower fertility of the males, by a maternal influence or by the direct influence of temperature on egg development. A combination of these factors is more likely to explain the variability in fertility.

Under both greenhouse and laboratory conditions fertility was higher at alternating temperatures than under constant ones. The variability of fertility within each treatment in Table 5 is possible produced by a maternal influence. The egg masses incubated represented all the egg masses with very high, intermediate or low number of eggs, oviposited on different days after emergence of the females. It was noted that in general the viability of the eggs laid toward the end of the oviposition period was lower than those laid at the beginning.

The subtropical origin and consequently the temperature for the highest reproduction of the OLR, which is approximately equal to the temperature range (15.5 - 24°C night-day) recommended for the culture of

roses in the greenhouse, explains the excellent adaptation of this insect to greenhouse conditions, why it has become such an established pest, and why during the summer months the highest densities of the OLR are observed. We are recommending a growing temperature for roses that coincides with the optimal temperature for the best growth, survival and reproduction of the OLR.

Velocity lines based on developmental rates of the different stages of insects at certain temperatures are used to estimate developmental rates at any given temperature, and are needed when designing temperature-dependent spray programs. The developmental rates for the total larval stage obtained in this study were essentially similar to those observed by other authors[1/] (Nelson 1936, Atkins et al. 1957, AliNiazee et al. 1957). However the mean duration of the larval stage reported by Atkins et al. (1957), who reared the OLR on cotton was longer at 26.7 thd 32.2°C than those observed in this study. This enhanced development at higher temperatures over that on the host plant may be attributed to the availability of some nutrients in the artificial diet (AliNiazee et al. 1971), not available at high temperatures from the host plant. This indicates that larval development at temperatures higher than 25°C is more sensitive to nutrition than at lower temperatures.

None of the above mentioned studies included age specific developmental rate observations of both sexes. However in this study the age- and sex-specific developmental rates were studied at a wide range of constant temperatures. Therefore the velocity lines obtained can be used to accurately calculate age-specific developmental rates at any

---

[1/] Date superimposed on the hyperbolas in Figs. 3, 7, and 8 for eggs, larvae and pupae respectively.

temperature. Yet fluctuating temperatures are characteristic of the environment of most insects and models and programs based upon constant temperature studies may be unrealistic in simulating field populations (Hagstrum & Hagstrum 1970). The same authors indicate that insects develop more rapidly at fluctuating temperatures than at constant temperatures when the maximum and minimum of the fluctuating temperatures are within the optimal range for the organisms.

For the egg and pupal development, at the 19°C mean fluctuating temperature (24-15.5°C day-night) an increase of the developmental rate over that at the corresponding constant temperature was observed, although the night temperature does not fall within the optimal range for development of these two stages. At the 20.5°C mean fluctuating temperature (24-18°C day-night) and 23°C mean fluctuating temperature (29.5-18°C day-night) an increase and a decrease respectively in the developmental rate of eggs and pupae over that of the corresponding constant temperatures was obtained. This follows the general observation made by Hagstrum & Hagstrum (1970). The first range coincides with the optimal range for development, while the day temperature of the latter exceeded the optimal temperature range. For the larval stage none of the fluctuating temperatures increased or decreased the developmental rate significatively over that observed at the corresponding constant temperatures.

The larval diet did not affect the development rates of the OLR. The rates for all stages at fluctuating temperatures obtained in the laboratory were equal to the ones observed in the greenhouse. The thermal constant (K) calculated from the developmental times at constant temperatures for the egg, larval and pupal stages was equal to that

calculated for these developmental stages in the greenhouse. This indicates that K from constant temperatures also accurately estimates the developmental rates for the OLR developing at fluctuating temperatures. Since a linear relationship was obtained for all age classes of the OLR (Figs. 3, 4, 5, 6, 7, and 8), this was expected. Where the linear relationship between developmental rate and temperature holds, each developmental process has a characteristic K and requires a fixed number of degree-days to bring it to completion (Wigglesworth 1967). Therefore, for calculations of application frequency in temperature-dependent spray programs, the thermal constant (K) for the egg, larval and and pupal stage is reliable and can be used to predict the time necessary for the development of the OLR in the greenhouse at different tempera tures. The use of the thermal constant instead of the developmental time at the various temperatures for the calculation of the spray frequency proved to be very satisfactory, since as shown in the experiments where the schedules were used a complete control of the OLR was obtained. The thermal constant can be used to calculate temperature-dependent spray schedules for the control of the OLR in any greenhouse at all temperatures at which this insect has a normal development.

