STUDIES ON THE ECOLOGY AND BEHAVIOUR OF ~~THE~~ ~~LARVAE OF Plutella~~ PLUTELLA xylostella ~~(LINNAEUS)~~ (MACULIPENNIS) (CURTIS), ~~(LEPIDOPTERA : PLUTELLIDAE).~~

by

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ABSTRACT

Plutella xylostella (L.) (Lepidoptera : Plutellidae) is a universal pest of cabbage. Populations of this species were studied both in constant environment rooms and in field conditions. The lengths of the different instars, and the fecundity,, were determined in the laboratory at 20°C. The behaviour of the larvae was recorded with particular emphasis to the recently hatched larvae and to density. The effects of size and shape of the leaves on behaviour and survival of the larvae as well as the effects of starvation in later instar larvae, in the laboratory, were recorded. The dispersion pattern of the larvae was recorded throughout development. The effects of the leaf toughness on survival was studied. The behaviour of the adults was recorded.

In the field, mortality factors were studied by exclusion cage techniques. These included exclusion of birds, soil predators, small aerial predators, parasites and rainfall. Mortalities from the different causes were assessed for the different instars. The importance of overlapping causes of mortality was demonstrated and as an exercise life tables were constructed.

Suggestions are made on how natural methods of control could be enhanced in order to minimise dependance on insecticides for control of this pest.

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1. INTRODUCTION

1.1 THE CONCEPT OF PEST.

Agriculture is one of the oldest activities of man, and since Neolithic times when the early man started cultivating vegetable products he presumably found that this was interfered with by many pests and diseases. Nowadays it is apparent that pests, such as insects, are actively competing with man. Thus a 'pest' can be defined as an organism which is in competition with man for some resource or which is an obstacle for his activities. As has been pointed out, insects are amongst the most serious pests since they are especially harmful to man's activities notably in relation to his health, crops and livestock.

1.2 CONTROL OF INSECT PESTS.

Most insects are plant feeders and as such they are the main pests of agriculture. No cultivated plant has been found entirely free of insects, and although it does not mean that all phytophagous insects are pests, most can be considered as potentially injurious to man's crops. However man has replied to the pests' competition by fighting back with all available means, and the development of such means can be traced back to the sounds and gestures supposed to have been made by man in prehistoric times through prayers or magic in latter times, and then to more refined methods such as the use of substances (ashes, chalk, plant juices, etc.) in the old civilizations. Later on (Medieval age up to a few dozen years ago) alchemy and chemistry offered better alternatives;

however, it was not until the discovery of the insecticidal properties of synthesised DDT that a major breakthrough took place in pest control. Subsequently many synthetic insecticidal chemicals have been developed and increasingly used. The unquestionable success of DDT, especially in public health, led to the chain-reaction type of production and use of many different chemicals with the undesirable consequences which were highlighted in somewhat exaggerated form by Rachel Carson (1963). One of the many consequences of the use of insecticides is the resurgence of pests as a result of induced resistance, another is the elevation to pest status of previously unimportant insects by the destruction of their natural enemies, or by eliminating their competitors. For example, in human and animal health the Diptera most characteristically demonstrate the above problems, whereas in agriculture the Hemiptera (s.l.) and the Lepidoptera exemplify them especially well.

1.3 Plutella xylostella (L.) AS AN IMPORTANT PEST.

One of the many Lepidoptera which has been subject to the consequences described above is the diamond-back moth, Plutella xylostella (Linnaeus). This is widely distributed throughout the world (Map 1) and is a very serious pest of cruciferous crops in many regions. With the frequent use of DDT this pest became resistant to DDT as early as 1953, as reported by Ankersmit (1953). It required about 30 to 40 generations to develop resistance, and is probably the first crop pest to be recorded as resistant to DDT.

The adaptability to different climatic conditions and its recognised status as a major pest in temperate and tropical regions makes the study of P. xylostella important from the economic as well as from the biological point of view. Therefore it is not surprising to find that many papers dealing with this insect are published. Table 1.3.1 gives the number of papers involving P. xylostella published in the last twenty-five years (1947-1971) (compiled from the Review of Applied Entomology

COMMONWEALTH INSTITUTE OF ENTOMOLOGY

DISTRIBUTION MAPS OF PESTS

Series A (Agricultural), Map No. 32 (revised). December 1967.
Published at:—56 Queen's Gate, London, S.W.7.

Pest: *Plutella xylostella* (L.) (*maculipennis* Curt.)

(Lep., Plutellidae) (Diamond-back Moth)

Host Plants: Cultivated and wild Cruciferae, notably *Brassica* spp.



© Commonwealth Agricultural Bureaux, 1967

Map 1. World distribution of P. xylostella. (The Commonwealth Institute of Entomology has advised us that Chad, in Central Africa, should be included`.

and the Zoological Record). The papers were divided according to their main subject. Sometimes it was necessary to place one paper in two categories, in those cases the proportion allocated to each is given.

Table 1.3.1 - Papers involving P. xylostella published from 1947 to 1971

	Most of Paper	Half Paper
Taxonomy:	3	1
General Biology (including life-history, population dynamics, distribution, and host-plant records):	70	2
Parasites, Predators and Diseases (including Biological Control):	45	4
Chemical Control	80	5
Total recorded papers	204	

Many of those papers are on chemical control which seems to be justified because of the relatively high value of the crops (brassicas) which it attacks. Both yield and appearance, are affected by the larvae of P. xylostella.

No doubt the seemingly easiest way of maintaining a particular crop free of insects is by application of insecticides but to control P. xylostella two or more insecticides are sometimes mixed, and applications as frequent as one per week until harvest have been recommended.

In spite of the amount of work published there are proportionally few papers on the detailed biology and ecology of the insect. Those few papers are mainly concerned with the life-history and/or parasites and/or seasonal history under localized conditions. Therefore it was felt that there was a need for some work to be done on certain aspects which might contribute to a better understanding of the relations between individuals (specifically the larvae) and also between this species and other species which may interact with it, i.e. parasites and predators.

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 brassicae (L.), Mamestra brassicae (L.), Brevicoryne brassicae (L.). 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 most injurious to the plants. At the same time it seemed to be related to the general condition of the host plant, since it is most 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.

The present study was carried out as a contribution to the knowledge of the ecology and behaviour of P. xylostella especially in relation to the behaviour during the larval stage. It was hoped that this work would have general relevance to other insects which disperse on the host plant, and that it might indicate the significance of intra-specific mechanisms in regulation of numbers of insects.

2. REVIEW OF LITERATURE

2.1 ECOLOGY OF LEPIDOPTERA.

The Lepidoptera are among the most studied of insects. They have aroused curiosity since immemorial times because of the beauty of the imagos - especially the butterflies, and also for the damage caused by their larvae. Most of the early studies on these insects were on their morphology and taxonomy. Only in the last century were more detailed observations made on their general biology and phenology. Later, morphological and anatomical investigations were made. At the beginning of the present century there was a diversification into many disciplines, with the traditional ones being studied in more detail and new ones like physiology, ecology, and behaviour, being developed. Most of the research on these new fields was on insects of economic importance and obviously many of them on Lepidoptera.

Outstanding early publications on ecology include the work of Hering (1926) on the general biology of Lepidoptera and Williams (1930) on butterfly migrations. Lately there have been some remarkable long term comprehensive research studies, generally team projects. For example the work of Baltensweiler (1966, 1968) on Zeiraphera griseana Hubner (Tortricidae) in the Alps; Embree (1965) on Operophtera brumata (L.) (Geometridae) in Canada; Ito (1969) on Hypanthria cunea Drury (Arctiidae) in Japan; Klomp (1968) on Bupalus piniarus L. (Geometridae) in Holland; Koyama (1970) on Leucania separata Walker (Noctuidae) in Japan; Morris (1963) and collaborators on Choristoneura fumiferana (Clemens) (Tortricidae) in Canada; Varley & Gradwell (1965, 1968) on

Operophtera brumata in Great Britain; Wellington (1960) on Malacosoma pluviale (Dyar) (Lasiocampidae) in Canada.

In more specific fields are the works of Dethier (1959 a, 1959 b) on host plant preference; Jacobson (1965) on sex attractants; Johnson (1969) on migration and dispersal; Schoonhoven (1969) on food plant selection; and Shorey and collaborators on biology and mainly on sex pheromones (Shorey et al., 1966, 1968a, 1968b).

2.2 ECOLOGY OF CRUCIFEROUS CROP PESTS.

Many papers have been published on ecology of Lepidoptera attacking cruciferous crops. Some major examples are as follows:

2.2.1. General crucifers pests.

Bonnemaison (1965) reviewed extensively, although very generally due to the scope of the review, the most important pests of cruciferous crops throughout the world and their control; Hirata (1967a, 1967b, 1968) has been studying a group of caterpillars of economic importance on cabbage in Japan; Pimentel (1961a, 1961b) has dealt with the structure of communities and inter-specific competition on Brassicas in U.S.A.; Oatman & Platner (1969) made a study of the dynamics of populations of the insects on cabbage in U.S.A.

2.2.2. Pieris spp. (Pieridae).

David & Gardiner (from 1952 onwards) have worked on the behaviour and natural enemies (parasites and diseases) of P. brassicae (L.) under laboratory conditions in Great Britain; Dempster (1967, 1968, 1969) reported the effects of DDT control on P. rapae (L.) in Great Britain; Faure (1926) examined the biology and parasites of P. brassicae in France; Harcourt (1961, 1962, 1966) studied the population dynamics of P. rapae in Canada; Hirata (1967a, 1967b, 1968) has researched on the general biology, ecology and population dynamics of several pests of cabbage

including P. rapae crucivora Boisduval in Japan; Hovanitz & Chang (1962, 1963) have reported on the insect-host plant relationship of P. rapae in U.S.A., although Hovanitz work in Lepidoptera (mainly in Rhopalocera) is very wide including taxonomy, philogeny, evolution, biology, ecology, etc.; Kobayashi (1962, 1968) studied the population dynamics of P. rapae in Japan; Matsuzawa (1958) made a detailed study of the ecology of Apanteles glomeratus (L.) a parasite of P. rapae crucivora in Japan; Moss (1933) reported on the natural control of Pieris spp. in USA; Oatman (1966) investigated on the dynamics of field populations on several cruciferous pests including P. rapae in U.S.A.; Richards (1940) made a comprehensive study of the biology and ecology of P. rapae in Great Britain, this is probably the most detailed study, up to date, of this species in Great Britain and gives the caracteristics of the different species of Pieris in Great Britain, descriptions of all the stages, food plants and their relative importance, life history, phenology, diapause, population dynamics, and natural regulation; Takata (1962) has summarized his work on the host preference of P. rapae crucivora in Japan; Williams (1938) gave a general account of the migration of P. brassicae.

2.2.3. Mamestra brassicae L. (Noctuidae)

Bonnemaison (1960, 1961a, 1961b, 1961c, 1962a, 1962b) studied thoroughly the main factors affecting the fecundity and fertility of this species in France; Hirata (1955, 1967b, 1968) studied the biology, ecology and population dynamics of M. brassicae and two other pests of cabbage in Japan; Ito & Miyashita (1955) studied the dispersion and mortality of this species in a chinese cabbage field in Japan; van der Laan (Ed.)(1967) edited a book which brings several references to the use of viruses as controlling agents in different countries; Matsumoto (1956) made a study of the light-trap catches of the adults and the factors affecting the occurrence of the moths in Japan; Misaki (1956) investigated the effect of temperature on the diapause of M. brassicae in Japan.

2.2.4. Trichoplusia ni (Hubner) (Noctuidae)

The bionomics of this species have been very well studied in the United States of America, where it is a major pest of Brassicas, and it is one of the insects in which the investigations on sex pheromones were initiated. Except where stated all the references are from U.S.A.

Berger (1966) gives an account of the sex pheromone and its synthesis; Chippendale et al. (1965) have studied the nutrition of this species; Elsey & Rabb (1967, 1970) studied its biology on tobacco as food plant; Goble, in Canada, has followed the seasonal occurrence for several years and reported that in 1968 this species occurred in higher numbers than in any of the previous twenty years (Goble, 1968); this increase in number seems to have occurred in Venezuela in the same year, when it became a serious pest, whereas previously it was uncommon; Greene (1968) discussed the distribution of eggs and larvae on cabbage as a basis for sampling efficiency; Henneberry, Howland, Kishaba, Toba and some others have investigated the biology and mainly the reproduction of this species with emphasis on its sex pheromone both natural and synthetic and the use of chemosterilants (some selected papers by those authors are: Henneberry et al. 1967a, 1967b, 1968; Howland et al. 1969; Kishaba et al. 1966, 1967; Toba et al. 1968, 1970); Jacobson et al. (1968) reported the synthesis of female pheromone; King (1966) studied the seasonal changes of the adults during nine years in relation to temperature and rainfall; Oatman & Platner (1969) investigated the ecology of T. ni in the field in U.S.A.; Sutherland (1966) made a detailed study on the biology, ecology and population dynamics of this and other Lepidoptera species in U.S.A.; Wolfenbarger (1967a, 1967b) estimated the seasonal abundance of this species as well as the variations of infestations as affected by two different host plants.

2.2.5. Plutella xylostella (L.) (Plutellidae).

This species is the subject of the present investigation so no detailed account of the literature will be given here because many of the papers will

be quoted later in the text. As it has already been pointed out many of the published papers on P. xylostella refer to its chemical control, many others are devoted to the study of the natural enemies, mainly parasites, predators and diseases and to biological control; finally there are many dealing with bionomics including biology, life-history, ecology, population dynamics, geographical distribution and host-plants. However, many of the papers in the latter category (or bionomics) are only either records of uncommon host-plants or simply notes on the occurrence of P.xylostella and other pests on cruciferous crops, some time with some additional data on local conditions (climate, vegetation, etc.). Nevertheless, there are several important papers reporting, more or less comprehensively, the biology and natural control of P.xylostella.

In a review of the literature of pests of crucifers, Bonnemaison (1965) quotes P.xylostella as being of importance in cruciferous crops. Pimentel (1959, 1961a, 1961b) in a series of investigations on the communities of animals, mainly arthropods, on Brassicas, refers to P.xylostella as one of the important pests.

Some other papers have been published which deal in more detail wit the general bionomics of this species, for example, Abraham and Padmanaban (1968) in India; Atwal (1955) in Australia; Biever & Boldt (1971) in U.S.A.; Brethes (1923) in Argentina; Edwards (1930) in Jamaica; Gupta & Thorsteinson (1960a, 1960b) in canada; Hassanein (1958) in Egypt; Ho Thian Hua (1965) in Malaya; Kanervo (1936) in Finland; Khristova (1957) in Bulgaria; Lee (1968) in Hong-Kong: Muggeridge (1930) in New Zealand; Oatman & Platner (1969) in U.S.A.; Reichardt (1919) in USSR; Shaw (1959) in Great Britain; Stepanova (1962) in USSR; Sutherland (1966) in U.S.A.; Taylor & Bardner (1968a, 1968b, 1970) in Great Britain; Thorsteinson (1960) in Canada; Vos (1953) in Java; and Way et al. (1951) in Great Britain.

There are some very comprehensive papers on this species, namely those of Harcourt (see references by Harcourt and Harcourt et al.

from 1955 onwards) who has worked on the biology and population dynamics of P. xylostella and other caterpillars on cruciferous crops in Canada; Robertson (1939) who described in detail the morphological characteristics of the different stages and gives thoroughly account of the bionomics and control in New Zealand; and Ullyett (1947) who has made one of the most exhaustive investigations on this species with particular emphasis in natural control in South Africa.

Finally there are two very important papers on parasitism and biological control of P. xylostella : Delucchi et al. (1954) in Italy, and Hardy (1938) in Great Britain.

Other major contributions to knowledge of P. xylostella which are directly relevant to the present work will be discussed in detail later.

2.3 EFFECTS OF DENSITY.

2.3.1. Effects of density on insects.

Animals in general are affected in different ways by their density, mainly in the amount of food and space available for each individual. Each species is affected in a particular way and what could be a disastrous density for one species might be the optimum for some others.

No attempt will be made here to review the effects of density in man and other animals except insects. For those subjects there is ample recent information in Ehrlich & Ehrlich (1971) and Taylor (Ed.) (1970) in relation to man. Wynne-Edwards (1962) deals with the aspects of population density leading to social behaviour in most of the groups of animals but with particular reference to the higher phyla. The Proceeding of the Advanced Study Institute on "Dynamics of Numbers in Populations" (1971) is probably the most recent comprehensive volume on all aspects of dynamics of populations, including effects of density in different groups of animals both vertebrates and invertebrates.

As regards insects, there has always been an interest in the study of the effects of density on those species which tend to form aggregates, especially if these aggregates last in such a way as to be important in inducing changes in biology, physiology or behaviour. The interest is usually increased for economic reasons if the species are pests.

There are two types of effects of density, namely effects on the same species (or intra-specific effects) which will be discussed later in more detail, and those on other species (or inter-specific), notably parasites and predators and also competitors. These latter effects will only be referred to in particular cases, and details on them may be found in van der Boer & Gradwell (Eds.) (1971), Holling (1959, 1961, 1966), Watt (1959), and Varley & Gradwell (1970).

The intra-specific effects of density can be divided (although there is not a clear line of separation) into what is generally regarded as a series of changes in the biology and the behaviour of the individuals but without any major change in their morphology and physiology, and what is more easily recognisable since it also includes changes in morphology and physiology ('Group Effect'). The 'Group Effect' is normally associated with the following changes in the individuals : darkening of the skin, increase in the rate of development, increase in the number of larval instars, decrease in size and weight, decrease in fecundity and longevity, change in hormonal activity (i.e. increase in juvenile hormone), increase in general activities (i.e. mobility, feeding, etc.), initiation or increase of aggregation, initiation or increase of migratory stimulation. A precise summary of the effects of group in different insects but mainly in locusts is given in a review by Uvarov (1961) who emphasises the fact that the studies on density effects on insects have normally concentrated on changes in coloration and morphology of individuals, while the more important physiological and behavioural effects have not been investigated, although may be expected (Uvarov, 1961). More than eleven years have passed since these remarks were made and they still stand as valid as

ever. With a few exceptions, mostly on Orthoptera (Albrecht, 1962; Uvarov, 1966), Aphids (Way, 1968), and Lepidoptera (to be discussed later) there have been no new studies on the behavioural and physiological changes occurring in insects when their densities change.

Some of the more relevant papers on the effects of density on insects (except Orthoptera and Lepidoptera) are those by Barbosa & Peters (1970) who gives a list of papers dealing with the manifestations of overcrowding in different species, Cohen (1968) on development time of Drosophila melanogaster Meig. (Diptera : Drosophilidae) on chemically defined diets; Crombie (1944) on different effects in grain-infesting insects, mainly Coleoptera; Davis (1945) on longevity in Trogoderma versicolor Creutz. (Coleoptera : Dermestidae); Dempster (1968) on mortality, development, and fecundity of Arytaina spartii (Guerin-Meneville) (Homoptera : Psyllidae); Ebelin & Reierson (1970) on Blatella germanica (Dictioptera: Blattidae) in choice-boxes; Greenough et al. (1971) on crowding of Aedes aegypti (L.) (Diptera : Culicidae); Ikeshoji & Mulla (1970) on chemical factors produced by the larvae of Culex pipiens quinquesfasciatus Say (Diptera : Culicidae) in overcrowded conditions; Jacklin et al. (1968) on Conotrachelus nenufar (Herbst) (Coleoptera : Curculionidae) on apples; Kalabukhov (1935) on longevity and feeding in Apis mellifera L. (Hymenoptera : Apidae); Kiritani et al. (1966) on egg and larval survival of Nezara viridula L. (Hemiptera : Pentatomidae); Kisimoto (1959) on Nilaparvata lugens Stal (Homoptera : Araeopidae) wing polymorphism; Krishnan et al. (1969) on larvae of Culex fatigans Wied. (Diptera : Culicidae) in the laboratory; Mac Lagan & Dunn (1936) on the reproduction of Calandra orizae L. (Coleoptera : Curculionidae); Martinez-Beringola (1966) on development time of Ceratitis capitata Wied. (Diptera : Trypetidae); Mertz & Robertson (1970) on Tribolium castaneum (Hbst.) (Coleoptera : Tenebrionidae); Miller & Thomas (1958) on D. melanogaster size and longevity; Milne & Giese (1970) on mortality and dispersal of Corthylus columbianus Hopkins (Coleoptera : Scolytidae); Moore & Fisher (1969) on Aedes aegypti (L.) and Aedes albopictus (Skuse)

(Diptera : Culicidae); Nakamura (1969) on the progeny population of Callosobruchus chinensis L. (Coleoptera : Bruchidae); Osborn et al. (1970) on Musca domestica L. (Diptera : Muscidae) fecundity; Park et al (1939) on larval and pupal duration in Tribolium confusum Duval (Coleoptera : Tenebrionidae); Quraishi (1965) on swarming, mating and density of Anopheles stephensis mysorensis Sweet (Diptera : Culicidae); and Way (1968) on Aphis fabae Scopoli and Brevicoryne brassicae L. (Homoptera : Aphididae).

2.3.2 Effects of density on Lepidoptera.

Overcrowding is harmful to insects but there are also subtle beneficial effects of aggregation (Group Effect; Coll. Intern. Centr. nat. Rech. scient., No. 172, 1968). Lepidoptera have been well studied in this connection. Some insects may be exposed to the effects of density from hatching and in this respect the oviposition habits of the species concerned are important. For example, in many species which show larval differences due to group effect, the eggs are laid in masses or if singly very close to each other, i.e. Spodoptera spp. (Noctuidae), Pieris brassicae L. (Pieridae). However, other species may lay isolated eggs and still be subject to the group effect, i.e. Alabama argillacea (Hubner) (Noctuidae).

Apart from general reviews as those of Barbosa & Peters (1970), Chauvin (1952), Le Masne (1952) and Uvarov (1961), it is necessary to emphasise the outstanding investigations carried out by Iwao in relation to phase variation and other effects of crowding in Leucania separata Haworth (Noctuidae) and some other Lepidopteran species (Iwao, 1962, 1968; Iwao & Wellington, 1970); and by Wellington (1960) on Malacosoma pluviale (Dyar) whose work is reviewed below.

Andersen (1956) reports on the effects of crowding in Endrosis sarcitrella L. (Oecophoridae); Calcagnolo & Sauer (1955) give an account of the change of coloration in A. argillacea; Cayrol (1957) discusses the

effect of group on the development of Plusia gamma L. (Noctuidae) and its correlation with different environmental factors; Darling (1939) mentions the biological meaning of crowding in Phalera bucephala L. (Notodontidae); Doull (1953) discusses phase coloration in larvae of several species of Lepidoptera; Drooz (1966) shows the effects of rearing density on the biology of Ennomos subsignarius (Hubner) (Geometridae); Edwards (1945) gives an account of larval gregariousness in Lepidoptera; Flanders (1933) shows how the density is limited in populations of Sitroga sp (Gelechiidae); Franz & Laux (1965) enumerate the individual differences found in Malacosoma neustria (L.) (Lasiocampidae); Gruys (1970) reports on the effect of larval density on growth of Bupalus piniarus L. (Geometridae); Klomp (1958) discusses the relationship between larval density and adult fecundity in B. piniarus; Leonard (1968, 1970) has comprehensively investigated the effects of density on the biology of Porthetria dispar (L.) (Lymantriidae) and one of his most important conclusions is on the increase of survival of the larvae under crowding conditions; Long (1953, 1955, 1959), Long & Zaher (1958), and Zaher & Long (1959) have also studied, very thoroughly, the effects of density in several species mainly Noctuidae; Martyn (1965) relates the density of oviposition with other environmental factors to the egg and larval survival in Oncopera intrincata Walker (Hepialidae); Sasakawa & Yamazaki (1967) report on the effect of population density on larval coloration suggesting that it is determined by density during the first instar, and on development of larvae and pupae in Cephonodes hylas L. (Sphingidae); Sevastopulo (1944) reports on the effects of overcrowding on Deilephila nerii L. (Sphingidae); Smith et al. (1949) relate the flight of Colias sp. (Pieridae) to the larval population density; Snyman (1949) reports on the influence of population density on the development and oviposition of Plodia interpunctella Hubner (Pyralidae); Takahashi (1953, 1956, 1961, 1962) has made a detailed study of the effects of population density with special reference to the power of reproduction and the population fluctuation of Ephestia cautella Walker (Phycitidae); Tetley (1947) points out the variability accompanying the

population increase in a colony of Argynnis selene (Nymphalidae); Titschack (1937) gives an account of the effects of mass breeding on the individual Tineolla bisselliella Hummel (Tineidae); Ullyett (1945) shows how density affects the reproductive rate of Ephestia Kuhniella Zell. (Phycitidae); Wafa & Eid (1967) report on the effect of density on weight and chemical composition in Bombyx mori L. (Bombycidae); and finally the remarkable work of Wellington (1960, 1964) on the qualitative changes occurring in the individuals of Malacosoma pluviale (Dyar) (Lasiocampidae) in natural populations during changes in abundance; he concludes that there are two main types of larvae according to their behaviour (active and sluggish) and two other intermediate types; then according to the proportion of each type, the appearance and habits of the whole colony as well as its mortality will be established; larval behaviour has been proved to be influenced by the parental moths, that is inactive moths oviposit near their birthplaces and most of its offspring are also inactive whereas active moths travel farther to oviposit and their progeny comprise a high proportion of active individuals.

2.3.3. Effects of density on Lepidoptera attacking crucifers.

There are few papers dealing with the effects of density on Lepidoptera attacking cruciferous crops. Most are on two species; Mamestra brassicae L. (Noctuidae) and Pieris brassicae L. (Pieridae) which show colour and morphological changes with increase in density. The most important papers on M. brassicae are by Hirata (see Hirata, from 1954 onwards) on phase variation, especially on the effects of density on coloration, food consumption, weight, rate of development, diapause, and population regulation.

The most comprehensive papers on P. brassicae are by Long (1955, 1959), Long & Zaher (1958) and Zaher & Long (1959) who report on density effects on the biology, morphology, physiology (especially in relation to coloration, size and weight), and behaviour. Some other relevant

papers are those by Cherchi (1952) on artificial gregariousness; and Wardzinski (1937) on growth and development as related to the density.

Kobayashi (1963, 1965) discusses the dispersive behaviour in the laboratory of larvae of Pieris rapae crucivora Boisduval reared under solitary and crowded conditions and concluded that there is no aggregative behaviour caused by the mutual attraction among individuals (except sometimes and very slightly in larvae reared in crowded conditions). He also reports on the influence of adult density on the oviposition site; Henneberry & Kishaba (1966) report on the pupal size, mortality, longevity and reproduction of Trichoplusia ni Hubner (Noctuidae) reared at several densities.

3. DESCRIPTION OF THE DIFFERENT STAGES OF P. xylostella.

The different stages have been described and illustrated accurately by many authors. A summary is given below.

3.1 THE EGG

Abraham & Padmanaban (1968) describe the egg as minute yellowish-white (0.5 mm). Bartell (1966) describes it as pale yellow at oviposition, darkening as the embryo develops until shortly before eclosion when the dark head capsule and body of the larvae can be seen looped beneath the now transparent chorion. The surface of the chorion is finely sculptured with a pattern of small circular bosses but it is very thin and plastic and the egg rather delicate. The shape is flattened oval, some 0.51 mm (range 0.49-0.52 mm) in length and 0.27 mm (range 0.26 - 0.28 mm) in width. Harcourt (1956) describes it as oval, flattened, pale green to lemon-yellow, the surface embossed with a pattern of small, circular, raised areas, the larval outline visible before hatching. 0.44 mm length, 0.26 mm width in average. Hardy (1938) describes it as oval, light yellow with a sculptured surface, the colour disappears and embryo becomes visible before hatching. Length 0.8 mm approximately. Robertson (1939) describes it as oval, light yellow, the chorion embossed with a pattern of small, circular, raised areas; approximately 0.49 mm length, 0.26 mm width. Shaw (1959) describes it as oval, pale greenish yellow and about 1/64 in. (=0.40 mm). Ullyett (1947) describes it as small, oval, yellow.

3.2 THE LARVA.

Abraham & Padmanaban (1968) describe the newly hatched larva as pale-white with pale-brown head; the full grown larva about 10 mm long, light green, moderately stout, attenuated at each extremity, smooth, with short, scattered, bristly hairs. Harcourt (1956) describes it as subcylindrical and relatively hairless, with five pairs of prolegs; the body of the first instar entirely lacking in pigmentation except for patches, the head is dark brown; later instars similar to first but more pigmented spots on body, head capsule is lighter mottled with dark brown pigment; at the end of the final instar the body is greenish. Hardy (1938) describes the newly hatched larva as about 2 mm in length, 8-9 mm when full grown, bright green, but with variations such as red and yellow forms. Robertson (1939) gives the most detailed descriptions and illustrations of the larval stages, especially of the chaetotaxy : First instar: - Head width, 0.163 mm, very dark brown; body almost entirely lacking pigmentation; Second instar: - Head width, 0.264 mm; only distinguishable from first instar by microscopic examination; head very dark, body shows little trace of pigmentation; Third instar: - Head width, 0.378 mm, head colour very variable, body may appear pale green; Fourth instar: - Head width, 0.628 mm, light in colour, body more or less colourless but later light green, and later on is more intense, red pigments and dark pigments may develop. Shaw (1959) describes the young larva as grey with very noticeable small black head, the mature larva being light green, spindle shaped and about $\frac{1}{2}$ in. (=12.7 mm) long, head lighter than when young. Ullyett (1947) describes the newly hatched larva as small, green, about 2 mm long.

3.3 THE PREPUPA.

Harcourt (1956) affirms that there is no ecdysis between the last larval instar and this stage, the two differing only slightly in general appearance; the prepupa is more contracted in form, especially in the

region of the head and Thorax, and is pale green. Hardy (1938) mentions the prepupa as being the responsible for spinning the cocoon but does not describe it. Robertson (1939) again gives the most detailed description of the prepupae, he also affirms that there is no ecdysis marking the beginning of the prepupal stage; he describes it as having the head and three thoraxic segments drawn up closely, the Thorax increases in circumference, the abdomen decreases; from bright green changes to pinkish fawn; a cuticular covering is formed beneath the larval skin, which becomes loosened and can be removed without injury to the prepupa; all the chaetotaxy is described in detail (as in the larval stages); he suggests that the most noticeable features of the thorax are the wings which have become everted and lie external to the body; he also gives detailed illustrations. Ullyett (1947) affirms that the fully grown larva spins a cocoon in which it prepupates, but does not describe the prepupa.

3.4 THE PUPA.

Abraham & Padmanaban (1968) describe the pupa as about 6 mm long, inside a loose-mesh silken cocoon. Harcourt (1956) describes it as obtect, cephalic end rounded, body widest in thoracic region, and tapering toward the caudal segment, mouth parts clearly defined, mesothoracic wings long, average 7 mm long, pale green and becomes light fawn with brownish markings, enclosed in neat, open-network, silken cocoon open at both ends, last larval skin remains at anal end within cocoon. Hardy (1938) describes it as about 7 mm, light green or white later brown or black, loosely enclosed in fine net cocoon spun by the prepupa. Robertson (1939) gives the most detailed description of all; he describes it as light green, pinkish fawn or almost colourless, but almost black before emergence of the adult; obtected type, cephalic end rounded, body wides in thoracic region and tapers toward the caudal segment; he gives illustrations and shows the differentiation

in the sexes. Shaw (1959) describes it as enclosed within a fine net cocoon, light green but dark brown later. Ullyett (1947) describes it as green first, brown later, inside a delicate cocoon formed by a fine network of white, silken threads.

3.5 THE ADULT.

Abraham & Padmanaban (1968) describe the adult as having 14 mm of wing expanse, narrow wings with pale marks on them, when at rest appear together as diamond-shaped median dorsal patches. Harcourt (1956) describes it as small, slender, greyish-brown, wing expanse slightly more than $\frac{1}{2}$ in. (=12.7 mm) at rest forewings slightly upturned at the posterior end, creamy-yellow dorsal band with irregular black border and three ondulations, hind wings dark grey, females lighter in colour, markings less distinct. Hardy (1938) describes it as small, slender, greyish-brown, wing expanse about 10 mm, at rest wings slightly turned-up at rear end, creamy-yellow band with irregular black border and three ondulations; he also quotes Meyrick (1927) description as follows: "Length 11-16 mm, head ochreous-white, tuft of palpi long, forewings narrow, fuscous, more or less ochreous tinged, often with darker strigulae, towards costa paler and sometimes whitish-sprinkled, a paler or whitish-ochreous dorsal streak from the base of the tornus, upper edge whitish and thrice sinuate upwards, edged with darker suffusion, hind wings grey ". Robertson (1939) does not describe it but quotes the description of Hudson (1918) as follows (here summarized): "... wing expansion over $\frac{1}{2}$ in. (=12.7 mm). Antennae ringed with black near the middle and apex, forewings rather narrow, with apex acute in the male, and the termen oblique; brown often purplish-tinged, paler in the female; the male has a broad cream-coloured dorsal streak from base to near tornus, often edged with black towards disc; in the female this stripe much less distinct,

often merged in the general ground colour; there is a series of indistinct black dots below the costa and another series on the dorsum. The hind wings are grey."

4. LIFE HISTORY

4.1 INTRODUCTION.

The life history of P. xylostella has been studied in varying detail in most parts of the world, from the equatorial tropics to polar regions.

Some examples are: Atwal (1955) in Australia; Biever and Boldt (1971), Marsh (1917) and Miner (1947) in U.S.A.; Brethes (1923) in Argentina; Harcourt (1957) in Canada; Hardy (1938) in Great Britain; Hassanein (1958) in Egypt; Ho Thian Hua (1965) in Malaya; Kanervo (1936) in Finland; Khristovar (1957) in Bulgaria; Lee (1968) in Hong Kong; Moriuti (1956) in Japan; Reichardt (1919) in USSR; Ripper (1928) in Germany; Robertson (1939) in New Zealand; Ullyett (1947) in South Africa; and Vos (1953) in Indonesia.

In order to confirm the results of those investigators who worked in similar conditions to ours, a series of experiments to study the biology of this insect were done under constant temperature conditions; also some experiments were done under variable conditions which would indicate better what may be happening under field conditions.

4.2 MATERIALS AND METHODS.

4.2.1. The rooms.

The experiments were carried out in controlled environment rooms at a constant temperature of 20 $\pm$ 1°C and with 16 hours light (08.00 to 24.00) per day from six 125-watts fluorescent tubes,

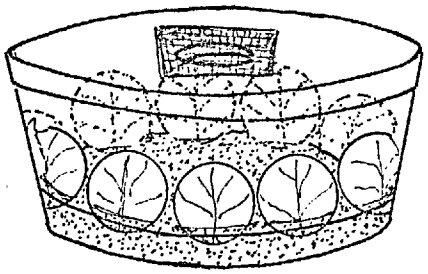
2.40 m long. Relative humidity was not controlled but remained between 44-52% during the day and up to 14% higher at night. This was because the refrigeration operated less often at night and so "froze out" less of the water transpired from the plants. As a means of comparison, as well as to have an idea of the possible variation which probably occurs under field conditions, observations were made in the laboratory under variable temperature from domestic-type central heating (average 20°C) and variable daylight coming through a glass window; to reduce the side-light effect, the cages were rotated 90° every day, and their position with respect to the window was changed. The relative humidity was not controlled.

4.2.2. The cages.

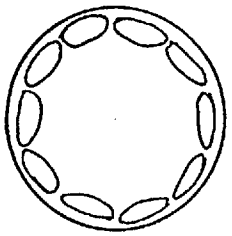
The cages used were circular transparent plastic boxes (9.5 cm bottom diameter, 10.5 cm top diameter, and 4.5 cm height) with transparent lids which had a 2.5cm hole in the centre, covered with terylene, to give ventilation. Inside the cages had a 5 mm layer of moistured silver sand to hold and provide water to the leaf discs (Fig.1 a).

4.2.3. The leaf discs.

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 (Fig.2), 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 (see fig.1b). Water was regularly added to the sand in order to keep the discs as fresh as possible.



a



b

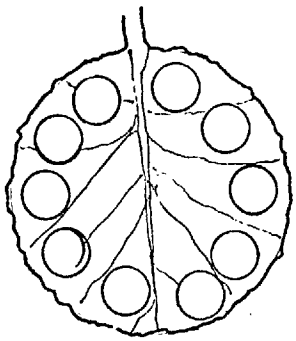


Fig. 1. (left). a. Circular cage with leaf discs inside.
b. Position of leaf discs inside the cages.

Fig. 2. (right) Distribution of discs in the leaf.

4.2.4. The experiments.

Adults were allowed to oviposit for short periods of about six hours; the date and number of eggs were recorded; also the date when hatched was recorded; this was the basis for estimation of the incubation period. For the larval developmental period, recently laid eggs were collected with a fine paint brush and placed on a moistured filter paper inside a plastic petri dish. Immediately the larvae hatched they were picked up with a fine paint brush and placed on the upper surface of the leaf discs as near to the centre of the disc as possible. Observations were made regularly, usually more than once in a day. Leaf discs were replaced when necessary but they were only removed when the larvae had moved onto the new ones.

4.3 RESULTS.

4.3.1. Developmental time.

The results obtained under both constant and variable conditions

are summarized in Table 4.3.1.

From Table 4.3.1 it can be seen that the total duration of the larval stages at constant and variable temperature was not significantly different. At 20°C constant temperature the total life duration was 41.4 days; with larval (first to fourth instar) duration of 12.7 days (12.6 days at variable temperature); larva and pre-pupa duration of 14.0 days (13.8 days at variable temperature), larva, pre-pupa and pupa duration of 21.2 days (23.1 at variable temperature). Therefore it seems that the main effect of the variable temperature was to increase the length of the pupal stage. The difference in the developmental time between constant and variable temperature was variable, being least for the first instar larvae and greatest for the pupae probably due to the few observations at the variable temperature. The mean developmental times were longer at constant temperature except in the fourth instar and pupa. The difference in the first instar was 0.040 days; in the second instar it was 0.389 days; in the third instar it was 0.166 days; in the fourth instar it was 0.500 days (longer at variable temperature); in the pre-pupae it was 0.136 days; and in the pupae it was 2.333 days. The variable conditions, perhaps, increased the rate of development.

4.3.2. Longevity and Fecundity.

Longevity and fecundity were studied in the constant temperature conditions (20°C) described above. The results given below form part of a series of experiments on the effects of density on P. xylostella and the details of the materials and methods used are given in the corresponding chapter.

Table 4.3.1. - Life Cycle

Stage	Constant Temperature (20°C)			Variable Temperature ($\bar{x}$ = 20°C)		
	Number observations	Range (days)	Time in days (mean ± standard error)	Number observations	Range (days)	Time in days (mean ± standard error)
Egg	349	3-5	3.19 ± 0.02			
Larva 1st instar	46	2.5-6	3.71 ± 0.11	18	3-5	3.67 ± 0.16
Larva 2nd instar	46	2-5	3.07 ± 0.17	17	2-3.5	2.68 ± 0.12
Larva 3rd instar	41	2-4	3.20 ± 0.14	17	2-4.5	3.03 ± 0.21
Larva 4th instar	38	1-6	2.75 ± 0.20	16	2.5-5	3.25 ± 0.19
Pre-pupa	37	1-2	1.32 ± 0.11	16	1-2	1.19 ± 0.10
Pupa	6	7	7.00 ± 0.00	3	9-10	9.33 ± 0.33
Adult	30	5-26	17.13 ± 1.18			

The longevity was recorded in mated females only, and there was a great difference between those which were kept in the presence of the host plant (i.e. a piece of cabbage leaf inside the oviposition cage) and those kept in its absence. Those kept in the presence of the host plant lived for a maximum of sixteen days, those kept in its absence lived for twenty-eight days (almost twice as long) (Fig. 3). This difference may be because females, in the presence of the host plant, laid more eggs than in its absence and therefore deteriorated more quickly, having fulfilled their biological function.

Fecundity was recorded in terms of eggs laid daily (figs. 4 and 5). The adults were paired on the day of emergence and normally the females started to lay within twenty-four hours although, in the absence of host plant, there was a pre-oviposition period of one day in a few females. The maximum number of eggs laid by one female in any day was fifty six in the absence and eighty six in the presence of the host plant. The females generally laid until the day they died, although those kept in the absence of host plant laid no eggs at all for up to ten days and then began laying, sometimes laying more than they did previous to the 'resting' period (Fig. 5). This is no doubt due to behavioural rejection by the female in absence of the host plant, but later it was forced to oviposit as eggs accumulated inside.

The average number of eggs/female laid in the absence of host plant was 162.9 compared with 246.4 in the presence of the host plant (Table 4.3.2).

