STUDIES ON THE BEHAVIOUR OF THE LARVAE OF *Plutella xylostella* (LINNAEUS) (LEPIDOPTERA: PLUTELLIDAE), A WORLD PEST OF CRUCIFEROUS CROPS. NORMAL AND 'SPACING' BEHAVIOUR[1]

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Resumen

Las larvas recién emergidas de Plutella xylostella *(L.) construyen galerías de manera que nunca llegan a encontrarse unas con otras, reduciendo la probabilidad de competencia por alimento, espacio y riesgo de ser encontrados por enemigos naturales. Los experimentos realizados se llevaron a cabo bajo condiciones controladas a 20 ± 1°C, 16 h luz/día y a una humedad relativa entre 44-52%, en cajas plásticas transparentes de forma circular. En cada caja se colocó discos (2.5 cm diámetro) de hojas de repollo en forma vertical, sobre una capa de arena silverada que sirvió de sostén.*

El movimiento de las larvas se observó desde que emergieron hasta que finalizaron la construcción del capullo, considerándose tanto el movimiento de larvas emergiendo de huevos separados o en grupos. Las observaciones del primer instar se realizaron desde la eclosión hasta el primer lugar de alimentación y después del primer sitio de abastecimiento.

Cada larva se arrastra y realiza movimientos "sensitivos" con su cabeza por varios minutos hasta que se ve estimulada por otras larvas inicia su autoalimentación. Las larvas provenientes de huevos individuales tienden a padecer de hambre pero carecen de estímulo de otras larvas. Después de la primera muda las larvas se alimentan sobre la hoja y no en galerías, separándose unas de otras al detectar cambios en la calidad del sustrato, colgándose de los hilos de seda que producen, por movimientos compulsivos fuertes, etc. Su distribución induce a una dispersión de áreas sobrepobladas, evitando así una sobre explotación del alimento disponible. En casos de baja densidad de población, la búsqueda de las larvas aumenta la probabilidad de encuentros entre larvas, con el consecuente estímulo para alimentarse.

Introduction

Plutella xylostella (Linnaeus) (Lepidoptera: Plutellidae) is a very common pest of cruciferous crops, with a wide distribution around the world. Although *P. xylostella* lays many eggs on a leaf either singly or in groups, the larvae rarely form aggregations as happens with some other pests of crucifers (i.e. *Pieris aripa* Boisduval, *Pieris brassicae* (L.), *Mamestra brassicae* (L.)). In normal field conditions, even at high densities, the larvae, especially the last

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instars, have a pattern of distribution whereby they seem to avoid direct contact and hence keep distinct feeding 'territories'. This dispersion pattern was thought not to be due to chance effects but to a mechanism by which larvae spaced themselves from each other at a certain minimum distance. This 'spacing' mechanism seems to be present in all the larval stages and was thought to be important, especially during the last two instars which are the more injurious to the plants. At the same time it seemed to be related to the general condition of the plant, since it is more apparent on the less tender leaves.

This is important from the economic point of view since larvae, especially the bigger ones, will tend to move to areas not previously attacked and will therefore tend to damage all parts of the plant.

From the statistical analysis of the distribution of the larvae under different densities and at different ages (4) it was shown that at low or high densities the degree of aggregation was very high for the recently hatched larvae and decreased with age to become random or sometimes regular in the older larvae, and finally increased again before pupation. This statistical analysis gives a clear idea of the distribution of the larvae. However, it does not explain the mechanism whereby the larvae distribute themselves ('spacing' mechanism). Therefore it was decided to do some direct observations on the behaviour of the larvae in an attempt to relate behaviour with distribution and survival.

A series of experiments were designed in order to observe and record the behaviour of the larvae from pre-hatching until pupation under different density conditions.

The objetives were to determine: a) how the larvae distribute themselves throughout the leaves of a plant; b) whether there was any interference between larvae at the different stages; c) whether the population density was an important factor influencing the behaviour of the larvae, their distribution, and their success or failure to reach the adult stage and reproduce.