The role of temperature in the population ecology of the OLR has several important implications in the development of a pest management program. Although temperature effects the developmental rate of the OLR, it had little effect on its survival and fecundity within the normal range of temperatures under both laboratory and greenhouse conditions. The range of growing temperatures recommended for the rose culture coincides with that for the highest rate of reproduction of the OLR. With a knowledge of the effect of temperature on development, survival and

reproduction, a temperature-dependent pest management program of population control can be designed to guide the rose grower in the effective planning of OLR control during commercial rose production.

Critical population level for the insecticide applications

The population level at which the insecticide application should be made is one of the most critical steps for an economically sound pest management program. Because of the relatively high fecundity, the low mortality of the larvae once established, and the wide range of dispersal of the OLR, the critical population level for insecticide applications for this insect on roses was estimated to be one egg mass per 11 plants. This is approximately equivalent to one first instar larvae per plant.

This critical population level of the OLR was obtained making the following considerations: at a mean fluctuating temperature of 21°C (24-15.5°C day-night) which is generally recommended for rose production, there are approximately 80 eggs per egg mass. With a first instar larval mortality of 50%, 40 first instar larvae will establish a feeding site. The significant dispersal (Table 15) occurs within 24 inches of the plant where the egg mass was laid. Having a distance between plants of 12 inches, the theoretical distribution of the attack from Table 15, would be 20 larvae on the plant where the egg mass had been laid, 13 on 4 plants at a 12 inch redius, and 6 on 6 plants at a 24 inch radius. This gives a total of 11 plants attacked ty the first instar larvae from a single egg mass.

If not controlled, approximately 25% of these larvae would attack shoots or flower buds and the rest would form webs with leaflets (Table 14). No marketable flowers would result from the shoots and flowere buds attacked by the OLR larvae. Therefore a critical level would be one

egg mass per 11 plants. The insecticide application should be made a certain number of days later, depending on the degree of incubation of the eggs and the greenhouse temperature. However, egg masses occur in different stages of development and are difficult to detect. Therefore it is quite difficult to make the decision of how many days after the egg mass was found an application should be made.

A more convenient diagnostic for an insecticide application is one first instar larva per plant. This level might seem very low, but it means if one larva is present on a particular plant, at least one egg mass was laid on another plant as much as 24 inches away. Most probably more first instar damage can be found on other plants or branches at this low population density. Furthermore, if not controlled at this level, the damage caused by the larvae to shoots, buds and leaves of the rose plants will be higher than the 5% permitted under the tentative standards for cut hybrid tea roses. This damage could even reach 25% of marketable flowers per plant at a given moment, if we consider that a) one plant has a production of 28 flowers per year, b) approximately seven weeks are required for the production of a flower from cut or pinch (Laurie et al. 1969). This gives four flowers per plant in each of the seven periods per year, and at the critical level of one larva per plant it means that one marketable flower will be lost because of the attack of either a shoot, bud or leaf, which represents a level of 25% damage.

Temperature-dependent spray schedule

As stated in the introduction, one of the factors which may explain why the OLR is difficult to control, was considered to be the lack of proper timing and frequency of the insecticide applications. Accurate

timing is essential for an effective pest control program.

To obtain maximum control insecticides are generally applied in one or two ways (Nat. Aca. of Sci. 1969). An application is recommended when the insect first appears, which requires the careful observation of the insect population in the field, usually at intervals of no more than a week. With this method an application is recommended when the OLR first appears in the greenhouse. However, since it is almost impossible to detect the initiation of an OLR infestation (i.e., the first egg mass laid by a fertile female in several square feet of greenhouse bench), this method was not considered to be useful for the control of the OLR.

In the second method an application is recommended when both the pest and the host plant have reached a certain stage of development, these stages being dependent on environmental factors, overwintering stage of the pest, planting time of the host plant, etc. (i.e., key events in the development of both pest and host plant).

The problem of timing insecticide application for the control of insects native to temperate zones and its many ramifications involved the second method have been studies by several authors (Harrison & Press 1971, Nat. Acad. of Sci. 1969). These insects which are mostly host specific overwinter in a certain stage of development. At a particular time, depending on the environmental conditions appropriate for both pest and host plants, they start the new generation in the spring. As soon as they reach a particular stage and density for which applications are recommended, insecticides are applied. However, for multivoltine, polyphagous species like the subtropical OLR the problems of timing insecticide applications under greenhouse conditions have not been well

studied.