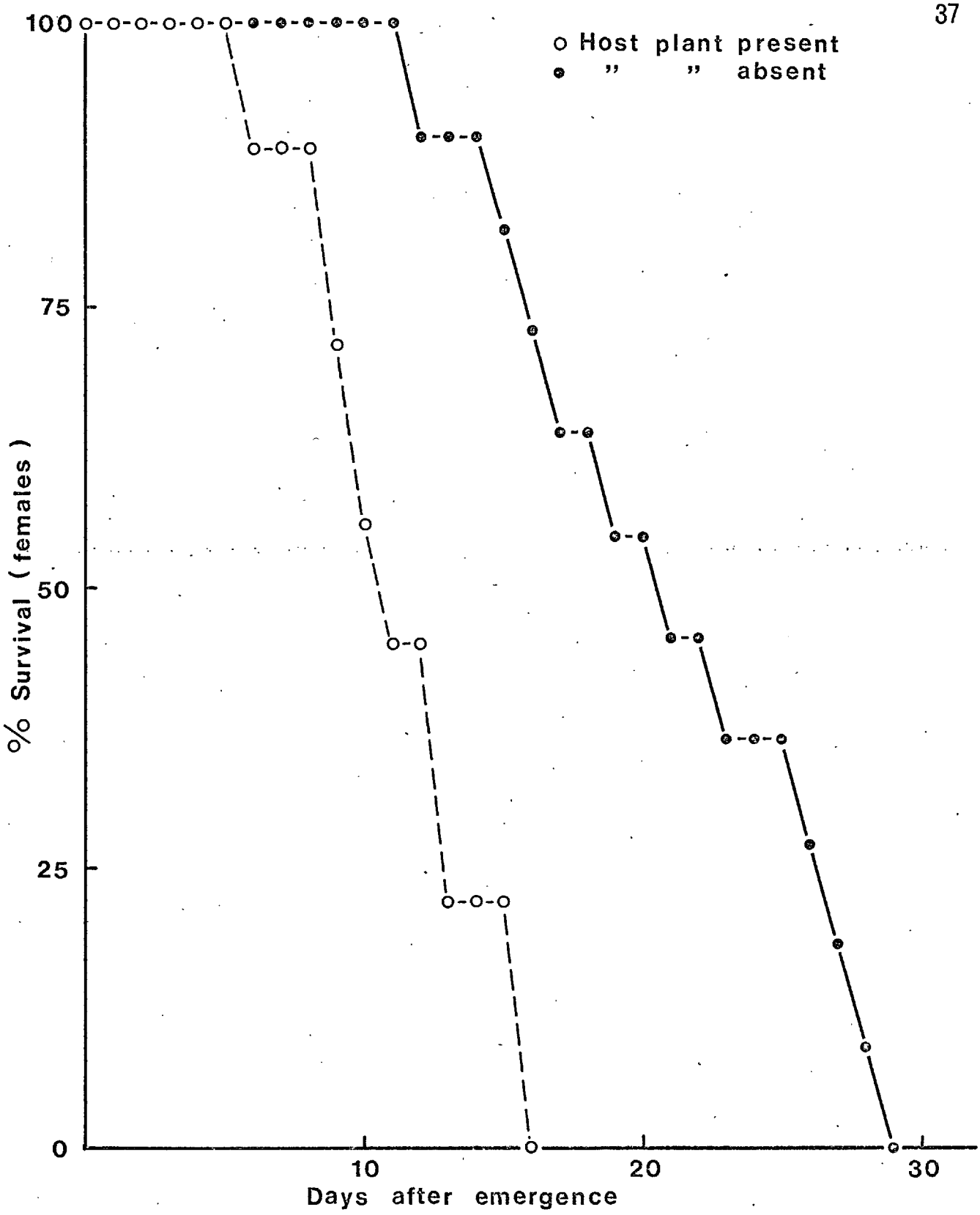


Fig. 3. Adult (females) longevity

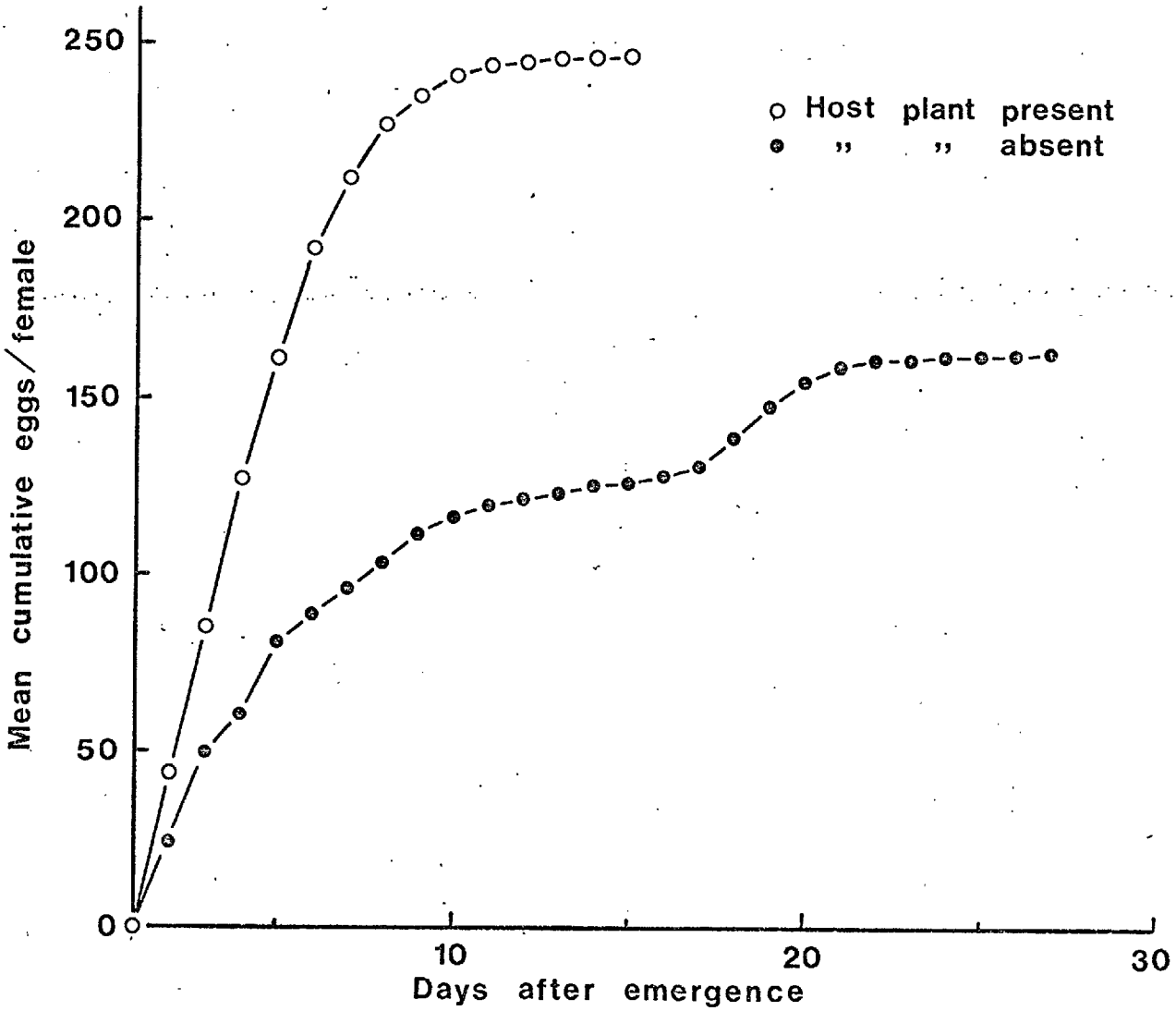


Fig. 4. Fecundity (mean cumulative number of eggs per female).

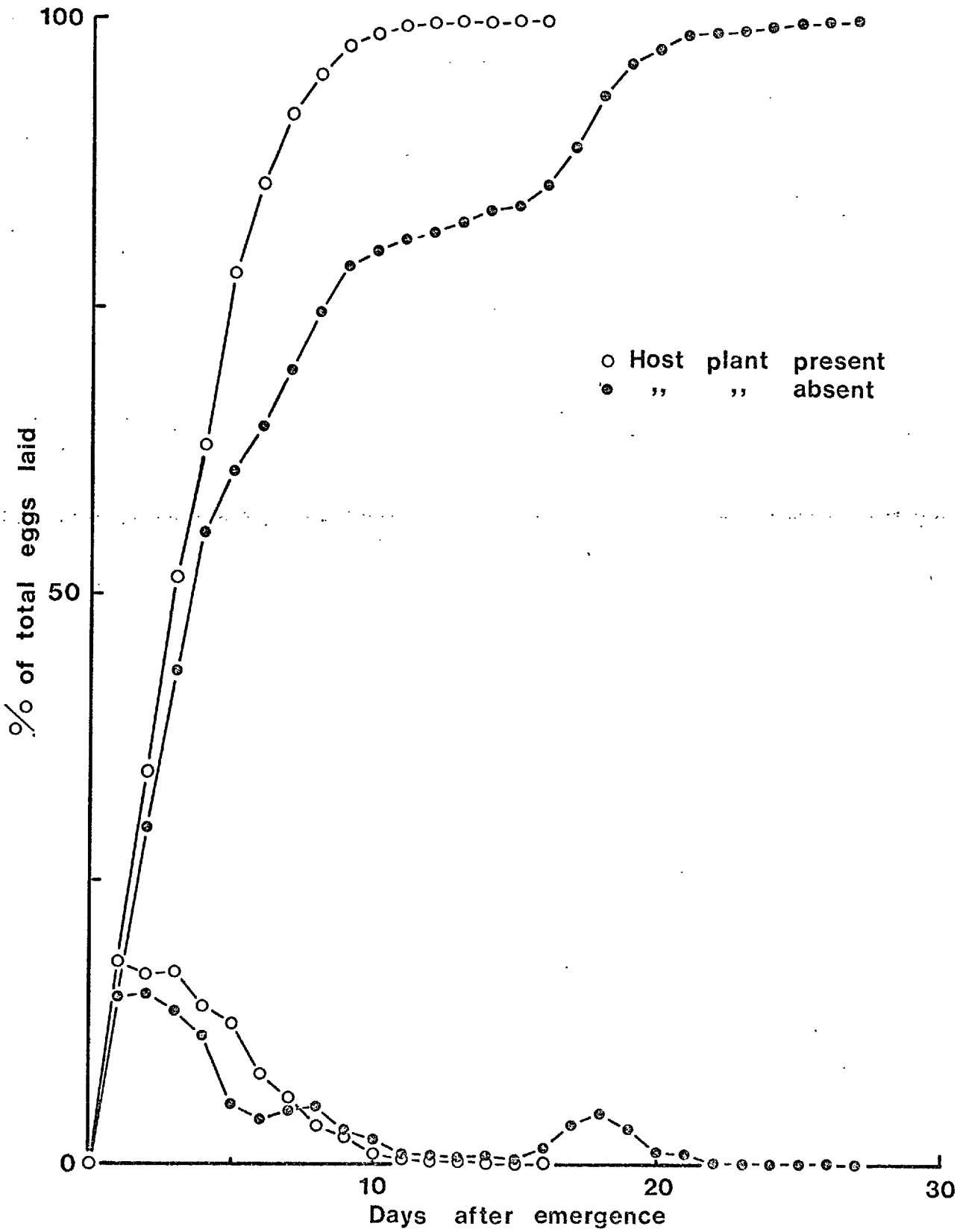


Fig. 5. Oviposition pattern (daily and cumulative).

Table 4.3.2. - Longevity and fecundity

	Number observed	Mean + (Range) oviposition period (days)	Mean longevity (days)	Eggs/female (Mean ± S.E.)
Females in presence of host	8	11.3 (7-16)	11.4 (8-16)	246.4 ± 29.9
Females in absence of host	11	18.6 (5-27)	19.7 (11-27)	162.9 ± 11.2

As stated above no significant pre-oviposition period was found, in contrast to Hillyer & Thorsteinson (1969) who found a mean pre-oviposition period of 4.2 days for mated females and 8.6 days for virgin ones. They also found that, of sixty seven freshly emerged females, only nine contained eggs, the rest had only immature oocytes in the ovaries. In the present study virgin females were dissected within a few hours after emergence. The ovaries were all normally developed and contained mature eggs, immature eggs and oocytes. It is difficult to differenciate the oocytes in the last section of the ovarioles, about 1.00 mm length, therefore they were not counted. The mean number of recognisable oocytes contained in the four ovarioles of each ovary of newly emerged females were:

Right ovary: 123 eggs + oocytes
Left ovary: 131 " "
Total: 254 " "

4.4 DISCUSSION.

Table 4.3.3 compares the life cycle of P. xylostella recorded by others under different conditions with those obtained under the present investigations at Silwood Park. As it can be seen the date are from countries, both temperate and tropical, throughout the world.

Some other data, not included in Table 4.3.3, but of interest for comparison are those of Given (1941) in New Zealand who found that in the laboratory the mean duration of the larva was 10.5 days, and the maximum duration of the adults was 108 days. Hillyer & Thorsteinson (1969) working in laboratory conditions in Canada found the mean duration of the pre-oviposition period in mated females to be 4.2 days with fecundity of 148.9 $\pm$ 32.0 eggs per female, and in the virgin females the mean pre-oviposition period was 8.6 days with 79.0 $\pm$ 15.9 eggs per female. Shaw (1959) found that in field conditions in Scotland (Great Britain) the larval stage took 21 days and the total life cycle 42 to 49 days. Way et al. (1951) found that in laboratory conditions (24°C) in Great Britain the maximum number of eggs laid by the females was 391.

Finally, from Table 4.3.3 it can be clearly seen that P. xylostella has a high degree of adaptation to different climatic conditions and also that temperature is the climatic factor most important in the development of this insect, especially in the development of the larval stage. This is very important for the species since it enables it to tolerate a wide range of temperature conditions characteristic of its wide distribution in different latitudes.

Table 4.3.3. - Life Cycles in different countries.

Author & Country	Abrah. &Prad. 1968 India	Atwal 1955 Australia	Biever & Boldt 1971 U.S.A.	Harcourt 1957 Canada	Hardy 1938 Gt.Britain	Hassanein 1958 Egypt	Ho Thian Hua 1965 Malaya		Kristova 1957 Bulgaria	Lee 1968 Hong Kong	Robertson 1939 New Zealand	Stepanova 1962 Leningrad	Ullyett 1947 South Africa	Vos 1953 Indonesia	Salinas 1972 Gt.Britain
Temperature Rel.Humidity		20°C	23±1°C 60±5%	Field	20°C	Field	Highland	Lowland	Average 25°C	Lab.(?)	Average 17.5	20°C	Field	Highl. (16-25°C) Lowl. (25-30°C)	20 ±1°C 44-52%
Egg	3-6		3	4-8 Mean: 5.6	4.5		6.2	2.0		2-8			(incl. in the data below		3.2
Larva 1st instar				3-7 4.5			3.4	1.4			4				3.7
2nd instar				2-7 4.0			3.1	1.0			2-4				3.1
3rd instar				2-8 4.1			2.2	1.2			3-5				3.2
4th instar				2-10 4.9			5.2	2.0			2-6				2.8
Total larva	14-21	10.6	11	9-30 17.5	10.5	10.4-29.7	13.8		8-11	13-16	12-17	23	Summer: 14 Winter: 18-21	Highl.: 21 Lowl.: 15	
Pre-pupa											(incl. in Liv: 1.5-2)				1.3
Pupa.	7-11	7.3	5	5-15 8.5	8.0		7	3.2		6-11					7.0
Adult ♂	6-13		(26±1°C) 7.7	3-58 12.1	14-28	6.3-15.4	16.5-23.9								
Adult ♀		max. 20	8.1	7-47 16.2		5.7-10.3	15.4-21.1				11-28				5-28 17.1
Pre-Ovipos.				0						1-2					
Oviposition			max. 14	6.4-15.1 10.3	13		12-18								
Peak Ovipos.			3	1			1-3								
Eggs/		max. 264±26.8	55-226 mean:139	18-356 159	69-248	92-364	81-379				87-427		max. about 300		95-602 246.4±2
Total Life-cycle	30-51		27	47.8	32-50		46.2			22-37 Mean:29.5					23.5-61.0 41.4

5. BEHAVIOUR

5.1 INTRODUCTION.

In normal field conditions, even at high densities, the larvae, especially the last instars, have a pattern of distribution whereby they seem to avoid direct contact and hence keep distinct feeding 'territories'.

From the statistical analysis of the distribution of the larvae under different densities and at different ages (see Chapter on Dispersion) it can be seen 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 very 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 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 objective was to determine:

a. how the larvae distribute themselves throughout the leaves of a plant (Dispersion).

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.

Five examples of the detailed behaviour of the larvae at low densities are given below. These examples are representatives of different situations commonly found in the field. After the detailed account of larval behaviour a general summary of the behaviour of all the stages is given.

5.2 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, the leaf discs and the set-up of the experiments were similar to those previously described.

The leaf discs were distributed and numbered inside the cages in the same disposition in which they were in the leaf (Fig. 6a). Each leaf disc was divided (not actually marked) into sixteen quadrats numbered from left to right and from top to bottom (Fig. 6b).

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.

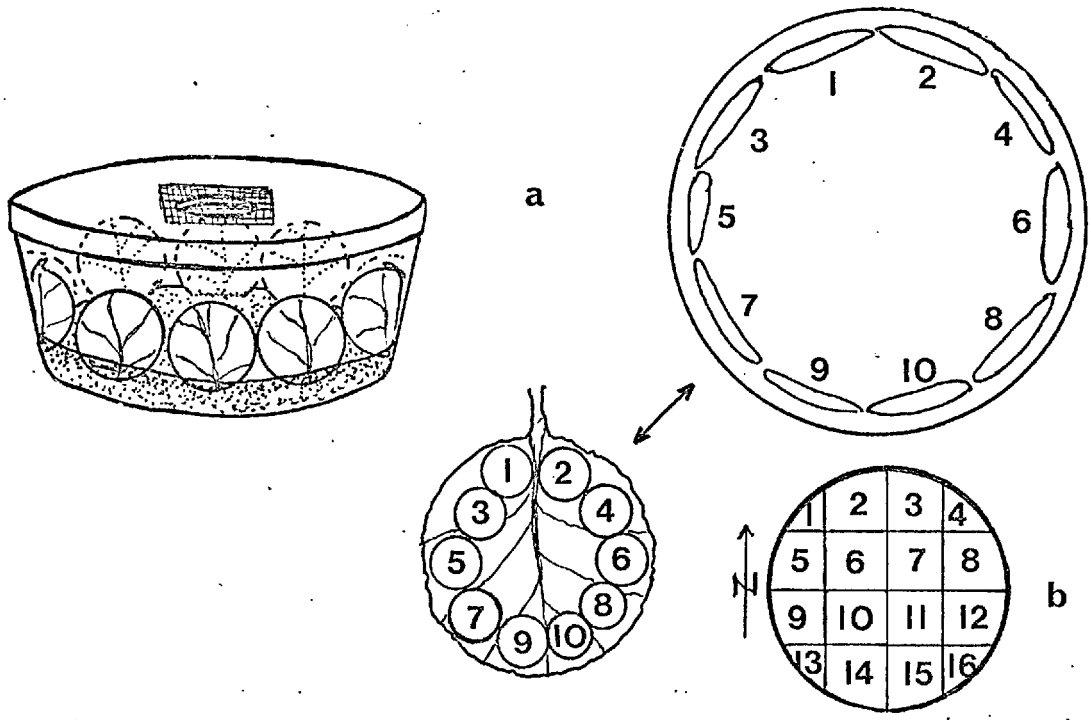


Fig.6. a. Position of leaf discs in the cage and in the leaf.
b. Division of leaf disc in 16 quadrats. Arrow points to the North referred to in the text.

5.3 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 plants 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, distance from egg to 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.

5.4 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 put 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 then 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 larvae to get easily out of the egg shell.

5.5 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. A detailed account of the behaviour of the recently hatched larvae as well as that of the different instars of the larvae is given in Appendix 1 (pp. 279-307).

Those 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 cine-camera, 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).

5.5.1. 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 lasts from two or three seconds to $\frac{1}{2}$ 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 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 behaviour 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 those 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.

5.5.2. First instar.

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 (Harcourt, 1957). 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 abdominal tip is out of the entrance 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, 1957) 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 'making' 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 of the gallery, and 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

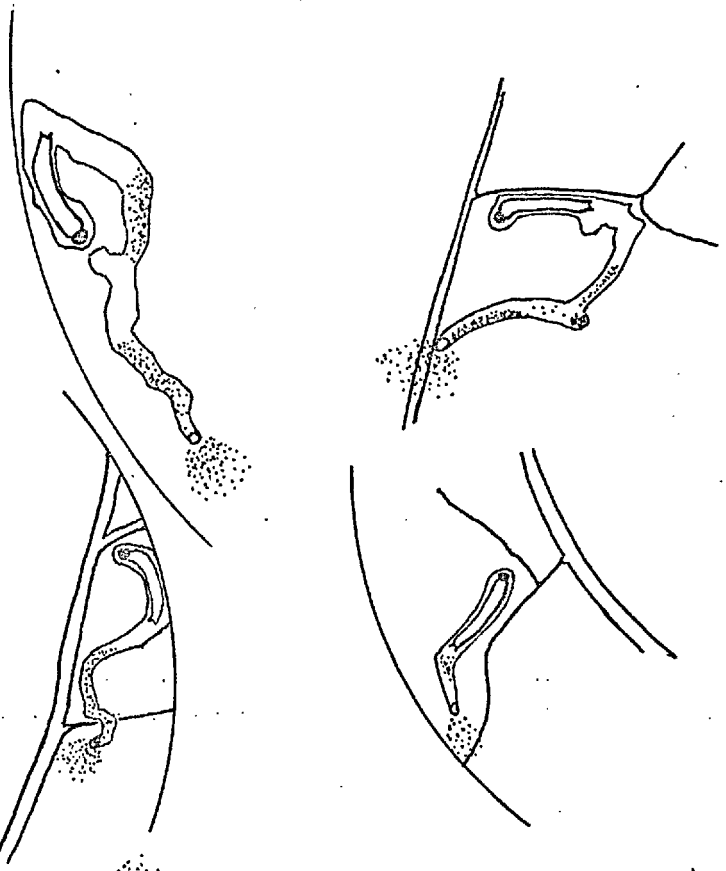


Fig. 11

Fig. 12

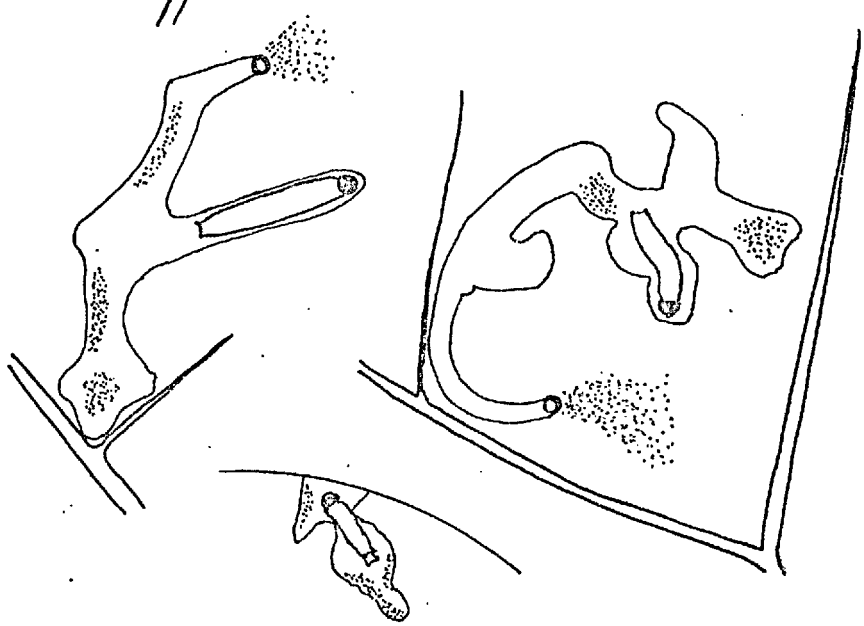


Fig. 13

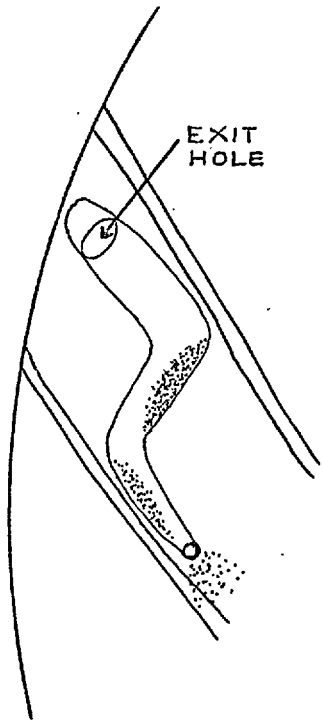


Fig. 14

Fig. 11. Gallery showing faecal deposition.
Fig. 12. Change of direction of gallery after meeting unsuitable leaf tissue.
Fig. 13. Reverse gallery-making after meeting unsuitable leaf tissue.
Fig. 14. Gallery showing exit hole.

deposits (Fig. 11).

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 (Fig. 12). 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 (Fig. 13). Most commonly it makes a hole at the end of the gallery and goes out to make a new gallery (Fig. 14). If there are two or more larvae in a small leaf (10 cm^2 or less), when they meet they may reverse and crawl in different directions, but commonly they tend to stay together either in the same hole (Fig. 9b) or in different holes (Fig. 9a). 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.

5. 5. 3 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 of 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.

5.5.4. 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.

5.5.5. 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 fourth 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.

5.5.6. 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 it 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.

5.5.7. 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.

5.6 '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 epidermis. 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 (Fig. 15).

In general, the larva may have means of detecting any change in the condition of the leaf tissue. Thorsteinson (1953, 1960) 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 (Thorsteinson, 1960), and the anatomical disposition of the cells in the leaf, as was demonstrated by Rudder and Brett (1967) for varieties of Kale (loosely arranged cells and abundance of air space in susceptible varieties, and densely compact cells without air space in those resistant. The chemical factors are discussed in detail by Thorsteinson (1960) and Gupta and Thorsteinson (1960).

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 whether it is its own gallery (Fig. 16); also it will change the direction of the gallery to avoid areas where changes in the leaf tissue have occurred (Fig. 16). 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 (Fig. 17). 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 (Fig. 18), or when the leaf toughness changes near the edges of the leaf (Fig. 19).

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 dispersion of 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 then 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

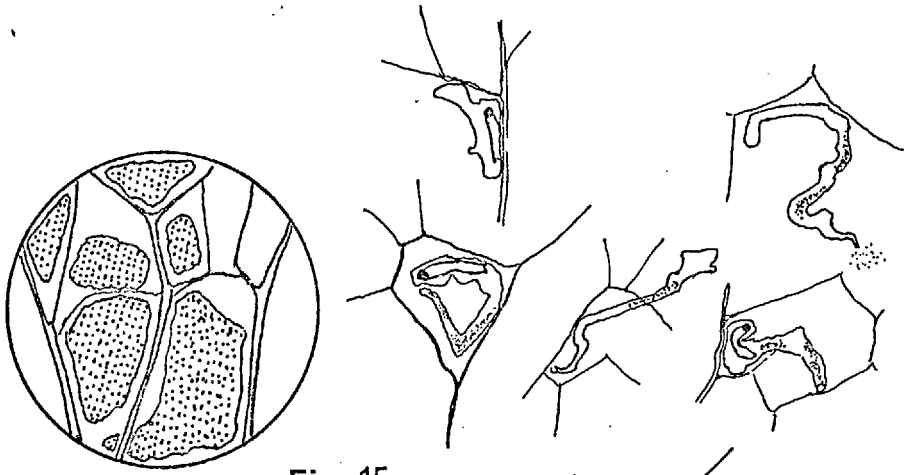


Fig. 15



Fig. 17

Fig. 16

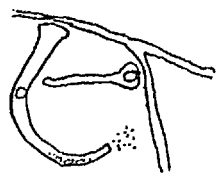


Fig. 18

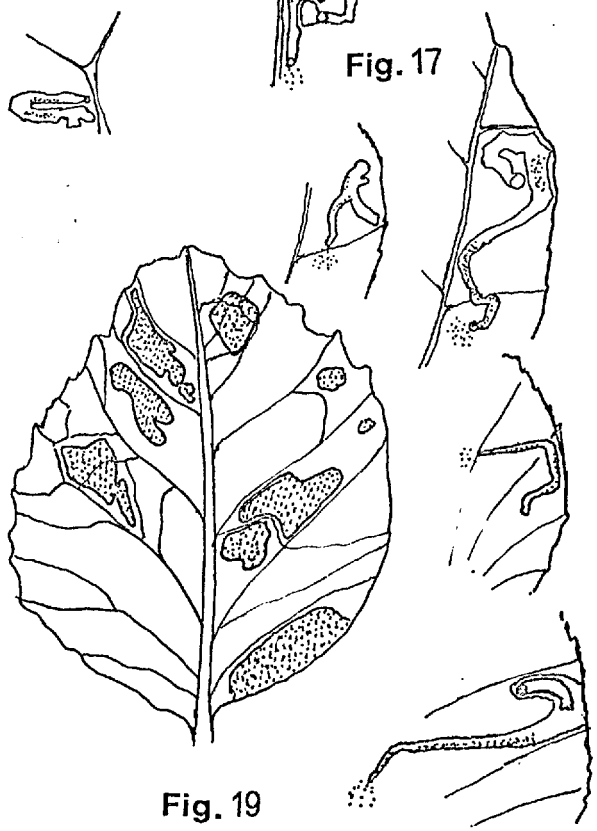


Fig. 19

Fig. 15 to 18. Shape of galleries and holes given by veins.
Fig. 19. Change of direction of galleries and holes near the edge of the leaf.

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.

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 larva 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 population 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.

6. EFFECTS OF THE SIZE AND SHAPE OF THE LEAVES, AND OF THE DENSITY OF THE LARVAE ON THE BEHAVIOUR, DISPERSION AND SURVIVAL OF *P. xylostella*.

6.1 INTRODUCTION.

Some experiments were made in order to determine the effect of the size and shape of the leaf on the behaviour, dispersion and survival of the larvae, especially the young ones, at different densities. Comparisons were made of behaviour of those larvae kept on whole plants and on leaf discs.

6.2 MATERIALS AND METHODS.

Rectangles of the following dimensions were cut from tender leaves of young cabbage plants.

5.0	x	2.0	cm
5.0	x	1.0	"
5.0	x	0.5	"
2.5	x	1.0	"
2.5	x	0.5	"
1.25	x	1.0	"
1.25	x	0.5	"

The rectangles were placed in circular plastic cages (10.0 cm diameter x 4.5 cm height), already described. The part corresponding to the bottom of the leaf was inserted about 1 to 2 mm in the wet sand to provide constant flow of water inside the leaf tissue. Recently hatched larvae were placed in the centre of each leaf rectangle, at the following densities:

1	larva	per	rectangle
2	"	"	"
4	"	"	"
8	"	"	"
16	"	"	"
32	"	"	"

6.3 RESULTS.

6.3.1 EFFECTS ON LARVAL BEHAVIOUR, DEVELOPMENT, AND MORTALITY.

6.3.1.1. Gallery making stage.

1 larvae per rectangle. - The larvae reared singly in the different rectangles did not show any noticeable difference from single larvae on leaf discs or on whole leaves. The larva followed the general pattern of behaviour already described which includes wandering, spinning, 'sensing', and biting the leaf surface, until it made a hole and eventually a gallery. Again the larva avoided, as generally happens, to eat through: thick veins, the borders of the rectangles, and its own previously made gallery. In the rectangles 0.5 cm wide, the galleries were obviously more irregular in direction because the distance between the side borders is shorter

and the larva was compelled to turn its gallery more often.

2 larvae per rectangle. - The larvae in pairs per rectangle did not show any detectable difference from those at similar number per leaf disc or per whole leaf. The galleries in the 0.5 cm wide rectangles were more irregular than those in 1.0 cm wide rectangles because the distance between borders is shorter. The result in narrow rectangles is a series of irregularly directed mines very often shorter than normal (Fig.20). Also if a thick vein is across the leaf rectangle the larvae will most probably make all the galleries on only one sector of the rectangle, avoiding crossing the thick vein (Fig.20).

4 larvae per rectangle. - When the density was increased to 4 larvae/rectangle the behaviour of the larvae changed. They became more active in making holes and it can be clearly seen in Table 6.3.1 that only 15 hours after hatching the mean number of holes increased from the usual one gallery per larva which is expected under low density to over ten galleries / larva in the smallest rectangles. This increase in the number of galleries is most probably due to mutual disturbance during the critical stage of starting the galleries and perhaps after gallery formation. In the smallest rectangle most of the feeding places counted were punctures and very few were galleries.

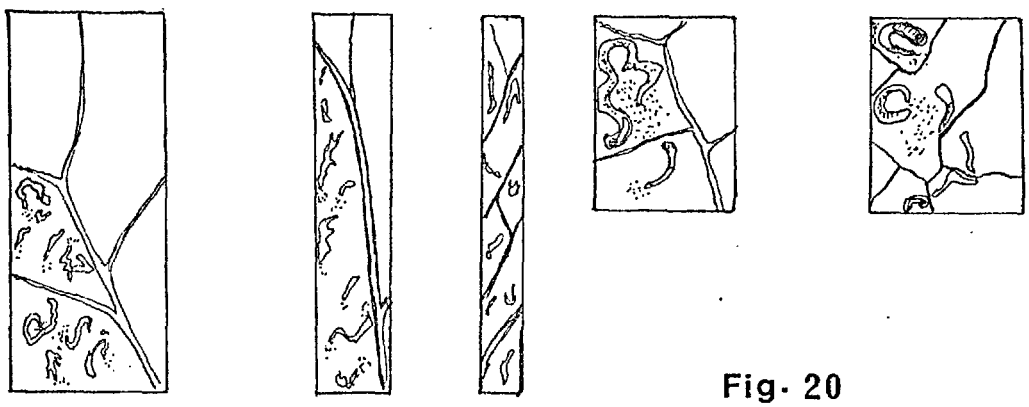


Fig. 20

Fig.20. Larvae feeding on one side of leaf. Avoiding thick veins.

Table 6.3.1 - Mean number of feeding places per larva. 15-18 hours from time of hatching.

	Size of leaf rectangle (cm)						
Larvae/ rectangle	5x2.0	5x1.0	5x0.5	2.5x1.0	2.5x0.5	1.25x1.0	1.25x0.5
1	1.0	1.0	1.0	2.0	3.0	1.0	1.0
2	1.0	1.0	1.0	1.0	1.0	1.0	1.0
4	4.3	5.0	3.8	3.8	6.3	10.8	10.0

6.3.1.2. Developmental time (including pre-pupation).

Table 6.3.2 - Larval developmental times (days) and mortalities (%).

	Number of larvae per rectangle				
	1	2	4	8	32
Mean No. days	14.8	14.2	11.6	16.8	16.3
Mortality of Larvae (%)	28.6	14.3	50.0	91.1	92.9

From Table 6.3.2 it can be clearly seen that at densities of one and two larvae per rectangle the times taken by the larvae to develop were 14.8 and 14.2 days respectively. When the density was increased to four larvae per rectangle the developmental time was reduced to only 11.6 days. This reduction in the period development can be regarded as

as beneficial for the insect since it can reach the pupal stage in a shorter period of time if food is likely to be in short supply.

The times for the larval stage increased to 16.8 and 16.3 days at densities of 8 and 32 larvae per rectangle. This can be interpreted in terms of optimum density of larvae per unit of available space or habitat, in other words it can be said that the larvae may require a certain stimulus which is provided by the presence or contact with other larvae but which has a limit, and when that limit is exceeded the effect is detrimental to the development of the larvae. Densities of one or two larvae per rectangle may be inadequate for the optimum stimulation, but at four larvae per rectangle the rate of development was at an optimum, but increases above densities caused the development period to be prolonged.

6.3.1.3. Larval mortality.

From Table 6.3.2 it can be seen that the mortality of the larvae was higher at the density of one larva per rectangle (28.5%) in comparison with that of two larvae per rectangle (14.3%). This may be insignificant but may also be a consequence of the suggestion that a mutual beneficial stimulus is provided by the larvae. In this case the stimulus may be necessary from the beginning of the larval life, since the mortality of the isolated larvae occurred during the first instar. When the density was increased to more than two larvae per rectangle the mortality increased rapidly, so less than 10% of the larvae survived at the higher densities.

6.3.2 EFFECTS ON SIZE AND WEIGHT OF PUPAE AND WEIGHT OF ADULTS.

Table 6.3.3. - Length (mm) and weight (mg) of pupae, and weight (mg) of adults.

	No. of larvae per rectangle			
	1	2	4	32
Mean pupal length (mm)	6.0	6.2	5.9	5.3
Mean pupal weight (mg)	5.9	6.0	5.6	4.9
Mean adult weight (mg)	3.5	4.0	3.4	2.7

Table 6.3.3 shows that the density of the larvae had a great effect on the size and weight of the pupae and adults. The mean size of the pupae was greater from larvae reared at low densities but the pupae and adults reared singly were a little smaller than those reared at 2 larvae/rectangle. This supports the suggestion made above that the larvae need the presence of some other larvae for optimum development. The density of 4 larvae/rectangle can be considered to have a negative effect when the number of feeding places of early stages are counted and also when the mortality is calculated; however it had a favourable effect on the pupal size and weight and also on the adult weight (Table 6.3.3). This supports the results obtained for developmental time and suggests that at this density the larvae tend not only to feed faster but to utilise better the food consumed, which eventually results in larger size and

higher weight of the pupae and adults. However there was a nullifying effect expressed as an increase in larval mortality with the increase in density.

The size and weight of the pupae are positively correlated in both sexes as it is shown in Fig.21. In all cases there was a high significance of the regression coefficient (Table 6.3.4).

The fecundity of the adults is also positively correlated with the weight (Hillyer & Thorsteinson, 1969), therefore the pupal size or weight can be used as an index of the fecundity.

Finally it can be said that any increase in fecundity combined with a shorter period of development is probably of importance in the preservation of the species.

Table 6.3.4. - Correlations between length and weight of pupae and adults.

Pupae	Length (mm)		Weight (mg)		b	Sb	t=b/Sb	r
	Range	$\bar{x}$	Range	$\bar{y}$				
Males	4.96-6.80	5.94	3.4 - 8.3	5.80	2.3274	0.1654	14.071**	0.8744
Females	5.36 - 7.20	6.09	5.3 - 9.8	6.65	2.6625	0.1765	15.084**	0.8880
Males (semi-starved)	4.72 - 6.40	5.74	3.2 - 7.6	5.50	0.7752	0.0819	9.465**	0.8248
Females (semi-starved)	4.64 - 6.92	5.86	3.7 - 9.6	6.00	0.8168	0.0949	8.607**	0.8313
Adults	Pupal length		Adult weight					
Males (semi-starved)	4.72 - 6.40	5.84	1.7 - 4.8	3.23	0.4113	0.0959	4.289**	0.6591
Females (semi-starved)	4.92 - 6.92	6.08	2.4 - 7.1	4.40	0.7874	0.1502	5.242**	0.7452

** $P < 0.01$

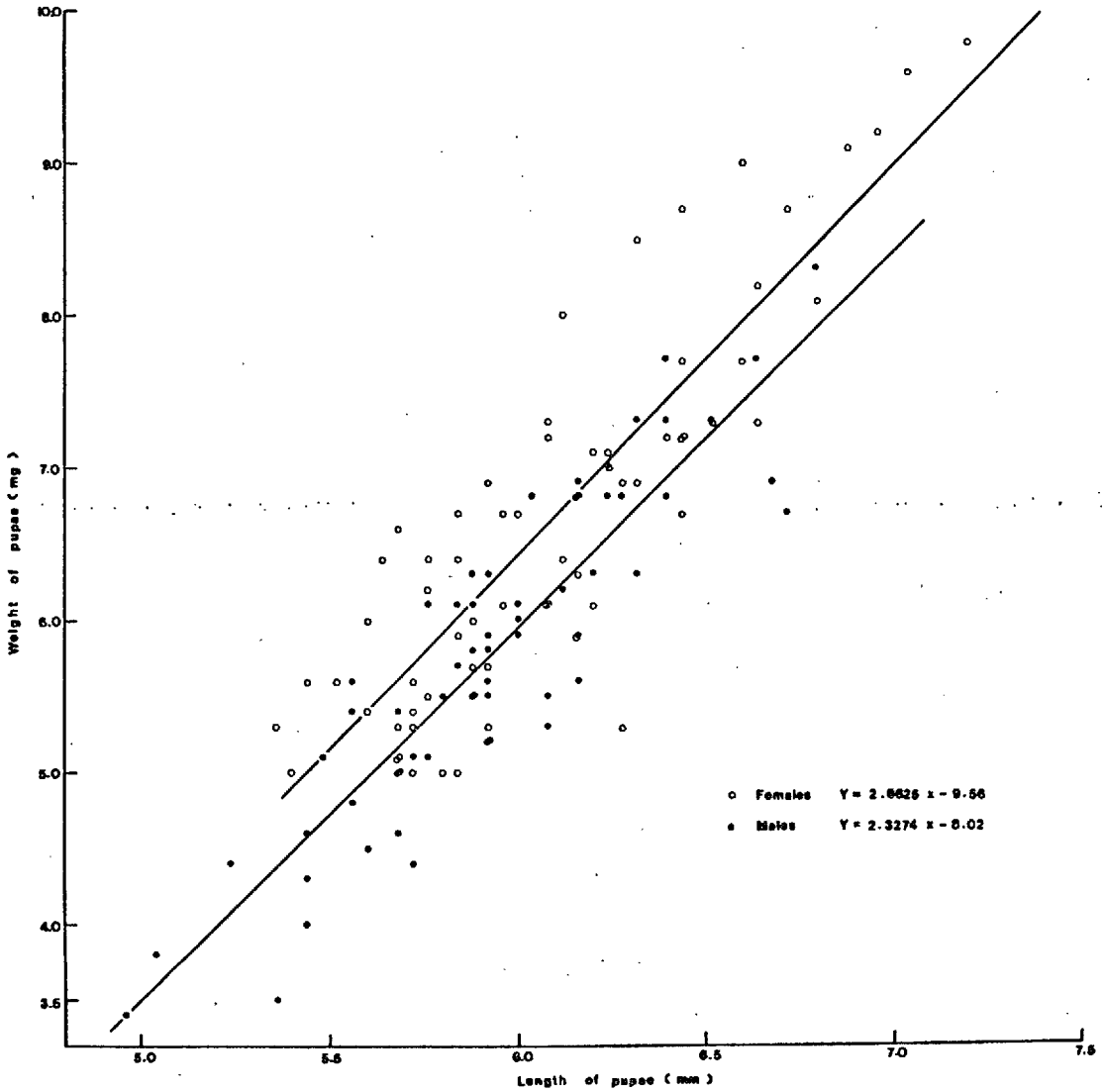


Fig. 21. Correlations of weight and length of pupae.

6.4 DISCUSSION.

Summarizing it can be said that the size and shape of the leaf has a certain influence on the behaviour of the larvae. The size seems to be more important than the shape since the larvae, in any stage, require a certain amount of space to move (even at the gallery-making stage).

In relation to the shape of the leaf it seems that the narrower the leaf the more unsuitable it becomes for the larvae, since the distance between borders (which are usually unsuitable) is reduced.

The density of the larvae is probably the most important of the factors studied. For example there was a correlation between the number of larvae and the number of feeding punctures and galleries made by the larvae. At low densities there was a low number of punctures but with an increase in the number of larvae (from 2 to 4 larvae/leaf) the mean number of feeding places increased 4 to 10 times depending on the size of the leaf; however further increases of the number of larvae did not result in a direct increase of the number of feeding places because the disturbance was so high that many larvae died before they could actually make a mine.

The mortality was in general positively correlated to the number of larvae and negatively correlated to the size of the leaf, i.e. the higher the number of larvae the higher the mortality, and the smaller the leaf the higher the mortality.

The density also had an influence on the time required by the larva to develop into a pupa, although the number of larvae per leaf seems to be more important than the actual size of the leaf. This is illustrated by the fact that the increase of developmental time when the size of leaf decreased was insignificant. The decrease in time of development for 4 larvae/leaf may suggest an optimum density since further

increases in density resulted in longer developmental time.

The size and weight of the pupae as well as the weight of the adults was inversely related to both the density of the larvae and the size of the leaf. The higher the density (either higher number of larvae or smaller size of leaf) the smaller the size and weight of the pupae as well as the weight of the adults. As these two are related to the fecundity it can be deduced that the higher the density the lower the fecundity. This effect of density on fecundity and also on developmental time are very important in the maintenance of populations and therefore in the preservation of the species since a short generation time with highly fecund individuals under favourable conditions may lead to higher populations, and vice-versa, long generation time with poorly fecund individuals even in favourable conditions will tend to low populations.

7. BEHAVIOUR OF THE LARVAE UNDER STARVATION (THIRD AND FOURTH INSTARS)

When the larvae are subjected to starvation some physiological and behavioural changes occur. The changes in physiology are not going to be discussed. Changes in the behaviour may be drastic. The larvae become aggressive and irritable, being disturbed by any slight nearby movement. The individual larva normally reacts to the disturbance by moving away and, if another touches it, both larvae crawl away in different directions. When the contact is strong they do very rapid twitching movements of the thorax and/or abdomen. In some cases the twitching movements are made so rapidly that the whole larva is displaced from its initial place. In some extreme cases of starvation the larva may acquire cannibalistic tendences and if a weakened larva is found by a stronger one, the normal biting associated with their encounter changes into the stronger larvae feeding on the weak one. This cannibalistic behaviour has apparently not been reported before. A description of such behaviour is as follows:

One 3rd-instar larva from a group of starved larvae was moulting into 4th-instar on the wall of a cage. Probably due to starvation conditions, the cuticle of the last abdominal segment did not separate from the newly moulted larva, thus sticking it to the exuvia which in turn adhered to the cage wall. The larva was struggling in an attempt to get free. Another 4th-instar larva arrived and started

to bite the penultimate abdominal segment of the larva which was stuck. Despite the very strong movement of the 'attacked' larva, the 'aggressor' continued to bite until it made a hole on the dorsal part of the abdominal segment through which the haemolymph started to flow out. The attacked larva did not cease to struggle in an unsuccessful effort to escape from the continuous biting of the aggressor larva, which was feeding on the fluid coming out of it (Fig. 22). After the haemolymph came a semi-liquid green material, probably part of the gut contents. The process had now taken 30 minutes. The aggressor larva stopped for about one minute, and then moved to the frontal part of the attacked larva where it started to bite its thorax. The attacked larva still struggled. The aggressor stopped and moved away for about one minute, then returned to bite on the abdominal segments. The attacked larva still struggled. The aggressor larva continued eating at the abdomen of the attacked larva. At this stage the following change of behaviour was observed in the aggressor : every time the attacked larva struggled, the aggressor became more aggressive and made very rapid attacks in the form of a series of bites all over the abdomen, biting any part of the abdomen that it grasped. By this time about 45 minutes had passed. Once the aggressor had eaten most of the flowing green material from the body of the attacked larva, it started to eat the right pleura of the 4th-abdominal segment. The attacked larva now did not struggle but just moved the anterior part of the body. The aggressor passed to feed on the thorax. One hour after the attack started the aggressor was eating the thorax and trying unsuccessfully to bite the head capsule of the prey. Then the aggressor moved again to the abdomen and made a hole on the ventral side of the last abdominal segment. It continued eating for half an hour more and then stopped. The attacked larva now almost empty of body contents was motionless. Five minutes later the aggressor started to eat again

at the last abdominal segment of the attacked larva and in about five minutes it ate all the cuticle of that segment, including the prolegs. Then, 1 hour 45 minutes from the beginning, the aggressor started to eat and rest for alternating periods of about 3 to 5 minutes. Next morning (it was not observed during the night) all the attacked larva had been eaten. There was nothing left, not even the head capsule.