Materials and methods

The experiments were carried out in the controlled environments rooms at 20 ± 1°C, 16 hours of light per day and 44-52% relative humidity. The cages used were circular transparent plastic boxes (9.5 cm bottom diameter, 10.5 cm top diameter, and 4.5 cm height) with transparent lids which had a 2.5 cm hole in the centre, covered with terylene, to give ventilation. Inside the cages had a 5 mm layer of moistured silver sand to hold and provide water to the leaf discs (Fig. 1).

The leaf discs were taken from tender leaves about 60-80 cm^2 area, of young cabbage plants. From each leaf, ten discs of 2.5 cm diameter were cut, five on each side of the central vein, and placed in a vertical position in a circle inside the cage. They were placed in the same position as they were in the leaf, with the upper surface facing the centre of the cage and slightly touching each other but separated about 0.5 cm from the cage wall (Fig. 1). Water was regularly added to the sand in order to keep the discs as fresh as possible.

The leaf discs were distributed and numbered inside the cages in the same disposition in which they were in the leaf (Fig. 1). Each leaf disc was divided (not actually marked) into sixteen quadrants numbered from left to right and from top to bottom.

Eggs about to hatch were observed and the hatching process was recorded. Larvae which hatched at the same time were transferred to leaf discs in the way previously described, and their behaviour recorded.

Results

The behaviour of the recently hatched larvae is very important in determining their survival since that survival depends on their ability to make an initial hole in the leaf surface. It is possible that many factors, apart from climate, are involved. For example those related to the plant might include: species and variety, age of the plant, age and position of the leaves, toughness of the leaf tissue; those related to the insect might include: initial number of eggs, dis-

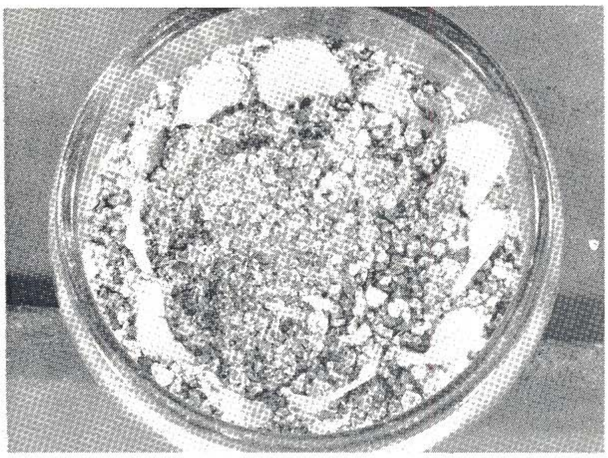

Fig. 1. Position of leaf discs in the cage.

tance from egg, whether the eggs are laid separated or touching, site of oviposition (stem, lower or upper surface, etc.), time when the eggs are laid; the latter is also related to the synchronization of hatching of two or more eggs within a group or batch.

PRE-HATCHING AND HATCHING BEHAVIOUR

The egg, when laid, is creamish in colour and later becomes yellow although the chorion remains transparent. One day before hatching the egg becomes dark (brownish) and under magnification the larva can be easily seen coiled inside the chorion with the head and the tip of the abdomen touching each other. When the larva is ready to hatch it starts to move inside the egg, especially the head. Soon afterwards it starts to make a hole by biting the chorion. At the beginning the head movement is vertical, that is up and down; two or three minutes later the hole is big enough to emerge part of the head through. Then the larva starts to eat the edge of the egg shell in order to make the hole bigger. At this stage the larva is biting continuously although is not always able to remove pieces of the egg shell. Two or three minutes later it stops for about five seconds and continues to bite for 10 to 15 seconds, stops again and repeats this alternative bite-and-stop for about two or three minutes until the hole is big enough to push the head entirely out of the egg. The larva pushes its head out of the egg and retracts it almost immediately. Then starts a pattern of behaviour in which it alternatively pushes the head out, bites the egg shell and stops all movements, each phase of the sequence lasting for three or four seconds. It continues for about five minutes until the hole is big enough for the larva to get easily out of the egg shell.