These two methods were not considered useful for the OLR. Therefore a spray schedule based on the insects development at different temperatures was found to be the most appropriate for control in the greenhouse. A grower will never find an OLR population of only susceptible larval instars, which could be eliminated with one insecticide application. He will observe the presence of all stages from egg through adult, which means that several application will be needed, each directed against the susceptible larval instars, to eliminate the pest. Under these conditions a temperature-dependent spary schedule (Table 16) will be required to obtian an effective and economic control of the OLR. This schedule should be followed exactly, since a change in the recommended frequency of insecticide applications at the respective temperature will cause a change in the effectiveness of the control program. If shorter intervals than those calculated are used, unnecessary and wasteful applications will be made, because susceptible larval instars will already have been eliminated by the previous application and the next stage (eggs) will not have developed into a susceptible age-class (first instar larvae). A longer interval than that recommended will allow susceptible age-classes (for example third instar larvae) to develop into non-susceptible ones (fourth instar larvae). This will result in economic damage to rose plants. The proper timing schedule was calculated precisely to avoid this damage. Both shorter and longer intervals between insecticide applications than the recommended ones will cause the need for more applications and it is quite possibe that the pest will not be eliminated, increasing condiderably the cost of OLR control.

In the insecticidal experiments, where the applications were made according to the temperature-dependent spray schedule (Table 16) complete control of the pest was obtained with all insecticides but aldicarb and B. thuringiensis (Tables 18 and 20). This control was achieved even with carbaryl, previously reported ineffective against the OLR (Naegele & Jefferson 1964, Ota 1969). In Ota's (1969) tests trichlorfon and mexacarbate gave only good control after one application, which indicates that the OLR would have become a problem again after several weeks. In the present study, by using a proper number and frequency of applications, which controlled the susceptible stages of the population, an excellent control was obtained with these two insecticides.

Smith (1969) reported that dichlorvos is effective against the first three instars of the OLR and has little residual activity. Although he recommends six applications of dichlorvos at weekly intervals for the control of this pest, he indicates that 10 applications are needed to eliminate the OLR in the greenhouse. Using the same insecticide at the corresponding temperature-dependent spray schedule obtained in this study (Table 16) at a mean fluctuating temperature of 20 or 22°C, only four applications at a 16 and 13 day interval respectively would be needed to eliminate the OLR. The use of the temperature-dependent spray schedule eliminates the pest in a much shorter time and with six less insecticide applications than the currently recommended control program. The number and frequency of insecticide applications in our timing schedule as compared to Smith's (1969) recommendation decreased considerably, because his schedule was not based on the developmental rates of the susceptible larval instars at different temperatures.

Selection of the best insecticides for the control of the OLR

Once the critical population level has been observed and the decision has been made to follow a timing schedule, the next step is to select the best insecticide for the control of the OLR.

In this study the efficacy of several insecticides was evaluated and the selection of the best materials was based on the following criteria: toxicity, residual activity and non-phytotoxicity.

Many times the inadequate control of insects with insecticides is caused by the capacity of certain insects to metabolize foreign compounds. The last instar larvae of the OLR seem to have this capacity, since its microsomal oxidase activity is very high and similar to the mean epoxidase activity obtained for twelve other polyphagous lepidopterous species as reported by Krieger et al. (1971). These enzymes exist in insects for the metabolism of potential toxic compounds present in their natural food (Gordon 1961). They are higher in polyphagous species because these insects have a greater possibility to encounter different toxic compounds in the many plants they feed on. Since the microsomal oxidase enzymes in the midgut of lepidopterous larvae are responsible for the detoxification process of stomach insecticides it was not surprising that the last instar larvae of the OLR was able to metabolize some insecticides and survive the applications.

Mexacarbate showed a 100% control of the fourth and a high activity against the last instar larvae, because it is a contact as well as a stomach insecticide. This material is reported to irritate the larvae which makes them leave the webs and expose themselves to its contact action (Smith 1965, Ota 1969). Methomyl and Sevimol, which also act as contact insecticides do not induce this larval irritation and therefore

did not show the same efficacy as mexacarbate.

The relatively low susceptibility to stomach insecticides by the late instar larvae reported in the literature can be explained by the high microsomal oxidase activity, rather than by the protection given to the larvae be their webbed retreats and the feeding within them, as suggested by several authors (Nelson, 1936, Smith et al. 1965, Lynn 1969, Ota 1969). Although the larvae hide within these webs they come out to feed on treated leaves.

Despite the high microsomal oxidase activity, there was a relatively high mortality (Table 19) observed for the last instar larvae in all treatments. This can be explained by the residual activity of the materials. In these experiments four applications at eight day intervals had been made. This resulted in an uninterrupted presence of the insecticide on the leaves. Apparently the enzyme system in the midgut of of the OLR is depleted by the continuous ingestion of the insecticide. It is possible, however, that the larvae would have survived a single application of the materials.

Residual activity of the insecticides is another important parameter in the efficacy of temperature-dependent spray schedules, since the frequency of insecticide applications is affected by the residual activity of the insecticide used. The longer the residuality, the longer the intervals between sprays, provided that the residual activity exceeds the developmental time of the susceptible stages.