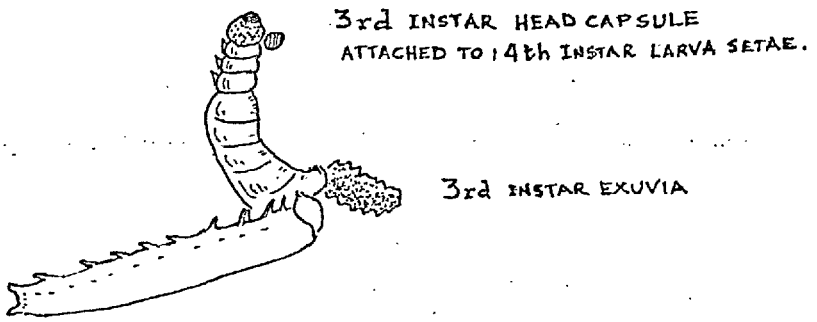


Fig. 22. Cannibalism induced by starvation.

8. ADULT BEHAVIOUR

8.1 NORMAL BEHAVIOUR.

The adult (in cages under constant environment rooms) emerges from the cocoon and immediately places itself in a vertical position with the head upwards on a leaf vein or on the stem of a plant; the expansion of the wings starts by the adult extending them downwards. The resting position is typically horizontal with the body all at the same level and the antennae directed backwards and practically lying on the wings. The 'alert' position is with the frontal part of the body raised, the tip of the wings on the leaf (due to the inclination of the body), and the antennae moving as if 'sensing' the air. The adult generally 'rests' on a leaf, near the petiole or on the lower surface, and when disturbed it invariably flies towards the lighted area of the cage. A few hours after emergence the adult is in a condition to mate and it usually does provided that there are adults of the opposite sex!

8.2 MATING BEHAVIOUR.

Observations were made in constant environment conditions as described, and in cages (36 x 36 x 36 cm) with the sides covered with muslin and the top and front made of transparent perspex. Inside the cage a pot with a young cabbage plant was introduced and also several adults of both sexes, recently emerged.



Fig. 23. Male and female in copula.

The adults went to the cage walls or the leaves of the plant. The female seemingly releases a sex pheromone hitherto unreported for Plutella. If the sex pheromone is perceived by a male it immediately moves towards the place where the pheromone is presumably concentrated, i.e. near the female. Then the male opens its wings and moves them at a high speed while walking sideways or backwards, pointing the tip of the abdomen with the valves wide open towards the place where the pheromone is presumably concentrated; the male keeps doing that and moving in different ways but always returning to the same place until it finds the female. When the male finds the female contact is made almost immediately. If the female has moved away the male tries to mate with any female or even male that it finds in its place, at the same time it keeps doing its fast wing-beating which is then alternated by very short periods of 'resting' in which the male stops the wing-beating but continues walking and searching for the female (only rarely stops completely). Eventually the unsuccessful male stops completely the pre-mating behaviour and continues its normal behaviour. The pre-mating behaviour of the female is almost imperceptible being only noticed on certain occasions by an increase in the speed of its movements. If the male finds a receptive female it tries to approach her with the tip of the abdomen. When the male is near the receptive female she changes her position, rather more frequently than normal (probably when she perceives the wing-beating of the male), then opens her wings and points the abdomen towards the male. The male searches with the tip of the abdomen until it gets the tip of the femaleabdomen, then it clasps the female abdominal tip and folds its wings; subsequently the female folds its wings too, which partially rest on the male ones (Fig. 23); during the copula they face away from each other. Immediately after they clinch in copula all the distinctive movements cease except for those of the abdomen which can only be observed from underneath.

The duration of the copula is variable from a few minutes up to several hours. If they are disturbed during the copula they try to move away but as the female is generally bigger and stronger, she drags the male to a safer place. Only under strong disturbances or when they are recently joined, will they separate. After the copula finishes they separate without any special pattern of behaviour.

8.3 OVIPOSITION BEHAVIOUR.

Some time after the copula, generally the same day or one day after, the female is ready to lay eggs. The pattern of oviposition is simple and begins with the female walking along the leaf surface. When the place is apparently favourable she starts to probe the leaf surface with the tip of the ovipositor which is partially stretched out. If suitable the female bends the abdomen and stretches the ovipositor completely out, then the egg is released. The egg is normally covered by a film of liquid substance which serves as a sticking substrate for the egg. After the release of one egg the female may move away although more commonly she moves only a short distance and starts again to probe on the leaf surface with the ovipositor and eventually releases another egg. Very often the female lays the eggs in groups of variable number. Also different females at different times may lay eggs beside other eggs previously laid or even beside empty egg-shells. In that way groups of eggs can build up in numbers (in the constant environment rooms). For example, in eleven young plants with four leaves each, the number of eggs laid by a group of females during the first day was recorded (Table 8.3.1.).

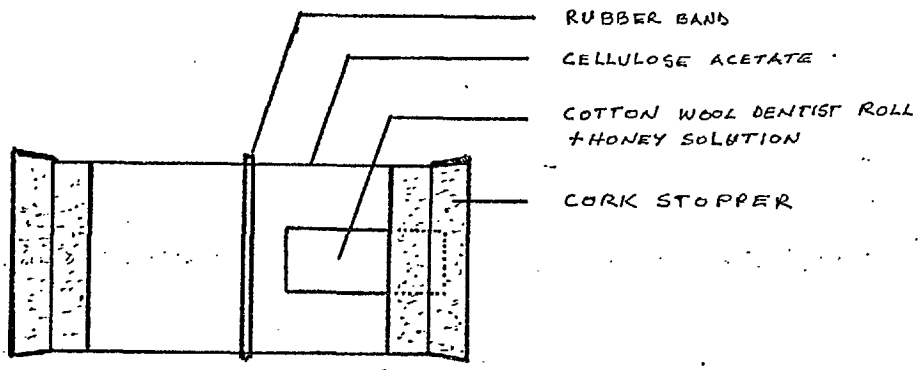


Fig.24. Fecundity cage.

Table 8.3.1. - Number and percentage eggs per group.

Number of eggs per group	1	2	3	4	5	5+
Total	1238	538	237	160	70	225
%	50.2	21.8	9.6	6.5	2.8	9.1

From Table 8.3.1 it can be clearly seen that the largest proportion of eggs was laid singly (in this case singly means more than 1 mm separate). In the group of more than five eggs the numbers ranged from 6 to 13.

8.3.1 Oviposition substrate preference.

The preference of the females to lay eggs on different textured surfaces was recorded.

Materials and methods. - Recently emerged adults were paired in individual cages ('Fecundity' cages) especially developed for the study of the oviposition. These cages each consisted of a piece of thin transparent cellulose acetate (5 x 10 cm) rolled into a cylinder shape and held in shape by two cork stoppers 2.5 cm diameter at each end and a rubber band on the middle (Fig.24). These cages have the advantages of being small and easy to store, not breakable, and can be extended flat for examination and collection of the eggs, and for cleaning. One of the cork stoppers had a hole in the centre to hold a half of a dental cottonwool roll impregnated in honey solution. Inside the cage, a piece of leaf from a young plant was introduced together with the pair of adults. Every day the adults were transferred to new cages, and the number of eggs laid on each of the different surfaces was recorded (Table 8.3.2.).

Results. - From the analysis of variance it was found that there were significant differences between the treatments ($F=3.446$; $P < 0.05$). The method of Keuls, as described in Snedecor (1956), showed that the number of eggs laid in the cottonwool was significantly lower than in the other treatments. The number of eggs laid in the cork stoppers was statistically similar to those on the lower surface and on the upper surface of the leaf.

From Fig. 25 it can be seen that most eggs were laid on the leaf surface, mainly on the lower surface. The second largest proportion was laid on the cork stoppers. It can be seen that both surfaces are firm but rather unsmooth or uneven. These results agree with those of Gupta & Thorsteinson (1960b) who found that the eggs were preferentially laid in concavities of leaves and stem, and significantly more eggs were laid on pebbled, grooved or pitted polyethylene surface than on a smooth substrate of the same material.

Table 8.3.2. - Oviposition surface preference.

Surfaces	Plants									Total	$\bar{x}$	St. Error
	A	B	C	D	E	F	G	H	I			
Leaf, lower	113	29	116	108	75	28	25	24	29	547	60.78	±13.91
Leaf, upper	15	39	110	78	55	54	5	58	20	434	48.22	±11.01
Cellulose acetate	101	40	32	50	36	89	39	12	42	441	49.00	±10.62
Cork	136	164	12	9	32	136	25	12	68	594	66.00	±20.86
Cotton wool	11	2	4	10	6	7	1	6	3	50	5.56	± 1.14
Total	376	274	274	255	204	314	95	112	162	2066	229.56	±31.25

Fig.25

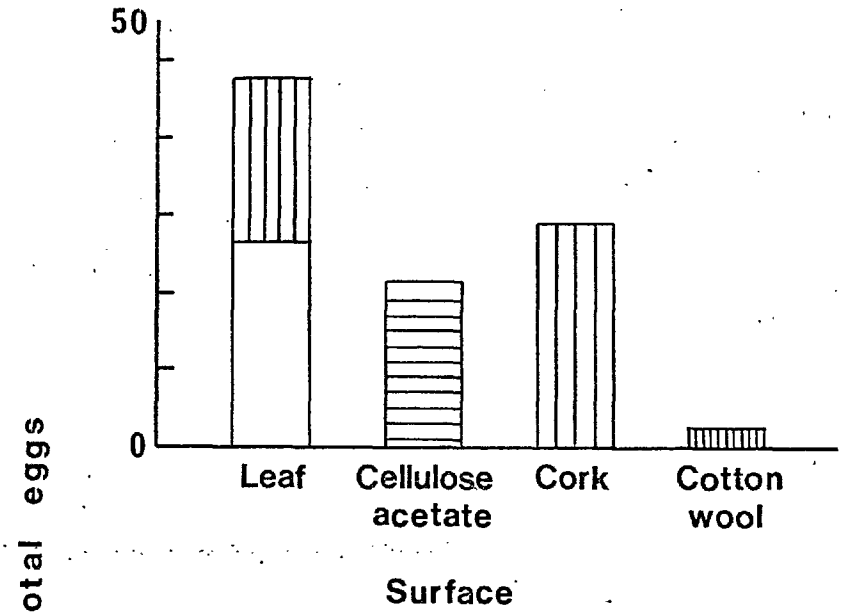


Fig.26

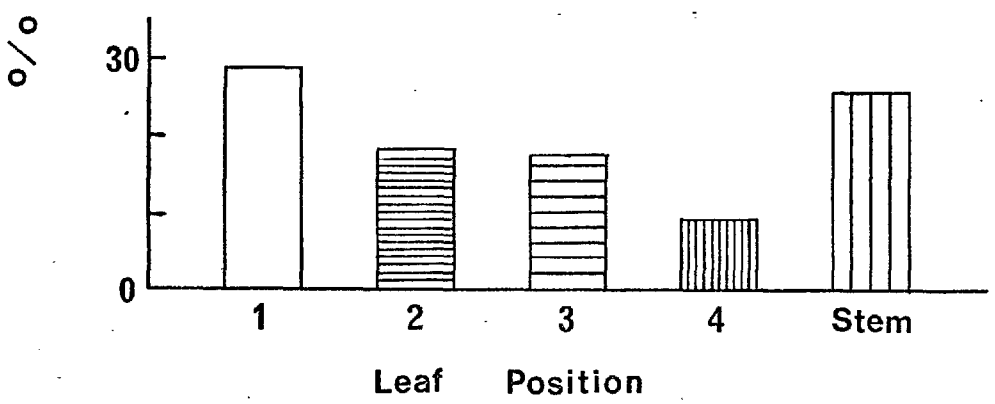


Fig.25. Oviposition. Surface preference.
Fig.26. Oviposition. Leaf-position preference.

8.3.2 Leaf position preference.

The preference of the females to lay eggs on particular leaves of the same plant was investigated in controlled environment rooms.

Materials and methods. - Young cabbage plants with tender leaves were used. Eleven of those plants were left with only four leaves : one mature (low position, No.1) one less mature (medium height, No.2) one young (medium height, No.3), and one very young (top position, No.4). All the leaves were distributed in such a way that they did not overlap. The plants were trimmed of the new growths, and the top growing point. Then they were introduced in cages (36 x 36 x 36 cm) with top and front made of transparent perspex and sides of muslin. Groups of adults (about 20 males and 20 females) were introduced in the cages and left freely to oviposit on the plants. Twenty four hours later the plants were removed and the number of eggs laid on each leaf as well as in the stem was recorded (Table 8.3.3.).

Table 8.3.3. - Oviposition leaf preference.

Leaf	A	B	C	D	E	F	G	H	I	J	K	Total	$\bar{x}$
1	16	2	37	38	121	66	144	36	80	105	83	728	66.18
2	17	18	15	17	85	88	68	62	46	1	40	457	41.55
3	5	11	7	12	40	36	44	190	77	2	17	441	40.09
4	14	19	8	4	28	38	16	60	31	12	--	230	20.91
Stem	17	57	127	7	99	74	--	87	77	45	63	653	59.36
Total	69	107	194	78	373	302	272	435	311	165	203	2509	228.09

Results. - From the analysis of variance it was found that there were differences statistically significant between the treatments ($F = 2.86$; $P < 0.05$).

The ranking method of Keuls as described in Snedecor (1956) showed that all the leaves and stem were statistically different in relation to the preference by the females to oviposit on them (except between the leaf No.1 and the stem, and between leaves 2 and 3).

Table 8.3.4 shows the comparison of the means, the differences between means are followed by (in brackets) the least significant difference for each range.

Table 8.3.4 - Comparison of leaf position preference.

Leaf	$\bar{x}$	$\bar{x}$-20.91	$\bar{x}$-40.09	$\bar{x}$-41.55	$\bar{x}$-59.36
1	66.18	45.27 (22.50)	26.09 (21.11)	24.63 (19.16)	6.82 (15.93)
Stem	59.36	38.45 (21.11)	19.27 (19.16)	17.81 (15.93)	
2	41.55	20.64 (19.16)	1.46 (15.93)		
3	40.09	19.18 (15.93)			
4	20.91				

From Table 8.3.4 and Fig.26 it can be seen that the order of preference of the leaves was according to the position on the plant, and that the stem was as preferred as the leaf No.1. This particular preference by the position of the leaves may be related either to real preference or may be due to the fact that there was a certain difference in size; leaf No.1 was generally larger than the No.2, and so on.

In relation to the preference of the stem it may be related to the grooviness of the surface which may stimulate a higher oviposition than on smooth surfaces (Gupta & Thorsteinson, 1960 b) although it may

also be due to a certain change in the oviposition behaviour of the females when in cages. Harcourt (1957) reports that most eggs in the field are laid on the lower surface of the leaves (63.4%) and that females laid mainly on the leaves but when the plants were small they laid on stems and petioles. Females closely confined may therefore oviposit abnormally by laying more eggs on the stems of the plants and on the sides and bottom of the containers.

9. STUDIES ON CAUSES OF MORTALITY AND ON DISPERSION IN LABORATORY POPULATIONS OF P. xylostella.

9.1. INTRODUCTION.

Experiments were carried out in controlled environment rooms in order to determine the development, mortality and dispersion of populations of P. xylostella in conditions where all the external factors were similar except the initial density of the eggs or larvae, and the quality of the host plant. These seem likely to be important factors in determining the duration of development, the mortality and the dispersion of the larvae, so their action on the larvae was examined from hatching up to pupation.

9.2. MATERIALS AND METHODS.

9.2.1. The rooms.

The rooms were similar to those already described in the Chapter on Life-history of P. xylostella. They were maintained at 20 $\pm$ 1°C constant temperature, with 16 hours/day light from six 125-watt fluorescent tubes, 2.40 m long. Relative humidity was not controlled but remained at 44-52% during the day and up to 14% higher at night.

9.2.2. The cages.

The cages were made of a wooden frame (36 x 36 x 36 cm) with the floor and back wall of hardboard, the sides were covered with muslin netting, and the top and front door were of transparent perspex (Fig.27). They were big enough to hold one cabbage plant in a 15 cm diameter pot or four smaller ones in 10 cm diameter pots. The cages were placed on benches about 15-25 cm. below the fluorescent tubes. The light intensity at the level of the plant leaves was about 12,000 ft - candles.

9.2.3. The plants.

The plants used were always cabbage (Brassica oleracea var. capitata L.). They were grown under greenhouse conditions until they reached a size (leaf area) suitable for the experiments. The number of leaves was reduced in order to make easier the observations of the early stages. Usually the youngest leaflets as well as the senescent ones were cut off (Fig.28).

9.2.4. The leaves.

The leaves used in the experiments were those in the medium region of the plant, neither senescent nor still part grown. Some leaves were trimmed and others removed in such a way that overlapping of the leaves was minimal. In most experiments the leaves were relatively tender, but initially, no serious attempt to measure the toughness was made although the nature of the leaves was recorded qualitatively. The area of the leaves varied from 10 to more than 300 cm^2 according to the size of the plant and to each experiment. Details of each experiment will be given appropriately in the text.



Fig. 27. Laboratory cages.



Fig. 28. Cabbage plant, trimmed to four leaves, showing damage by P. xylostella.

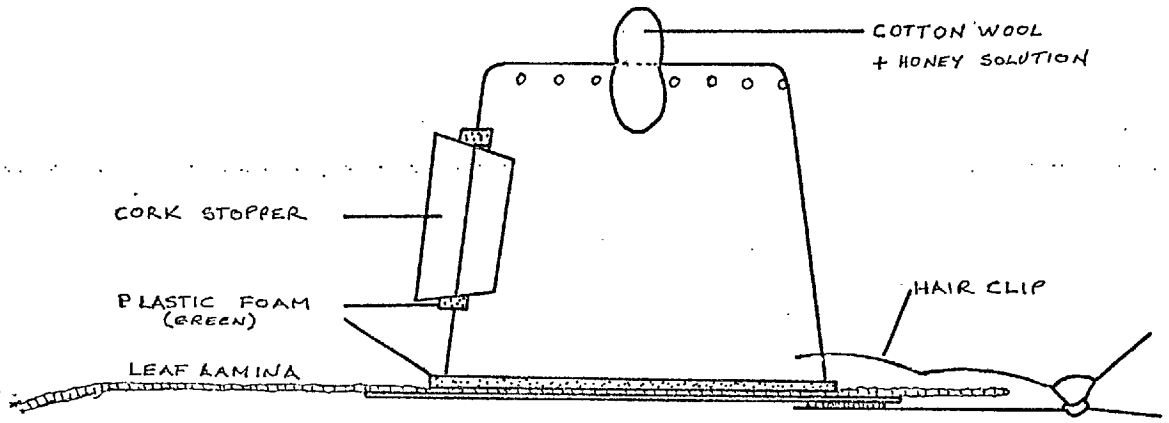


Fig. 29. Oviposition cage.

9.2.5. The oviposition cages.

Small oviposition cages were used in order to confine one or more females to one selected place where the eggs were going to be laid (Fig.29). Each cage was made of a transparent plastic circular box (45 mm height, 53 mm open diameter, and 40 mm bottom diameter). A 30-mm diameter hole was made on one side and a 5 mm diameter hole was made on the centre of the bottom. About ten 1-mm diameter holes were made around the edge of the bottom (see Fig.29). The big hole and the mouth of the box were lined with green plastic foam to avoid damage to the plants, and to avoid the escape of the moths. A piece of cellulose acetate sheet 6 x 6 cm) was used as the lid of the cage and was held in position by a spring-type hair clip (Fig.29).

When required the cage was placed on the selected leaf and held together with two or three wire clips (Fig.29). Adults of P. xylostella were introduced through the big hole which was then closed with a cork stopper. A cotton wick moistened with honey solution was placed through the small hole to feed the moths. The smaller holes provided aeration and prevented condensation of moisture inside the cages.

9.2.6. The stock culture of the larvae.

All the experiments were carried out using P. xylostella larvae from a stock culture that was started in October 1968 from larvae and pupae obtained from Jealott's Hill Research Station, Bracknell, Berkshire. Adults were placed in a cage of the type described above (36 x 36 x 36 cm, muslin covered, top and front door of transparent perspex) (Fig.27), with one young cabbage plant. A dental cotton roll moistened with honey solution was pro-

vided as a source of food for the adults. The females laid eggs readily on the plants. The culture has been maintained since then without difficulty or apparent variation in quality of individuals.

The normal hygienic rules of breeding Lepidoptera were maintained in order to preserve the health of the stock. These included cleaning the cages thoroughly with hot water and soap, providing healthy food plants without fungal disease, changing the food plant regularly before it deteriorated; watering the plants as often as required, providing food for the adults (cotton wool moistened with honey solution), etc.

Every time one experiment was to be started, pupae were collected and isolated in order to obtain adults of the same age. The pupae were taken out of cocoons by tearing the cocoons off with a watchmaker's forceps. The pupae were sexed under a stereo-dissecting microscope. The sexing was easy since the pupal last abdominal segments with the genital features are distinct for each sex. If required, the pupae were measured with a calibrated reticule eye-piece, and weighed in an electric balance sensitive to 0.1 mg.

The newly emerged adults were transferred either to another cage where whole plants were presented to them or to the oviposition cages described above in which they were confined to a selected place in one leaf.

9.3 EXPERIMENT TO DETERMINE DEVELOPMENT, MORTALITY AND DISPERSION.

This experiment was done in order to determine the rate of development, the mortality and the dispersion of P. xylostella at high initial densities of larvae.

9.3.1. Materials and methods.

The experiment was carried out under the conditions described above. Two cabbage plants (A and B) in 15-cm diameter pots were used. Both plants were similar in age, growth condition, etc. They were each trimmed to seven young leaves of the same size and position. The leaves were traced on paper and their areas measured with a planimeter calibrated to 0.1 cm^2. Two readings were made which usually gave a discrepancy of less than 0.5 cm^2. The mean was used as the leaf area. The total leaf area of plant A was 627.6 cm^2, and of plant B was 689.1 cm^2. Each leaf was divided in sixteen parts by quadrats drawn with a blue ink felt tip pen (Fig. 30). It proved not to be toxic to the plants or the larvae.

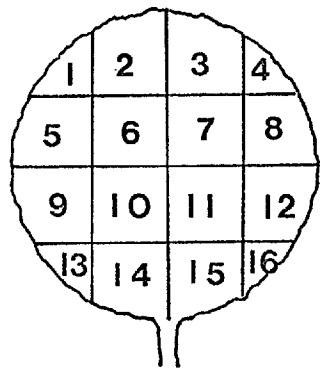


Fig. 30. Leaf showing 16-quadrats division.

Those quadrats helped when counting and recording the position of the eggs and larvae.

The two plants had tender leaves. Each plant was placed in one cage and a group of twenty moths put in each cage. The following day the moths were removed and the eggs on each leaf were carefully counted. Any eggs on petioles, stem, lower surface of leaves, or anywhere except the upper surface of the leaves were removed with a soft paint brush. Two batches of eggs were however left on the lower surfaces of two leaves of plant B to make the total number of eggs per plant as high as in Plant A. The number of eggs on each leaf is given in Table 9.3.1. (The oldest leaf is No. 1).

Table 9.3.1. Density of eggs.

	Plant A			Plant B		
Leaf	No. eggs	Area (cm^2)	Density (Eggs/ 100 cm^2)	No. eggs	Area (cm^2)	Density (Eggs/ 100 cm^2)
1	14	95.8	14.6	10	90.6	11.0
2	18	98.4	18.3	16	95.5	16.8
3	33	98.0	33.7	32	100.1	32.0
4	38	95.5	39.8	57	115.6	49.3
5	13	82.4	15.8	45	98.5	45.7
6	13	85.0	15.3	15	104.3	14.4
7	23	72.5	31.7	5	84.8	5.9
Total/ mean	152	627.6	24.2	180	689.1	26.1

The eggs were examined every day and the number which hatched recorded. Live and dead larvae were also counted daily.

9.3.2. Results and Discussion.

Egg mortality.

Table 9.3.2 records the mortality of the eggs and the numbers of larvae which become established.

Table 9.3.2. - Egg mortality

	Plant A				Plant B			
Leaf	No. eggs	Larvae hatched	Mortality eggs (%)	Initial larvae/ 100cm^2	No. eggs	Larvae hatched	Mortality eggs(%)	Initial larvae/ 100 cm^2
1	14	14	0	14.6	10	10	0	11.0
2	18	18	0	18.3	16	16	0	16.8
3	33	15	54.6	15.3	32	32	0	32.0
4	38	21	44.7	22.0	57	57	0	49.3
5	13	13	0	15.8	45	45	0	45.7
6	13	12	7.7	14.1	15	15	0	14.4
7	23	23	0	31.7	5	5	0	5.9
Total/ mean	152	116	23.7	18.7	180	180	0	26.1

As can be seen there was a rather high mortality of the eggs on two of the leaves of plant A, but none on plant B. The cause of the mortality is not known - perhaps damage due to handling.

Larval and generation mortality.

The mortality of the larvae was assessed by counting every day the number of live larvae and taking the difference from those previously alive as the daily mortality. This daily mortality expressed as a percentage of the numbers of initial larvae, was transformed to

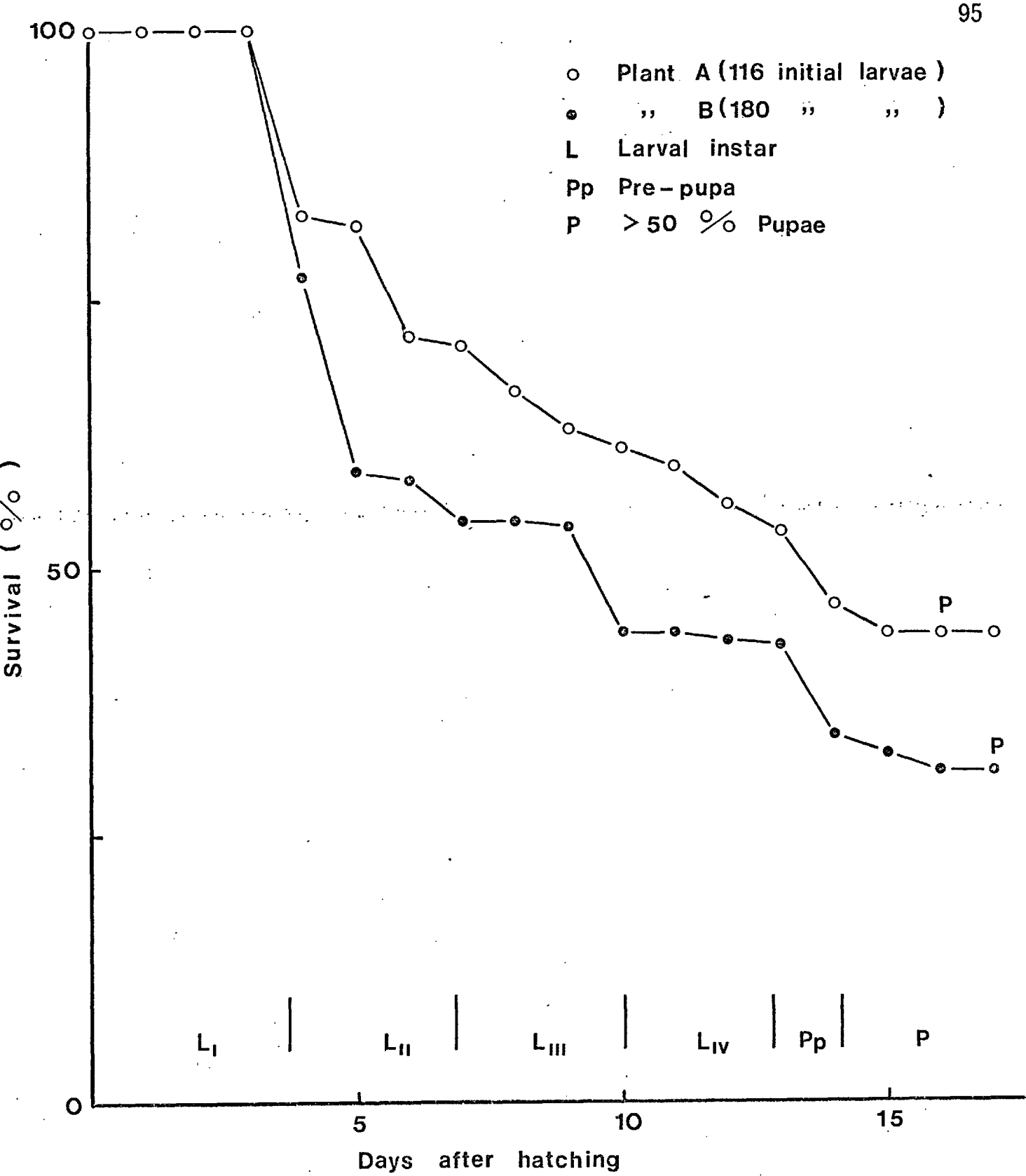


Fig. 31. Larval survival.

survival (by subtracting the percent mortality from 100, i.e. 100-30% mortality = 70% survival) and is shown graphically in Fig 31.

The mortality of the larvae was 56.0% in plant A and 68.9% in plant B. No mortality occurred in the pupal stage. The generation mortalities on each plant are summarized in Table 9.3.3.

Table 9.3.3. - Generation mortality of P. xylostella in two plants(a), and pooled data (b)

(a)

	Plant A			Plant B		
	Initial	Dead	Mortality (%)	Initial	Dead	Mortality (%)
Eggs	152	36	23.7	180	0	0
Larvae	116	65	56.0	180	124	68.9
Pupae	51	0	0	56	0	0
Adults	51			56		

(b)

	Plants A + B		
	Initial	Dead	Mortality (%)
Eggs	332	36	10.8
Larvae	296	189	63.9
Pupae	107	0	0
Adults	107		

As already mentioned there was a notable mortality of eggs on plant A (23.7%) compared with plant B(0%). However more larvae died on plant B, so the overall population of adults bred from each plant was similar. This may suggest that the egg mortality on plant A was compensated for by a higher larval mortality on B (probably due to intra-specific competition) but it could be fortituous. Nevertheless Fig.31 shows graphically that, based on hatched larvae, there was a higher final survival (individuals reaching the adult stage) in plant A (more than 11%). This can be associated with the initial density of the larvae, 18.5 larvae/100 cm^2 in plant A compared with 26.1 larvae/100 cm^2 in plant B; and this suggestion is supported by the fact that most of the mortality occurred in the early stages of the larvae (51% of the total mortality in plant A, and 61% in plant B, occurred during the first and second instars, see Fig 31), especially during the first week of the larval life, when they were starting to disperse, and probably 'needed' more space per initial larvae to burrow their galleries as shown in the Chapter on Behaviour.

9.4. EXPERIMENT TO DETERMINE DEVELOPMENT, MORTALITY AND DISPERSION.

This experiment was done as a repetition of the previous one.

9.4.1. Materials and methods.

The experiment was carried out under the conditions described above. Two young cabbage plants (A and B) with medium tough leaves were used. Both plants were similar in age, growing conditions, etc. They were trimmed to four and five leaves respectively, to provide leaves of the same size and position.

The procedure in general was the same as in the previous experiment. The plants were placed in individual cages and a small group of moths (about twenty) was put in the cages and allowed to lay eggs. The next day the moths were removed and the eggs on each leaf carefully counted. All eggs not in the upper surface were removed.

The number of eggs laid on each leaf is given in Table 9.4.1., together with the area of the leaves. Leaf 1 is the oldest in the plant.

Table 9.4.1. - Density of eggs.

	Plant A			Plant B		
Leaf	Eggs	Leaf area (cm^2)	Density (Eggs/ 100 cm^2)	Eggs	Leaf area (cm^2)	Density (Eggs/ 100 cm^2)
1	70	149.2	46.9	25	153.4	16.3
2	7	125.8	5.6	42	140.4	29.9
3	17	133.7	12.7	24	162.0	14.8
4	16	146.3	10.9	41	129.6	31.6
5	20	109.6	18.3			
Total/ mean	130	664.6	19.6	132	585.4	22.6

The eggs were examined every day and numbers hatched recorded. Live and dead larvae were also counted daily.

9.4.2. Results and Discussion.

Egg mortality.

Table 9.4.2 shows the mortality of the eggs.

Table 9.4.2. - Egg mortality.

	Plant A				Plant B			
Leaf	Eggs	Larvae hatched	Mortality eggs(%)	Initial larvae/ 100 cm^2	Eggs	Larvae hatched	Mortality eggs(%)	Initial larvae/ 100 cm^2
1	70	68	2.9	45.6	25	25	0	16.3
2	7	7	0	5.6	42	38	9.5	29.9
3	17	13	23.5	9.7	24	24	0	14.8
4	16	16	0	10.9	41	39	4.9	31.6
5	20	19	0.5	17.3				
Total/ mean	130	123	5.4	19.6	132	126	4.6	22.6

In this case the egg mortality was very small except on one leaf on plant A (23.5%).

Larval and generation mortality.

As in the previous experiment the highest mortality occurred during the larval stage, with no mortality during the pupal stage. The generation mortality is summarized in Table 9.4.3.

Table 9.4.3. a. - Generation mortality.

	Plant A			Plant B		
	Initial	Dead	Mortality (%)	Initial	Dead	Mortality (%)
Eggs	130	7	5.4	132	6	4.6
Larvae	123	47	38.2	126	42	33.3
Pupae	76	0		84	0	
Adults	76			84		

Table 9.4.3. b. - Generation mortality. Pooled data of table 9.4.3.a.

	Plants A + B		
	Initial	Dead	Apparent mortality (%)
Eggs	262	13	5.0
Larvae	249	89	35.7
Pupae	160	0	
Adults	160		

From Table 9.4.3. it can be seen that there was not much difference between plants A and B in relation to egg mortality which remained reasonably low at around 5%; but there was a slightly higher mortality of the larvae in plant A. As before this mortality occurred during the early stages of the larvae (74% of the total mortality in plant A, and 62% in plant B, occurred during the first and second instars, see Fig 32), and again, as in the previous experiment most of it was during the first week when the larvae begin to disperse.

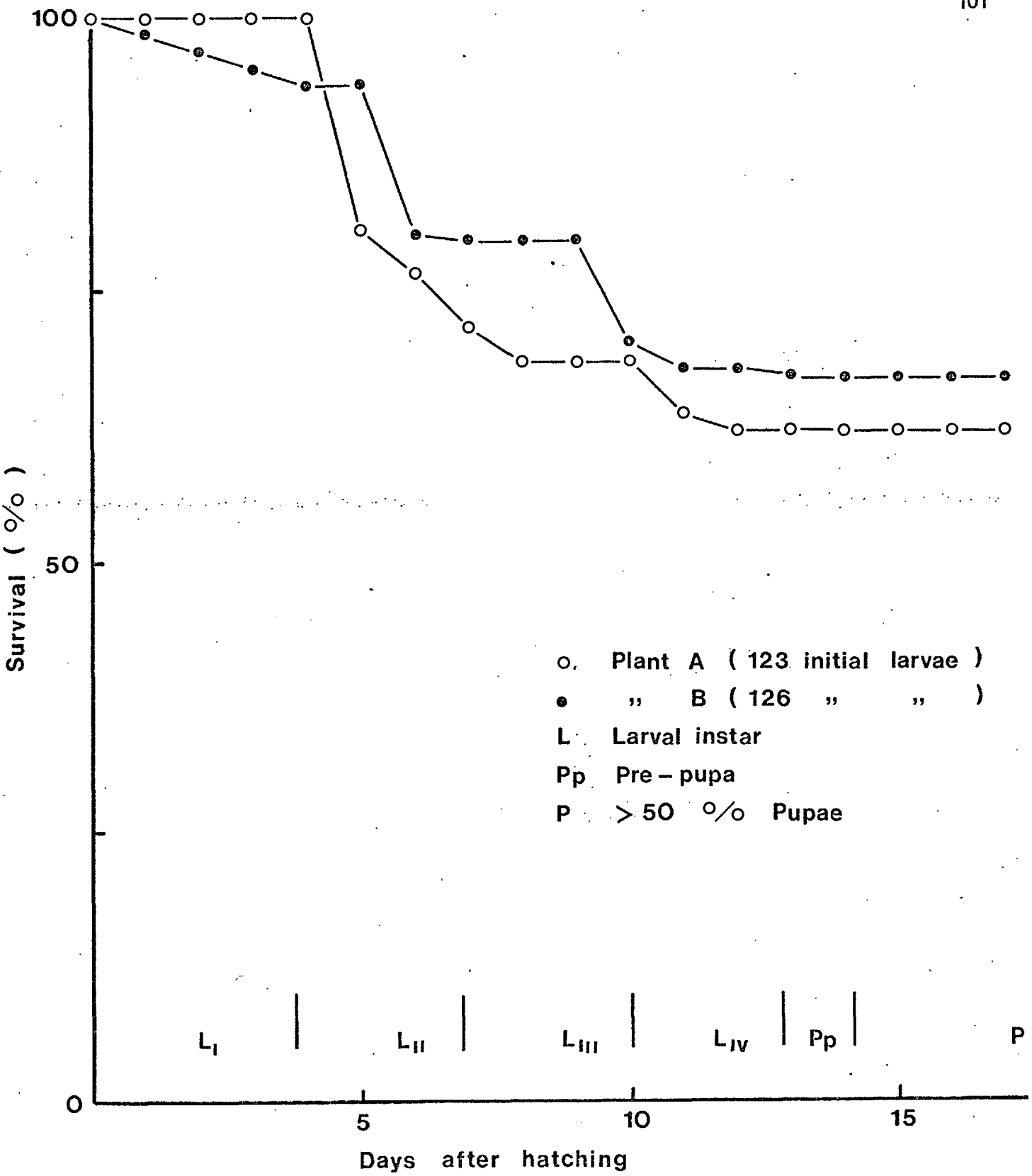


Fig. 32. Larval survival.

This suggests that there is intra-specific competition of the young larvae at high densities. However after the 'young-larvae' mortality the remaining larvae did not suffer any other notable increase in mortality. The population of individuals reaching the adult stage remained similar in both plants (Fig 32). No pupal mortality occurred.

When compared with the previous experiment it can be noticed (tables 9.3.3 and 9.4.3; Figs 31 and 32) that the overall mortality was slightly lower in this experiment. This mortality was mainly due, as mentioned above, to the mortality of the early instars (first and second) which is seemingly induced by intra-specific competition and therefore density dependent.

From those results it can be said that the total mortality of the larvae of P. xylostella is greatly influenced by the mortality of the early instars. Mortality in the remaining immature stages was small compared with that of the first and second instars and there is evidence of density dependent mortality in the early instars.

9.5. EXPERIMENT TO DETERMINE DEVELOPMENT, MORTALITY AND DISPERSION AT LOW TO HIGH DENSITIES.

This experiment was done to determine in one experiment the rate of development, the mortality and the dispersion of P. xylostella at low, medium and high densities, and so test the hypothesis that mortality is related to density. It was found in the two previous experiments that the initial density of the larvae might be an important factor influencing the mortality of the early larval stages. Therefore the present experiment was planned in order to compare

the mortality, development and dispersion of larvae at low and medium densities with those of larvae at a high density; and also to investigate the effect of toughness of the leaves which might be a factor affecting mortality by favouring or jeopardising the success of the recently hatched larvae in making the initial feeding hole.

9.5.1. Materials and methods.

The experiment was carried out under the same constant conditions as before. Three mature plants (A, B and C) with rather tough leaves were used. They were similar in age, growing conditions, etc. and were trimmed to four leaves of similar size and position on each plant.

The procedure was in general the same as in the previous experiments, except that the three older leaves of each plant were covered with cloth sleeves in order to stop the moths from laying on them. The sleeves were big enough to cover the petioles as well. About twenty adults were introduced in each cage and allowed to lay eggs on the youngest leaf, since the initial dispersion of the larvae could be better studied by restricting all the eggs to one leaf, and if possible to one place in the leaf. The moths were removed next day and the eggs on the upper surface were carefully counted. All other eggs were removed.

The area of the leaves and the number of eggs laid on each plant (on the youngest leaf) is given in Table 9.5.1.

Table 9.5.1. - Density of eggs. Eggs on leaf 4 only.

	Plant A			Plant B			Plant C		
Leaf	Eggs	Area (cm^2)	Density (Eggs/ $100cm^2$)	Eggs	Area (cm^2)	Density (Eggs/ $100cm^2$)	Eggs	Area (cm^2)	Density (Eggs/ $100\,cm^2$)
1		236.7			297.4			172.5	
2		296.2			244.5			166.7	
3		315.7			258.2			130.0	
4	80	347.8	23.0	270	323.3	83.5	425	118.5	358.7
Total/ mean	80	848.7	9.4	270	1123.4	24.0	425	587.7	98.2

As in the previous experiments, the eggs were examined every day and the number hatched were recorded. Live and dead larvae were also counted daily.

9.5.2. Results and Discussion.

Generation mortality.

Table 9.5.2 shows the generation mortality.

Table 9.5.2. - Generation mortality.

	Plant A			Plant B			Plant C		
	Initial	Dead	Mortality (%)	Initial	Dead	Mortality (%)	Initial	Dead	Mortality (%)
Eggs	80	56	70.0	270	4	1.5	425	5	1.2
Larvae	24	2	8.3	266	182	68.4	420	261	62.4
Pupae	22	0	0	84	6	7.1	159	8	1.9
Adults	22			78			151		

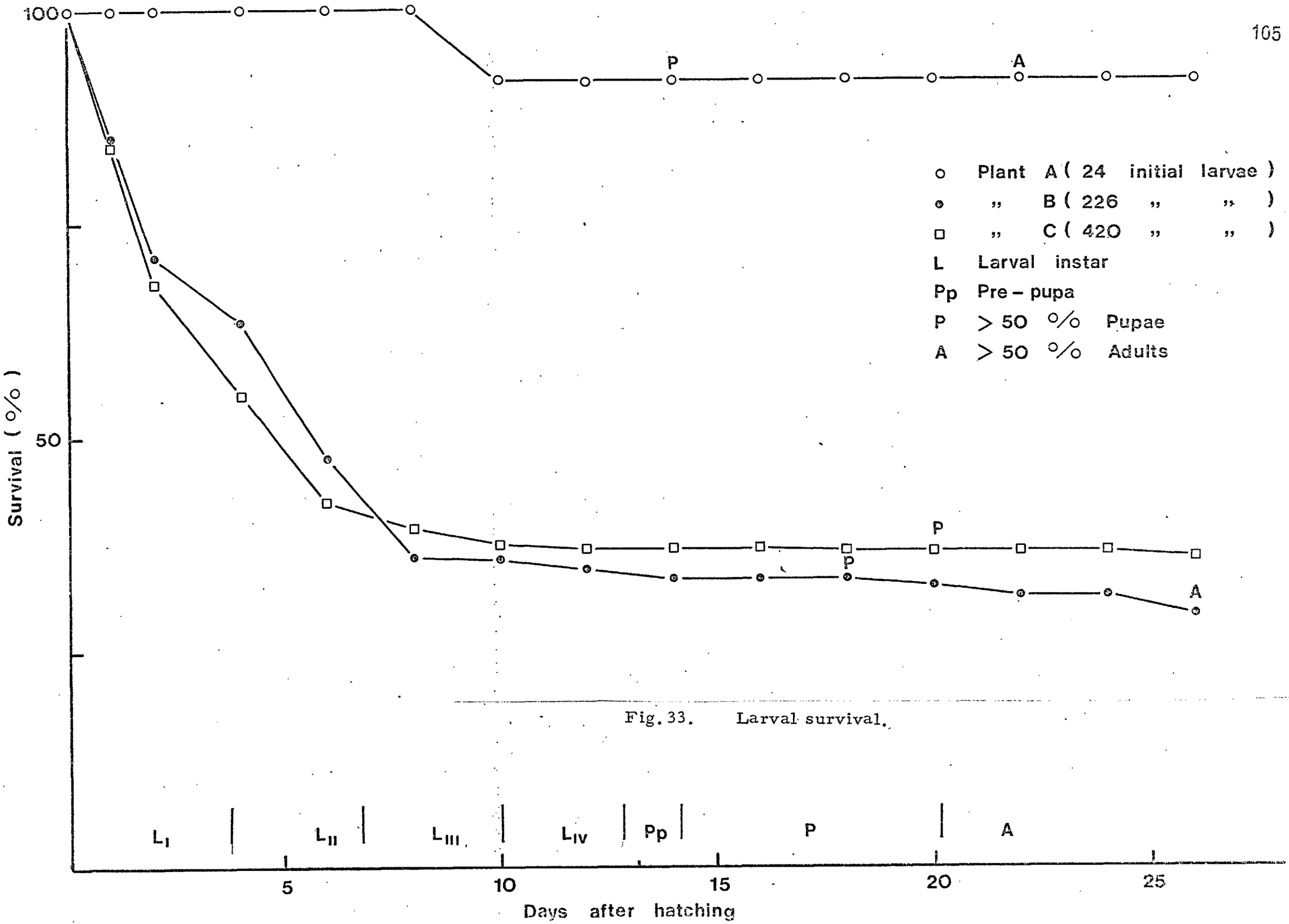


Fig. 33. Larval survival.