BEHAVIOUR OF THE LARVAE

The following description of the larval behaviour is mainly based on direct laboratory observations of the larvae throughout their development from hatching to pupation. These observations were made as frequently as possible. They were made by day as well as by night; however, the night observations had to be made with the lights on, which although for periods of no more than 2 or 3 hours per night, might alter the normal behaviour of the larvae. In order to observe whether there were differences in the behaviour of the larvae in darkness, a series of sequences were made with a time-lapse cinecamera, synchronized to an electronic flash in such a way that the larvae remained in the normal darkness all through the night except for the flash lightings (periods of less than 1/1000 second). The results showed that, apparently, there were no significant differences in the behaviour of the larvae in total darkness as compared with those observed under normal room lights. Therefore the descriptions of the behaviour during nocturnal observations can be regarded as valid as in total darkness (natural conditions).

First instar. From hatching to first feeding place

After hatching, the first instar usually wanders over and about the other eggs for a short period of time (varying from a few minutes to about two hours). This early wandering period of the recently hatched larva is characterized by a series of behavioural patterns. The duration of each pattern as well as the sequence and interval between them is variable.

Larvae from groups of eggs. – Just after eating its way out of the egg-shell the larva crawls over the other eggs, stops for two or three seconds on one egg and moves the head in a spinning-like movement (this takes from two or three seconds to 1/2 min.); actually it may be the first spinning of silk by the larva. After the 'spinning' movements the larva crawls out of the group of eggs onto to the leaf surface where after walking for 5 to 10 seconds it stops, raises the head well above the leaf surface and moves it widely from side to side. This movement seems to be a way in which the larva senses its environment by visual and/or chemosensorial impressions. From that stage there are two characteristic alternatives to the behavior of the larva. The first one is probably most common when the leaf is tender: the larva crawls further on the leaf surface for a short period of time (1 mm to several centimetres according to the time spent crawling; normally about 5 seconds). Then the larva stops and makes sensing-type movements for 2 or 3 seconds and continues crawling. This sequence may be repeated several times until the larva stops, starts to bite on the leaf tissue and eventually makes a hole. Sometimes the larva moves to another place after trying unsuccessfully to make a hole. The second alternative is most common when the leaf tissue is rather tough or when the eggs have been laid on the stem and is probably due to the first sensing impressions not being completely favourable. In this case the larva turns back onto the group of eggs and crawls over them while moving the head in a sensing type movement. If there is one egg about to hatch the larva goes almost directly to that egg and stands on it making the sensing movements for about 3 to 4 seconds. From there it moves to any other place in the group of eggs but generally tends to go to the empty shells of the eggs (including its own one) where it stops and makes sensing movements, or just passes over them. Every time the larva reaches the edge of the group of eggs it stops and turns back without attempting to go again onto the leaf surface. This pattern of behaviour may be repeated several times within a period of 5 to 10 minutes, and with certain variation in the duration of each stop or crawl. Finally the larva, after reaching the edge of the group of eggs walks out and crawls for periods of about 5 seconds which are alternated with short stops of about 3 seconds and sensing movements. It may return and crawl onto the group of eggs but almost immediately it crawls out again and repeats the 'crawl-stop-sense-crawl- . . .' sequence. After a variable period of time the larva stops and starts to bite the leaf until it makes a hole (or moves to another place and starts to bite repeating this until it eventually makes a hole).

Larvae from isolated eggs.– The behaviour of the larvae hatched from isolated eggs but with other eggs nearby is rather different from those hatched in groups of eggs. The larva eats its way out of the shell and immediately starts to crawl on the leaf surface until it meets another egg: the larva probes on that egg by doing a movement like that of spinning (which, in fact can be the first silk spinning of the larva), it continues spinning on the egg (as the spinning advances it crawls onto the egg) until it covers the whole surface with the spinning movement. Then the larva moves around until it finds another egg and repeats the process.