The descrepancy between the residual activity of all materials on roses and beans requires an explanation. The shorter resuduality of B. thuringiensis, mexacarbate and trichlorfon on beans compared to roses (Table 17) was partially caused by the high temperature conditions under

which the experiment on beans was conducted. This induced a faster degradation of these materials. Also the counts made to evaluate the residuality were different for both tests and probably influenced the results. On beans the total mortality was obtained several days after the emergence of the first instar larvae, based on the number of larvae definitely established on the plants. On roses the number of established first instar larvae was taken at a given moment as an index of survival and no further observations wer made, although some of the larvae might have died after further feeding on the treated laeves.

In this study the residuality of carbaryl (8 days) and mexacarbate (3 days) against the first instar larvae of the OLR on beans was similar to that observed against the second and third instar by Ota (1969). However, the residuality was not the same for trichlorfon and methomyl. Trichlorfon was used at the same dosage, yet in this test it was still 84% effective after four days, while Ota (1969) observed no activity after three days. Methomyl applied in this study at 0.5 lb active ingredient per 100 gallons of water showed a residual activity of eight days, while Ota (1969) at 0.25 lb observed no residuality after three days.

The higher dosage of methomyl and the different instars against which the residual activity was evaluated can only in part explain the difference between the results of this study and Ota's. In his field tests methomyl at the 0.5 lb dosage was surprior to all other insecticides. Ota (1969) explained part of the discrepancy he obtained with this material and other insecticides in his residual studies and field tests by indicating that "the larvae remain within the rolled leaves that make their nests and feed on untreated leaves for a few days, then

they move to the new foliage developing after application of the spray." In this study, however, it was observed, that the larvae always came out of their webs and fed on the treated leaves surrounding the web and not within the retreat. If the larvae are not disturbed they remain within the web and do not move to new foliage.

In this study B. thuringiensis showed the longest residual activity (10 days). This material was followed by Sevimol, methomyl and Orthene which had an activity of 8 days and by mexacarbate and trichlorfon with an activity of 5 days.

Although good control and the longest residual activity was observed with B. thuringiensis, this material was not considered as one of the best insecticides. Applications did not eliminate all individuals of a given susceptible age class, a characteristic assumed for an insecticide to be used in the temperature-dependent spray schedule programmed in in this study. This bacteria is like a chemical stomach poison, in that it must be ingested to kill. Therefore, one of the reasons why a 100% kill was never observed on roses could be the lack of a complete coverage of the plant which would ensure the consumption of a lethal dosage of spores by all larvae. On beans, however, where because of the non-waxy surface of the leaves an apparent better coverage was possible, all first instar larvae died.

In addition the physical properties of a chemical allow a complete solution and an uniform distribution of the toxic principle on the treated surface. With the non-soluble spores, however, even with a good coverage it is possible to obtain a less uniform distribution, which would leave some parts of the leaflets without the toxic substance (spores). It is quite probably that B. thuringiensis could be included

in this type of spray program if the obstacle of coverage on roses can be overcome.

Another reason for the incomplete kill of the OLR larvae by this bacteria could be, that since death only occurs several days after ingestion of the spores, it is possible that larvae considered "alive" at the moment of the count could have died some days later.

Although methomyl and Sevimol gave excellent control of the OLR and showed long residual activity, these two materials were phytotoxic to "Red American Beauty" roses at the dosage employed, and therefore could not be recommended insecticides. It is interesting to observe that the phytotocicity of methomyl, which was even more conspicuous on beans, has not been reported previous to this study, even though this material has been used on roses. Since the Ortho Chevron Spreader was also mixed with the other insecticides, the damage cannot be attributed to the use of this surfactant. However, a specific incompatibility may exist between methomyl and this surfactant.

Carbaryl alone was not considered phytotoxic, but when it is mixed with molasses (Sevimol) a discoloration and unhealthy aspect of the whole plant was observed. This unhealthy aspect could only be attributed in part to the higher mite infestation on plants treated with this insecticide. Moreover, Sevimol left a white residue on the treated leaves, which could cause a rejection under the tentative standards for roses. In general the phytotoxicity of both materials can at least partially be attributed to the relatively high greenhouse temperature (25°C mean fluctuating temperature) which is normally not used for rose culture.

With Orthene, mexacarbate and trichlorfon complete control of the

OLR was obtained, when these materials were applied according to the temperature-dependent spray schedule.

Orthene, however, had a longer residual activity than the other two materials, and besides killing the first three instars showed a high activity against the fourth and a good activity against the last instar of the OLR. Orthene also gave excellent control of spider mites, even at a 16 day spray interval.

The residual activity of both mexacarbate and trichlorfon was five days. Mexacarbate controlled the first through the fourth instar and showed a high activity against the last larval instar, while trichlorfon did not have as good an activity against the fourth larval instar and was almost ineffective against the last one. Mexacarbate gave good control of spider mites at an eight day spray interval, while trichlorfon did not show any activity against this pest. Therefore Orthene and mexacarbate were selected as the best insecticides for the control of the OLR on roses in the greenhouse.