From Table 9.5.2 it can be seen that there was an exceptionally high mortality of eggs in plant A. This reduced the initial density of the larvae on plant A to a low level. The cause of the failure of the eggs was not known but it is suspected that they may have all been laid by a single infertile female.

The mortality of the larvae was variable according to the initial density, and seemingly it was related to the density since those larvae in plant A which were at a low density suffered a very low mortality (8%) while those at the high densities (plants B and C) were subjected to heavy mortalities (68% and 62% respectively, see Table 9.5.2 and Fig 33). Again, as in the previous experiments most of the mortality occurred during the early stages of the larvae, except in plant A probably due to low larval density (i.e. 85% of the total mortality in plant B, and 96% in plant C, occurred during the first and second instars, see Fig 33; no mortality occurred at this time in plant A); also, as before, this mortality occurred during the first week of the larval life when the larvae begin to disperse. However, surprisingly, the total mortality was not directly related to the density because it was similar in plant C where there were 385.6 recently hatched larvae/100 cm^2 of leaf 4 as in plant B where there were 82.3 initial larvae/100 cm^2 of leaf 4. Perhaps at very high densities the effects of intra-specific competition are ameliorated by a 'gregaria' effect, i.e. a phase change. However, the lack of replication makes this suggestion very speculative on the available evidence.

9.6 EXPERIMENT TO COMPARE DEVELOPMENT, MORTALITY AND DISPERSION AT LOW, HIGH AND VERY HIGH DENSITIES.

This experiment was done as a confirmation of the previous one in order to check the effects of intra-specific competition by comparing the rates of development, the mortality, and the dispersion of P. xylostella at low, high and very high densities. In the previous experiments it was found that the mortality of the larvae seemed to be related to their initial density, since at high and very high densities the mortality of the early larval stages was higher than at low density.

9.6.1. Materials and methods.

The experiment was carried out under similar conditions to previous experiments. Three mature cabbage plants (A, B and C) were used. The plants were similar in age, growing conditions, etc. and were trimmed to five leaves each. Care was taken to use plants with similar sized leaves, in the same position, and not overlapping.

The general experimental procedure was the same as in previous experiments, except that the oviposition cages were used to restrict the moths to a selected place on a leaf. This had the advantage that no sleeves were needed and it was not necessary to check for eggs laid in other parts of the plant. The cages were placed on one side of the apical end of the youngest leaf, on the upper surface. A group of about twenty adults was introduced in each cage and allowed to lay eggs. Next day the oviposition cages and moths were removed from plants A and B, and one of those oviposition cages (with moths) was placed on one side of the youngest

leaf of plant C together with the previous oviposition cage for one day more in order to obtain a very large number of eggs. Next day the cages were removed, and the eggs on all plants were counted. To obtain the required densities some eggs were removed, especially from Plant A where only ten eggs were needed.

The areas of the leaves and the number of eggs laid on each plant (on the youngest leaf) are given in Table 9.6.1.

Table 9.6.1. - Density of eggs per plant. Eggs on leaf 5 only.

	Plant A			Plant B			Plant C		
Leaf	Eggs	Area (cm^2)	Density (Eggs/ $100cm^2$)	Eggs	Area (cm^2)	Density (Eggs/ $100cm^2$)	Eggs	Area (cm^2)	Density (Eggs $100cm^2$)
1		103.1			201.2			135.1	
2		146.7			238.2			158.6	
3		147.4			194.0			206.6	
4		171.9			251.2			236.1	
5	10	199.8	5.0	190	291.6	65.2	641	265.1	241.8
Total/ mean	10	768.9	1.3	190	1176.2	16.2	641	1001.5	64.0

Again, as in previous experiments, the eggs were observed every day, and numbers hatching were recorded. Live and dead larvae were also counted daily.

9.6.2. Results and Discussion.

Generation mortality.

Table 9.6.2 gives the mortality of each of the stages and Fig 34 shows graphically the survival of larvae and pupae.

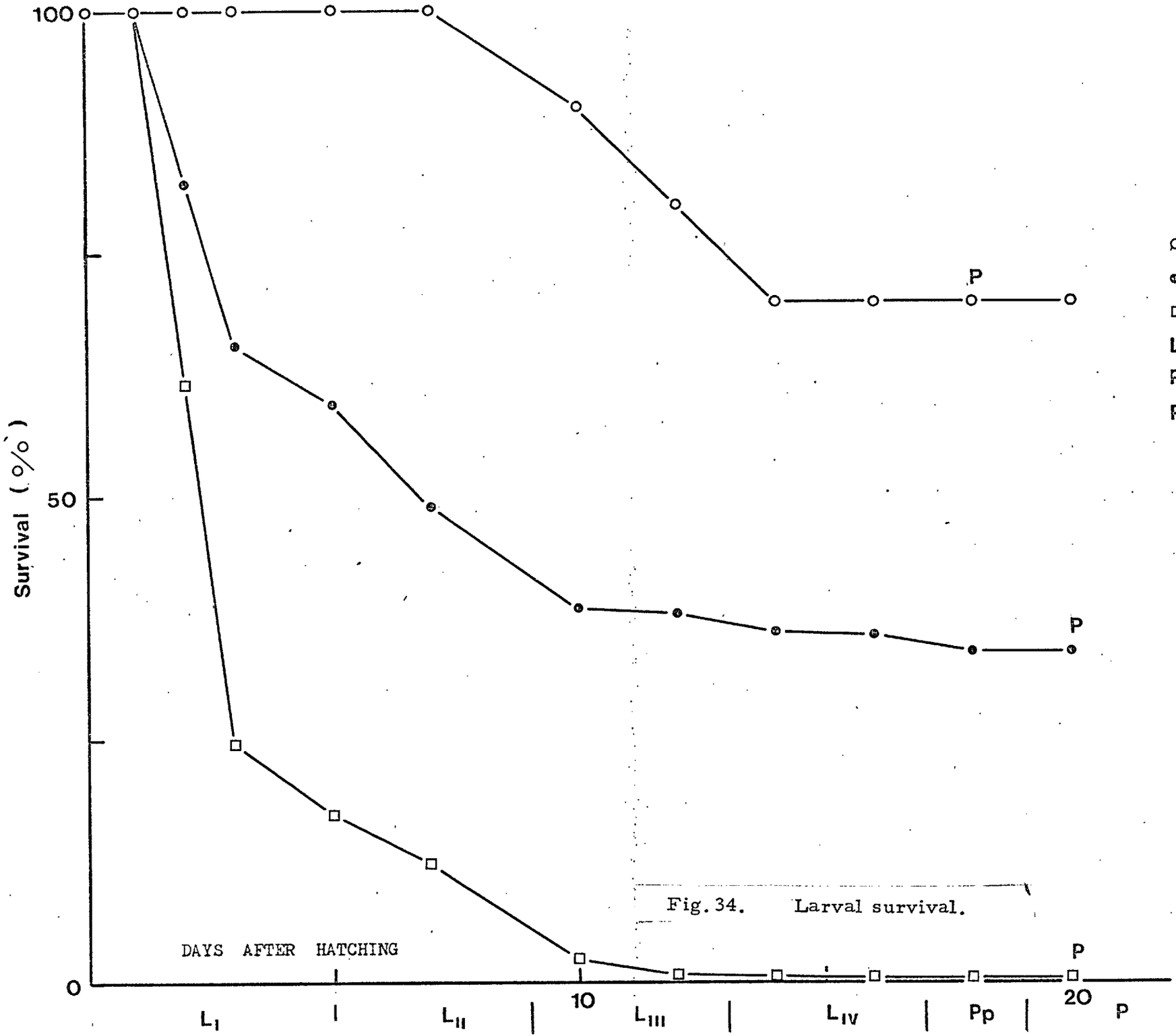


Fig. 34. Larval survival.

○ Plant A (10 initial larvae)
● „ B (188 „ „)
□ C (550 „ „)
L Larval instar
Pp Pre – pupa
P > 50 % Pupae

Table 9.6.2. - Generation mortality.

	Plant A			Plant B			Plant C		
	Initial	Dead	Mortal-ity (%)	Initial	Dead	Mortal-ity(%)	Initial	Dead	Mortal ity (%)
Eggs	10	0	0	190	2	1.1	641	91	14.2
Larvae	10	3	30.0	188	124	66.0	550	547	99.5
Pupae	7	0	0	64	0	0	3	0	0
Adults	7			64			3		

From Table 9.6.2 it can be seen that there was no egg mortality in plant A and it was very low in plant B; however in plant C some eggs failed perhaps due to infertility. In spite of this, the range of initial densities of larvae was obtained as planned, i. e. low (10 larvae), high (188 larvae) and very high (550 larvae).

In terms of mortality of larvae, the present results (Table 9.6.2; Fig 34) confirmed those of the previous experiments concerning the effect of density on mortality. From Table 9.6.2 it can be seen that the mortality was strongly related to the density, i.e. it was density dependent.

A graphical representation of the above results is given in Fig 34 which also shows that, as in the previous experiments most of the mortality occurred during the early stages of the larvae except in plant A in which there was no mortality in the first and second instars probably due to the low density (5.0 larvae/100 cm^2 of leaf 5). 77% of the total mortality in plant B (with high initial density of 64.5 larvae/100 cm^2 of leaf 5), and 88% in plant C (at very high initial density of 207.5 larvae/100 cm^2 of leaf 5),

occurred during the first and second instars (see Fig 34); this mortality as in previous experiments occurred during the first week of larval life which is the period when the larvae begin to disperse. In plant C at the very high initial density, the population practically collapsed by the third day after hatching (about 80% mortality) and ten days after hatching only 2% of the initial population remained (Fig 34). It is possible that the recently hatched larvae, in dispersing to other leaves, naturally disturbed each other and some fell onto the ground or did not establish a feeding place and eventually died of exhaustion or dessication. The processes of mutual disturbance are described in detail in the Chapter on Behaviour of the larvae. There was no pupal mortality. Thus intra-specific competition does not affect the delicate processes during pupation, at least in terms of survival to the adult stages. Effects on the viability of adults are described in the Chapter on Life-history.

9.7. EXPERIMENTS TO COMPARE DEVELOPMENT, MORTALITY, AND DISPERSION AT HIGH, LOW, AND EXTREMELY LOW (ISOLATED LARVA) DENSITIES, ON TOUGH AND TENDER LEAVES.

These experiments were done in order to compare the rate of development, the mortality, and the dispersion of P. xylostella at high and low densities and at a density of only one larva per plant. An additional stress was also included, namely the use of tough-leaved plants since this quality is likely to increase the difficulties for early instars larvae.

In the previous experiments the mortality of the larvae, especially during the first and second instars was seemingly density dependent and when a certain population density was reached, generally at the end or after the second instar, the intensity of the mortality ceased and the population remained fairly constant. This level of population density seems to be related to the initial density of the larvae. For example, at low initial densities of about 5 - 10 larvae/100cm^2 of leaf (the leaf in which the eggs are laid, not the total plant leaf-area), the level is reached when the initial intense mortality has eliminated about 20 - 30% of the initial population; when the initial density is high, more than 20 - 30 larvae/100 cm^2 of leaf, the level is reached when about 60% of the initial population is eliminated; when the population is very high, 50 - 60 or more larvae/100 cm^2 of leaf, the initial mortality is so high that the whole population collapses in less than ten days and only a few individuals (less than 1% of the initial population) reach the pupal stage.

9.7.1. Materials and methods.

The experiment was carried out under the same conditions as in the previous experiments. Three mature cabbage plants (A, B and C) with rather tough leaves were used in this experiment. The criterion of toughness is a subjective one; however in this case the leaves were considered tough when they were thick and hard, as normally occurs in senescent plants, or when young, or mature plants have been subjected to water stress in which case the leaves take a blueish coloration due to the production of wax. The texture of these leaves was rather leathery. The leaves were considered tender when they were turgescent and soft, generally thin, and green in colour; normally occurring in young plants or in those mature plants which have been well watered. Their texture is very smooth, never like leather. Medium tough or medium tender leaves were considered as those which being thick and from mature plants, were turgid but not so hard, with green to dark green colour (never blueish). Their texture was normally smooth.

The plants were similar in age, size, growing conditions, etc., and were trimmed to five leaves each, as near as possible the same size and position, and not overlapping.

The general procedure was the same as in the previous experiment. On plant C the moths were kept only for a few minutes until one of them had laid one egg. The oviposition cages with moths on plants A and B were left overnight and removed the next day.

The areas of the leaves and the number of eggs laid on each plant (on the youngest leaf) are given in Table 9.7.1.

Table 9.7.1. - Density of eggs. Only on leaf 5.

	Plant A			Plant B			Plant C		
Leaf	Eggs	Area (cm^2)	Density (Eggs/ $100cm^2$)	Eggs	Area (cm^2)	Density (Eggs/ $100cm^2$)	Eggs	Area (cm^2)	Density (Eggs/ $100\,cm^2$)
1		27.2			55.6			43.0	
2		77. 1			107.8			94.7	
3		90.6			89.5			109.6	
4		71.2			67.4			105.6	
5	1	47.8	2.1	5	53.3	9.4	132	58.7	224.9
Total/ mean	1	313.9	0.3	5	373.6	1.3	132	411.6	32.1

The eggs were observed every day and the numbers hatched were recorded. Live and dead larvae were also counted daily.

9.7.2. Results and Discussion.

Generation mortality.

Table 9.7.2 gives the mortality of each stage in the generation and Fig 35 shows graphically the survival of larvae and pupae.

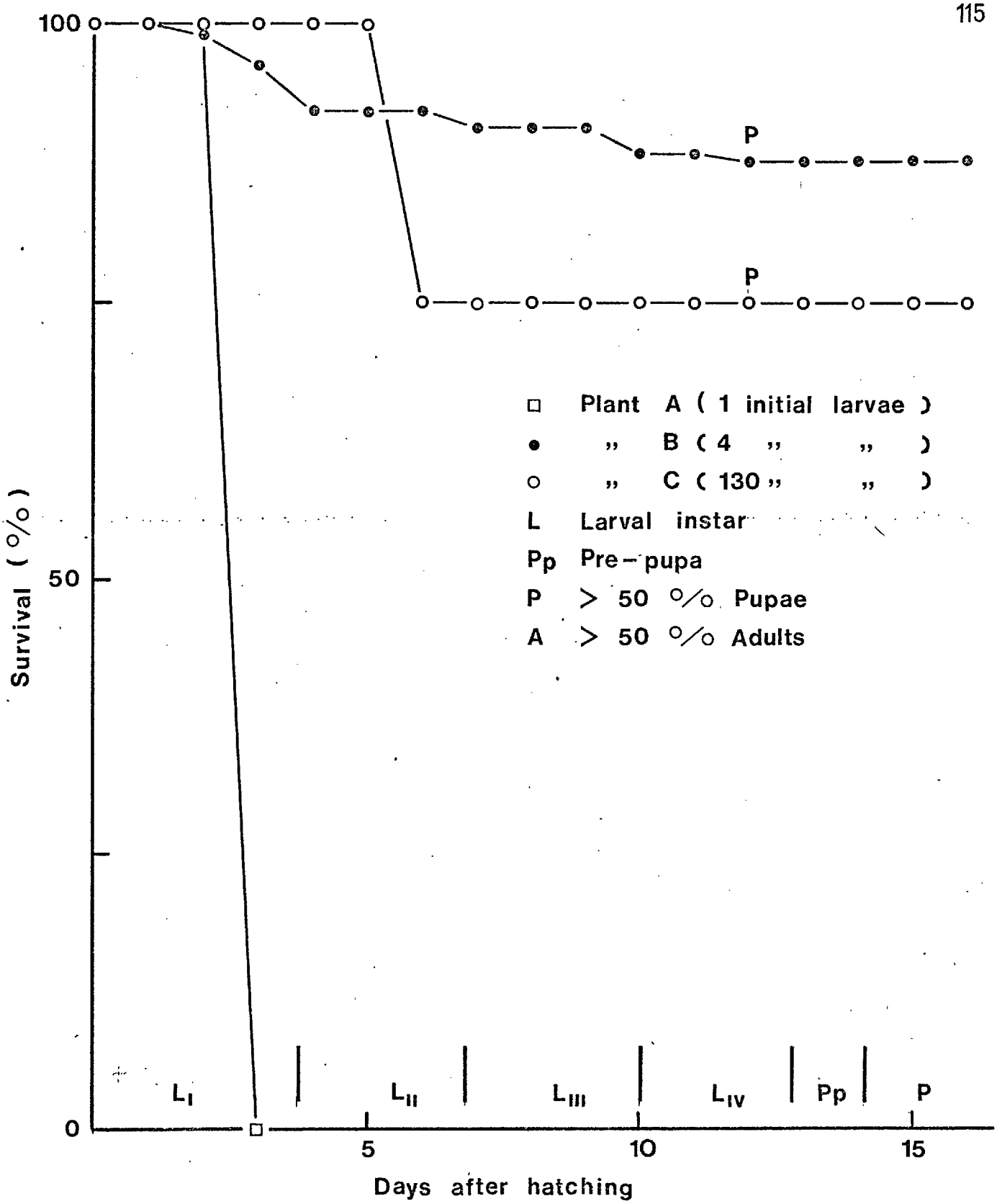


Fig. 35. Larval survival.

Table 9.7.2. - Generation mortality.

	Plant A			Plant B			Plant C		
	Initial	Dead	Mortality(%)	Initial	Dead	Mortality (%)	Initial	Dead	Mortality (%)
Eggs	1	0	0	5	1	20.0	132	2	1.5
Larvae	1	1	100.0	4	1	25.0	130	16	12.3
Pupae	0			3	0	0	114	0	0
Adults	0			3			114		

From Table 9.7.2 it can be seen that the egg mortality was low in absolute numbers although on plant B the failure of one egg to hatch made 20% of the mortality. This means that no statistical significance can be attached to the differences. The isolated larva was dead by the third day after hatching (Fig 35). The mortality of the larvae at low density (9.4 initial larvae/100 cm^2 of leaf 5) was rather low. The mortality of the larvae at high initial density (221.5 larvae/100 cm^2 of leaf 5) was contrary to expectation, low at 12% as compared with the previous experiments. Again, as in the previous experiments most of the mortality occurred in the early instars, i.e. 75% of the total mortality occurred during the first and second instars.

From these results it seems that the toughness of the leaves is not necessarily an important factor in the survival of the larvae of P. xylostella. The leaves when tough present a natural resistance to be pierced by the recently hatched larvae which may disperse in search for more suitable leaves. During the dispersion they may die by different causes as explained in the discussion of the previous experiment. This may be the reason of the death of the isolated

larvae. At the same time, the toughness of leaves seems to have a favourable effect on the larvae of P. xylostella at high density. This could be interpreted as the indirect and combined effect of dispersion of the early instars and mutual stimulation to bite on the leaf surface; in other words when high density populations of larvae hatch on tough leaves they try, as normal, to burrow galleries into the same leaf in which they have hatched, but if the leaf is tough they will try to find a more suitable place. This dispersion is favoured by mutual disturbance which occurs as a consequence of the high density of the larvae. Eventually they may find the right leaves or suitable places in the leaves and make their galleries. This suggestion is, however, very speculative and in general it seems as if 'toughness' is not necessarily detrimental.

9.8 EXPERIMENTS TO DETERMINE THE DEVELOPMENT, MORTALITY AND DISPERSION OF ISOLATED AND PAIRED LARVAE, ON TENDER LEAVES.

In the preceding and other preliminary experiments, larvae which hatched from isolated eggs on a plant died in a few days. Perhaps a certain minimum stimulus from another larva is valuable; in other words there are mutual beneficial effects at the beginning of the larval stage, up to a certain critical limit of density when mutual interference starts to have harmful effects.

The present experiments were therefore carried out in order to determine the rate of development, the mortality, and the dispersion of isolated larvae as well as larvae at very low density (2 larvae per leaf) and placed at different distances from each other.

Very young plants with tender leaves were used in order to minimize possible effects of leaf toughness, and also enable adequate replications in the space available in the constant environment rooms.

9.8.1. Materials and methods.

Three experiments were carried out in similar conditions to those of the previous experiments. Eight, six and eight plants (A to Q) respectively were used in successive experiments but since they were similar in size, age, growing conditions, etc. the results of the three experiments will be pooled. Each plant was trimmed to four leaves, which were more or less the same size, position in the plant and not overlapping.

The general experimental procedure was the same as in the preceding experiment. The moths were allowed to lay eggs on a stock culture plant during a period of about 24 hours. From this plant eggs which had been laid isolated (more than 2 cm from next egg) were taken with a water-moistened fine paint brush and transferred to the experimental plants where they were placed on the leaves, either isolated or in pairs. If in pairs, the eggs were placed at two different distances between them, either more than 20 mm or less than 1 mm. This would indicate whether the immediate presence of one egg or larva stimulated the other larva to establish itself, feed and survive.

9.8.2. Results and Discussion.

Generation mortality.

Table 9.8.1 gives the mortality of the immature stages in the generation.

Table 9.8.1. - Generation mortality.

Eggs laid:	Initial eggs	Mortal-ity(%)	Initial larvae	Mortal-ity(%)	Initial pupae	Mortal-ity(%)	Adults
Single	34	17.6	28	35.7	18	0.0	18
Paired <1mm	42	4.8	40	37.5	25	4.0	24
Paired >20mm	38	13.2	33	45.5	18	0.0	18

From Table 9.8.1 it can be seen that the overall mortality of the eggs (12%) was low although not as low as it would be expected, and this could be due to the effect of handling and transferring the eggs from the stock culture plant to the experimental ones. It also can be seen from Table 9.8.1 and Fig 36 that the larval mortalities did not show a definite effect of the treatments (35.7% when isolated against 37.5% when closely paired, or 45.5% when individuals of a pair were separated). Therefore, these results seem to indicate that the mortality was not influenced by isolation from other larvae at any rate when the leaf tissue is very tender.

The distances travelled by the recently hatched larvae from the egg to the first visible feeding place was measured in the last of the three experiments, for all the 49 newly hatched larvae. The results are shown in Table 9.8.2, together with the mean area of the leaves and the density of the initial larvae per 100 cm^2.

Table 9.8.2. - Distance (mm) from egg to first feeding place.

Eggs laid:	Mean leaf area (cm^2)	Mean larvae/ 100 cm^2	Distances (mean ± S.E.)
Singly	13.3	7.5	10.6 ± 3.63
Paired >1 mm	23.3	7.3	7.9 ± 1.36
Paired <1 mm	28.1	6.2	14.5 ± 2.13

From Table 9.8.2 it can be seen that the recently hatched larvae of P. xylostella crawled different distances according to the proximity of other larvae or eggs. For example, when the eggs were less than 1 mm apart or even touching each other, the distance travelled by the larvae before settling to feed was longer that when the eggs were isolated.

This could be interpreted as a mechanism to help the initial dispersion of the recently hatched larvae and avoid more drastic mortality.

9.9 EXPERIMENTS TO COMPARE THE DEVELOPMENT, MORTALITY, AND DISPERSION OF THE LARVAE AT DIFFERENT DENSITIES (ISOLATED LARVAE TO HIGH DENSITY) ON DIFFERENT TOUGHNESS AND SIZES OF LEAVES.

In previous experiments it was found that the mortality of the larvae was related to their initial density since, generally, more larvae died when the initial populations were more dense (in terms of initial larvae/100 cm^2 leaf) than when the density was low. Leaf toughness might also be important.

The present experiments were carried out in order to check those results by comparing the rates of development, mortality and dispersion of the larvae of P. xylostella under different densities (from isolated larvae to high density) on plants with leaves of different toughness.

9.9.1. Materials and methods.

The experiments were carried out under similar conditions to the previous experiments. Twenty nine cabbage plants were used. 24 were very young, small and with tender leaves; 5 were young and small but with tough leaves (the toughness of the leaves was achieved by depriving the plants of water for certain intervals of time). The size of the plants was in general similar. The plants were trimmed to four leaves each. The leaves were similar in size in each plant and not overlapping.

The general experimental procedure was similar to that of the preceding experiments, except that the eggs were laid on pieces of cabbage leaf in fecundity cages. The moths were placed in those

cages the day before setting up the experiments so as to have all the eggs of the same age. From the leaf-pieces the eggs were transferred to the experimental plants by means of a fine camel-hair brush moistened with water to help their removal. The eggs were placed isolated on each leaf or in small or large groups, in the latter case the eggs were placed in rows very close to each other, some of them either touching each other or in small compact batches. The leaf on which to place the eggs was variable, although usually the youngest was chosen. In the case of isolated eggs, sometimes they were isolated in one plant and sometimes isolated on one leaf (four leaves/plant), however the results can be regarded as 'isolated' for both since in previous experiments it was found that if the eggs were well separated they behaved in a similar way to fully isolated eggs.

9.9.2. Results and Discussion.

Generation mortality.

Table 9.9.1 gives the mortality of the immature stages.

Table 9.9.1. - Generation mortality.

Plant condition	Number of eggs	Egg density	%mortality during larval stage	%mortality during pupal stage
Tender leaves	22	Isolated	13.3	0.0
	40	Groups of 10	38.1	0.0
	490	Groups of 35-50	57.3	4.8
	110	Group of 110	59.6	27.8
Tough leaves	6	Isolated	60.0	0.0
	53	Group of 53	29.4	0.0
	75	Group of 75	64.6	0.0
	120	Group of 120	80.8	20.0

When the mortalities of the larvae at different densities on tender leaves are compared, it is seen that there was greater mortality among the grouped than on the isolated ones (Table 9.9.1). This confirms the results of previous experiments in which it was concluded that mortality of the young larvae is directly related to the density, i.e. density-dependent.

As before, on plants with tough leaves there was notable mortality among isolated larvae and then density dependent mortality among the grouped larvae. Unfortunately, no small groups were included in this set of treatments but the mortality of a group of 53 was less than among smaller groups on tender leaves. As previously noticed, grouped larvae seem to do better on tough than on tender leaves, perhaps because they affect each other less through their effect on the host leaf.

The distances travelled from the egg to the first feeding place could not be measured on leaves with groups of eggs because it was impossible to correlate every individual gallery with its initial egg. However, the distances were measured in some of the isolated larvae and in some of the small groups of larvae. Table 9.9.2 shows the distances in relation to the density of initial larvae.

Table 9.9.2. - Distance (mm) from egg to first feeding place.

Plant condition	Eggs laid	Mean leaf area (cm^2)	Mean larvae /100 cm^2	Distance (mean $\pm$ S.E.)
Tender leaves	Isolated	12.7	7.9	9.5 $\pm$ 2.03
	Grouped	19.4	27.1	17.6 $\pm$ 1.07

It can be seen that the recently hatched larvae of P. xylostella crawled different distances from the egg to the first visible feeding place, according to whether they were isolated or grouped. Thus, the isolated larvae travelled a distinctly shorter distance before starting to feed. This confirms results of previous experiments.

9.10. EXPERIMENT WITH PENETROMETER TO COMPARE TEXTURE OF LEAVES.

The texture of the leaves was usually described by their general appearance since for each experiment (except the last all the plants were of the same age, growing conditions, general appearance, etc.

9.10.1. Materials and methods.

Some measurements of texture were made with a penetrometer modified from the type described by Williams (1954). This penetrometer (Fig.36) consisted of a glass tube (5 x 1 cm) used as a holder, a piece of capillary tube (7 mm diameter) covered around with PVC tape to give a diameter of 7.5 mm. This holds a strip of leaf about 5 mm wide and 30 mm long in a straight and tight position. The 'reservoir' was made of a 15 mm wide strip of cellulose acetate rolled into a cylinder shape (23 mm diameter) and with a layer of cork (2 mm thick) as the base, through which a No. 8 entomological pin was placed. The general procedure was the same described by Williams (1954) using weighed silver sand. Five records were made per leaf.

9.10.2. Results.

The results in Table 9.10.1 show that there was little variation between plants (either young or mature) as measured by the readings of the penetrometer. There was also little variation between the leaves of each plant.

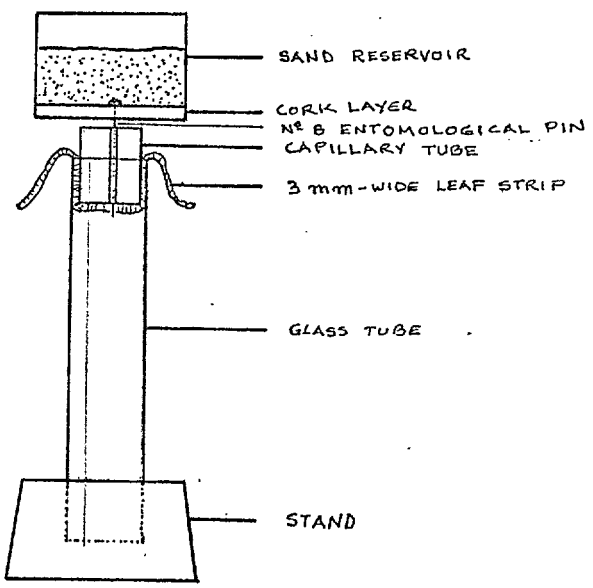


Fig. 36. Penetrometer used to 'measure' leaf toughness.

Table 9.10.1. - Leaf texture

General appearance		Penetrometer reading (g sand) (mean ± S.E.)		
Plant	Leaves	Mature leaf	Young leaf	Very young leaf
Young	Tender	1.16 ± 0.16	--	--
Young	Tender	1.01 ± 0.31	--	1.15 ± 0.05
Mature	Tough	1.43 ± 0.08	2.51 ± 0.08	1.80 ± 0.11

These results seem to agree with the experimental results in which it was demonstrated that the larvae did not suffer more mortality on tough than on tender leaves of 'very young', 'young' or even 'mature' plants. This suggests that the texture of the leaves is not very important for the survival of the larvae. For the gallery-making stages (first and some second instar larvae) the distribution of the cells within the leaf tissue seems to be important. For example, Shade & Wilson (1967) working on Oulema melanopus (L.) (Coleoptera : Chrysomelidae) found that the first instar larvae had mouth parts 77.1 microns thick when open and that out of 18 food plants all those which were favourable (11) had a distance between leaf veins of 144 ± 34 microns (average ± S.D.) which allows the mandibles to go in and bite, whilst all those unfavourable (7) had distances between leaf veins of 65 ± 16 microns which does not allow the insect to bite and feed because the weak first instar larvae cannot tear the veins apart or force its mandibles between them. Rudder & Brett (1967) found that in the leaves of Kale the cells were more compact and their walls thicker in the old leaves than in the young succulent ones, they also found that the Kale varieties

susceptible to the attack of P. xylostella had leaf tissue with loosely arranged cells and abundance of air space while those resistant had densely compact cells without air space. For example after seven days the larvae on young (tender) leaves of a resistant variety of Kale had higher mortality (45%) than those on young (tender) leaves of a susceptible variety (25%), but on mature (tough, harvest maturity) leaves the difference in mortality between resistant and susceptible varieties was not so big (80% and 70% respectively), and in old hardened leaves of either variety no larva at all survived; on cabbages they found that the red varieties are more susceptible than the green varieties; for example the mortality of the larvae after 7 days of hatching was 25% on young leaves of red cabbage and 35% on young leaves of green cabbage; however no larva survived on old hardened leaves.

9.11. DISPERSION OF THE LARVAE.

9.11.1. Introduction.

The dispersion of a population is defined as the pattern of distribution of the animals in space, and may be of considerable ecological significance (Southwood, 1966).

There are many indices and mathematical models which describe the populations of animals or plants in space. Insects, especially those which are pests of agricultural crops, tend to be highly concentrated in areas in which the food plant is grown; therefore the variance of their populations is greatly larger than the mean, and hence that they are described by the negative binomial distribution (Bliss & Fisher, 1953). In spite of this

artificial concentration of individuals in cultivated plants, sometimes more than one distribution may fit the data or alternatively none of them fits significantly. On the other hand when the size of the sampling unit is changed, the value of dispersion parameter K of the negative binomial also changes; therefore the type of distribution changes, thus limiting the comparison of the distributions to those in which the same size of sampling unit has been used (Southwood, 1966). It is commonly found in agricultural entomology, that the sampling unit used is the whole plant; therefore when the data of the populations are analysed, they usually fit the negative binomial. Several examples of those types of changes are given by Southwood (1966). Harcourt (1960b) analysed the data on field counts of the immature stages of P. xylostella on cabbage and found that, using the whole plant as the sampling unit, they significantly fitted the negative binomial.

Another way of expressing the distribution of the population is by measuring the degree of aggregation of the individuals. As mentioned above, there are many indices which express that aggregation. Amongst the most common are: the 'index of dispersion' which is calculated as the ratio of the variance to the mean (the larger the index the more aggregated the individuals); the 'K' parameter of the negative binomial (the smaller 'K' the more aggregated the individuals); 'Morisita's index of dispersion' (the larger the index the more aggregated the individuals); and 'Lloyd's mean crowding' (the bigger, the more aggregated). Details of calculations and their implications are given in Southwood (1966).

9.11.2. Materials and methods.

In the present investigation two sizes of sampling unit were used for the analysis. In the laboratory experiments the leaves were divided in 16 quadrats, as described before, and the quadrat was chosen as the sampling unit. In the field experiments the sampling unit used was the whole leaf because of difficulty in separating quadrats on each leaf. The data were arranged as frequencies and fed into the Imperial College Computer and all the necessary parameters calculated.

9.11.3. Results.

The results are given in Appendix - Tables (9.11.1 to 9.11.10) and Figs 37 and 38. The appendix-Tables give in the first column 'Morisita's index of dispersion' which is considered as one of the most valuable expressions of contagiousness. The second column gives the 'index of dispersion' ($s^2/\bar{x}$) which is a basic measure of the dispersion. The third and fourth columns give the probability of the difference between the expected and observed values when the chi-square test (the 'alternative test') for goodness of fit was applied to Poisson and negative binomial respectively. The fifth column gives the dispersion parameter, K, of the negative binomial. The last column gives the value of 'Lloyd's mean crowding'.

Figs 37 a and b show the variation of two different indices of dispersion (Morisita's and $s^2/\bar{x}$) with relation to the age of the immature stages of P. xylostella, at medium density of larvae per plant (116-180) initial larvae per plant, respectively). Figs 37 c to f show the variation of Morisita's index of dispersion with age of the larvae at different densities of initial larvae per plant,

low (10-24), high (123-266), and very high (420-550). Fig 38 shows the variation of the Morisita's index with the age of the larvae under field conditions when all parasites and predators were excluded so that only intraspecific competition (and to a lesser extent rainfall) was affecting the densities and therefore the distributions.

9.11.4. Discussion.

From Appendix-Tables 9.11.1 to 9.11.8 and Fig 37(a to c) it can be seen that, in laboratory populations, the degree of aggregation of the immature stages of P. xylostella at medium densities, is variable throughout its development. The eggs are highly aggregated (high values for the aggregation indices) and so are the larvae during the first and part of the second instar because of their mining behaviour which, as explained in the Chapter on Behaviour, is characterized by the burrowing of mines in the proximity of the eggs; however as the mines grow longer the larvae either meet thick leaf veins or other larval galleries which force them to go out and start to construct other mines somewhere else. This behavioural pattern at medium and high densities (and also the density-induced mortality) makes the larval population change from highly aggregated to less aggregated and even to random in a relatively short time. This is shown in Fig 37 a to c by the steep decrease of the curve and also in Fig 39 by the change in height of histograms showing the percentage of the total population which is living on each leaf at different dates. As the larvae grow bigger they disperse more evenly throughout the different leaves of the plant. Normally there is little movement from plant to plant. The larvae tend to remain in that even distribution up to the end of the larval stage when they tend to aggregate before pupation (i.e. higher aggregation indices, see Figs 37 and 38). This is also shown

in Appendix-Tables 9.11.1 to 9.11.8 in which at the beginning of the larval stage the distribution fits better to the negative binomial distribution, later with the increase in age they fit better the Poisson distribution and at the end of the stage, near pupation, they fit again the negative binomial distribution. The general shape of the curve formed when plotting the indices of aggregation (Morisita's or $s^2/\bar{x}$) is concave (hyperbolic type) with a certain flat sector in the middle corresponding to the active 'spacing' of the larvae.

As mentioned before, the overall pattern of dispersion is generally affected by both the initial density of the larvae and the mortality of the early instars. The higher the density the higher the mutual disturbance and the higher the early instar mortality, therefore the larvae take shorter time to get evenly distributed over the leaves. At lower densities the mortality is also lower and the larvae (especially the early instars) remain longer in their original feeding place hence maintaining a similar level of aggregation for longer time.

In field populations, when natural enemies were excluded in order to show only the effects of intra-specific competition Appendix-Tables 9.11.9 and 9.11.10 and Fig 38), the eggs and recently hatched larvae are, as expected, highly aggregated (Morisita's index of dispersion values from 8 to 21), but immediately after the first instar they begin dispersion to other leaves, which is accompanied by some mortality according to the density. They disperse until they reach a certain pattern of distribution which fits the negative binomial (Morisita's index of dispersion about 2-3) at which they stay without significantly changing (Fig 38). For pupation the population remains in a

similar distribution, showing only a slight tendency to aggregation (Fig 38). The plants were much larger and rougher surfaced than in the laboratory experiments so pupation sites were probably not so limited.

In general it can be said the larvae of P. xylostella tend to be aggregated at the time of hatching because the adults lay the eggs close to each other or in small groups (see Chapter on Life history). This initial aggregation may help the larvae during the first hours of life because it may encourage them, by mutual stimulation, to feed and construct their galleries. Later the populations tend to be more sparse and the distribution tends to be random, or even tend to reach uniformity and then fit better to the Normal distribution (regular). This may imply a spacing mechanism by which the larvae tend to be near to each other (probably for mutual stimulation) but at the same time keeping a certain distance so as not to interfere or disturb themselves. This spacing is mainly induced by the behaviour of the larvae which tend to wriggle away from any mechanical disturbance such as the touch of another larva, and then settle again. If the disturbance persists the larvae may wriggle out of the leaf and, by hanging from a silk-thread, move to another leaf at a lower level. This type of behaviour is not commonly recognised among Lepidoptera or other insects, although Kennedy & Crawley (1967) describe in detail what they called the 'space-out gregariousness' (or 'social' aggregation) of aestivating Drepanosiphum platanoides (Schrank) (Hemiptera : Callaphididae) on sycamore leaves, in which the adult aphids settle gregariously although maintaining a minimum distance such that each is only occasionally touched by another; when a settled aphid is touched by another it will move away and settle nearby, but when a walking

aphid is touched it will also move away but shortly afterwards it will settle nearby (if not touched it will continue walking). This spaced-out gregariousness has a beneficial effect enabling the aphids to escape when they are attacked by predators. It might be acting in the same way in dense populations of larvae of P. xylostella; that is when the larvae are disturbed they twitch or wriggle with an intensity proportional to the disturbing effect of the predators. At the same time such dispersion minimises over-population and therefore perhaps minimises starvation by allowing (or forcing) individuals to migrate from overpopulated to under-populated areas of the plant, and even away from the plant. However it is noteworthy that this mechanism does not appear to work at the earlier stages perhaps by limiting the numbers of individuals by causing early-instar mortality it ensures that surviving larvae will have adequate food, space and other requisites to complete development.

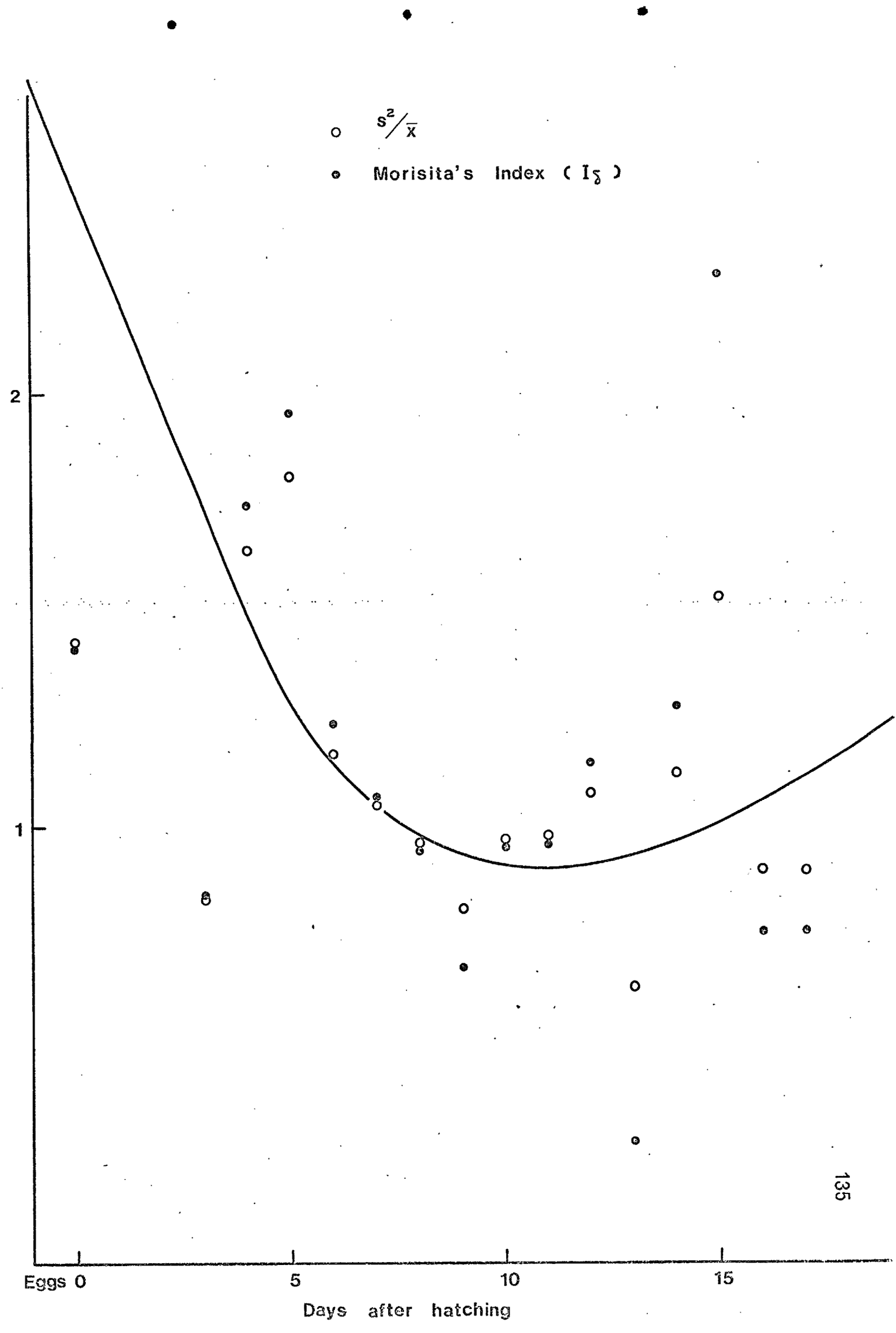


Fig. 37.a. Dispersion of larvae in laboratory populations.