When that egg is covered by spinning, the larva moves, finds another egg and the process is repeated. The process is repeated for about five minutes. At irregular intervals the larva stops and remains motionless for a period from 2 or 3 seconds to one minute. This pattern of behaviour may be occasionally altered as, for example, when the larva meets an empty egg-shell; in that case the larva makes the spinning movements but very quickly, which may be caused by a special stimulus. Another example of change in the pattern of behaviour is when the larva meets a group of eggs; in this case the larva crawls quickly onto them and makes the sensing-type movements and keeps crawling and making the sensing movements for 4 or 5 seconds up to 3 minutes. If there is an egg about to hatch or an empty egg shell the larva stands on it and spins on it or on the egg next to it for a short period (up to 1 min.). Then it moves to the edge of the group and stops. Sometimes it tries to crawl out of the batch but when half its body is on the leaf surface it turns back, then either repeats the process or spins on the eggs at the edge. The larva repeats the sequence of crawling to the edge, spinning and going to another place on the edge for 3 to 4 minutes. At irregular intervals the larva usually meets one of the eggs about to hatch; in that case it stops and spins on it or on the next egg for about one minute, then raises its head and thorax and makes sensing movements for about 5 seconds. After about 20 minutes from hatching the larva stops longer between crawls and also makes sensing movements more frequently. If the larva is near a group of eggs it usually crawls onto it and alternates the sensing movements with the spinning on the eggs; it may also attempt to bite the eggs (generally without success); then it crawls off and on the group of eggs for several times. This sequence is repeated several times. During one of these crawls the larva may go to a natural depression on the leaf and try to bite there: this may be achieved after a certain period of time (around 5 min., but variable, most probably affected by the toughness of the leaf). If the larva does not succeed in the first attempt it moves away and starts the sequence of 'crawling-sensing-crawling' for 5 to 8 minutes, then stops while making the sensing movements, starts a very fast spinning-like movement on the leaf surface, without trying to bite it, for about 2 minutes. Then it changes to normal spinning for about 2 minutes more. Then the larva starts to bite but alternates the biting with spinning for about 30 seconds, when it then starts to bite continuously and rather rhythmically for about three to four minutes (this period is very variable, probably influenced by the leaf toughness) after which it eventually succeeds in making a hole which is marked by rapid increase in intensity and speed of the biting movements. Three minutes after starting, the hole is big enough for the mandibles to go in, five minutes after starting it is big enough for half the head to go in, ten minutes after starting the whole head is inside the hole.

First instar. After first feeding place

Once the larva succeeds in making a first hole on the leaf surface it usually stays there eating the spongy mesophyll which is softer than the palisade tissue (2). It only stops to rest to excrete or when disturbed. The feeding results in a gallery inside the leaf tissue. This is usually larger than the width of the larva and obviously increases in width when the larva body increases.

At the beginning most of the body is on the leaf surface, in that case the larva expels excrement by simply rising the tip of the abdomen and expelling semiliquid pellets. Later when a gallery is made (up to 2 or 3 times the length of the larval body), to excrete the larva walks backwards in the gallery until its abdomical tip is out of the entrace hole, then it expels the faeces. Normally the larvae start to feed on the lower surface, consequently, most of the opening holes of the galleries are on that surface; therefore when the larvae expel the faeces at relatively high speed they are scattered on the lower leaves. However, a considerable proportion of first instar larvae, (between 10 and 30% in the present investigation; 23.3% in Harcourt (2)) feeds on the upper surface. In this case the pellets can often be seen on the upper leaf surface around the gallery. The pellets are expelled at a relatively high speed away from the gallery opening. This can be interpreted as a means of avoiding accumulation near the entrance of the gallery, with subsequent decomposition of tissue and proliferation of fungi. Also it can be seen as a way of 'marking' the place as a 'territory' which another larva may consequently avoid. However, as the length of the gallery increases the distance necessary for the larva to go to the entrance hole also increases; then the larva goes backwards a certain distance, from 2 or 3 up to about 10 mm, and deposits the pellets on a place on one side. If the gallery is curved the pellets might be deposited on a bend. As the gallery increases in length the pellet deposit place is changed; thus in a long gallery it may be possible to see two, three or more pellet deposits.