From this study the following recommendations will guarantee efficient commercial control of the OLR:

1.) Insecticide applications must begin when the density of one first instar larva per plant is reached, or a damage higher than 5% permitted under tentative grades for cut hybrid tea roses may result.

2.) When this level is reached, the best insecticides for control of the susceptible larval instars are Orthene and mexacarbate.

3.) These materials must be applied at a frequency calculated from the temperature-dependent spray schedule in Table 16 based on the greenhouse conditions. At the recommended greenhouse

temperatures of 20 an 22°C (mean fluctuating temperature) this corresponds to four and three applications at 20 and 19 day intervals respectively.

BIBLIOGRAPHY

Adkisson, P. L., E. S. Vanderzant, D. L. Bull and W. E. Allison. 1960. A wheat germ medium for rearing the pink bollworm. J. Econ. Entomol. 53:759-62.

AliNiazee, T. M., E. M. Stafford and C. Fukushima. 1971. Rearing of the omnivorous leaf roller in the laboratory on artificial diet. Ann. Entomol. Soc. Am. 64:1172-73.

AliNiazee, T. M. and E. M. Stafford. 1971. Evidence of a sex phermone in the omnivorous leaf roller Platynota stultana (Lepidoptera, Tortricidae): Laboratory and field testing of male attraction to virgin females. Ann. Entomol. Soc. Am. 64:1330-35.

AliNiazee, T. M., C. D. Lynn, E. M. Stafford and D. A. Luvisi. 1970. Integrated control of grape pests: Effectiveness of cryolite and standard lead arsenate against the omnivorous leaf roller. Calif. Agri. 24(12):8-10.

Andrewartha, H. G. and L. C. Birch. 1961. The Distribution and Abundance of Animals. The Univ. of Chicago Press. Chicago Ill. p. 129-205.

Atkins, E. L., M. H. Frost, L. D. Anderson and A. S. Deal. 1957. The omnivorous leaf roller, Platynota stultana Walsingham, on cotton in California: Nomenclature, life cycle, life history, and bionomics (Lepidoptera, Tortricidae). Ann. Entomol. Soc. Am. 50:251-59.

Atkins, E. L., M. H. Frost, A. S. Deal and H. T. Reynolds. 1957a. The omnivorous leaf roller, Platynota stultana Walsingham on cotton in southern California: Damage and control. J. Econ. Entomol. 50: 59-64.

Barnes, W. and A. Busck. 1920. Notes and new species of Tortricidae. Contrib. Nat. Hist. Lepid. N. A. 4(3):213-14.

Bohart, R. M. 1942. Platynota stultana as a pest of field grown carnations. J. Econ. Entomol. 35:399-403.

Bourne, A. I. 1936. Value of electric traps against orchard insect pests. Mass. Agr. Exp. Sta. Annual Rep. for 1935. Bull. 327, 47-49.

Busck, A. 1933. In: Minutes of the 499th regular meeting of the Entomological Society of Washington, Oct. 5, 1933. Proc. Ent. Soc. Wash. 35(8):191-92.

Bursell, E. 1964. Environmental Aspects: Temperature. In: The Physiology of Insecta I. Ed. M. Rockstein. Acad. Press. N.Y. p. 284-317.

Campbell, I. M. 1962. Reproductive capacity of the genus Choristoneura Led. (Lepidoptera, Tortricidae). I. Quantitave inheritance and genes as controllers of rates. Can. J. Genet. Cytol. 4:272-88.

Campbell, R. L. and G. B. Ward, Jr. 1971. Insecticides tested against Platynota stultana on Euonymus. J. Econ. Entomol. 64:1556.

Chant, D. A. 1966. Integrated Control Systems. In: Scientific Aspects of Pest Control. Nat. Acad. of Sciences. Nat. Res. Council, Washington, D.C. 470 pp.

Chemagro. 1972. 1973 Product guide. Chemagro division of Baychem Corporation. Kansas City, Missouri. 235 pp.

Chevron Chem. Co. 1971. Experimental data sheet. Orthene (R). Ortho Div. San Francisco, Calif. 2 p.

Compton, C. C. 1941. Leaf tiers and leaf rollers. Can. Florist. 36: 140-143.

Cram, W. T. and N. V. Tonks. 1959. Note on the occurrence in British Columbia of the omnivorous leaf tier, Cnephasia longana (Haw.), (Lepidoptera, Tortricidae), as a pest of strawberry. Can. Entomol. 91:155-56.

Essig, E. O. 1926. Insects of Western North America. The MacMillan Co. New York. 737-738.