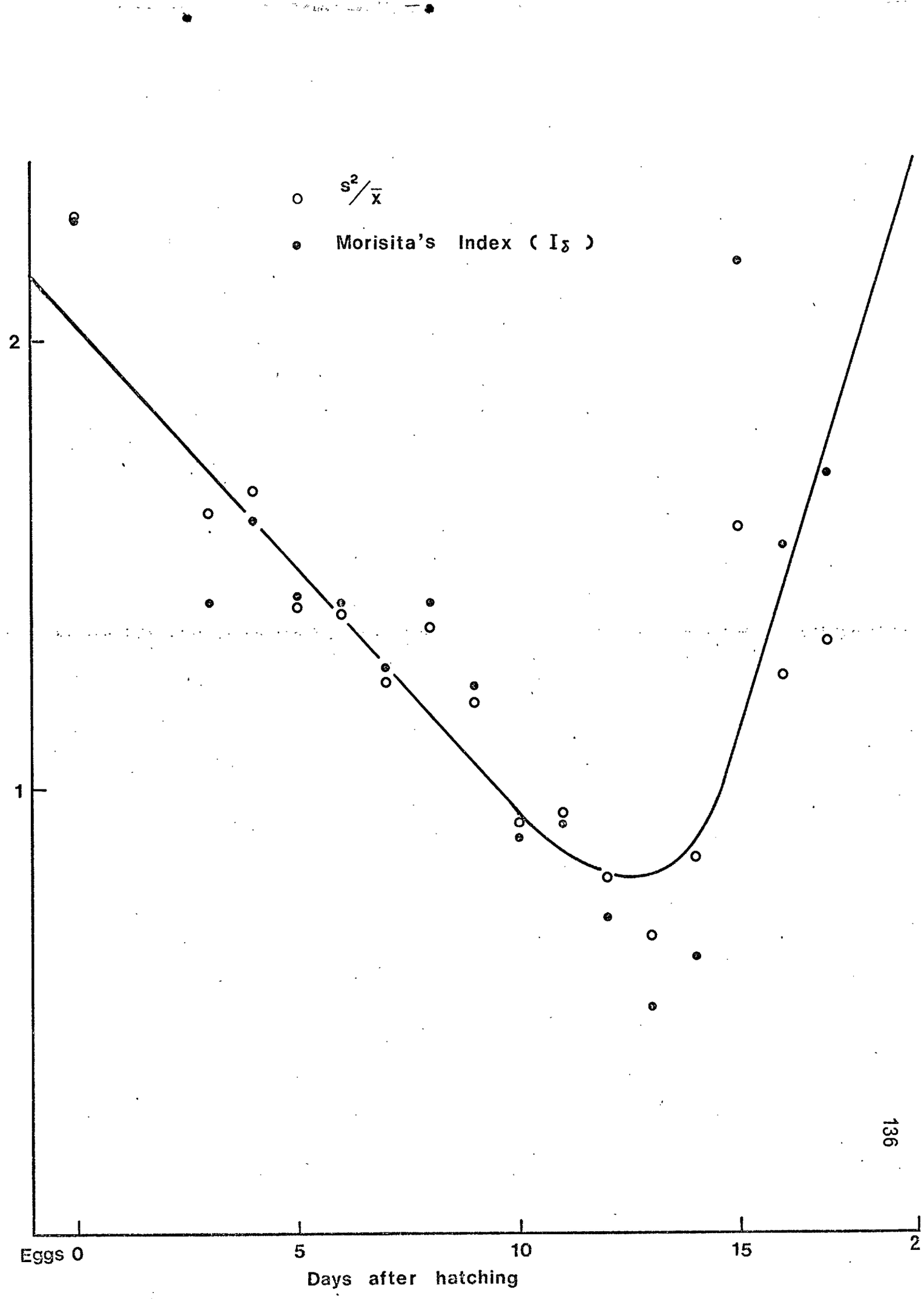


Fig. 37.b. Dispersion of larvae in laboratory populations.

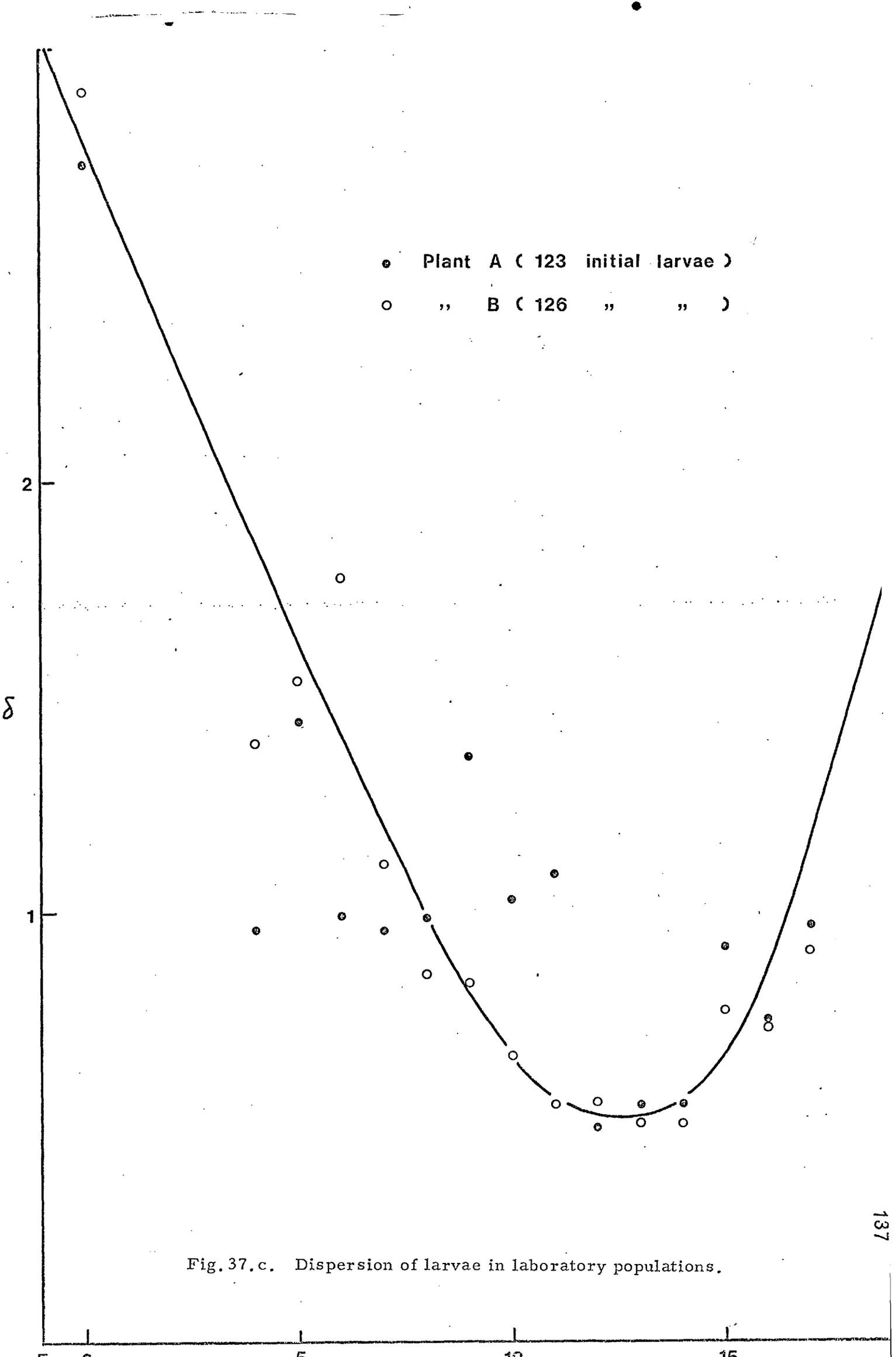


Fig. 37.c. Dispersion of larvae in laboratory populations.

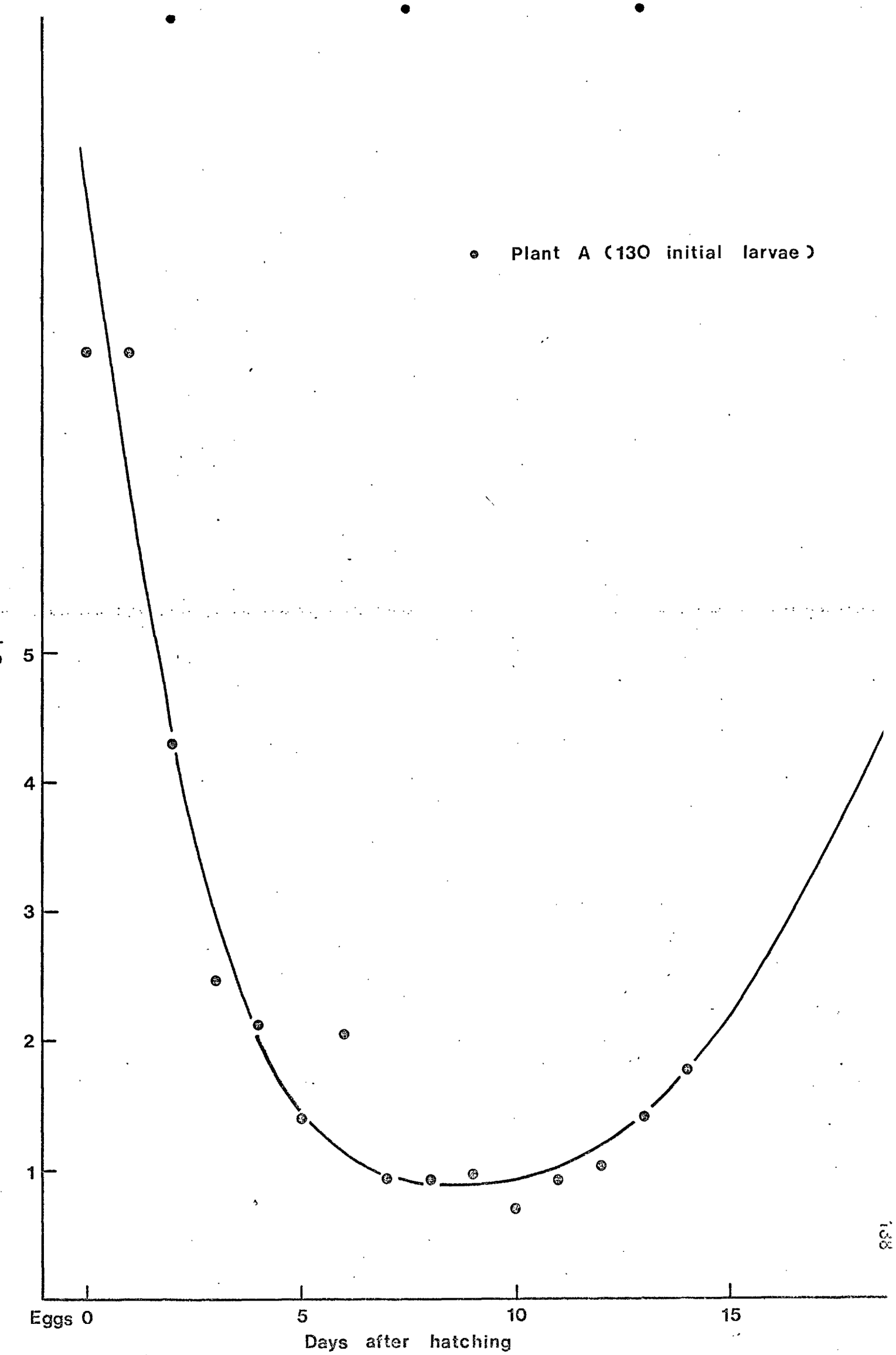


Fig. 37.d. Dispersion of larvae in laboratory populations.

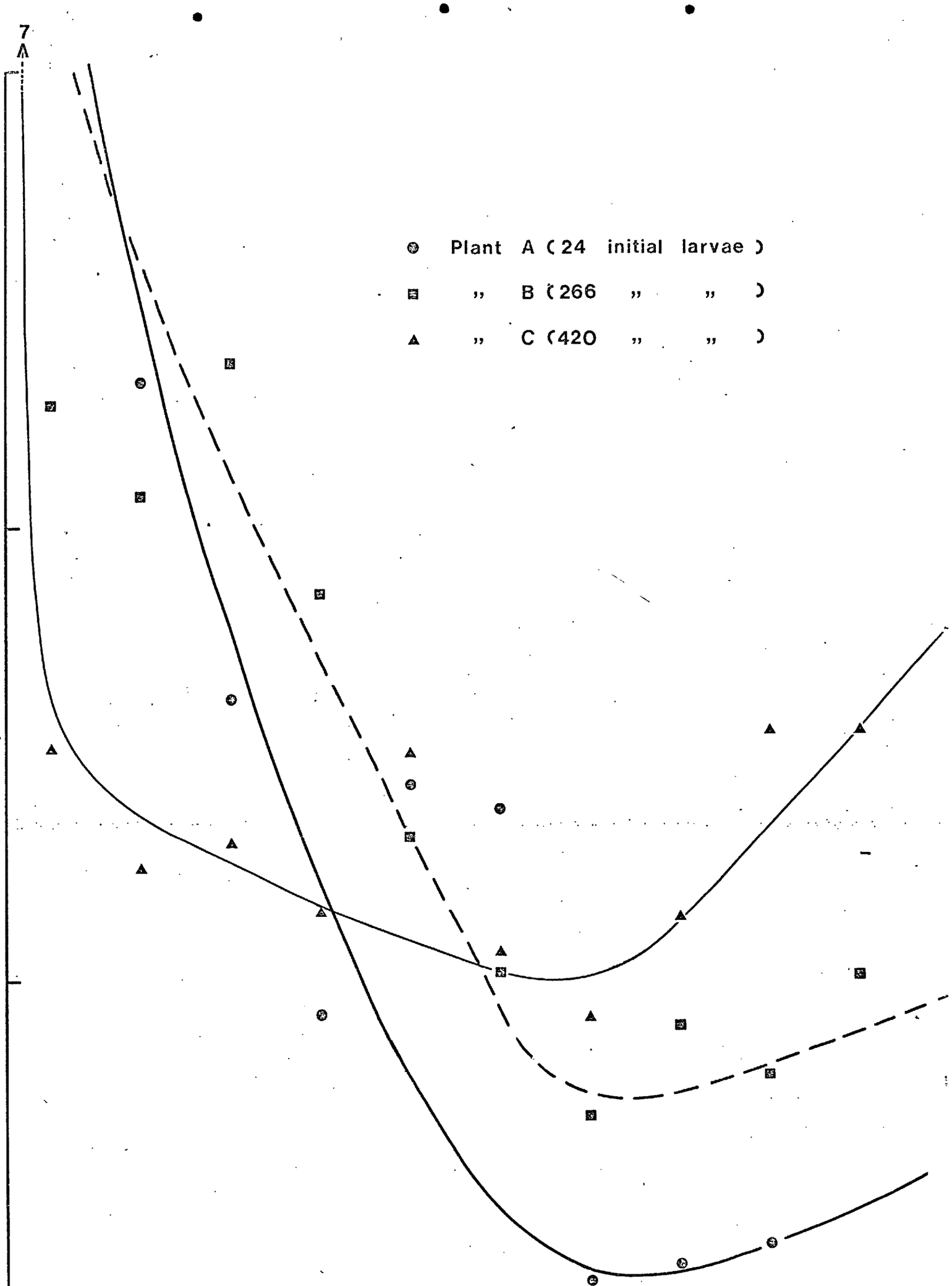


Fig. 37.e. Dispersion of larvae in laboratory populations.

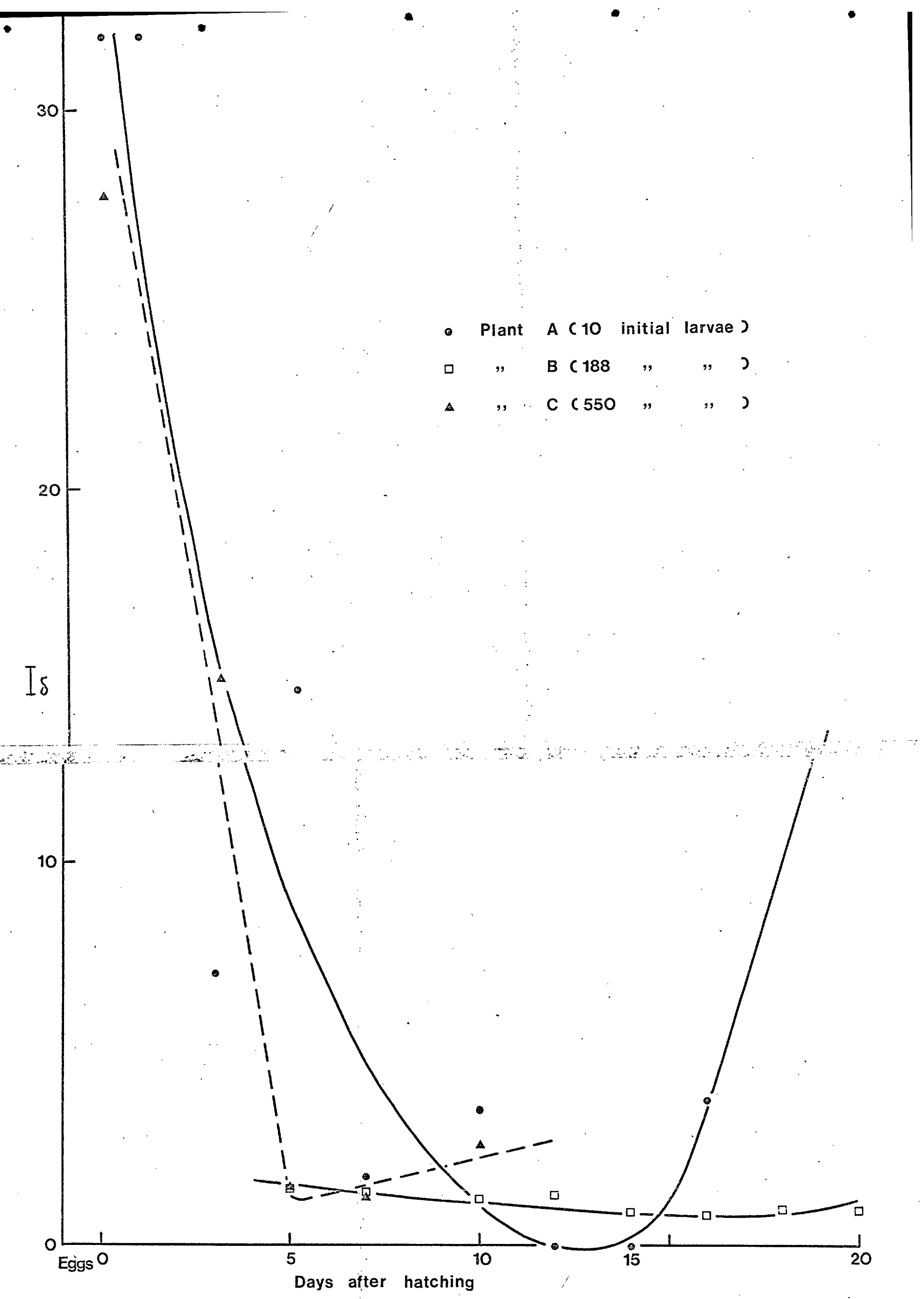


Fig. 37. f. Dispersion of larvae in laboratory populations.

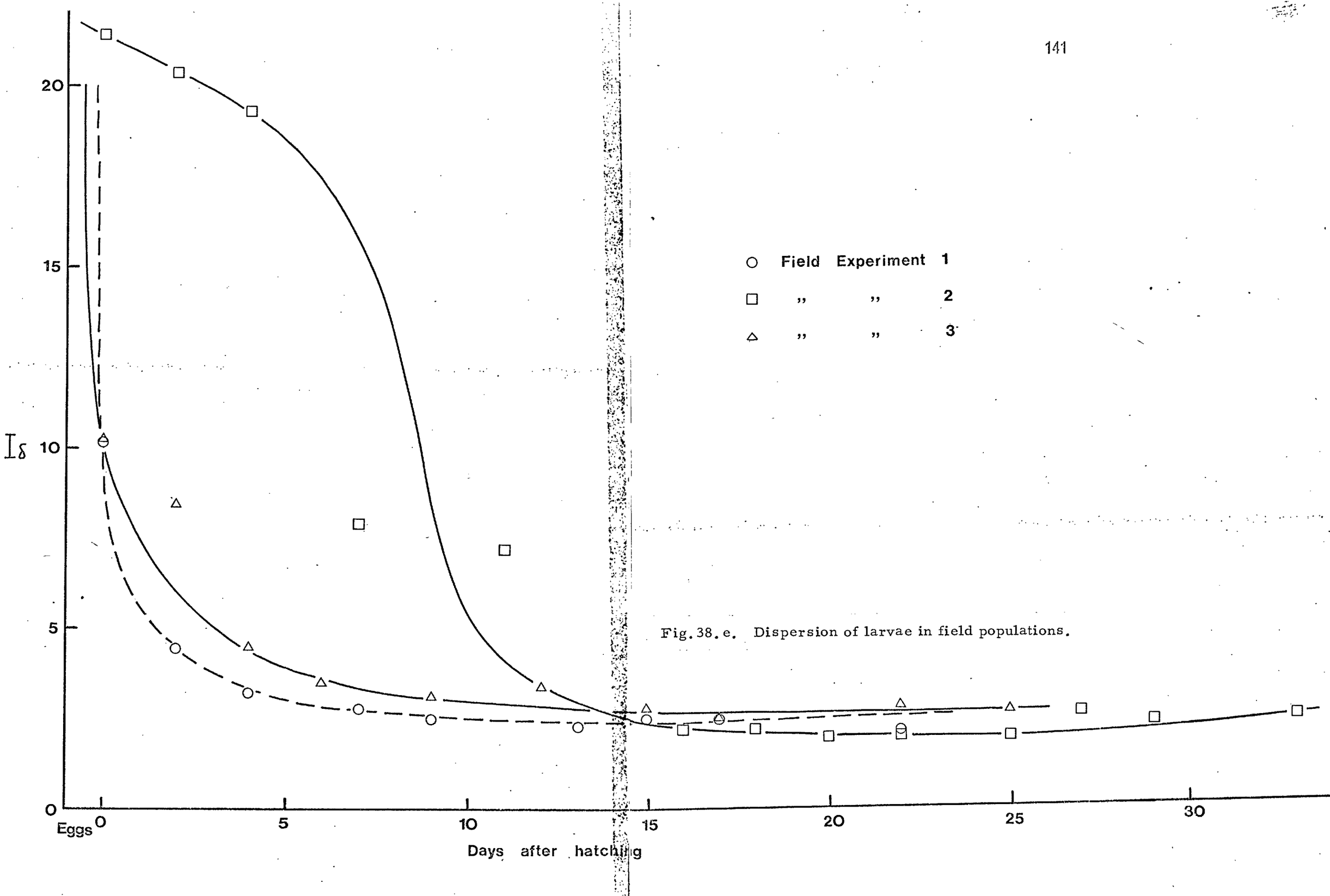


Fig. 38. e. Dispersion of larvae in field populations.

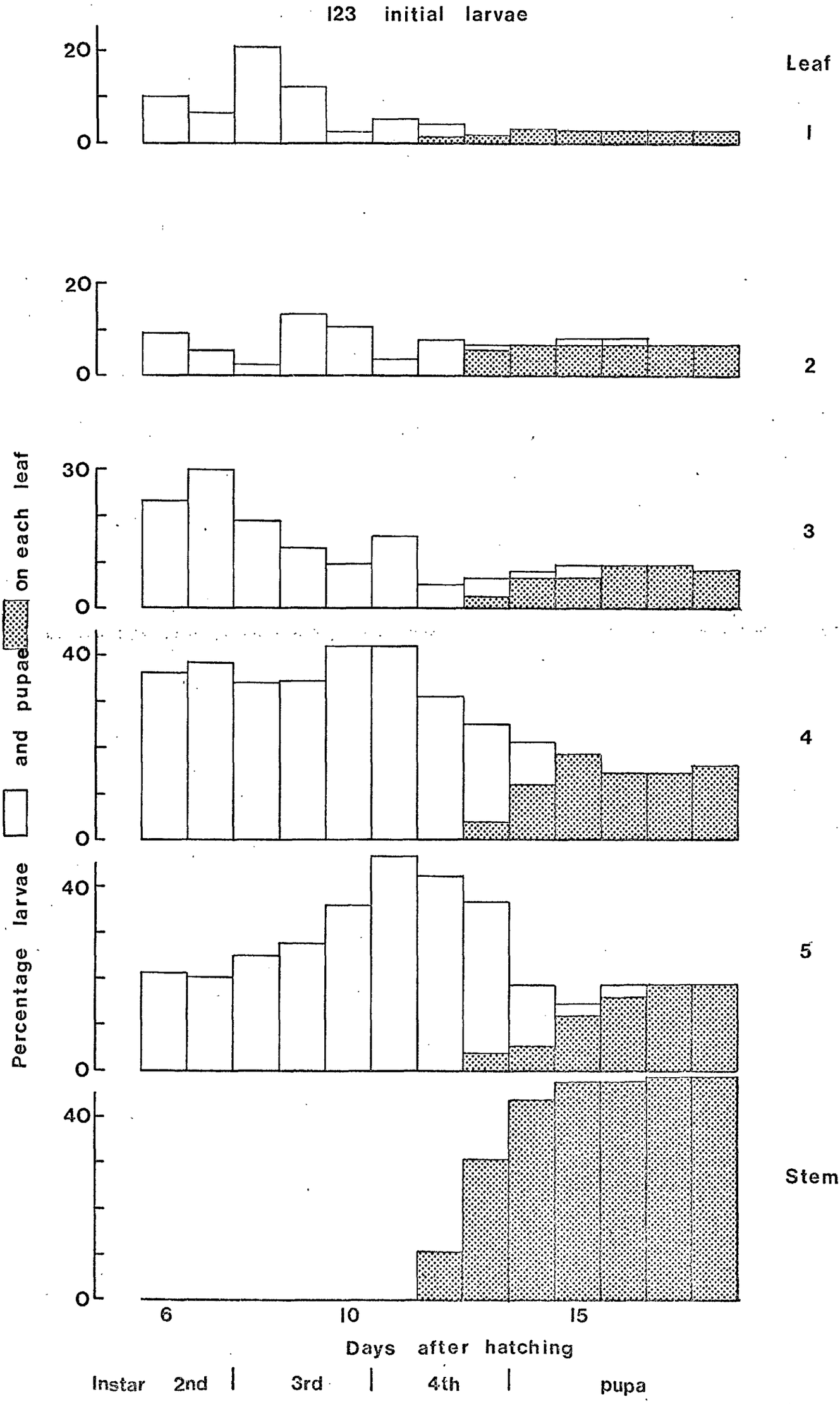


Fig. 39. Distribution of larvae on the leaves (as % of total larvae).

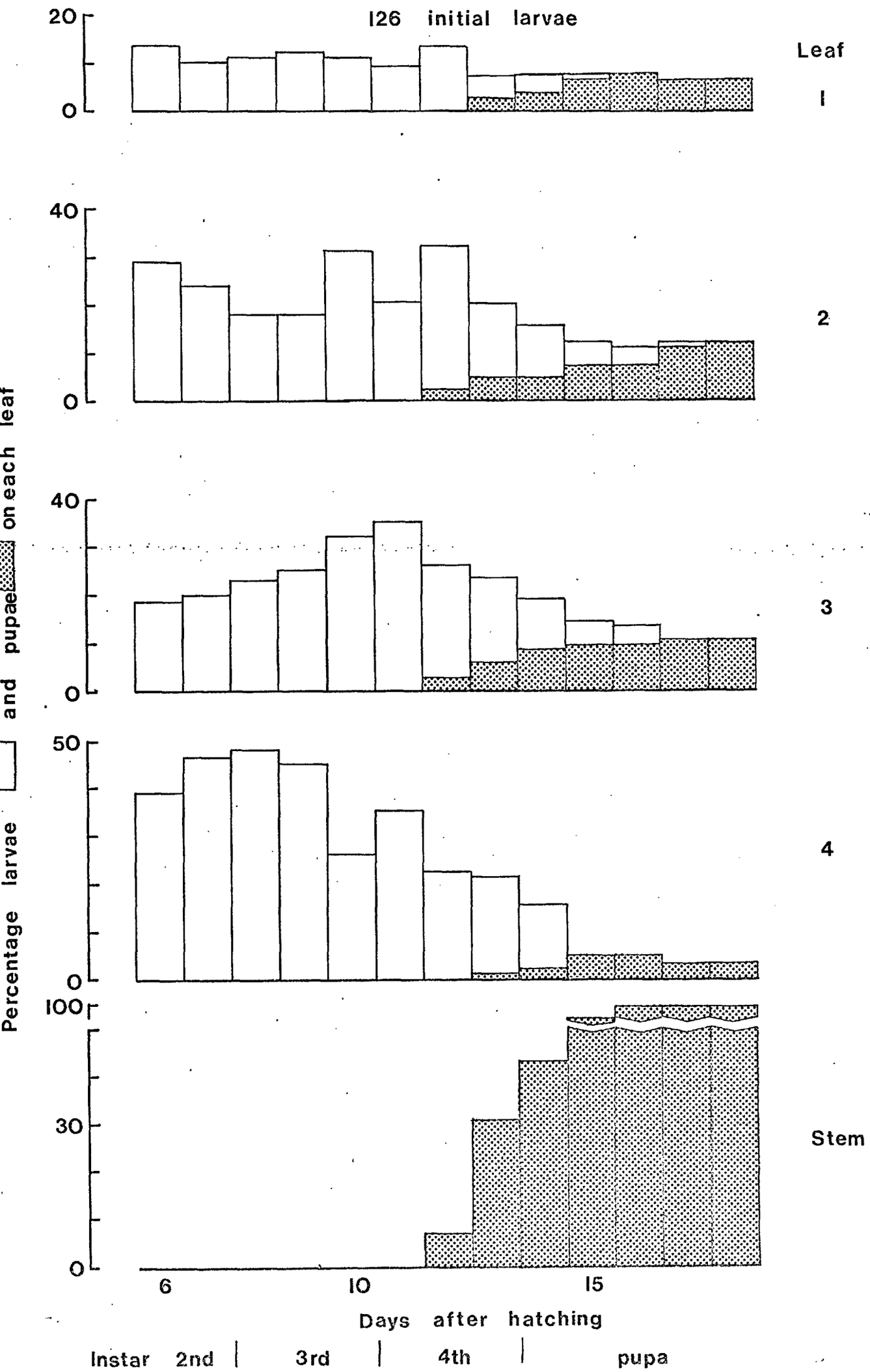


Fig. 39. a. Dispersion of larvae in laboratory populations.

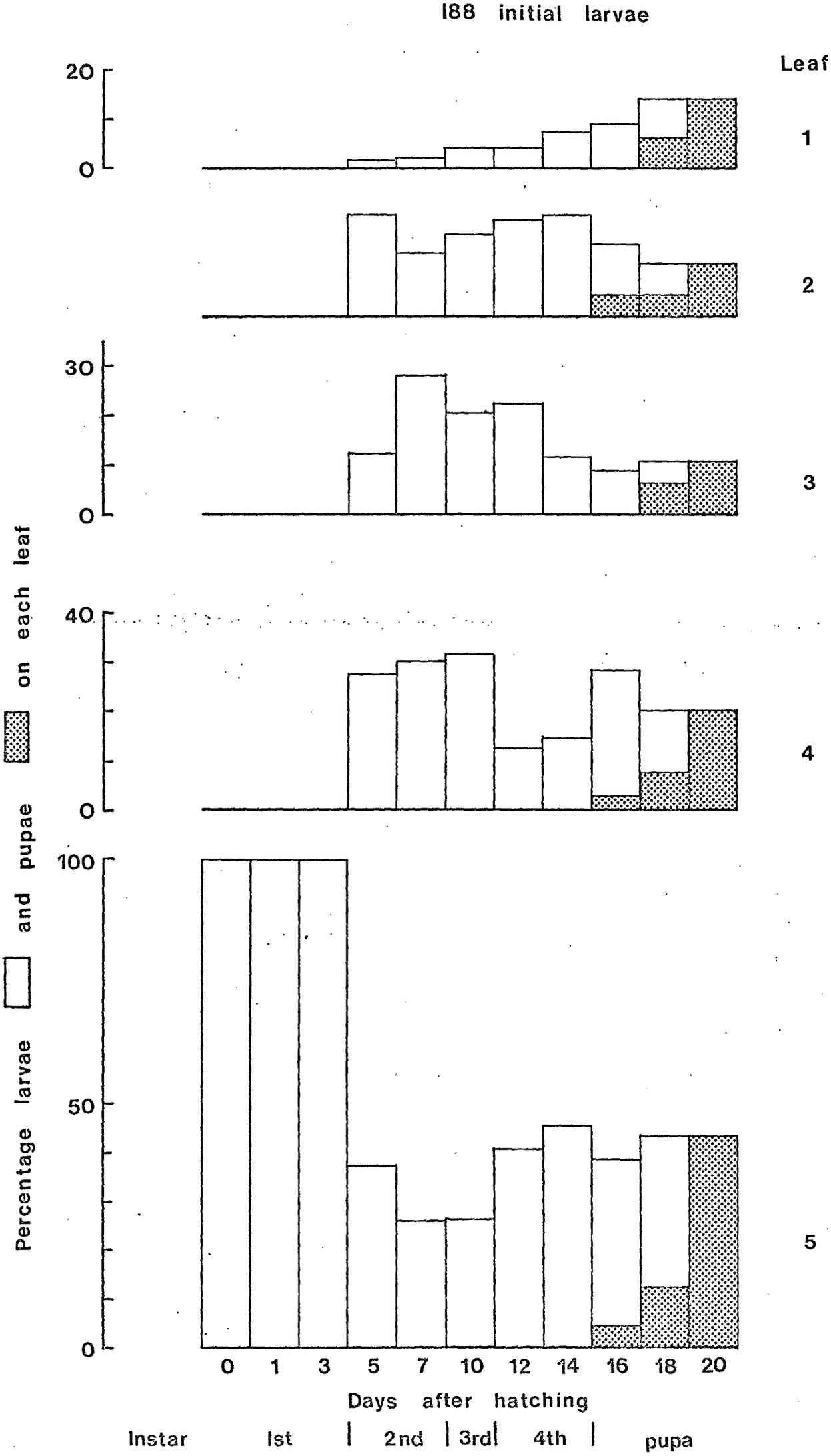


Fig. 39. b. Dispersion of larvae in laboratory populations.

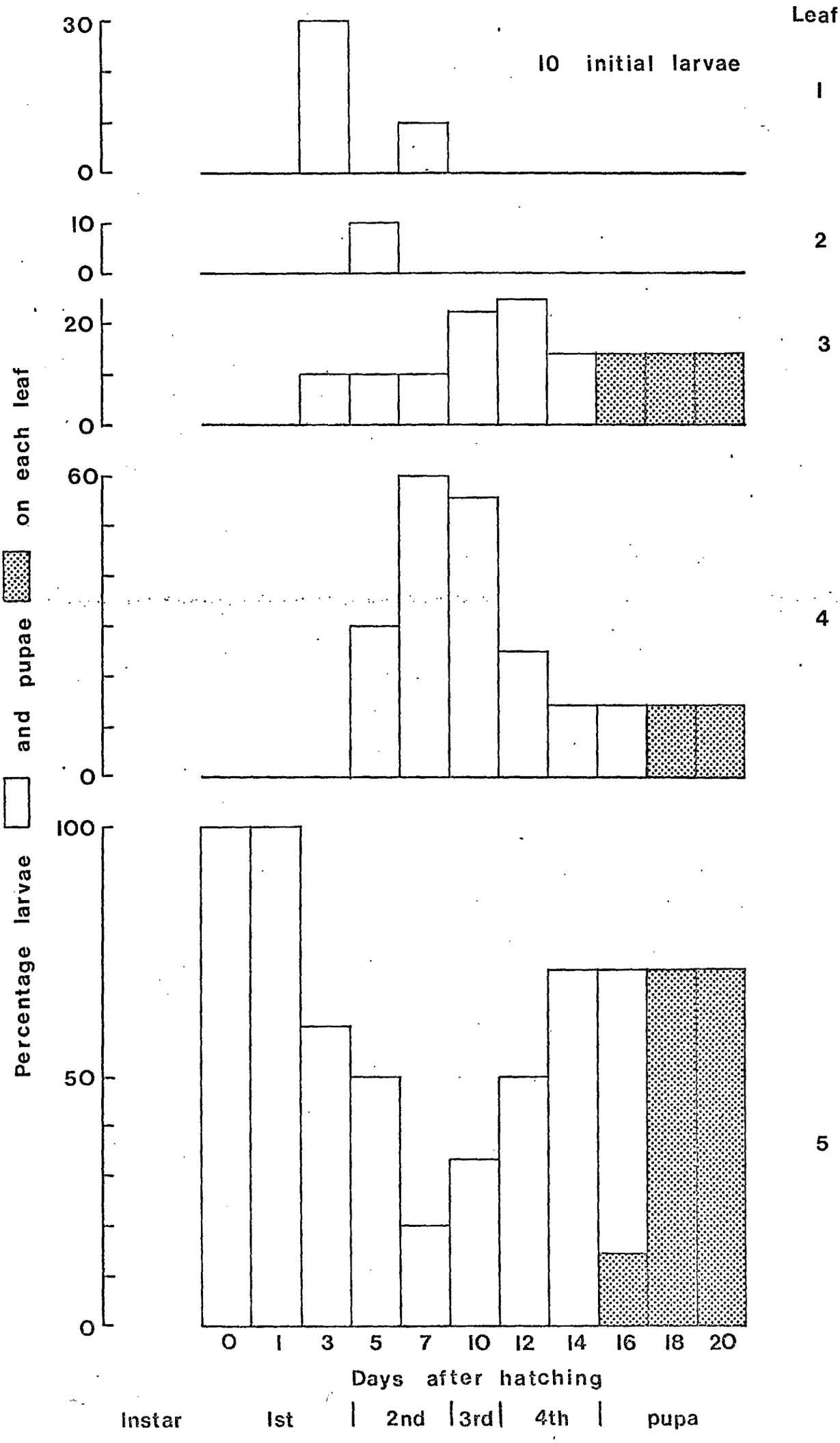


Fig. 39. c. Dispersion of larvae in laboratory populations.

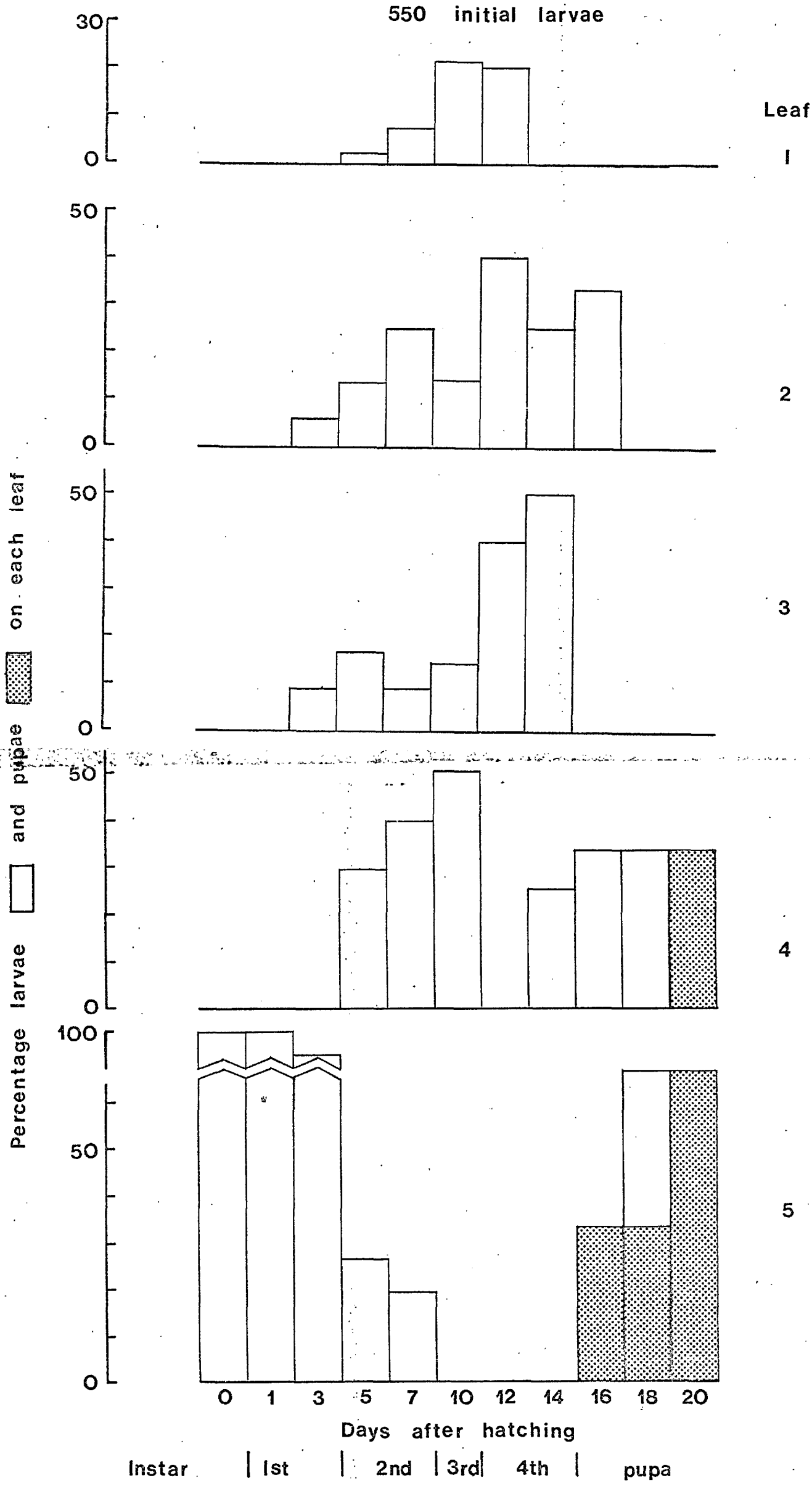


Fig. 39. d. Dispersion of larvae in laboratory populations.