Usually, the galleries are directed in a straight line; however, the leaf tissue is crossed by veins, the larva eats across thin veins but avoids the thicker ones. In some cases the galleries turn to one side. There are some instances in which there is no alternative route for the larva to make the gallery. In such cases the larva may try to turn in different directions until eventually it retreats and burrows in an opposite direction. Most commonly it makes a hole at the end of the gallery and goes out to make a new gallery. If there are two or more larvae in a small leaf (10 cm^2 or less), when they meet they reverse and crawl in different directions, but commonly they tend to stay together either in the same hole or in different holes. Normally the larva remains in the gallery until the end of the first instar when it goes out, generally to the lower surface of a nearby depression of the leaf or vein where it moults. Here, the larva spins a patch of silk and, prior to ecdysis, adopts a motionless position with the body straight and swollen.

Second instar

After the moult, the creamy coloured larva remains motionless for about one hour (sometimes much longer). Then it moves out of the moulting place and after crawling for about 2 or 3 minutes starts to make a new hole which may be increased as a gallery or more commonly as a window-type hole, usually on the lower surface. The galleries made at the beginning of the second instar are usually shorter than those made in the first instar. The holes are almost invariably 'window' type, that is all the leaf tissue is eaten except the upper epidermis. Normally, one larva makes more than one hole, that is, changes feeding place.

In this second instar the larva eats through veins slightly thicker than in the first instar. When two larvae meet they tend to crawl in different directions but do not show any sign of direct interference. At the end of the instar the larva moves to a secluded area such as a depression of the leaf or near a vein, and spins a patch of silk, then stays motionless for one hour until ecdysis takes place. It remains motionless about one hour after.

Third instar

About one hour after moulting, the larva usually moves to a place nearby and starts to make a window-type hole; sometimes it moves to another leaf. The holes made in this instar (from 7 mm diameter upwards) are bigger than those made in the previous instar and also the veins through which the larva eats are thicker. The larvae generally do not obviously upset with each other unless there are many per leaf. If a larva when wandering on the plant (leaf or stem) meets another which is stationary (feeding, spinning, 'resting', etc.), the latter makes a sudden movement of the thorax or abdomen depending on the part touched and continues its previous activity (feeding, etc.). This may be repeated a few times until the wandering larva goes away. However if the contacts persist or if it is a strong one (like trying to crawl over the other larva, or biting it), the stationary larva usually reacts with a very rapid twitching movement of the thorax or the abdomen (again depending on the part touched) which is usually strong enough to shake the other larva away. This movement may also be repeated several times until the disturbing larva goes away. The disturbing larva may also react against the stationary one by doing the same sort of rapid twitching movement and, after a few times, one of them will crawl away, usually the disturbing one. The third instar larva feeds mostly on window type holes, but also on holes through the whole leaf lamina. Then the larva ceases feeding and goes to a sheltered place, such as a leaf depression or near a thick vein, where it spins a patch of silk, then the body is straightened and very soon it swells; the larva remains motionless for one hour or more until the moult takes place.

Fourth instar

The new fourth instar larva is very light in colour and remains motionless for about one hour after ecdysis; then it starts to crawl away and goes to a new feeding place. The behaviour of the foruth instar larva is more or less similar to that of the third instar. At the beginning the larva usually makes window-type holes but later it feeds through the leaf lamina, including veins except those which are thick.

The larva is able to eat on almost any part of the leaf and once it has settled in one feeding place it generally remains in that place long enough to eat a big hole (up to eight hours, provided that it is not disturbed). During this time the larva alternates feeding and resting; the duration of each of these is variable. It also may move short distances (5 to 20 mm) or change the position of the body but always remains within its feeding area. It is not easily moved away by disturbance from other larvae although it reacts rapidly. The pattern of reaction is very much like that of the third instar although the movements are faster and stronger.