Fincham, J. R. S. 1954. Effects of a gene mutation in Neurospora crassa related to glutamic dehydrogenase formation. J. Gen. Microb. 11:236-46.

George, J. A. 1965. Sex phermone of the oriental fruit moth, Grapholita molesta (Busck) (Lepidoptera, Tortricidae). Can. Entomol. 1002-7.

Glass, E. H. and P. J. Chapman. 1952. The red-banded leaf roller and its control. N.Y. Sta. Agr. Exp. Sta. Geneva. Bull. 755, 42p.

Guppy, J. C. 1969. Some effects of temperature on the immature stages of the armyworm, Pseudaletia unipunctata (Lepidoptera, Noctuidae), under controlled onditions. Can. Entomol. 101:1320-27.

Hagstrum, D. W. and W. R. Hagstrum. 1970. A simple device for producing fluctuating temperatures, with an evaluation of the ecological significance of fluctuating temperatures. Ann. Entomol. Soc. Am. 63:1385-89.

Hall, I. M. and P. N. Dunn. 1958. Susceptibility of some insect pests to infection by Bacillus thuringiensis Berliner in laboratory tests. J. Econ. Entomol. 51:296-98.

Harrison, F. P. and J. W. Press. 1971. Timing of insecticide applications for the european corn borer control in sweet corn. J. Econ. Entomol. 64:1496-99.

Helgesen, R. G. and R. N. Freeman. 1971. Leaf rollers. New York State Flower Industries. Bull. 11, 6-7.

Hough, W. S. 1927. A study of the biology and control of the red-banded leaf roller. Virginia Agr. Exp. Sta. Bull. 259, 12p.

Henneberry, T. J. and A. N. Kishaba. 1966. Cabbage Loopers. In: Insect Colonization and Mass Production. Ed. C. N. Smith. Acad. Press. New York. p. 461-478.

Ignoffo, C. M. 1963. A successful technique for mass rearing cabbage loopers on a semisynthetic diet. Ann. Entomol. Soc. Am. 56:178-82.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Amer. Natur. 101:233-49.

Kaae, R. S. 1971. Biological studies on Clepsis peritana (Clemens) and Platynota stultana Walsingham, Tortricidae with emphasis on mating and ovipositional behaviour. Diss. Abstract 32(4):2210B-2211B.

Kenaga, E. E. and N. E. Allison. 1969. Commercial and experimental organic insecticides. Bull. Entomol. Soc. Am. 15(2):85-148.

Krieger, R. I., P. I. Feeny and C. F. Wilkinson. 1971. Detoxication enzymes in the guts of caterpillars: An evolutionary answer to plant defenses? Science 172:579-81.

Krieger, R. I. and C. F. Wilkinson. 1970. An endogenous inhibitor of microsomal mixed-function oxidase in homogenates of the southern armyworm (Prodenia eridania). Biochem. J. 116:781-89.

_____. 1969. Microsomal mixed-function oxidases in insects I. Localization and properties of an enzyme system effecting aldrin epoxidation in larvae of the southern armyworn (Prodenia eridania). Biochem. Pharmacol. 18:1403-15.

Lord Walsingham. 1884. X. North American Tortricidae. Trans. Entomol. Soc. Lond. p. 121-147.

Laurie, A., D. C. Kiplinger and K. S. Nelson. 1969. Commercial Flower Forcing. McGraw-Hill Book Co. N.Y. p. 327-351.

Lynn, D. C. 1969. Omnivorous leaf roller an important new grape pest in the San Joaquin Valley. Calif. Agr. 23(4):16-17.

Macdonald, D. R. and F. E. Webb. 1963. Insecticides and the spruce budworm. In: R. F. Morris. The dynamics of epidemic spruce budworm population. Mem. Entomol. Soc. Can. 31:288-310.

Mackay, M. R. 1962. Larvae of the North American Tortricinae (Lepidoptera: Tortricidae). Can. Entomol. Suppl. 28, 180pp.

Mastalerz, J. W. 1969. Environmental Factors- Light, Temperature, Carbon Dioxide. In: Roses. Ed. J. W. Mastalerz and R. W. Langhans. Penns. Flower Growers, N.Y. State Flower Growers Assoc., Inc., Roses Inc. p. 95-108.

Mc Gregor, E. A. 1934. Platynota stultana Wlsm. (Lepidoptera) damaging green oranges in southern California. J. Econ. Entomol. 27:974-7.

Meyrick, E. 1913. Lepidoptera, Heterocera, Familia Tortricidae. In: Genera Insectorum. Ed. P. Wytsman, V. Verteneuil and L. Desmet. Bruxelles. Fasc. 149 p. 58.

Miller, C. A. 1966. The black-headed budworm in eastern Canada. Can. Entomol. 98:592-613.