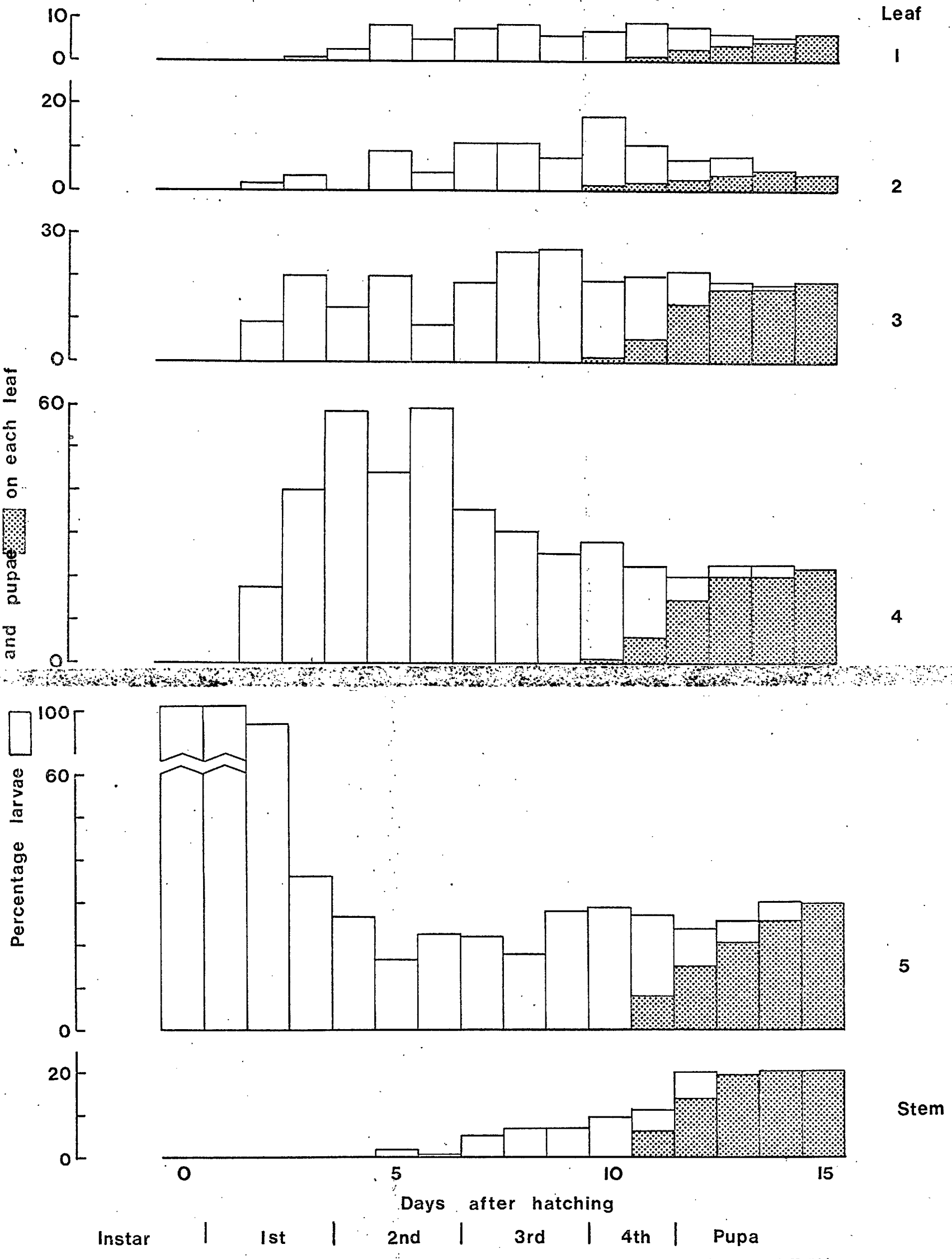


Fig. 39. e. Dispersion of larvae in laboratory populations.

10. STUDIES ON CAUSES OF MORTALITY IN FIELD POPULATIONS OF P. xylostella.

10.1. INTRODUCTION.

A series of field experiments were done in order to determine mortality and dispersion of populations of P. xylostella on B r ussels Sprouts in conditions where caging methods were used to protect them from different causes of mortality. It is known from the literature that parasites may kill many larvae of P. xylostella (Adashkevich, 1966; Anon., 1946; Delucchi et al. 1954; Harcourt, 1960a, 1963a; Hardy, 1938; Hassanein, 1958; Kopvillem, 1960; van der Laan, 1955; Lloyd, 1940, 1942; Miller & Hudson, 1953; Parker, 1971; Pimentel, 1961; Robertson, 1939; Todd, 1957; Ullyett, 1947; Yarrow, 1970), but little is known about the effects of parasitism and of the other mortality factors such as rainfall, birds and other predators on the dynamics of the species.

THE FIELD STATION
SILWOOD PARK

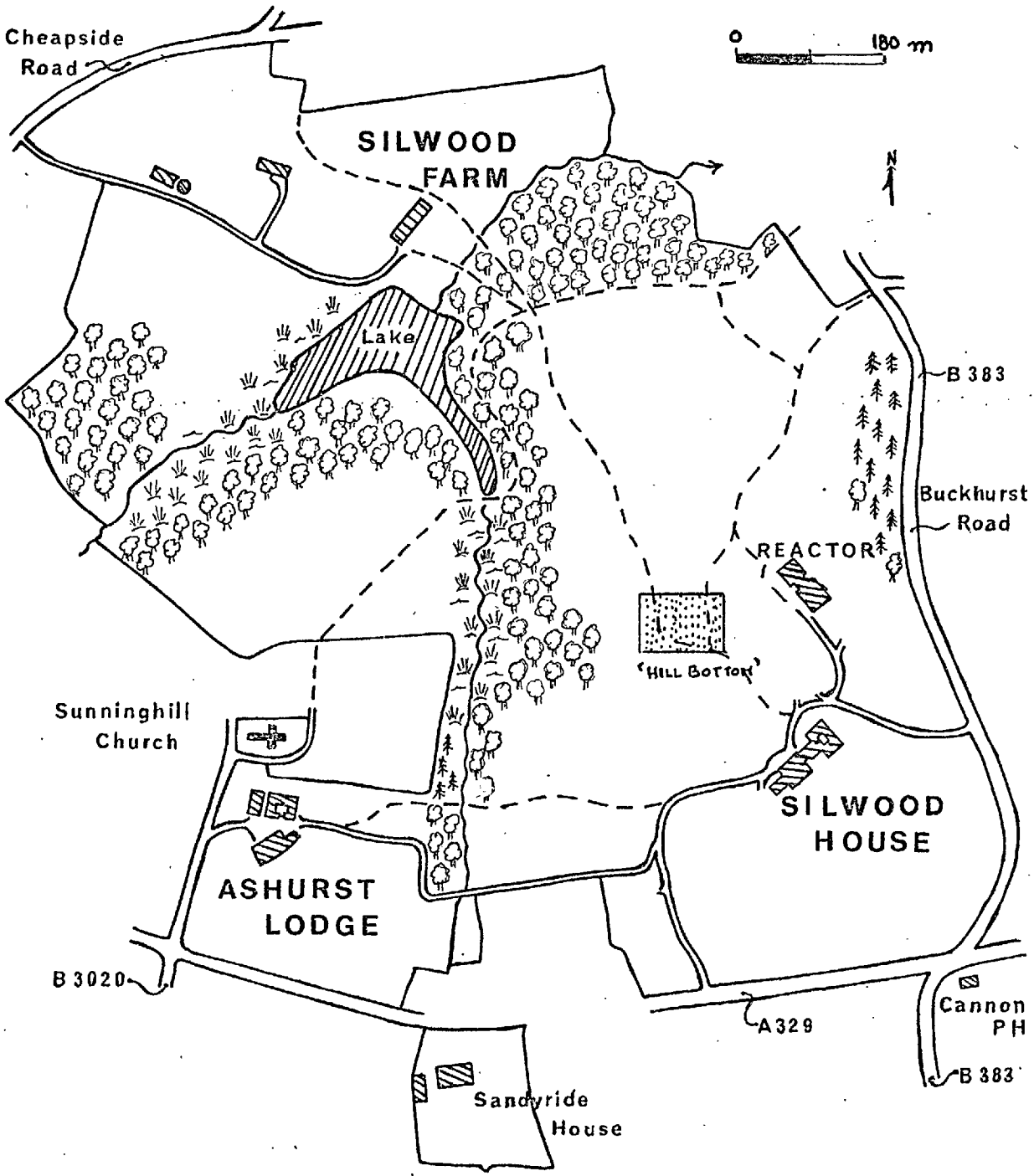


Fig. 40. Map of Silwood Park showing "Hill Bottom" area.

10.2. MATERIALS AND METHODS.

10.2.1. The field.

The field experiments were all carried out in the "Hill Bottom" area at the Imperial College Field Station, Silwood Park, Ascot, Berks. (Fig 40). The land slopes slightly from East to West. The soil is classified as Bagshot Sands, and is very sandy with small stones and basically of acid pH. The land was given 40 tons of cow manure per acre and lime was applied to give a pH of about 7. "Hill Bottom" is normally maintained under a crop rotation of Potatoes, Field Beans, and Brassicas. The chosen Brassica crop is Brussels Sprouts.

10.2.2. The plants.

The plants used in the field experiments were Brussels Sprouts, var. 'Irish Elegance' because the shape of the plant and distribution of leaves allowed relatively easy handling of the plant without damage during the observations. The larvae could also be seen with less difficulty than on cabbage plants where it was necessary to 'dissect' the plants leaf by leaf in order to obtain satisfactory records for population studies (Harcourt, 1955).

The field experiments were begun in mid-July when the plants had about twenty to thirty full grown leaves. By August the plants had about forty to fifty full grown leaves and by early September they were sixty or more.

The plants were set out in rows 91 cm apart in and between the rows (Fig 41).

10.2.3. The exclusion cages.

Cages were used in the field experiments in order to obtain information about the importance of the different mortality factors on P. xylostella larval and pupal populations.

The cages were made of a wooden frame (75 x 75 x 150 cm) and different materials were used on the walls and roof according to the factor or factors to be excluded. A door was provided to allow inspection of the plants.

To isolate all parasites and predators the cages were covered with Terylene netting (440 mesh per square inch = 10.45 cm^2) with holes small enough to isolate the parasites and predators without greatly altering the micro-climate (Fig 42) (Way & Banks, 1968).

To isolate birds the cages were covered with a string net (about 4 mesh per square inch = 10.45 cm^2) with holes big enough to let arthropod predators and parasites go freely in and out but too small for birds (Fig. 43).

To isolate rainfall a wooden frame bearing a transparent polythene roof (240 x 240 cm) was placed on top of a cage and secured against the wind by strong wires from each corner to stakes in the soil. The side walls of the cages were open so parasites, birds, and any other predators were unimpeded, at least from the sides (Fig 44).

To isolate crawling soil predators wooden frames (Fig 45) were put around the plants; outside these frames other frames made of four wooden boards (30 x 120 cm) were dug into the soil about 10 cm deep in order to prevent any possible subterranean predator coming in. All the ground inside both frames was treated with 2% dieldrin dust in order to kill any insect predators that might have crawled into that piece of ground. The part of the wooden frame which remained out of the soil was covered with a sticky band



Fig. 41. Brussels Sprouts experimental plantation.



Fig. 42. Cage to exclude all parasites and predators.



Fig. 43. Cage to exclude birds

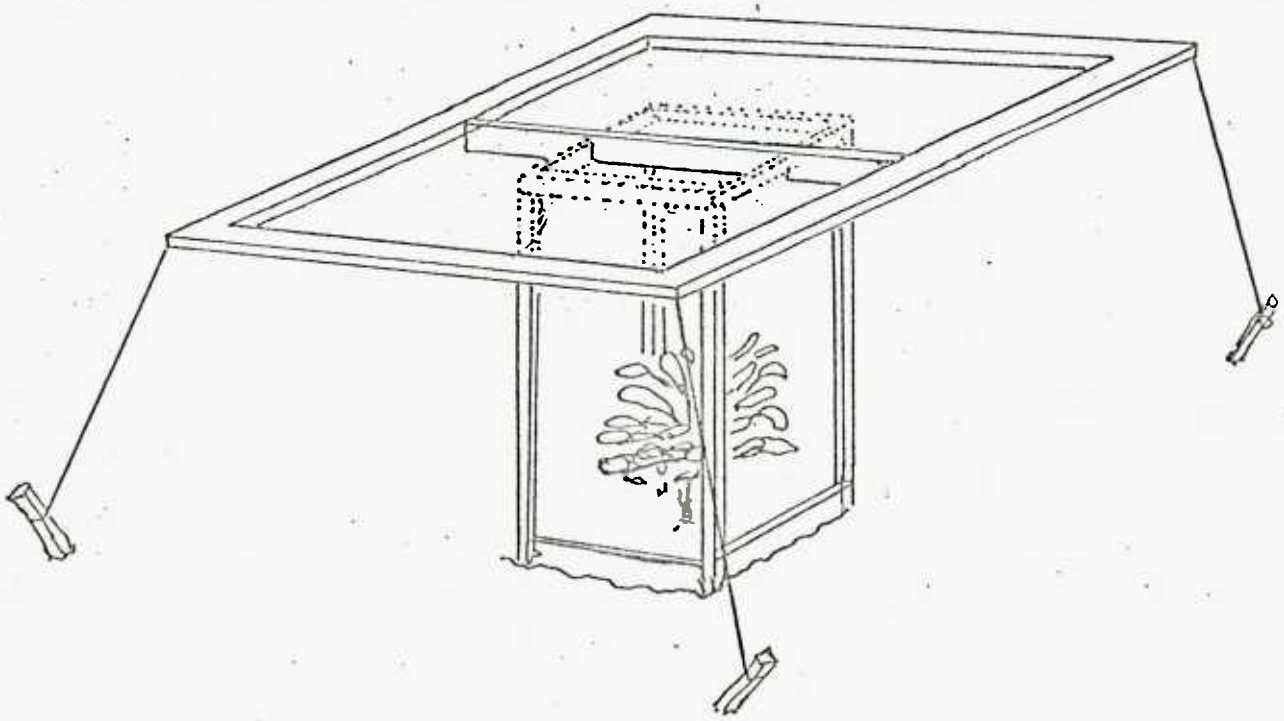


Fig. 44. **Cage to exclude rain.**



Fig. 45. Cage to exclude soil predators.



Fig. 46. Oviposition cage on plant.

(ICI Fruit Tree Grease Band) to stop any predators crawling into the area of the plant. Any flying predator could easily reach the plant as no other excluding material was used.

10.3 SETTING UP THE FIELD EXPERIMENTS.

10.3.1. Establishment of field populations.

Suitable Brussels Sprouts plants were selected, i.e. at least 5 metres apart, similar in size and appearance and at least five rows from the edge of the field.

All the insects were removed from the plants; the senescent lower leaves and the axillary buds were cut off, and the remaining leaves were trimmed. The leaves were labelled, and numbered from the bottom upwards. Cages, as described above, were placed over individual plants.

One oviposition cage (Fig 46) was placed on a single chosen leaf which was usually about 90 cm^2 and had enough space to hold the cage on one side of the central vein. The oviposition cage was secured with wire so that it did not damage the leaves. A group of about twenty P. xylostella adults from the laboratory culture was placed in the cage. After three days the oviposition cages with the moths were taken out.

10.3.2. Method of counting.

The initial numbers of eggs were not counted because they were laid on the leaf surface, on the walls and on the foam-lining of the oviposition cages. It was assumed that no externally caused egg mortality occurred under the experimental conditions since no parasites or predators of the eggs have been recorded (Thompson,

1946, Thompson & Simmonds, 1964). In the field infertility is normally insignificant, i.e. less than 1% (Harcourt, 1969), and it is assumed that this was the case in the present experiments.

The larvae were counted every two or three days. At the beginning it was very difficult to locate the larvae inside the mines and this could only be done by looking at the leaves against the light. Later the larvae started to disperse to different leaves and the time used in finding them increased.

The pre-pupae were easily identified in the field before and after cocoon formation and they were recorded as such, but in the results of the experiments they are tabulated under 'pupae' because it was impossible to follow individually every one before cocoon formation and also because some larvae became pupae during the period between two countings. Parasitism was counted by the presence of the parasite cocoon inside the P. xylostella cocoon. Predation of the larvae was assessed as being related to the disappearance from the plants. Pupal predation was more evident because they are stationary and every one is localized, therefore if predated they could be seen as either torn out of the cocoon or taken away with the cocoon leaving only the mark. The adults were assessed by counting the empty pupal exuviae from which adults had characteristically emerged.

10.3.3. Analysis of the data.

The data were analysed in terms of mortality. A short definition of the terms most commonly used when comparing the mortality factors within a generation will be given below; for details in their calculation see Southwood (1966) pp.291-293.

Apparent mortality. - This is the measured mortality the numbers dying as a percentage of the numbers entering the stage. Its main value is for simultaneous comparison either with independent factors or with the same factor in different parts of the habitat.
Real mortality. - This is calculated on the basis of the population density at the beginning of the generation; is given as a percentage of that density, and therefore is accumulative through the different stages of the generation. It is useful for comparing the role of population factors within the same generation.
Indispensable (or irreplaceable) mortality. - This is part of the generation mortality that would not occur, should the mortality factor in question be removed from the life system, after allowance is made for the action of subsequent mortality factors. It is often assumed that these will still destroy the same percentage independent of the change in prey density; clearly this assumption will not always be justified.

With relation to the analysis of the data, the mortality of the treatments and replicates were compared by the 'analysis of the variance'. The Least Significant Difference was taken as described by Snedecor (1956) as Hartley's test in which the means are ranged and different values of Q are used, one for each range of means. The formula is:

Least Significant Difference = Q x Standard Error of the Residue

(For details see Snedecor (1956) pp. 251-253).

10.4. FIRST FIELD EXPERIMENT (SUMMER 1969).

The experiment was carried out during the Summer (July-August) of 1969.

The main mortality factors to be assessed were: birds (predators), other predators, parasites, and rainfall.

10.4.1. Materials and methods.

The Brussels Sprouts plants were set in the field at the end of May and in June, and were allowed to develop into well grown plants by July. In the third week of July the plants were artificially infested and caged as previously described. Three plants were used for each treatment. The effect of the factors excluded was assessed by comparison with the populations of larvae on plants without cages.

The oviposition cages with the moths and unhatched eggs were removed one day after the hatching started in order to make all the larvae of about the same age.

No attempt was made to measure the size of the leaves as it was changing rather quickly and because of the difficulty in measuring the young, folded leaves of the 'head' of the plant. There were about twenty five completely open leaves per plant at the beginning (21 July 1969) and about forty when the experiment was finished (26 August 1969).

10.4.2. Results.

Effects of excluding all parasites and predators.

Table 10.4.1. - Plants protected from parasites and predators.

Mortality in successive instars (total of 3 replicates):

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	337	116	34.4	34.4	28.0
Larvae II	221	35	15.8	10.4	15.3
Larvae III	186	6	3.2	1.8	3.3
Larvae IV	180	0	0.0	0.0	0.0
Pupae	180	1	0.5	0.3	0.5
Adults	179	--	--	--	--
Total	337	158		46.9	

From Table 10.4.1 and Figs 47 and 48 it can be seen that, from an initial population of 337 newly hatched larvae the 'apparent' mortality during the first instar was more than double that during the second instar (see Table 10.4.1, 'apparent' mortality), and the second-instar 'apparent' mortality was about five times that of the third instar. There was no mortality of the fourth instar larvae and only one pupa died out of a total of 180 larvae which pupated.

The 'mean apparent mortalities' in different instars were significantly different ($F = 6.15$; $P < 0.05$) except between fourth instar and the pupa.

The highest 'apparent' mortality occurred during the first instar and notably on the plant with the largest number of initial larvae. The least 'apparent' mortality occurred on the plant with the smallest number of initial larvae. This suggests that 'real'

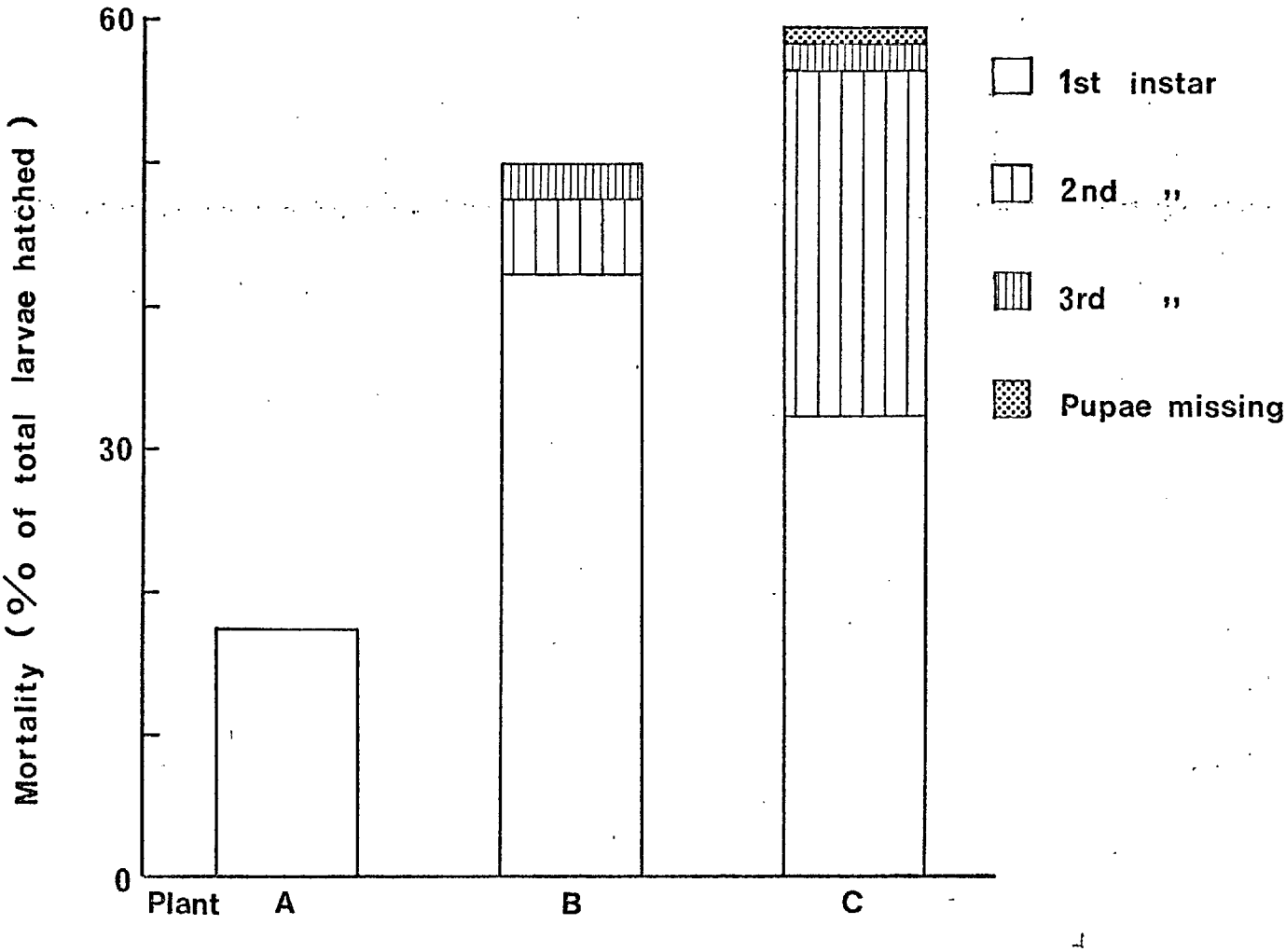


Fig. 47. a. Field experiment 1. Effects of excluding parasites and predators. Mortality.

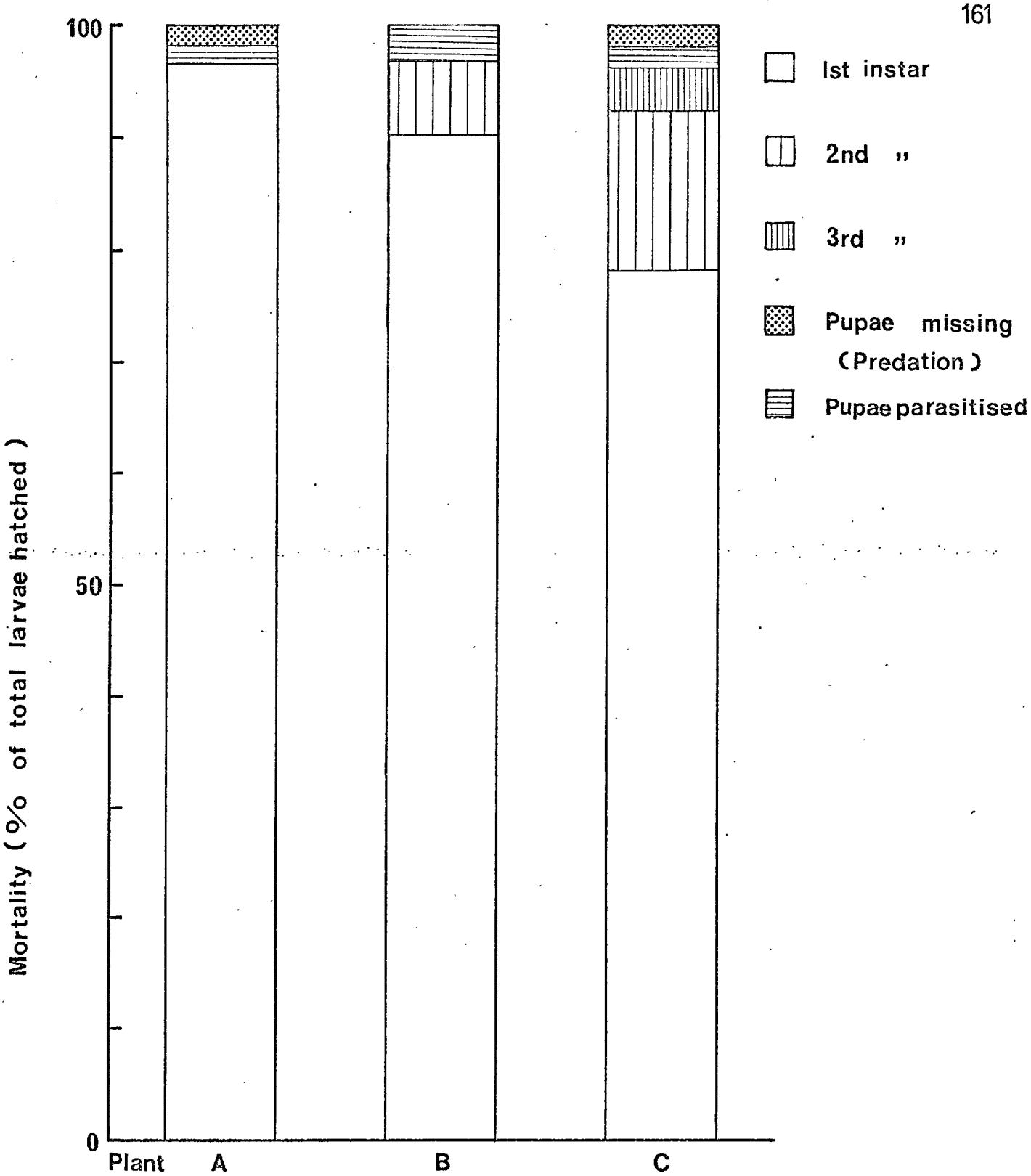


Fig. 47. b. Field experiment 1. Effects of excluding birds. Mortality.

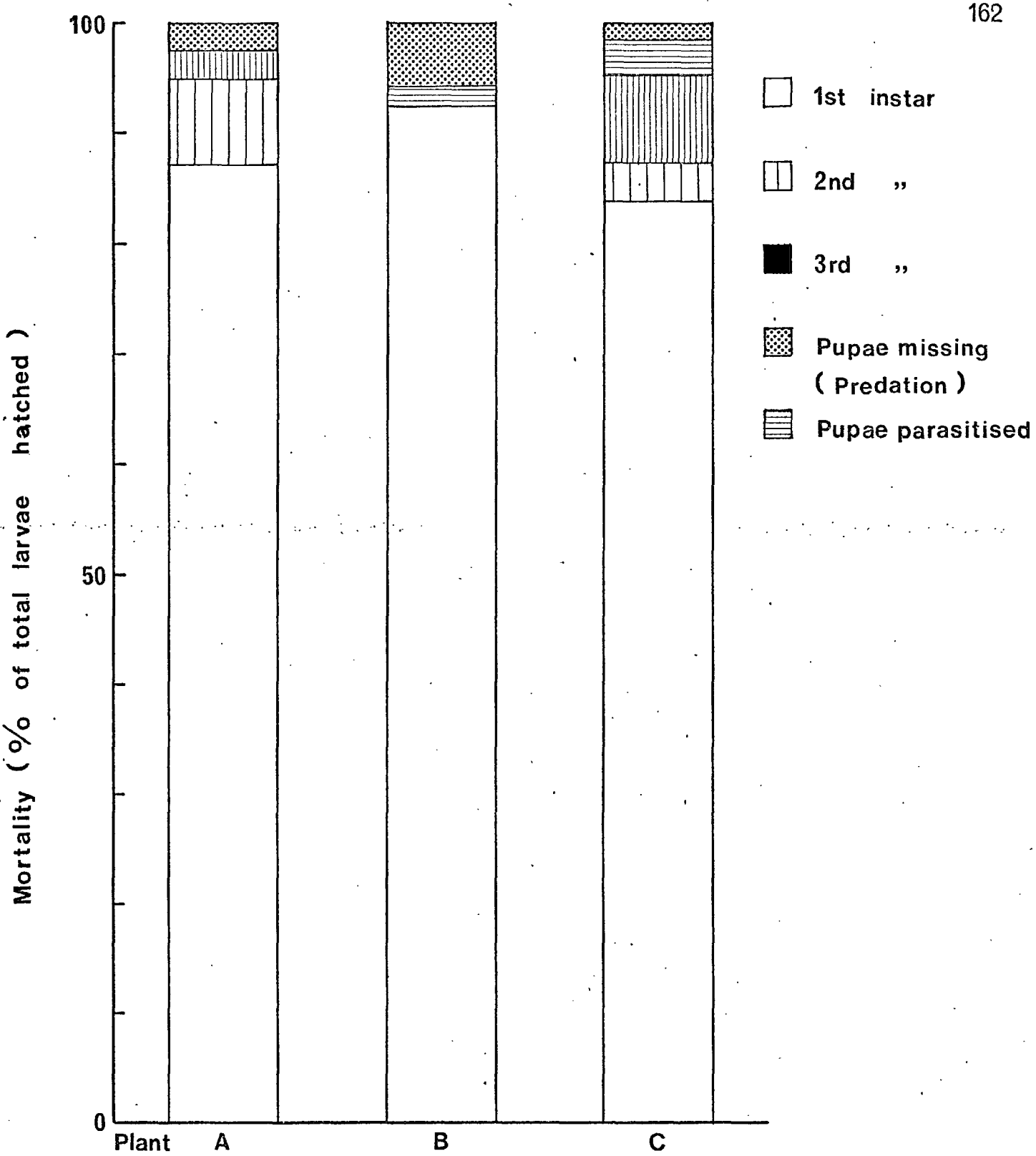


Fig. 47. c. Field experiment 1. Effects of excluding rainfall. Mortality.

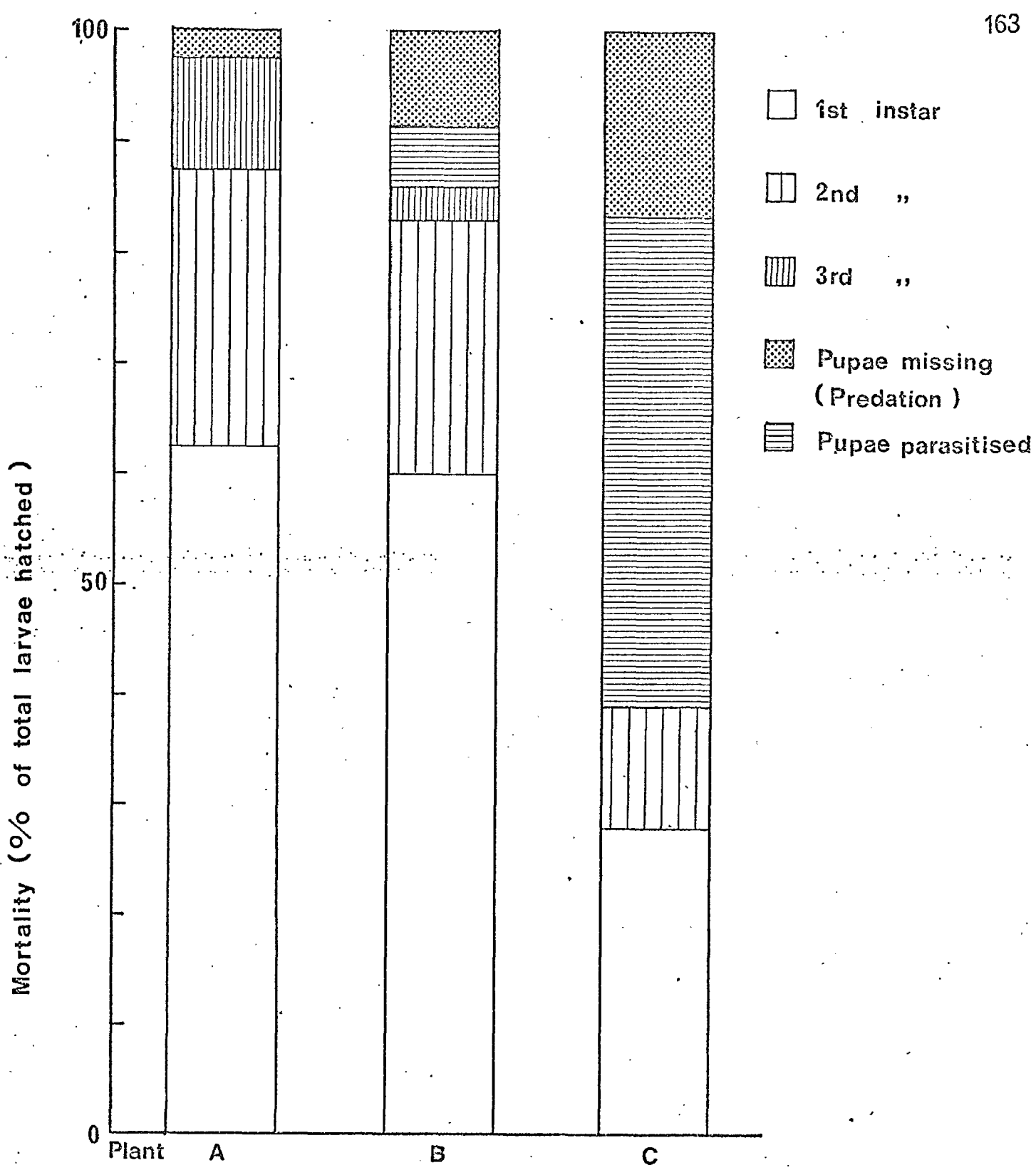


Fig. 47. d. Field experiment 1. Effects of all mortality factors. Mortality.

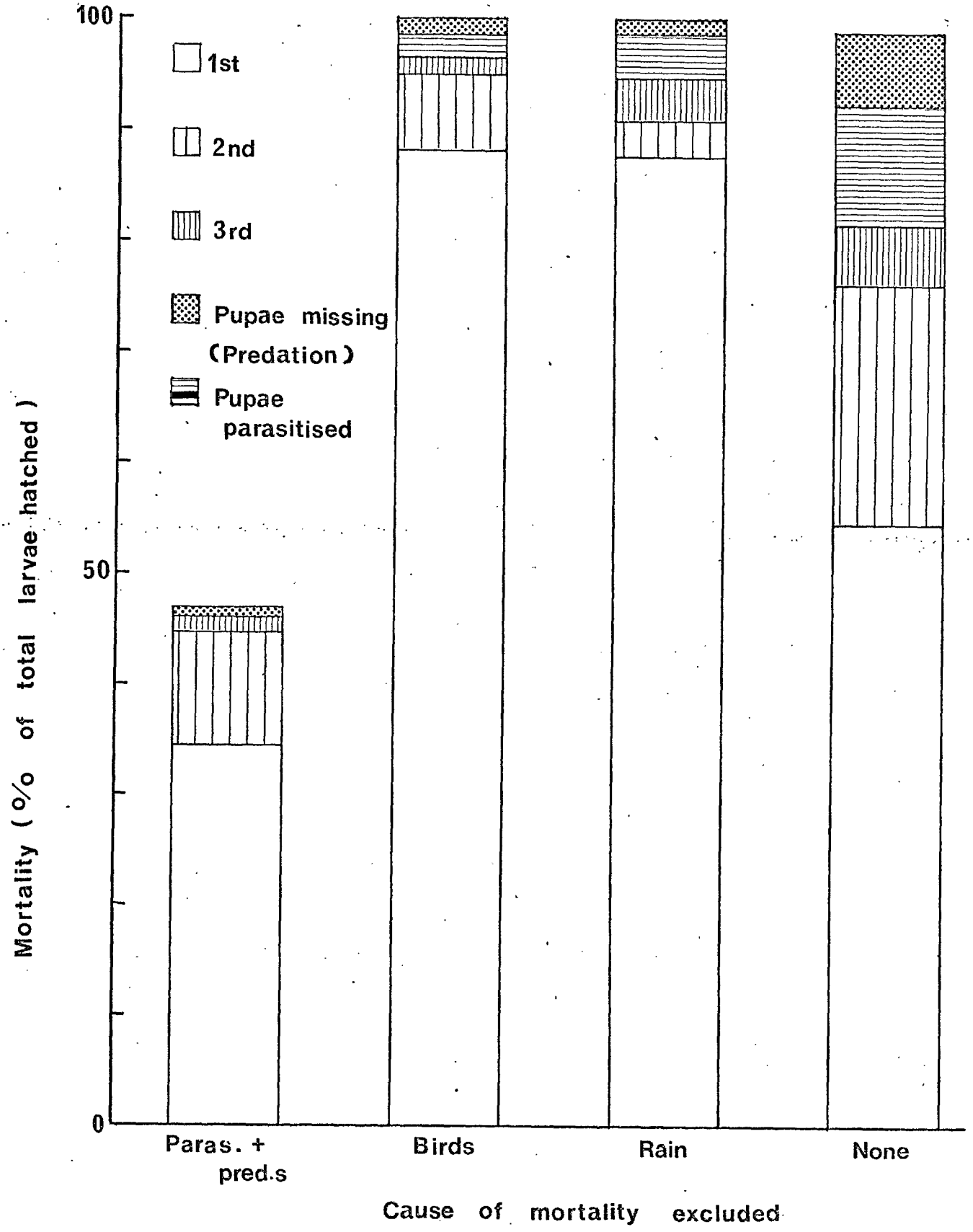


Fig.47.e. Field experiment 1. Effects of excluding different factors or none. Mortality.

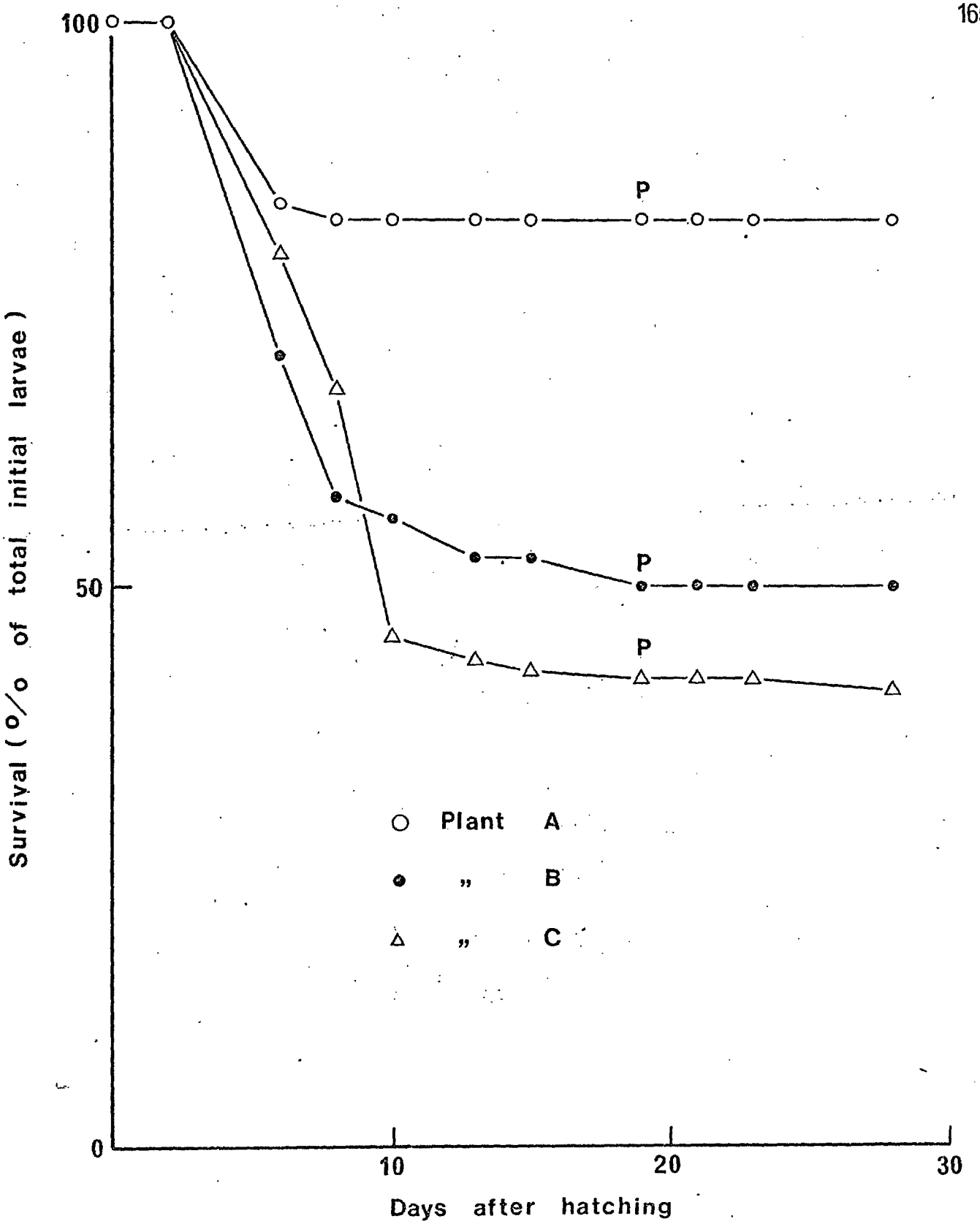


Fig. 48.a. Field experiment 1. Effects of excluding parasites and predators. Survival.

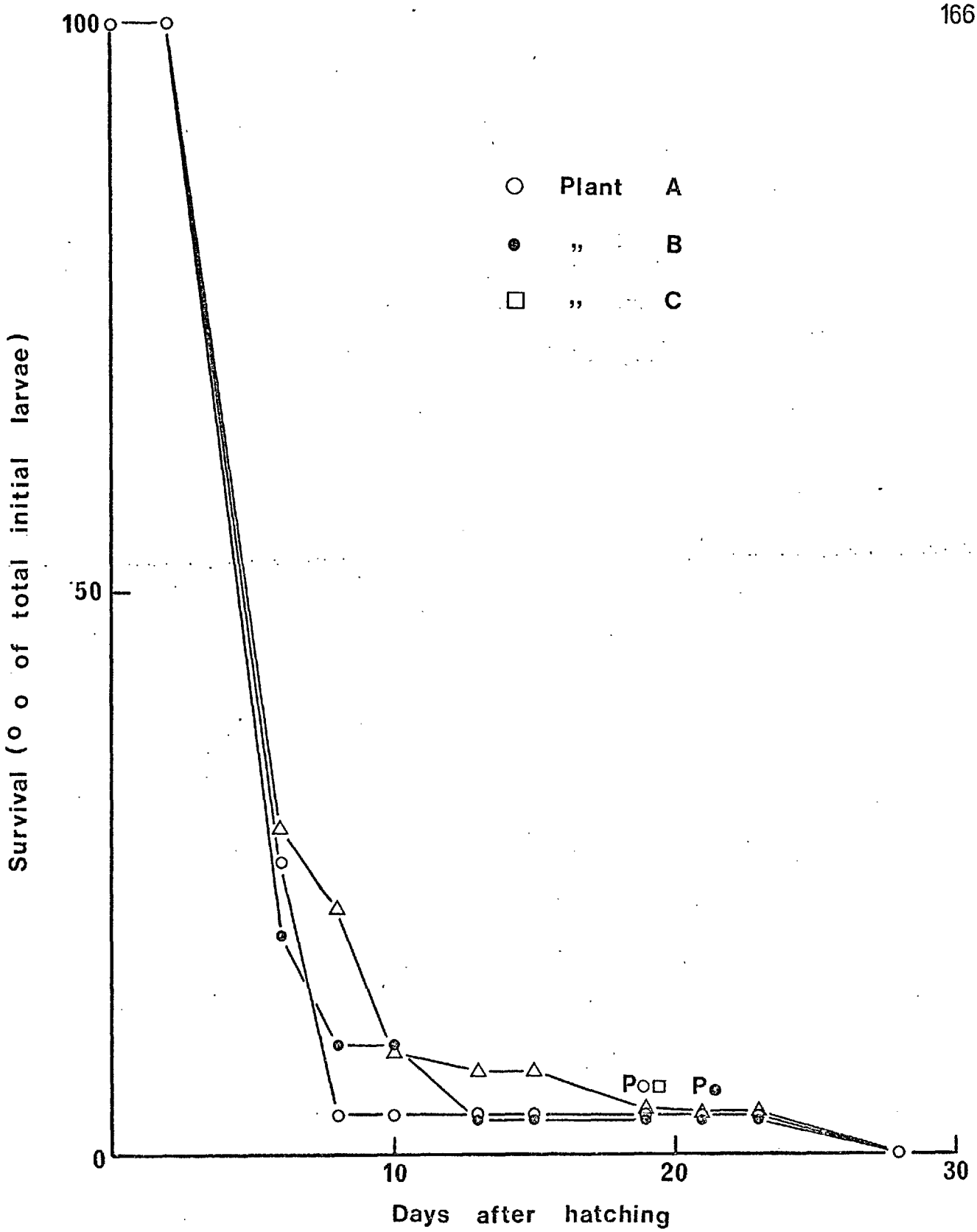


Fig. 48.b. Field experiment 1. Effects of excluding birds. Survival.