Pre-pupa

The larva goes to a sheltered place, apparently drier than the feeding place, i.e. a depression of the leaf surface, near a thick vein, or less frequently on the petiole or stem. In that place is starts to spin a patch of silk on the leaf surface. At this stage the body starts to change in colour to pinkish. When the larva has finished the patch of silk ('floor' of the cocoon) it remains straight and motionless for about two hours. The body continues changing in colour and starts to swell. Then the larva starts to make the walls of the cocoon. To do this the larva moves its head from side to side to stick the silk threads to the sides. Occasionally it turns through 190° and from there it spins short diagonal threads of silk, later remaining in its original position. The same pattern is repeated many times until a wide-mesh open net is made over itself.

When this open net is finished the larva does not turn its body completely any more but continues to spin the cocoon by turning the thorax to the sides as far as possible until it finishes the cocoon. Then the prepupa remains motionless for a variable period (normally about one day at 20°C temperature), after which it moults by a split along the midline of the thoracic cuticle splitting down to the tip of the abdomen. The emerging pupa wriggles to help the shedding of the cuticle. The larval skin slips to the abdominal end and remains there.

Pupa

When the pupa emerges, it is very light in colour, rather white-creamish and transparent. Shortly afterwards the pupal cuticle becomes opaque and yellowish. The colour remains unchanged for four or five days at room temperature. Then it starts to become darker and by the sixth day it is brown-greyish and continues darkening until it becomes totally dark brown (hours before the adult emerges). Minutes before the emergence of the adult, the pupa becomes rather blackish and all the features of the adult can easily be seen through the pupal cuticle. The ecdysis starts with the splitting of the cuticle in the midline of the thorax which continues down to the abdomen. The imago pushes its way out of the cocoon through the frontal end which is spun in such a way that it allows the adult to get out.

SPACING BEHAVIOUR OF THE LARVAE

Before describing the spacing behaviour of the larvae it is necessary to mention some characteristics of these larvae which are directly involved in such behaviour.

The first instar larva seems to have relatively weak mandibles which may condition its feeding behaviour. This is suggested by the fact that at the beginning it spends a relatively long time wandering, probing and trying to bite before the first feeding puncture is made. It may also be that the mandibles are initially not hard enough to bite the leaf tissue. This suggestion of weakness of the mandibles could be applied to the older instars which feed only on the sponge tissue, avoiding the thick veins, leaving the harder upper epeidermis. And even when they are able to eat through the whole thickness of the leaf lamina they still avoid the thick veins. In this way the larvae on a leaf tend to get into 'feeding cells' separated by the veins.

In general, the larva may have means of detecting any change in the condition of the leaf tissue. Thorsteinson (5, 6) demonstrated chemotactic (olfactory as well as gustatory) responses in the finding of the host plant, in inducing the larva to bite, and in the amount of leaf tissue eaten by the larvae as well as in the host finding and in the oviposition by the adults. Therefore it is most likely that the same type of response will induce the detection of leaf-tissue suitability by the larva. In the present investigation it was observed that recently hatched larvae started to eat quicker when the leaf tissue was cut.

This behaviour may be influenced by not only chemotactic stimuli, but also by physical and morphological factors which combined with those chemotactic stimuli to make leaf tissue suitable.

Some of the morphological factors of major importance are: the texture, the succulence, the toughness of the leaf (6), and the anatomical disposition of the cells in the leaf, as was demostrated by Rudder and Brett (3) for varieties of Kale (loosely arranged cells and abundance of air space in susceptible varieties, and densely compact cells without air space in resistant ones). The chemical factors are discussed in detail by Thorsteinson (5) and Gupta and Thorsteinson (1). The larva is so sensitive to the quality of the leaf tissue that it will never burrow a gallery beside another gallery which has been previously burrowed irrespective of whether it is its own gallery; also it will change the direction of the gallery to avoid areas where changes in the leaf tissue have occurred. When there is no other alternative route for the larva, it generally makes a hole in the epidermis of the leaf and gets out, to start a new gallery. But, as explained before, the larva is not only able to detect those abnormal changes in the plant tissue but also the more normal ones, for example when it meets a vein in the leaf which is less tender than the tissue around, or when the leaf toughness changes near the edges of the leaf.