Morris, R. F. and W. C. Fulton. 1970. Models for the development and survival of Hyphantria cunea in relation to temperature and humidity. Mem. Entomol. Soc. Can. 70:1-60.

Muller, H. J. 1942. Isolation mechanism, evolution and temperature. Biological Symposia 6:71-166.

Naegele, J. A. and R. N. Jefferson. 1963. Floricultural entomology. Annu. Rev. Entomol. 9:319-40.

Nat. Acad. of Sciences. 1969. Insect-Pest Management and Control. Principles of Plant and Animal Pest Control Vol. 3. Nat. Acad. of Sci. Washington, D.C. 508 pp.

Nelson, R. H. 1936. Observations on the life history of Platynota stultana Walsingham on greenhouse rose. J. Econ. Entomol. 29:306-12.

Ota, A. K. 1969. Control of Platynota stultana, a tortricid leaf roller in greenhouses. J. Econ. Entomol. 62:1279-82.

Powell, J. A. 1964. Biological and taxonomic studies on Tortricinae moths, with reference to the species in California. Univ. of California Publ. in Entomology 32, 317 pp.

Rathmell, J. K., Jr. 1969. Cutting and Handling Flowers. In: Roses. Ed. J. W. Mastalerz and R. W. Langhans. Penns. Flower Growers, N.Y. State Flower Growers Assoc. Inc., Roses Inc. p. 136-140.

Roelofs, W. L. and Kuo-Ching Feng. 1967. Isolation and bioassay of the sex pheromone of the red-banded leaf roller, Aegyrotaenia relutiana (Lepidoptera, Tortricidae). Ann. Entomol. Soc. Am. 60:1199-1203.

Smith, F. F. 1969. Insects and related Pests on Foliage, Flowers and Stems. In: Roses. Ed. J. W. Mastalerz and R. W. Langhans. Penns. Flower Growers, N.Y. State Flower Growers Assoc. Inc., Roses Inc. p. 220-25.

Smith, F. F., A. L. Boswell and S. W. Jacklin. 1965. Zectran insecticide controls the omnivorous leaf roller, a greenhouse pest. Down to Earth 20(4):18-22.

Steinhaus, E. A. 1979. Microbial Disease in Insects. In: Biological Control of Insect Pests and Weeds. Ed. P. DeBach. Reinhold Publ. Co. N.Y. p. 515-547.

Stern, V. M., R. F. Smith, R. van den Bosch and K. S. Hagen. 1959. The intergretated control concept. Holgardia 29:81-101.

Southwood, T. R. E. 1971. Ecological Methods. Chapman and Hall, London. 391 pp.

Thomson, W. T. 1972. Agricultural Chemicals. Book I, Insecticides. Thompson Publ. Indiana. 315 pp.

University of Illinois, College of Agriculture. 1968. Market grades and standards for carnation, chrysanthemum and roses. Agr. Exp. Sta. Bull. 727, 23 pp.

Uvarov, B. P. 1931. Insects and Climate. Trans. Entomol. Soc. Lond. 79:1-232.

Vanderzant, E. S. and R. Reiser. 1956. Aseptic rearing of the pink bollworm on synthetic media. J. Econ. Entomol. 49:7-10.

Wigglesworth, V. B. 1967. The Principles of Insect Physiology. Methuen and Co. Ltd. London. 741pp.

Wildon, C. E. 1946. Garden Roses. Michigan Spec. Bull. (revised) 227, 21pp.

Woglum, R. S. 1920. A recently discovered citrus pest, Platynota tinctana (Walker) in California. Calif. Dept. Agr. Monthly Bull. 9:341-43.

Zenner-Polania, I. and R. G. Helgesen. 1973. Effect of temperature on instar number and head-capsule width of Platynota stultana (Lepidoptera: Tortricidae). Environ. Entomol. 2:1823-27.

APPENDIX

Table 1A. Developmental velocity (%/day) of the immature stages of the OLR at various temperatures

Temp. °C	Egg	Larval type	Larval instars 1	2	3	4	5	6	Total larval stage	Pupae
15	3.5	males	7.5	9.9	8.4	7.7	4.0		1.3	3.8
		females B	8.1	8.5	8.1	7.7	7.3	3.4	1.0	
20	8.2	males	12.8	18.4	20.9	18.8	11.3		3.1	8.3
		females A	12.9	18.3	19.2	15.8	11.4		2.9	9.1
		females B	11.5	17.2	19.8	22.0	17.6	11.9	2.6	8.5
		all							2.9	8.4
25	14.9	males	24.2	24.9	37.8	37.3	22.0		5.9	14.1
		females A	23.5	32.2	33.9	33.0	20.4		5.4	15.7
		females B	18.6	30.9	34.7	41.6	32.8	19.8	4.5	15.9
		all							5.6	14.8
30	20.8	males	30.0	46.8	48.7	44.9	29.7		7.6	20.0
		females A	32.0	45.3	47.4	40.7	25.6		7.2	22.9
		females B	27.7	43.5	43.3	47.2	46.7	29.7	6.6	22.9
		all							7.4	20.9
35	22.9	males	33.2	47.1	53.3	45.8	28.3		7.8	19.2
		females A	33.4	47.4	49.8	40.9	25.8		7.4	21.7
		females B	30.1	44.5	47.6	43.9	34.7	26.5	6.0	19.7
		all							7.4	20.6