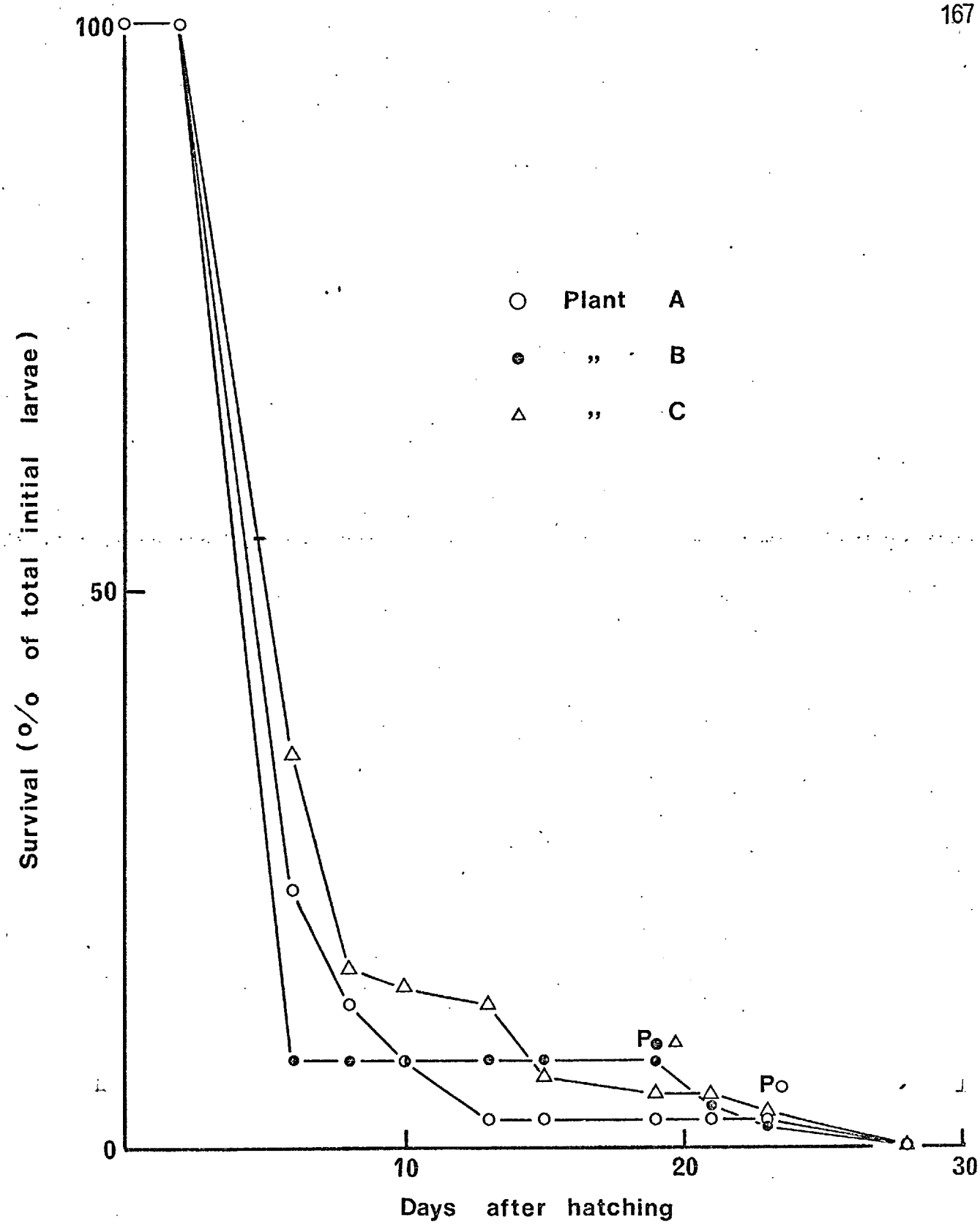


Fig.48.c. Field experiment 1. Effects of excluding rainfall. Survival.

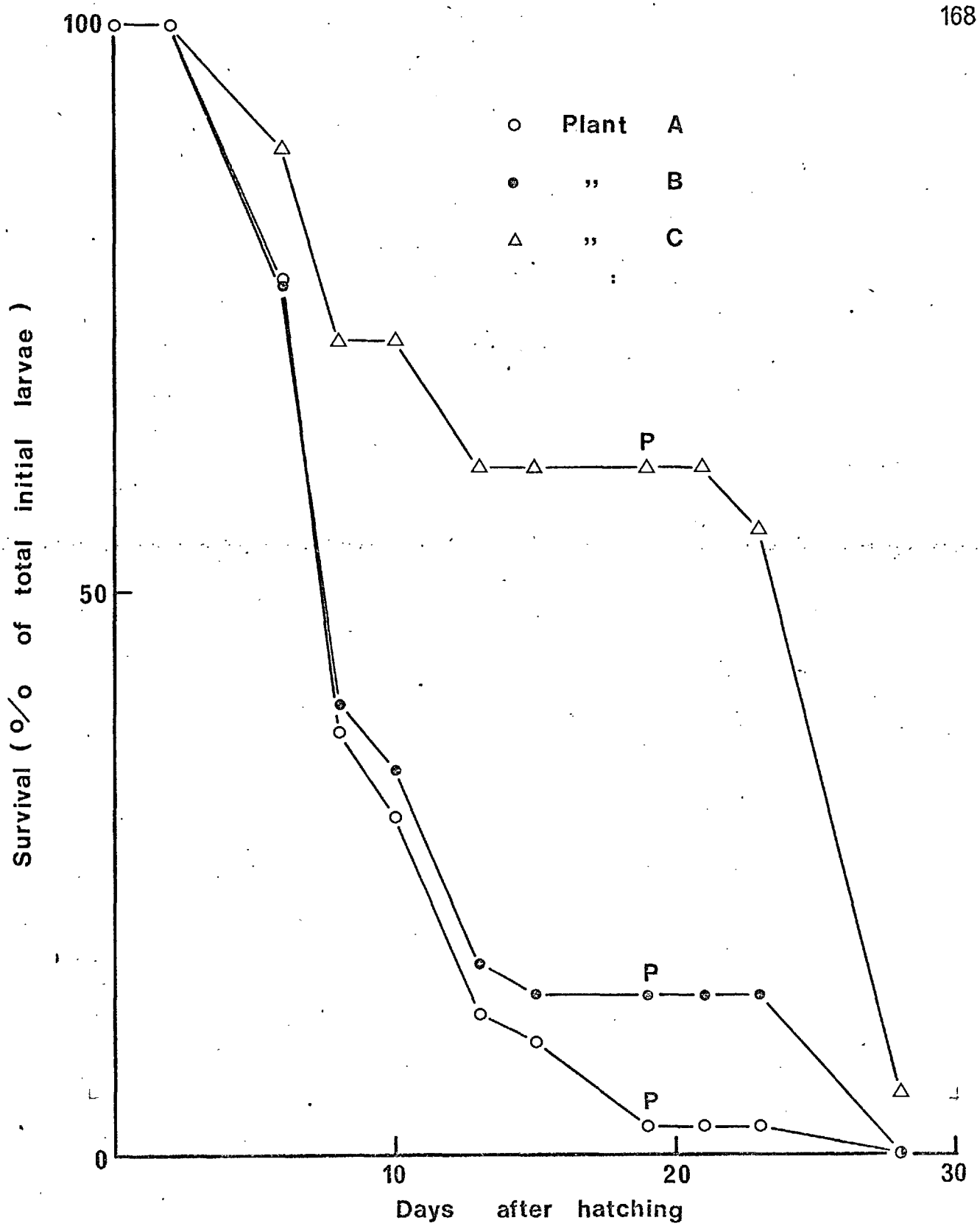


Fig. 48. d. Field Experiment 1. Effects of exposure to all mortality factors. Survival.

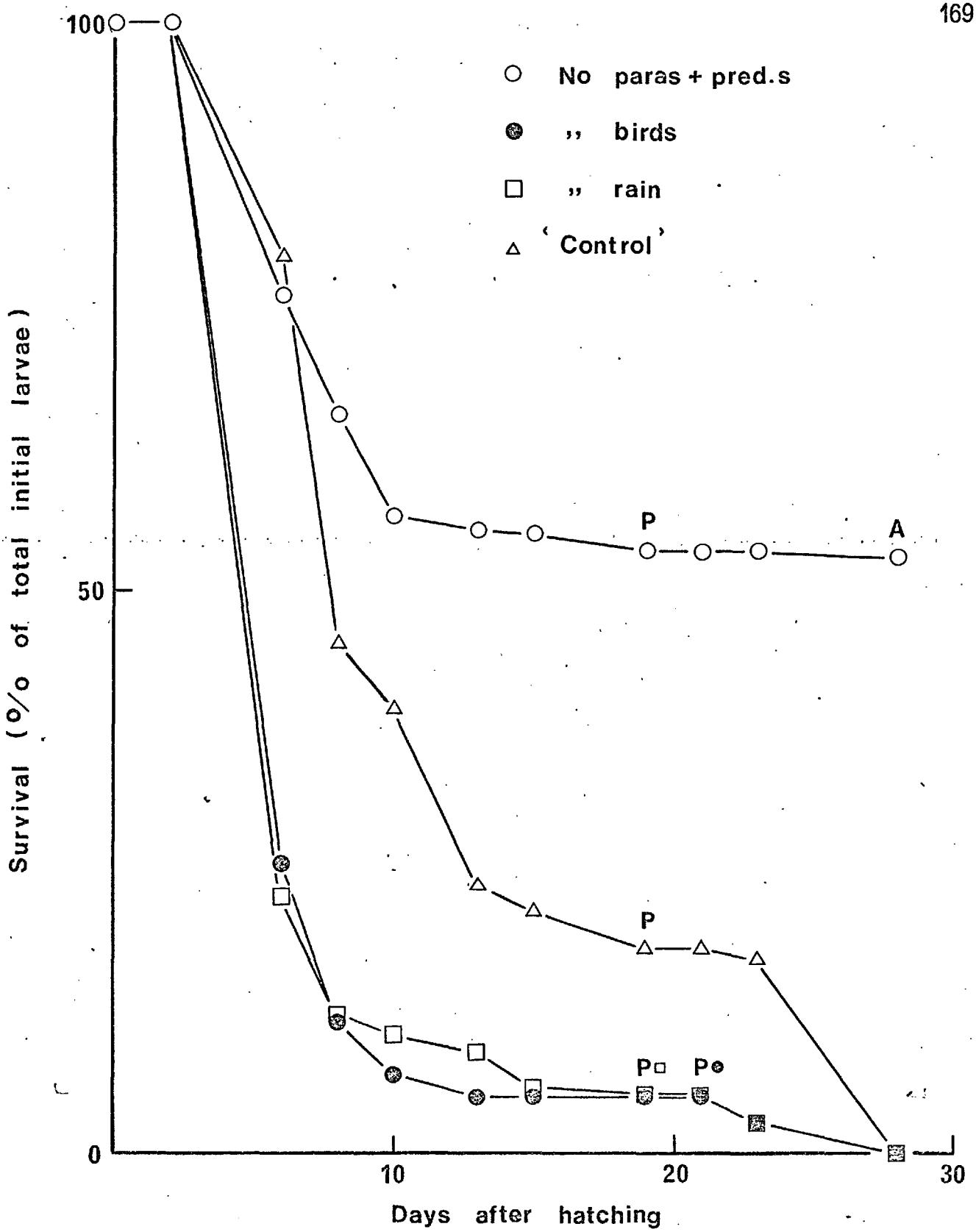


Fig. 48e. Field experiment 1. Effects of excluding different factors or none. Survival.

mortality was density related as indicated by the laboratory experiments previously described.

In conclusion, it seems that under those conditions the 'apparent' mortality of the larvae of P. xylostella was related in a density dependent manner to the density of the larvae, and inversely related to the age of the larvae.

Total 'real' mortality from newly hatched larva to adult was 46.9% based on the mean of the three replicates in which the 'real' mortality varied from 17.5% to 59.3%.

Effects of excluding birds.

Table 10.4.2. - Plants protected from birds. Mortalities in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	144	127	88.2	88.2	0.0
Larvae II	17	10	58.8	6.9	0.0
Larvae III	7	2	28.6	1.4	0.0
Larvae IV	5	0	0.0	0.0	0.0
Pupae	5	5	100.0	3.5	100.0
Adults	0	--	--	--	--
Total	144	144		100.0	

From Table 10.4.2 and Figs 47 and 48 it can be seen that the 'real' mortality of the larvae was very similar within all the replicates. The 'mean apparent mortalities' in different instars had highly significant differences ($F = 11.95$; $P < 0.01$), except between first instar and pupa, and between third and fourth instar.

There was a very high 'apparent' mortality in the first instar (88.2%) which was about two times that of the second instar (58.8%). The second-instar 'apparent' mortality was two times that of the third instar (only two larvae died in the third instar). No larvae died in the fourth instar, but the pupae all failed so no adults were produced.

The most striking feature of the results was that pupal mortality was total; 60% due to parasitism and 40% probably taken by predators, others than birds.

Effects of excluding rainfall.

Table 10.4.3. - Plants protected from rainfall. Mortalities in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	154	135	87.7	87.7	0.0
Larvae II	19	5	26.3	3.2	0.0
Larvae III	14	6	42.9	3.9	0.0
Larvae IV	8	0	0.0	0.0	0.0
Pupae	8	8	100.0	5.2	100.0
Adults	0	--	--	--	--
Total	154	154		100.0	

From Table 10.4.3. and Figs 47 and 48 it can be seen that the 'apparent' mortality of the larvae was similar within all replicates. The 'mean apparent mortalities' in the different instars were subjected to analysis of variance and showed that the differences were very highly significant ($F = 14.66$; $P < 0.001$); all the means of the mortalities were different except for those between the first instar and pupa, and between the second and the third instar.

As in the 'No Birds' treatment, there was a large 'apparent' mortality of the first instar (87.7%), this mortality was about 3.5 times more than that of the second instar but the latter was one third less than that of the third instar. In the fourth instar no larva died. Pupal mortality was total and was made up of 37.5% parasitised and 62.5% presumably from predation.

Effects of all causes of mortality (Control).

Table 10.4.4. - Fully exposed plants (Control). Mortalities in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	93	51	54.8	54.8	1.3
Larvae II	42	20	47.6	21.5	2.2
Larvae III	22	5	22.7	5.4	1.4
Larvae IV	17	0	0.0	0.0	0.0
Pupae	17	16	94.1	17.2	94.1
Adults	1	-	-	-	-
Total	93	92		98.9	

From the analysis of variance the 'mean apparent mortalities' in the different instars showed to have highly significant differences ($F = 10.66$; $P < 0.01$), except between first, second and third instars.

From Table 10.4.4 and Figs 47 and 48 it can be seen that the 'apparent' mortalities were initially less than in the previous two treatments but this was largely caused by one aberrant replicate.

A mean of 54.8% was lost in the first instar ('apparent' mortality), but this relatively low figure was compensated for in the second instar, 47.6% of which died. The second-instar 'apparent' mortality was two times that of the third. There was no mortality in the fourth instar and only one out of 17 pupae survived. The rest were parasitised (58.8%) or lost (35.3%) presumably by predation.

10.4.3. Discussion.

When all parasites and predators were excluded from the field populations (artificially infested plants) of P. xylostella, the larval mortality was related to the initial density. Most mortality occurred in the first instar but it is apparent from examination of the different replicates that some compensatory mortality occurred in the second instar. When the initial density was low (63 larvae on a plant) only 17.5% died during development to the adult stage, but with an initial density of 166 larvae on a plant, 50% died. This means that, irrespective of initial densities fairly similar numbers survived. It was unfortunate for the purposes of the present experiment that initial numbers varied and that numbers differed between treatments. However the results suggest that little loss from intraspecific competition occurred below about 60 larvae/plant. Perhaps therefore competition can be discounted in the other treatments, in which the initial numbers of larvae per plant ranged from 18 to 63.

First instar mortality.

Table 10.4.5. - First instar mortality.

Treatment	Total initial No.	No. dead	Real mortality (%)
No PP	337	116	34.4
No Birds	144	127	88.2
No Rain	154	135	87.7
Control	93	51	54.8

No PP = Excluded all parasites and predators

No Birds = Excluded all birds

No Rain = Excluded rainfall

Control = Fully exposed to all causes of mortality.

The analysis of variance of the mortalities of the above treatments showed that there were highly significant differences between the means ($F = 19.26$; $P < 0.01$) although no differences were found between replicates; no significant difference was found between the means of populations protected from birds and from rainfall.

From Table 10.4.5. and Figs 47 and 48 it can be seen that mortality ('real') of the first instar larvae was most in those populations protected only from birds or rainfall. The relatively small mortality on the fully exposed treatments was possibly an artifact due to one aberrant replicate. It could be however that the cages attracted those predators that presumably killed the first instar larvae.

Birds for obvious reasons, mainly the size and mining behaviour of the larvae, do not seem to attack the first instar larvae of P. xylostella, and did not seem to attack the other stages. They have been previously mentioned as important predators of P. xylostella in Great Britain by Ormerod (1892) during an outbreak of the pest in 1891; different bird species are cited including starlings, lap wings, herring gulls, common gulls, and many others. Also Theobald (1926) in Great Britain mentions sparrows and starlings eating larvae of P. xylostella. Harcourt (1963a) mentions that in Ontario, Canada, birds periodically landed on plants in search of larvae and pupae, the most common being Molothrus ater, Melospiza melodia and Agelaius phoeniceus, the last one was most common in early Autumn, when it descended upon the plots in large swarms. Ullyett (1947) mentions wagtails searching for larvae and pupae in South Africa. Kanervo (1936) also mentions birds as predators of larvae in Finland.

If the 'real' mortality in the populations excluded from parasites and predators ('No Parasites and Predators') is regarded as being due to the effects of density and to climatic and host plant factors, and it is subtracted from the 'real' mortality in the populations excluded from birds ('No Birds'), the difference (88.2 -34.4 = 53.8%) might be regarded as probably an underestimate of mortality due to rainfall (washing out the larvae or killing by direct mechanic effect of the droplets), and of predators other than birds. (As far as it is known parasites do not kill first instar larvae (Harcourt, 1969; Hardy, 1938)). Therefore the most likely alternatives must be rainfall, and predators other than birds, perhaps including soil predators such as Carabidae, and also Syrphidae, Chrysopidae (Chrysopa sp. larvae were observed eating third-instar and early fourth-instar larvae of P. xylostella) and spiders (Xysticus cristatus, Pisaura mirabilis, and an unidentified Lyniphiidae were seen eating larvae of P. xylostella).

Although there was a relatively large amount of rainfall during the first instar (Fig 53; 2 and 3 Aug 1969) it seems unlikely that this rainfall had any effect on the population because subtracting the first instar 'real' mortality in 'No Parasites and Predators' from that of 'No Rain' treatment (87.7 - 34.4 = 53.3%) gave a difference similar to that in 'No Birds' which was exposed to rain; also the mortality was greater than in the fully exposed treatments (Controls). The mortality can therefore be regarded as due to small predators of the kind that can get through the netting that excludes birds. Rain therefore was probably not an important factor in reducing the populations of first instar larvae; this is in general supported by the evidence that rainfall is rarely quoted as a mortality factor. Hardy (1938) suggests that there are only two short periods in which rain alone can be an effective controlling agent against P. xylostella; the first is the short interval between the eclosion of the larvae and the construction of a mine, and the second is the time immediately after emergence from the mine. He noted that an infestation of P. xylostella in 1936 was subjected to three weeks of almost continuous rain and bad weather, and yet no appreciable diminution in the number of larvae could be observed! Ullyett (1947) says that despite the reference by many authors to the mechanical effect of rainfall as an controlling factor, by washing the larvae off the plant or by drowning them in drops of water on the plant, no definite data have been produced to support this contention; he affirms that his study covered many periods of heavy rainfall and in no case was evidence obtained that appreciable numbers of larvae were destroyed in this manner. He concludes that the mechanical effect of rainfall may be discounted as a significant agent of control and that any decrease in the damage to a crop (and presumably in the larval population)

following rain is due to fungal or bacterial diseases which may attack the population in humid conditions. In contrast to the previous authors, Harcourt (1963a) stated that, during 18 generations, rainfall was responsible for an average of 55.6% (ranging from 0-94%) of larvae from hatching to the middle of the fourth instar, and a further 8.8% of the larvae from the middle of fourth instar to cocoon formation. The effect was mainly due to the larvae drowning in water pockets but also by being washed off the leaves; the mortality was more intense during cold weather because the larvae were more sluggish and/or longer exposure period. The mortality due to rainfall found by Harcourt (1963a) seems to be excessive. He also concludes that predators destroyed only a few of the feeding larvae. His results are therefore very different from those of the present investigation.

When the first-instar mortality ('real') of the entirely unprotected populations (Controls) is compared with that of the other treatments, it is noticed that it is higher than 'No Parasites and Predators' as expected and the difference (54.8 - 34.4 = 20.4%) is regarded as caused mainly by predators. However, and contrary to the expected, it was significantly lower than the mortalities of the populations protected against birds and against rainfall. As already indicated a possible explanation may be found in terms of effects of the cages on predators. Thus apart from attracting small predators, as already mentioned, the cages may protect the small predators from birds. This simply means that carabirds, syrphid and chrysopid larvae, spiders, etc, can crawl throughout the plant without being eaten by birds (perhaps also by shrewds and mice). In the plants protected from rain the large hood may also have deterred birds.

Mortality in later instars.

The results are summarized in Tables 10.4.6 and 10.4.7, and differences in significance are indicated.

Table 10.4.8 shows the overall 'real' and 'indispensable' mortalities of each instar in each treatment. The latter is especially valuable because it indicates the value of a mortality at each stage of the life cycle. The most striking features of the results are:

(1) Apparent compensatory mortality in the second and third instar. Thus, in the rain-free treatment the mortality on the second instar was small compared with that in 'No Birds' treatment (although only at the end of the instar did 10 mm of rain fall, (Fig. 53)). However, this was compensated for in the third instar and pupal stages. Similarly in the fully exposed treatment the first instar mortality was less than in 'No birds' and 'No Rain' treatments but this was entirely compensated for by greater mortality in the second and third instars and pupal stages.

(2) The lack of mortality during the fourth-instar larval stage. This suggests that the predators are small ones, only capable of killing the early instar larvae; also that birds are not important at all because they would surely tend to see and choose the larger, late instar larvae if they did, in fact, prey on P. xylostella.

Table 10.4.6. - Mortality of second, third and fourth instars, and of pupae.

Second instar			
Treatment	Total initial No.	No. dead	Apparent mortality (%)
No PP	221	35	15.8
No Birds	17	10	58.8
No Rain	19	5	26.3
Control	42	20	47.6
F = 0.58; No significant			

Third instar			
Treatment	Total initial No.	No. dead	Apparent mortality (%)
No PP	186	6	3.2
No Birds	7	2	28.6
No Rain	14	6	42.9
Control	22	5	22.7
F = 0.78; No significant			

Fourth instar			
Treatment	Total initial No.	No. dead	Apparent mortality (%)
No PP	180	0	0.0
No Birds	5	0	0.0
No Rain	8	0	0.0
Control	17	0	0.0

Pupae			
Treatment	Total initial No.	No. dead	Apparent mortality (%)
No PP	180	1	0.5
No Birds	5	5	100.0
No Rain	8	8	100.0
Control	17	16	94.1
F = 805.22 P < 0.001			

Table 10.4.7. - Field Experiment 1. Real and Indispensable mortalities during development of P. xylostella populations (Jul - Aug 1969)

	Real mortality				Indispensable mortality			
	Cause of mortality excluded				Cause of mortality excluded			
Instar	All natural enemies	Birds	Rain	None	All natural enemies	Birds	Rain	None
Larvae I	34.4	88.2	87.7	54.8	28.0	0.0	0.0	1.3
Larvae II	10.4	6.9	3.2	21.5	15.3	0.0	0.0	2.2
Larvae III	1.8	1.4	3.9	5.4	3.3	0.0	0.0	1.4
Larvae IV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pupae	0.3	3.5	5.2	17.2	0.5	100.0	100.0	94.1
Total mortality	46.9	100.0	100.0	98.9	-	-	-	-

Table 10.4.8. - Field Experiment 1. Causes of 'pupal' mortality

Treatment	No. entering prepupal stage	No. killed by parasites	No. disappeared	No. of Adults
No PP	180	0	1	179
No Birds	5	3	2	0
No Rain	80	3	5	0
Control	17	10	6	1

(3) The 'pupal' mortality. Table 10.4.8 shows the causes of mortality between the end of the larval stage and the emergence of the adults. This mortality was crucial because, despite very low densities, only one individual survived in the fully exposed treatments. In those treatments the main cause of mortality was parasitism by Nythobia eurocephaga Horstm., N. neocerophaga Horstm. and Apanteles plutellae Kurdj. which killed 58.8% of the initial 'pupae' (including pre-pupae and pupae), and disappearance which accounted for the loss of 35.3% of the total initial 'pupae', and most certainly was due to predation since tear marks could be seen on the cocoon remnants wherethe cocoon was attached to the leaf.

In contrast, the pupal mortality of the 'No Parasites and Predators' populations was almost nil (only one pupa missing).

In the other treatments the mortality of the 'pupae' was due partly to parasitism, which could be clearly detected by the presence of the parasite cocoon inside the P. xylostella cocoon. The parasite, of course, oviposits in the earlier stages, usually 2nd-, 3nd- or 4th-instar larvae but does not kill the host until it is about to pupate. The 100% (or virtually 100%) mortality was made up by 'disappearance' attributed to predators. For example in the 'No Birds' treatment 60% of the 'pupae' were killed by parasites and 40% disappeared, presumably taken by small predators able to go through the big holes of the excluding birds netting. In the 'No Rain' treatment, the assumed predators-induced disappearance was responsible for 62.5% of the pupae and 37.5% were killed by parasites.

In these two treatments no pupa survived, as mentioned before.

Summarizing, it can be said that, except the 'pupae', the first instar was the immature stage most susceptible to mortality by the total of the factors, both biotic and abiotic, including density effects. The larvae tend to become less susceptible to the effects of those factors as they grow bigger, suggesting that they may develop defensive mechanisms against predators; or by becoming less abundant and more evenly distributed on the plant, they naturally become less affected by their own density. The only possible divergence is that the second instar larvae may be affected by rainfall.

The'pupa' was the most susceptible of all the stages (to judge from indispensable mortality), and practically all were killed by parasites and probably predators.

There were therefore very effective biological control mechanisms operating in the field at this time (August 1969).

It is assumed that small predators caused most of the mortality though only sparse evidence was obtained of the species that were responsible. Birds and rainfall were unimportant but may not be so in other circumstances.

10.5. SECOND FIELD EXPERIMENT (LATE SUMMER - AUTUMN 1969).

The objective of this experiment was, as in the previous field experiment, to estimate the different causes of mortality of P. xylostella under field conditions, in this case in late season from 29 Aug.1969 to 31 Oct 1969.

10.5.1. Materials and methods.

The plants were in the same field as for the previous experiment and so they were now larger and older. At the beginning of the experiment each plant had about forty full grown leaves.

The selection and preparation of the plants and cages was as in the previous experiment except that one or two of the lowest leaves of the plants were left on the plant in order to allow them to touch the ground and let possible predators climb on the plants, as they would do normally. In those plants where parasites and predators were to be excluded the hanging lower leaves were, however, cut off.

At the end of August the plants were prepared and caged, and the leaves numbered with Indian Ink. Oviposition cages were placed on the lower surfaces of the leaves to avoid direct heating from the sun on the cages and also because the moths may prefer laying on that surface. Groups of about 10 adults were introduced in the oviposition cages as previously described. The moths were left for three days to lay eggs in the places they preferred (as in the previous experiment). They were removed but the cages were left on until the eggs began to hatch. The eggs hatched irregularly since they had been laid over a period of three days. So to avoid marked differences of ages of larvae, the cages, and unhatched eggs were removed from the leaves about 24 hours after hatching started. The numbers of recently hatched larvae per treatment ranged from 402 to 659.

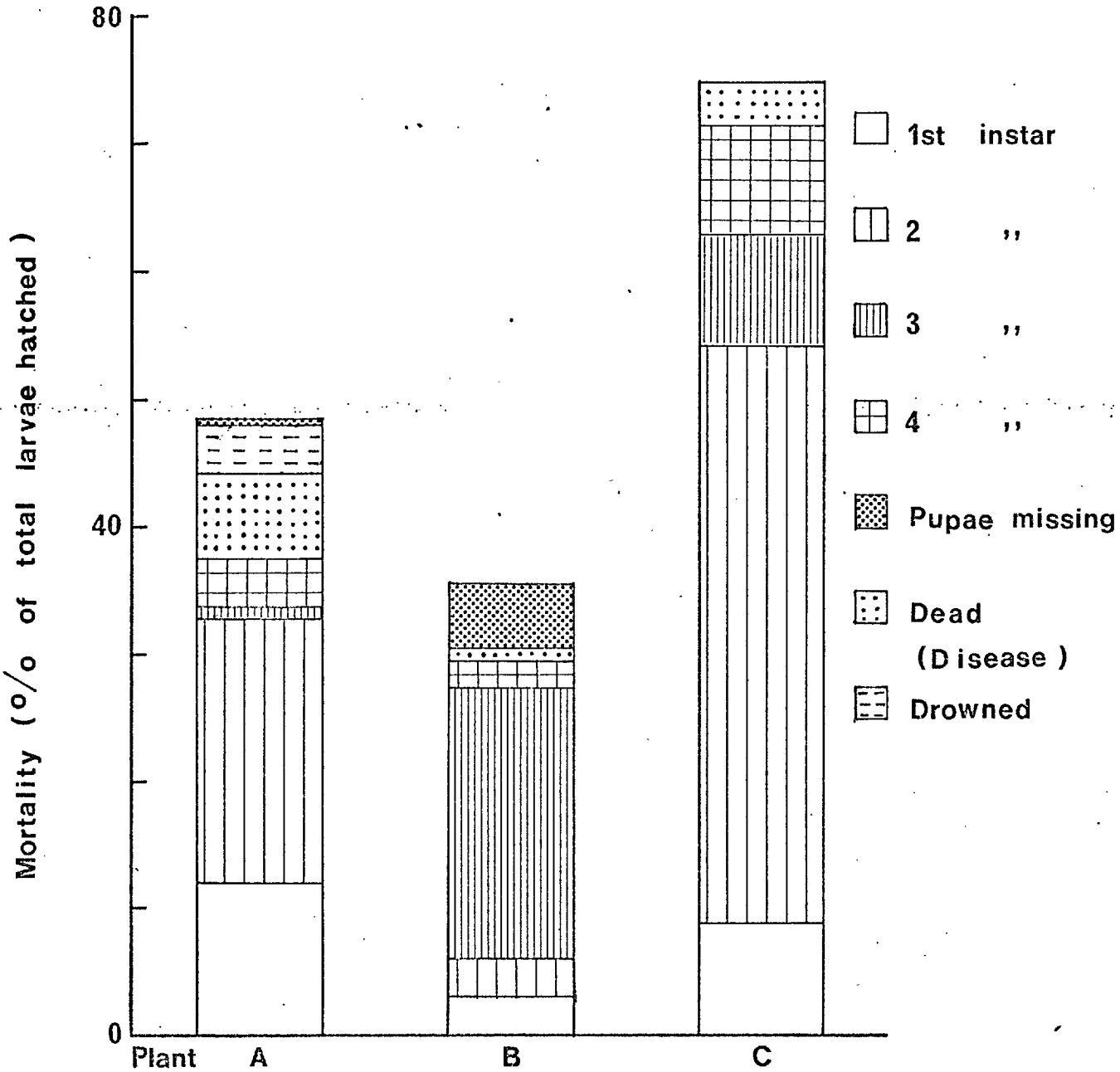


Fig.49.a. Field Experiment 2. Effects of excluding parasites and predators. Mortality.

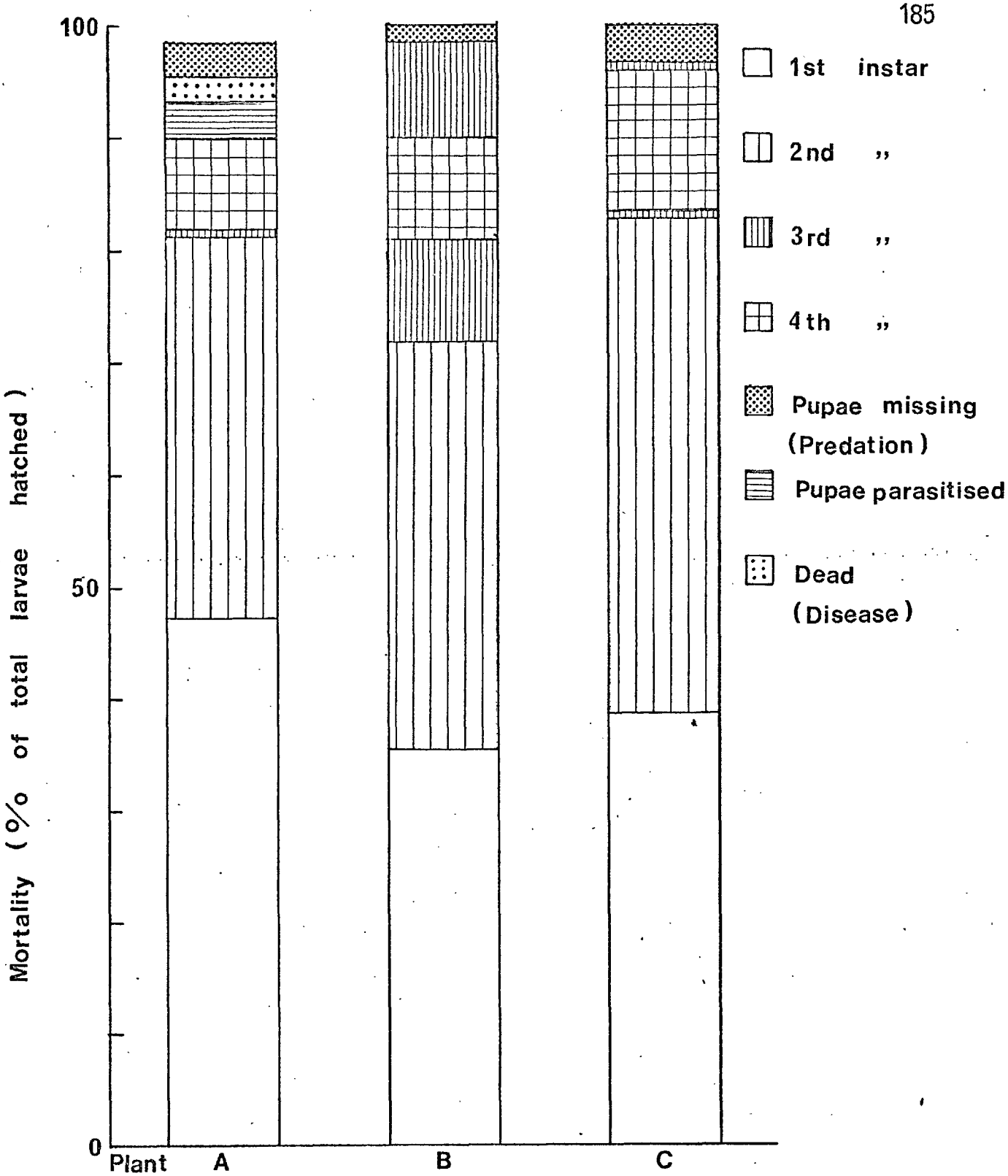


Fig.49.b. Field Experiment 2. Effects of excluding birds. Mortality.

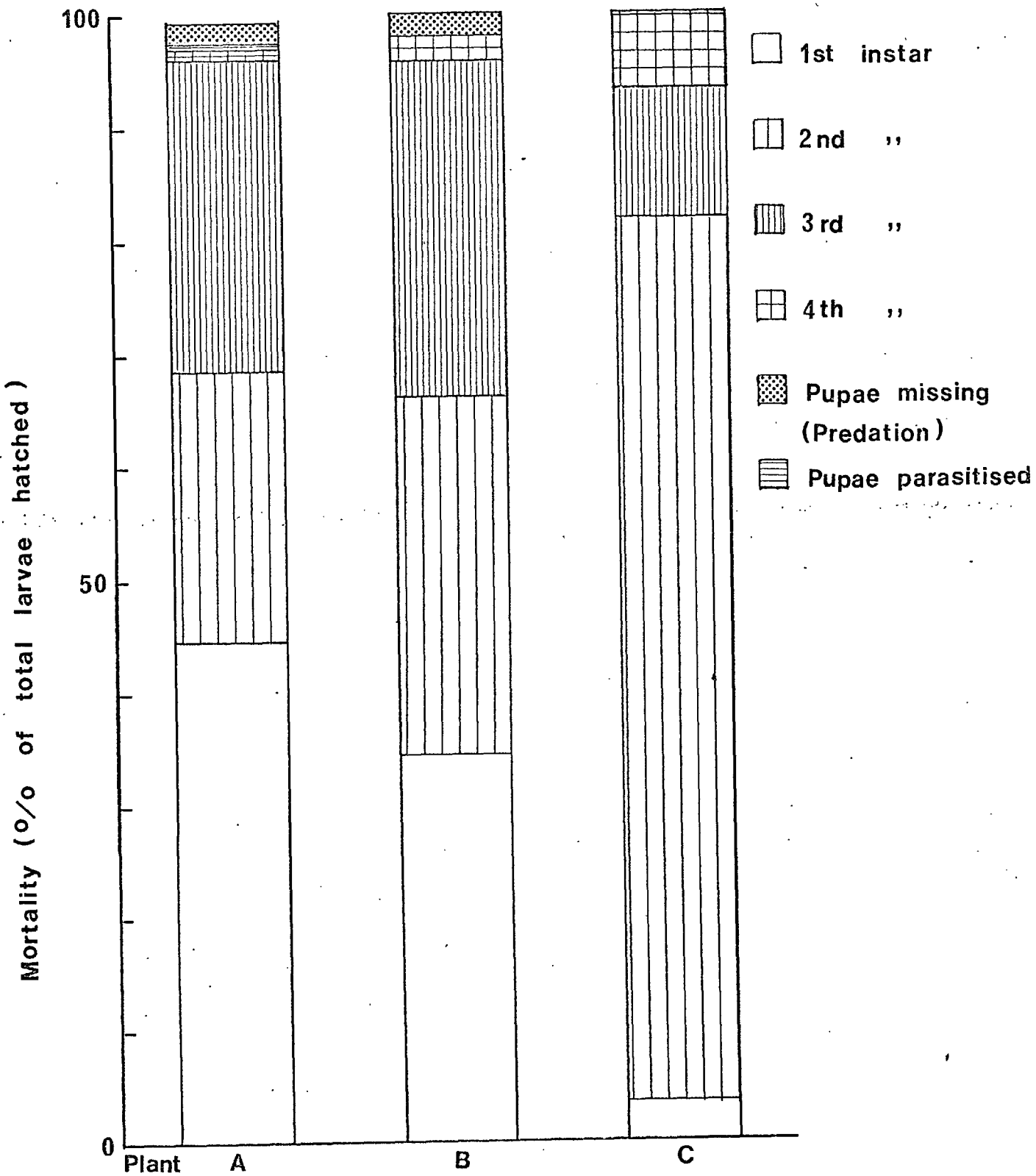


Fig.49.c. Field Experiment 2. Effects of excluding rainfall. Mortality.