Another important characteristic of the larvae in all the instars, which contributes to the 'spacing' of the larvae in the plant, is the ability (common to many Lepidoptera) of spinning a thread of silk which from immediately after hatching may serve as a guide or support for the legs and prolegs when crawling, but which has an apparently more important role in the larvae. For example, if there is a sudden disturbance such as a strong wind, shaking of the leaves, or interference by another larva, it is able to hang from the thread until the disturbance ceases and it regains the original position by twisting its body, grasping the thread with the mandibles and legs, and so climbing up to its original leaf, or it may lower itself to another part of the plant or even to the ground and to a neighbouring plant. This favours dispersal from the original population, which might be vital under conditions of high larval density or shortage of food.

Discussion

The behaviour of the recently hatched larvae is notable for the galleries or mines they construct. The mines never contact each other because before meeting another gallery the larvae emerge and start a new gallery somewhere else. In that way there is less direct competition for the host plant, the area (and hence time) to be searched by natural enemies is no doubt increased and in cases of high initial densities the surplus population of *P. xylostella* is eliminated, thus minimising the danger of over-eating the host plant. This helps to ensure that large adults which will be fit for reproduction are produced, since fertility is related to the weight of the adults. It was found in previous experiments that pupal length and weight, and adult weight were inversely correlated with larval density.

Older larvae tend to keep near to each other but mantain a certain distance apart– so called 'spaced-out' gregariousness. This spacing is ensured, at least partially, by the wriggling movements of the larvae when disturbed, and seem to be beneficial especially for escaping natural enemies or avoidance of other competitors either of the same or different species.

In general it can be said that the typical behaviour of *P. xylostella* larvae which is partially characterized by the relatively frequent change of feeding places, may be important in the survival of the population in, at least, two ways. Firstly, because it increases the probability of meeting each other according to the density of the population; therefore for each larvae it acts as a means of 'measuring' the population density, consequently it induces dispersal from the crowded areas and hence it avoids over-exploitation of resources such as food or space by the 'spacing' behaviour already described. Secondly, in cases where the populations density is very low, this 'moving' behaviour increases the probability of two larvae meeting and mutually stimulating to feed, which might be essential for the survival of the larvae.

Summary

The recently hatched larvae of *Plutella xylostella* (L.) make galleries in such a way that they never contact each other, minimising the probability of competition for food, space and risks of natural enemies. Experiments were carried out in controlled environment rooms (20 ± 1°C, 16 h light/day, 44-52% relative humidity). Transparent plastic circular boxes were used as cages. Leaf discs (2.5 cm diameter) of tender cabbage were distributed inside the cages, in vertical position. A layer of moistured silver sand held the leaf dics. The behaviour of the larvae was recorded from the moment they hatched until the cocoon was finished. The experiments included larvae hatching both from eggs in groups and isolated. The observations were made continuously and as frequently as possible. The first instar observations were divided from hatching to first feeding place, and after first feeding place. Each larva starts crawling and making "sensing" movements with the head. After several minutes and when stimulated by other larvae, the wandering larva starts to feed. Isolated larvae tend to starve as there is no stimulus from other larvae. After the first moult the larvae feed outside, not in galleries. The larvae have several ways of "spacing" themselves, for example by detecting changes in the quality of the leaf tissue, by hanging from threads of silk, by making sudden shaking movements, etc. The spacing induces the dispersal from crowded areas, hence avoiding over-exploitation of food and space. In cases of very low population density, the wandering of the larvae increases the probability of two larvae meeting and mutually stimulating to feed.

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