Table 1A (Continued). Developmental velocity (%/day) of the immature stages of the OLR at various temperatures

Temp. °C	Egg	Larval type	Larval instars 1	2	3	4	5	6	Total larval stage	Pupae
24-15.5	8.1	males	12.1	18.1	22.0	19.8	12.0		3.1	7.3
(19)		females A	11.2	17.8	20.0	17.8	11.2		2.9	8.1
		females B	7.4	20.5	24.3	23.4	28.1	12.4	2.6	8.2
		all							2.9	7.8
24-18	10.0	males	15.4	20.8	24.9	23.7	15.0		3.8	9.3
(20.5)		females A	16.5	22.2	24.2	20.3	14.1		3.7	10.4
		females B	13.7	19.3	24.0	25.2	24.1	12.9	3.0	10.3
		all							3.7	9.7
29.5-18		males	15.5	24.7	28.6	27.5	15.7		4.1	10.5
(23)		females A	16.0	24.5	26.3	25.5	14.1		3.9	11.7
		females B	10.2	25.7	29.4	33.4	21.6	14.0	3.1	12.4
		all							3.9	11.1

Table 2A. Comparison of developmental rates (%/day) of larval instars of the OLR at constant and fluctuating temperatures.

Larval instar	Temp. °C	Developmental rate observed at the mean fluctuating temperature ♂♂	♀♀ A	♀♀ B	Developmental rate calculated at the corresponding constant temperature[a] ♂♂	♀♀ A	♀♀ B	Observations ♂♂	♀♀A	♀♀B
1st	19	12.1	11.2	7.4	12.5	11.5	9.5	d[b]	d	d
	20.5	15.4	16.5	13.7	14.7	14	12	i[b]	i[c]	i
	23	15.5	16.0	10.2	19	16	16	d	=	d
2nd	19	18.1	17.8	20.5	17	16.5	15	i	i	i
	20.5	20.8	22.2	19.3	20.5	20.5	18	i	i	i
	23	24.7	24.5	25.7	28	27	25.5	d	d	=
3rd	19	22.0	20	24	19.5	16.5	18.7	i	i	i
	20.5	24.9	24.2	24.0	23	21	22.5	i	i	i
	23	28.6	26.3	29.4	30.5	27.5	29	d	d	d
4th	19	19.8	17.8	23.4	16.5	15.5	22.5	i	i	i
	20.5	23.7	20.3	25.2	21	19	25	i	i	i
	23	27.5	25.5	33.4	27.5	25	33.5	=	=	=
5th	19	12.0	11.2	28.1	10.5	11	15.2	i	i	i
	20.5	15.0	14.1	24.1	13	13	19.5	i	i	i
	23	15.7	14.1	21.6	17.7	16.5	26.5	d	d	d
6th	19			12.4			10			i
	20.5			12.9			12.5			i
	23			14.4			17			d

Total larval stage (both sexes)			% increase
19	2.9	2.8	0.5
20.5	3.7	3.4	1.0
23	3.9	4.2	-1.0

[a] Data obtained by interpolation from Figs. 2, 3, 4 and 5

[b] d = decrease in rate of development; i = increase in rate of development

c = developmental rates are equal.

Table 3A. Comparison of developmental rates (%/day) of the pupal stage of the OLR at constant and fluctuating temperatures.

Type	Temperature °C	Developmental rate observed at the mean fluctuating temperature	Developmental rate calculated at the corresponding temperature[a]	Observation
Males	19	7.3	7.0	i[b]
	20.5	9.3	8.8	i
	23	10.5	11.6	d[b]
Females A	19	8.1	8.1	=[c]
	20.5	10.4	9.4	i
	23	11.7	13.2	d
Females B	19	8.2	7.4	i
	20.5	10.3	9.6	i
	23	12.4	13.2	d
All pupae	19	7.8	7.4	3.1% i
	20.5	9.7	9.2	3.9% i
	23	11.1	12.2	12.6% d

[a] Data obtained by interpolation from Fig. 6

[b] i = increase in rate of development; d = decrease in rate of development

c = developmental rates are equal