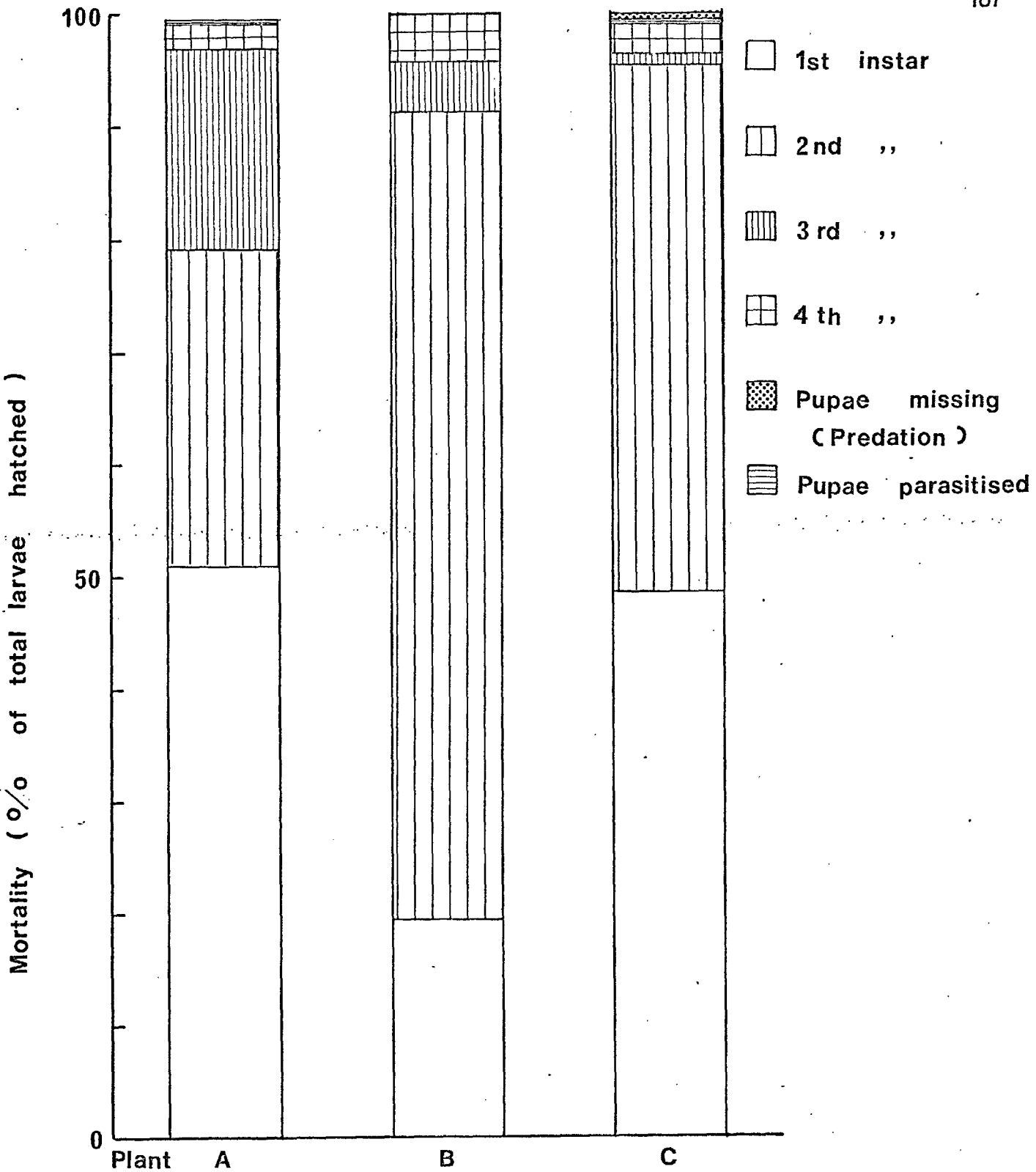


Fig.49.d. Field Experiment 2. Effects of exposure to all mortality factors. Mortality

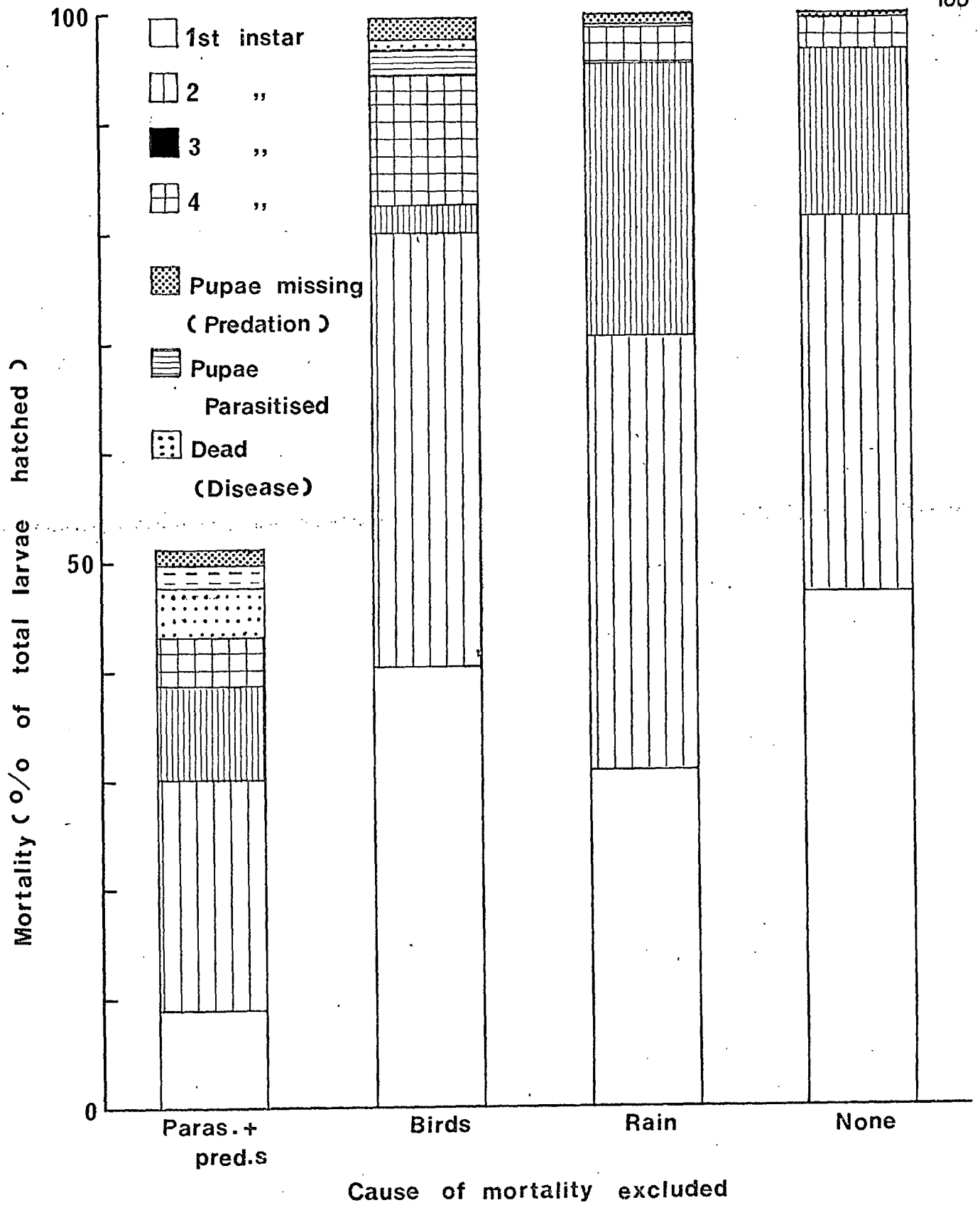


Fig.49.e. Field Experiment 2. Effects of excluding different factors or none. Mortality.

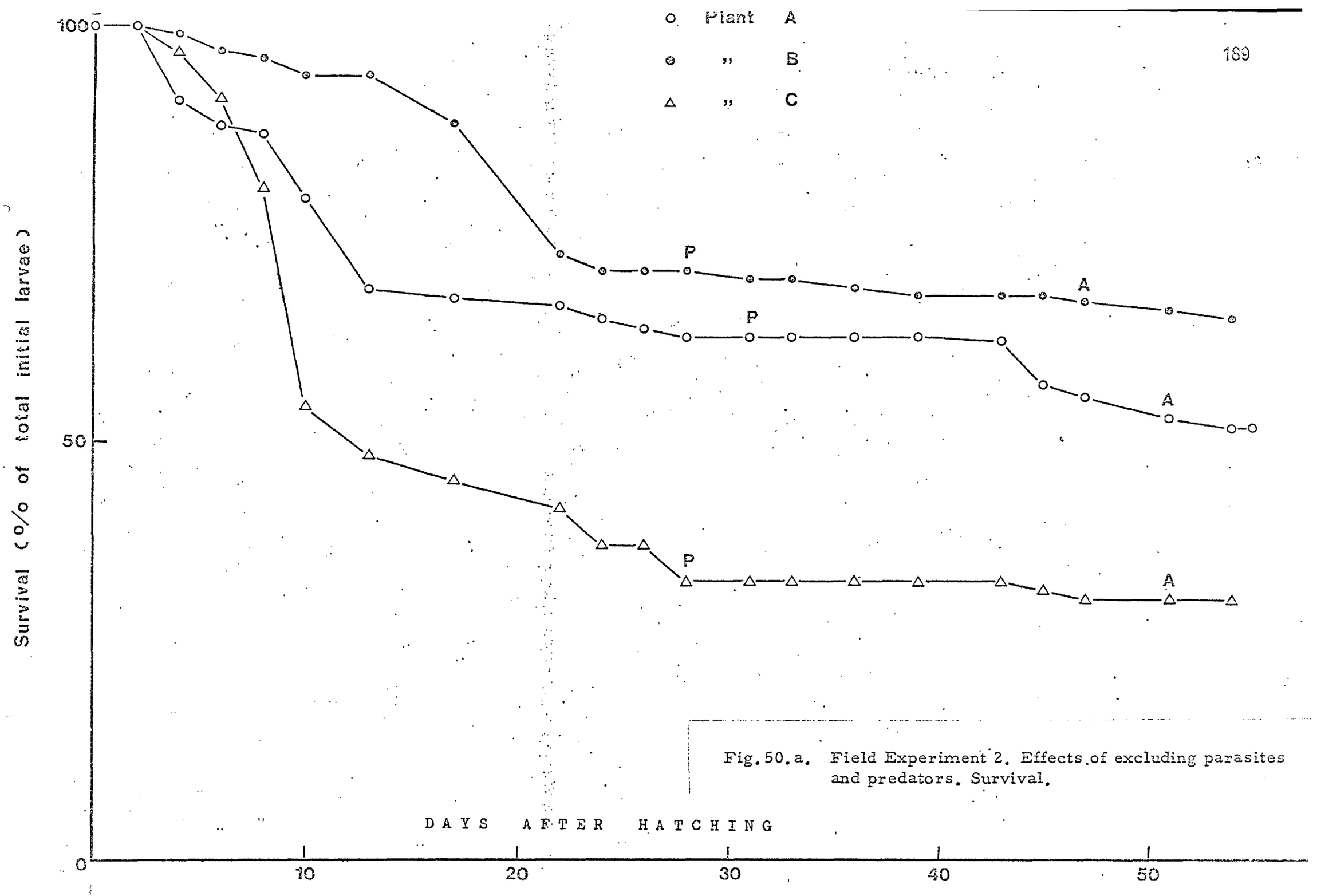


Fig.50.a. Field Experiment 2. Effects of excluding parasites and predators. Survival.

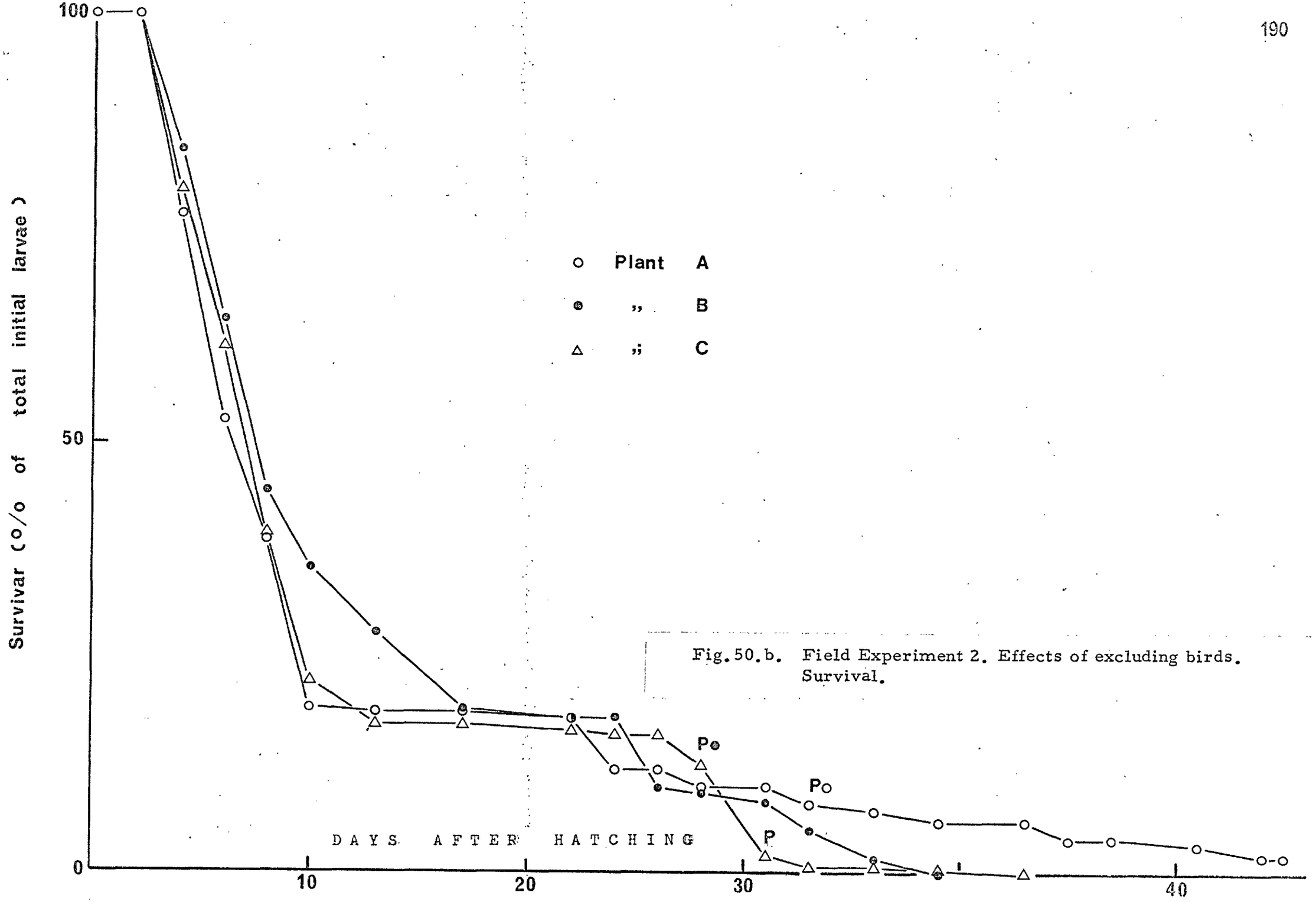


Fig. 50.b. Field Experiment 2. Effects of excluding birds. Survival.

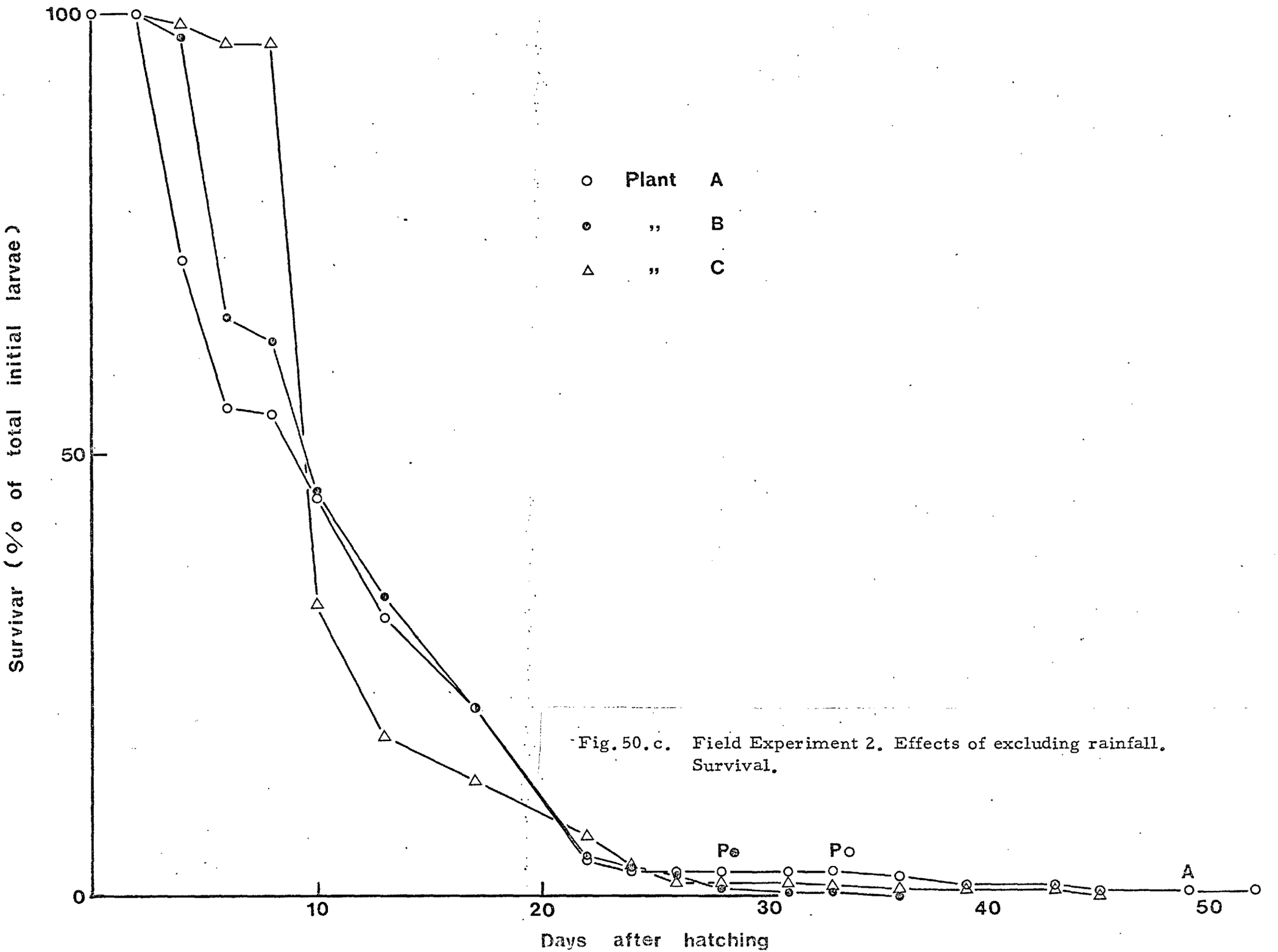


Fig. 50.c. Field Experiment 2. Effects of excluding rainfall. Survival.

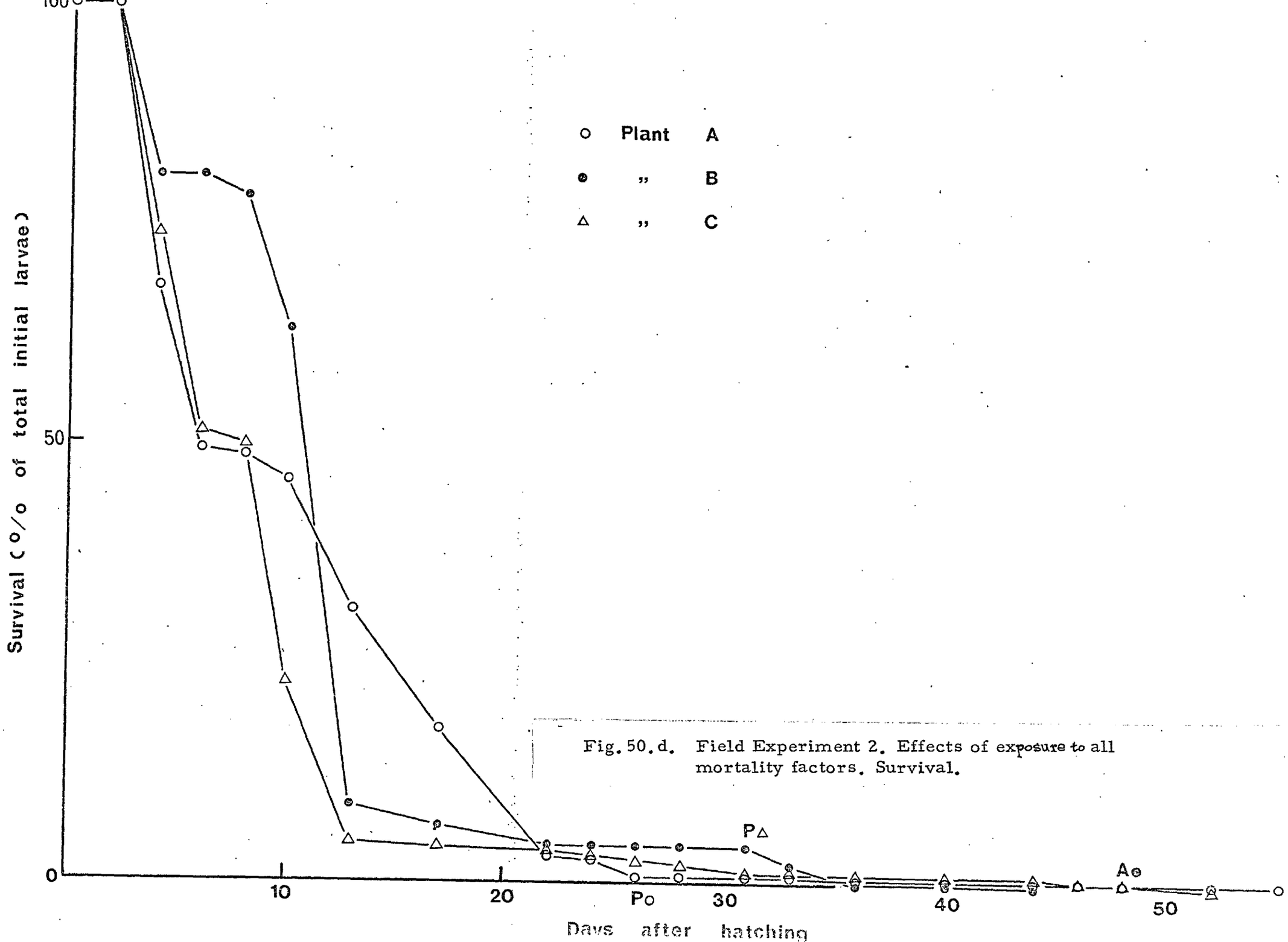


Fig. 50.d. Field Experiment 2. Effects of exposure to all mortality factors. Survival.

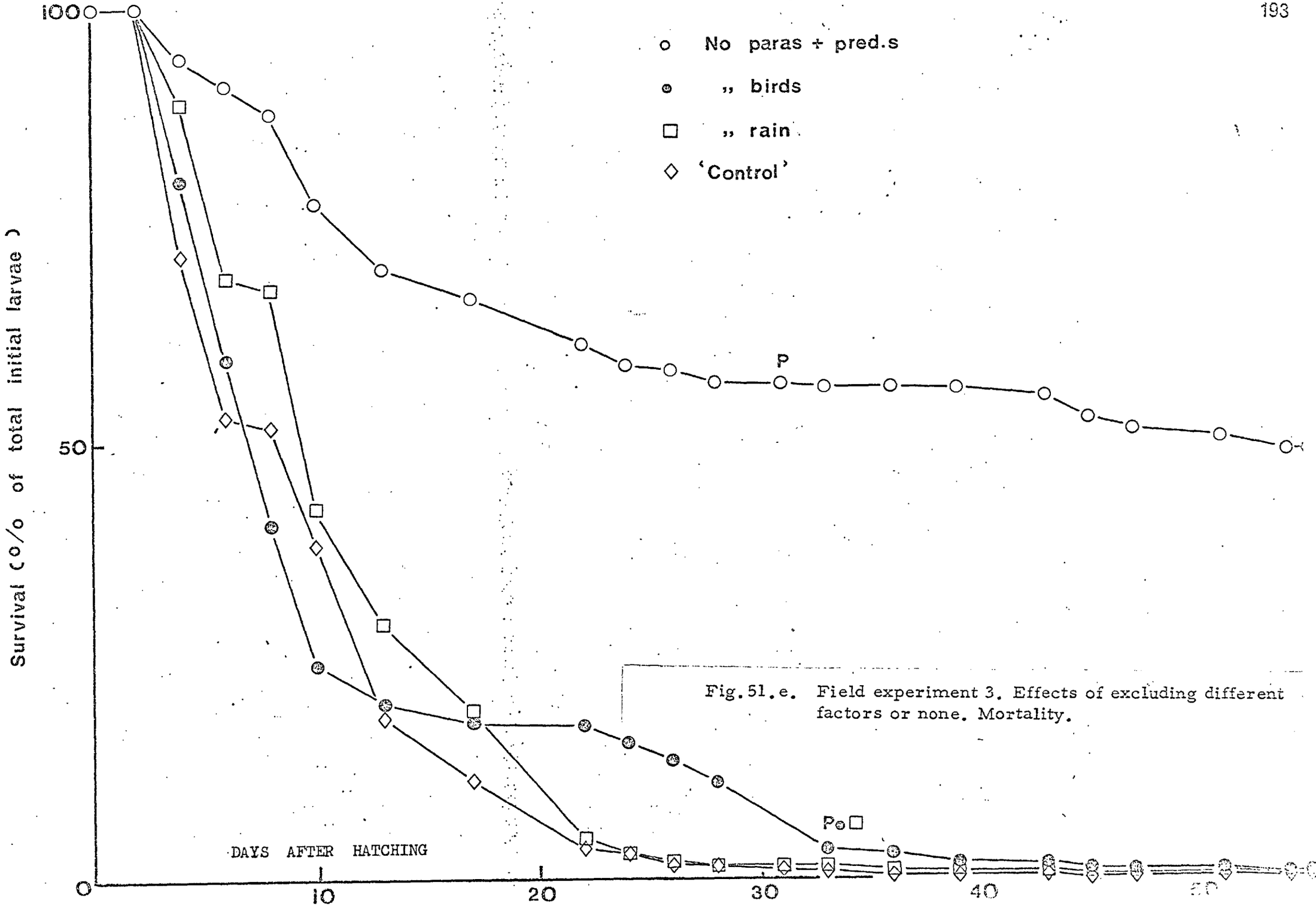


Fig.51.e. Field experiment 3. Effects of excluding different factors or none. Mortality.

10.5.2. Results.

Effects of excluding all parasites and predators.

Table 10.5.1. - Plants protected from parasites and predators. Mortality in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	402	36	9.0	9.0	4.9
Larvae II	366	88	24.0	21.9	15.5
Larvae III	278	32	11.5	8.0	6.4
Larvae IV	246	18	7.3	4.5	3.9
Pupae	228	32	14.0	8.0	14.0
Adults	196	-	-	-	-
Total	402	206		51.2	

From Table 10.5.1 and Figs 49 and 50 it can be seen that the 'apparent' mortality was small in the first instar compared with that in the first experiment. Density did not have a large effect although the highest mortality occurred in the plant with the greatest density.

The 'mean apparent mortalities' between different instars were not significantly different ($F = 0.95$). The results therefore differ from those of Field Experiment No.1 in which the first instar had the highest 'apparent' mortality. Some fourth instar larvae were also lost. Furthermore the pupal mortality was notably more than that in Field Experiment No.1. This rather high mortality was partly due to what seemed to be a disease and also some pupae were drowned in pockets of water formed in the depressions of the surface of the leaves.

Overall about 50% of the newly hatched larvae survived to the adult stage, as in Experiment No.1. The stages at which most mortality occurred were, however, very different.

Effects of excluding birds.

Table 10.5.2. - Plants protected from birds. Mortality in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	545	220	40.4	40.4	0.4
Larvae II	325	216	66.5	39.6	1.1
Larvae III	109	14	12.8	2.6	0.1
Larvae IV	95	64	67.4	11.7	1.1
Pupae	31	28	90.3	5.1	90.3
Adults	3	-	-	-	-
Total	545	542		99.5	

From Table 10.5.2 and Figs 49 and 50 it can be seen that mortalities('apparent') occurred in all the stages. The 'mean apparent mortalities' in the different instars had very highly significant differences ($F = 19.04$; $P < 0.001$), except between second and fourth instars.

The main features of the results were similar losses totalling 80.0% of 'real' mortality in the first two instars, some loss in the fourth instar, and as in Experiment 1, a crucial loss in the pupal stage.

Overall, 99.5% of the first instar larvae failed to become adults. Although 3 out of 545 became adults, the end-result was similar to that in Field Experiment No.1, except that much less of the mortality ('real') occurred in the first instar, some occurred in the fourth instar and unlike Experiment No.1 a few survived the pupal stage. These few survivors are, however, potentially important (see later life-tables analysis).

Effects of excluding rainfall.

Table 10.5.3. - Plants protected from rainfall. Mortality in successive instars (total of 3 replicates).

Instar	Initial No.	No.dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	659	204	31.0	31.0	0.1
Larvae II	455	261	57.4	39.6	0.4
Larvae III	194	163	84.0	24.7	0.8
Larvae IV	31	23	74.2	3.5	0.6
Pupae	8	7	87.5	1.1	87.5
Adults	1	-	-	-	-
Total	659	658		99.8	

From Table 10.5.4 and Figs 49 and 50 it can be seen that mortalities ('apparent') occurred in all stages. No statistically significant differences were found between the 'mean apparent mortalities' of the different instars ($F = 1.03$).

The main features of the results were the almost similar losses totalling 70.6% of 'real' mortality in the first two instars, the high mortality of the third instar and again a very important

loss during the pupal stage.

99.8% of the total initial larvae failed to become adult, giving similar results to those in Field Experiment No. 1, except that in that case near 90% of 'real' mortality occurred in the first instar whereas in the present experiment the mortality was spread over the three first instars; also in this case one pupa reached the adult stage, compared with none in Experiment No. 1.

Effects of all causes of mortality (control).

Table 10.5.4. - Plants fully exposed (Controls). Mortality in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	501	236	47.1	47.1	0.2
Larvae II	265	172	64.9	34.3	0.4
Larvae III	93	76	81.7	15.2	0.9
Larvae IV	17	13	76.5	2.6	0.6
Pupae	4	3	75.0	0.6	75.0
Adults	1	-	-	-	-
Total	501	500		99.8	

From Table 10.5.4 and Figs 49 and 50 it can be seen that mortalities ('apparent') occurred in all the stages. No significant differences ($F = 0.73$) were found between the 'mean apparent mortalities' in the different instars.

The most notable aspect of the results was the consistently decreasing values of the 'real' mortalities with the development of the larvae. The 'real' mortality during the first two larval stages

accounted for 81.4% of the total mortality.

99.8% of the initial larvae died before reaching the adult stage. Only one out of 501 became adult, so this can be said to be similar to the Experiment No.1, except that more third instar larvae died, some fourth instar larval mortality occurred and the pupal mortality was of necessity less because fewer survived to die in the pupal stage.

10.5.3. Discussion.

When all parasites and predators were excluded from the field populations of P. xylostella, the larval mortality ('apparent') unlike in the Experiment No.1, was not directly related to the density. The highest 'apparent' mortality occurred during the second instar; however, there was notable mortality in the other instars. The mortality was variable suggesting that some intra-specific competition may be acting on the larval populations.

An examination similar to that of the previous experiment can be attempted in order to identify the most important factors affecting the population at this later time of the year (Aug - Oct 1969).

The data are summarized in Tables 10.5.5 to 10.5.8 and the significances are indicated.

Table 10.5.6 shows the overall 'real' and 'indispensable' mortalities of each instar in each treatment. The most notable feature of the results was that, as in Experiment 1, protection from all parasites and predators greatly decreased developmental mortality ('real' mortality) to about 50% (Table 10.5.6) compared with 99.5 to 99.8% in exposed treatments. First instar mortality ('real') in all treatments (Table 10.5.6) was nothing like so pro-

Table 10.5.5. - Field Experiment 2. Mortality of different instars.

First instar

Treatment	Total initial No.	No.dead	Apparent mortality (%)
No PP	402	36	9.0
No Birds	545	220	40.4
No Rain	659	204	31.0
Control	501	236	47.1
F = 3.90; No significant			

Second instar

Total initial No.	No.dead	Apparent mortality (%)
366	88	24.0
325	216	66.5
455	261	57.4
265	172	64.9
F = 3.83; No significant		

Third instar

Total initial No.	No.dead	Apparent mortality (%)
278	32	11.5
109	14	12.8
194	163	84.0
93	76	81.7
F = 12.65; P < 0.01		

Fourth instar

Treatment	Total Initial No.	No.dead	Apparent mortality (%)
No PP	246	18	7.3
No Birds	95	64	67.4
No Rain	31	23	74.2
Control	71	13	76.5
F = 9.66; P < 0.05			

Pupae

Total initial No.	No.dead	Apparent mortality (%)
228	32	14.0
31	28	90.3
8	7	87.5
4	3	75.0
F = 1.73; No significant		

Table 10.5.6. - Field Experiment 2. Real and Indispensable mortalities during development of P. xylostella populations (Aug - Oct 1969).

	Real mortality			
	Cause of mortality excluded			
Instar	All natural enemies	Birds	Rain	None
Larvae I	9.0	40.4	31.0	47.1
Larvae II	21.9	39.6	39.6	34.3
Larvae III	8.0	2.6	24.7	15.2
Larvae IV	4.5	11.7	3.5	2.6
Pupae	8.0	5.1	1.1	0.6
Total mortality	51.2	99.5	99.8	99.8

	Indispensable mortality			
	Cause of mortality excluded			
Larvae I	4.9	0.4	0.1	0.2
Larvae II	15.5	1.1	0.4	0.4
Larvae III	6.4	0.1	0.8	0.9
Larvae IV	3.9	1.1	0.6	0.6
Pupae	14.0	90.3	87.5	75.0
Total mortality	-	-	-	-

Table 10.5.7. - Effects of different mortality factors on each instar (based on % Apparent mortality)

Instar	Birds	Rain	All parasites + predators
	Control - No Birds	Control - No Rain	Control - No PP
Larvae I	6.7	16.1	38.1
Larvae II	- 1.6	7.5	40.9
Larvae III	68.9	-2.3	70.2
Larvae IV	9.1	2.3	69.2
Pupae	-15.3	-17.5	61.0
Total (Real mortality)	0.3	0.0	48.6

Table 10.5.8. - Causes of 'pupal' mortality.

Treatment	No. entering prepupal stage	No. killed by parasites	No. disappeared	No. killed by disease	No. drowned	No. of adults
No PP	228	0	6	18	8	196
No Birds	31	15	10	3	0	3
No Rain	8	1	6	0	0	1
Control	4	2	1	0	0	1

nounced as in the Field Experiment No.1, where there was 34 to 88% mortality according to treatment (Table 10.4.7). This was, however, compensated for by mortality in the later instars as indicated by the figures for 'real' and 'indispensable' mortalities (Table 10.5.6).

Total 'real' mortalities during the first three instars in the three exposed treatments ranged from 82.6% in 'No Birds' to 95.3% in 'No Rain', to 96.6% in the 'Controls'. This might imply that birds were killing some larvae but this seems unlikely because in the fourth instar 11.7% (64 individuals) died in 'No Birds' compared with 3.5% (23 individuals) in 'No Rain' and 2.6% (13 individuals) in the 'Controls'. Again as in Experiment No.1, the fourth instar larvae would have been expected to be the most susceptible to birds (because they are larger and more conspicuous) and yet few were lost in the treatments exposed to birds.

As in Experiment No.1 pupal mortality was crucial as indicated by the date in 'indispensable' mortality (Table 10.5.6). The causes of pupal mortality are given in Table 10.5.8. For example, in the fully exposed plants (Controls) only one pupa survived to the adult stage; 50% of the individuals entering the stage were killed by parasites and 25% disappeared probably taken by predators.

Again as in Experiment No.1, very little probably insignificant mortality occurred in the 'No Parasites and Predators' populations, although in this case there was some mortality due to diseases (8% of the initial 'pupae'), and some pupae were drowned (3.5%) in pockets of water formed in the depressions of the leaves surface, and a few pupae (2,5%) were missing, probably fallen to the ground, the rest (about 86%) survived to adults.

In the 'No Birds' treatment 48.4% of the 'pupae were killed by parasites; 32.3% disappeared presumably eaten by small predators going through the netting; 9.7% were killed by disease, and 3 individuals (9.7%) were able to reach the adult stage.

In the 'No Rain' treatment the mortality of the 'pupae' was mainly due to disappearance assumed to be by predators and accounted for 75.0% of the initial 'pupae', while a further 12.5% was killed by parasites, leaving a 12.5% surviving 'pupae' to reach the adult stage.

The survival of pupae to the adult stage in the 'No Birds' and 'No Rain' treatments is in clear contrast with the Experiment No.1 in which all pupae were killed by parasites or predators.

Summarizing it can be said that during September and October (late season) the populations of P. xylostella had different developmental ('real') mortality as compared with the populations in July and August.

In this case the mortality ('real') was more distributed between the first two instars (in Experiment No.1 it is concentrated in the first instar), and there was appreciable mortality during the third and fourth instars in contrast to the Experiment No.1 in which very small mortality occurred in the third instar and none at all in the fourth instar. This increase in late larval mortality may be an indirect consequence of a longer developmental time due to the decrease in temperature (overall means : Aug. 16.0°C; Sept. 14.2° C; Fig 52) which makes the larvae for longer time available to parasites and predators and at the same time they become sluggish therefore being unable to escape rapidly from parasite or predator attack.

In general the mortalities in the different instar were tending to compensate for any lack of mortality in the previous stage, as can be seen from the 'real' and 'indispensable' mortalities.

The 'pupae', as in Experiment 1, was the most susceptible stage, as shown by the 'apparent' mortalities. Some pupae survived and produced adults in all the treatments but it is unlikely that those adults or their progeny would survive under the climatic conditions after late October and November.

Finally it can be seen from Table 10.5.7 that, in all the stages, parasites and predators (except 'birds') were the most important mortality factors. There was little rainfall during September (total Sept. rainfall : 8.6 mm; Fig 53), and the birds were seemingly unimportant.

10.6. THIRD FIELD EXPERIMENT (LATE SUMMER - AUTUMN 1970).

This field experiment was carried out during the period August to October 1970.

The objective of the experiment, was as in the previous experiment, to determine the main causes of mortality of the larvae under field conditions and especially to confirm the results of the previous experiment in which parasites and predators were the most important mortality factors. Since rainfall albeit scarce (Fig 53) had little effect on the mortality of the larvae in the two previous experiments (see Figs 48 and 50), it was decided not to use the cages which protect the larvae against rainfall. Instead a

set of three cages was used in order to protect the plants from soil predators. Small predators seemed to be very important, however, no idea was available about which predators were most important, either 'soil predators' which climb and crawl through the stems and the lower leaves touching the ground, or 'flying predators' which come by air and land on the plants.

10.6.1. Materials and methods.

Again this experiment was carried out at "Hill Bottom", on Brussels Sprouts plants. The plants were transplanted to the field about May and at the beginning of the season (May-June) suffered water stress. They were allowed some time to recover, and also some replanting was carried out. By July the plants were in condition to start the experiment (about thirty full grown leaves) but the population of Brevicoryne brassicae (L.) had increased in such a way that all the plants were infested. The less infested plants were selected in the field and marked. They were then sprayed with a selective non-persistent insecticide, nicotine sulphate 0.05% solution to remove the aphids. One week later the cages were placed over the plants and one week later, although the plants seemed to be clean of aphids, the spraying was repeated. By the beginning of August the plants were ready and the experiment was set up. There was some irregularity in the size of the plants that were used, as a consequence of the period of drought mentioned above.

The plants were left with twenty full grown leaves each. All the youngest and oldest leaves were cut off, and so were the buds from the axils. The petioles were trimmed of leaf tissue. The tops of the plants were cut off and the youngest leaf to be left was that with enough space to hold an oviposition cage (about 25 cm^2 area). This was done so that the plants could be easily searched for

P. xylostella larvae. Some other leaves were removed from different heights on the stem of the plant in order to give a good 'spread' of ages (especially medium and young groups) of leaves and to have the same number (twenty) of leaves per plant, and regular distribution of leaves up the stem. In those plants from which parasites and predators were going to be excluded,and those from which soil predators were excluded, all the lowest leaves were removed to avoid any of them touching the ground and thus allowing predators to climb on them. Three cages per treatment were used to give a total of nine caged plants, plus three plants without cages to be used as 'controls', as in the previous experiments. Cages used were also as in the previous experiment. To isolate the soil predators, wooden-frame cages without netting were used and the ground area inside the frame was covered with dieldrin dust (2%) as described in Materials and methods.

Oviposition cages were then placed on the youngest leaf of each plant,which was about 40 cm^2. They were placed on the lower surface of the leaf, as explained before, to avoid direct sun heating and because they prefer to lay on that surface. Small groups of adults (about ten) were introduced and honey solution provided as food; they were left to oviposit for three days. The honey solution was replaced daily. After three days the adults were removed and the oviposition cages left in their places to allow the eggs to incubate. The oviposition cages were removed about twenty four hours after the first larvae hatched, in order to have uniformity in instar age.

The initial number of recently hatched larvae per treatment ranged from 379 to 826.

10.6.2. Results.

Effects of excluding all parasites and predators.

Table 10.6.1. - Plants protected from parasites and predators. Mortality in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	826	12	1.5	1.5	1.2
Larvae II	814	15	1.8	1.8	1.5
Larvae III	799	28	3.5	3.4	3.0
Larvae IV	771	32	4.2	3.9	3.6
Pupae	739	51	6.9	6.2	6.9
Adults	688	-	-	-	-
Total	826	138		16.7	

From Table 10.6.1 and Figs 51 and 52 it can be seen that the 'apparent' mortality in the first instar was very small compared with the same first-instar mortality in Experiments 1 and 2. Density did not have a great effect although the highest mortality occurred in the replicate with the highest density.

The 'mean apparent mortalities' between different instars were not significantly different ($F = 1.33$).

The first instar had the least mortality ('apparent' and 'real') of the developmental stages, and as in Experiment 2 it was very small, in that way differing from Experiment 1 in which the first instar suffered the highest mortality. The 'real' mortality in the

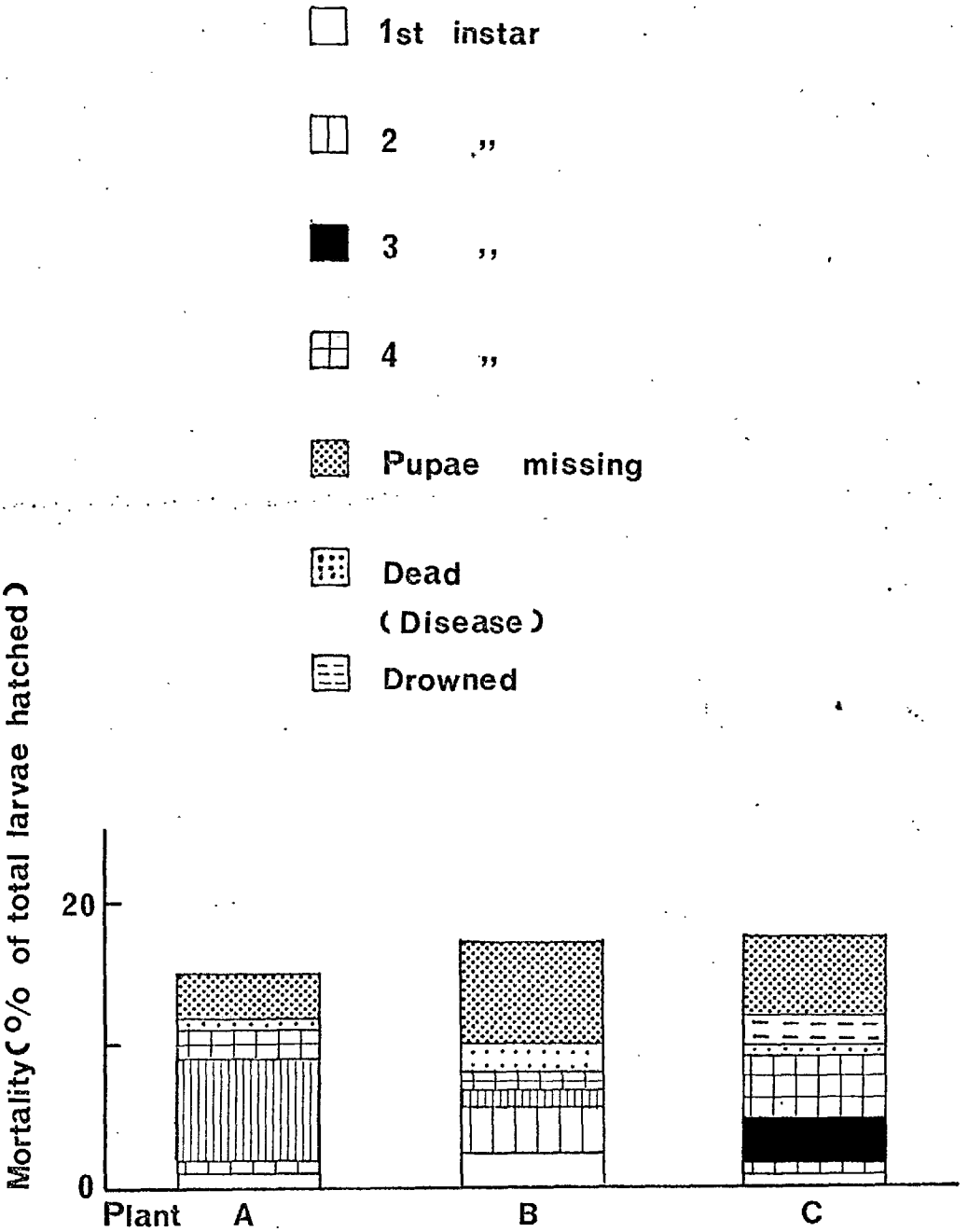


Fig.51.a. Field experiment 3. Effects of excluding parasites and predators. Mortality.

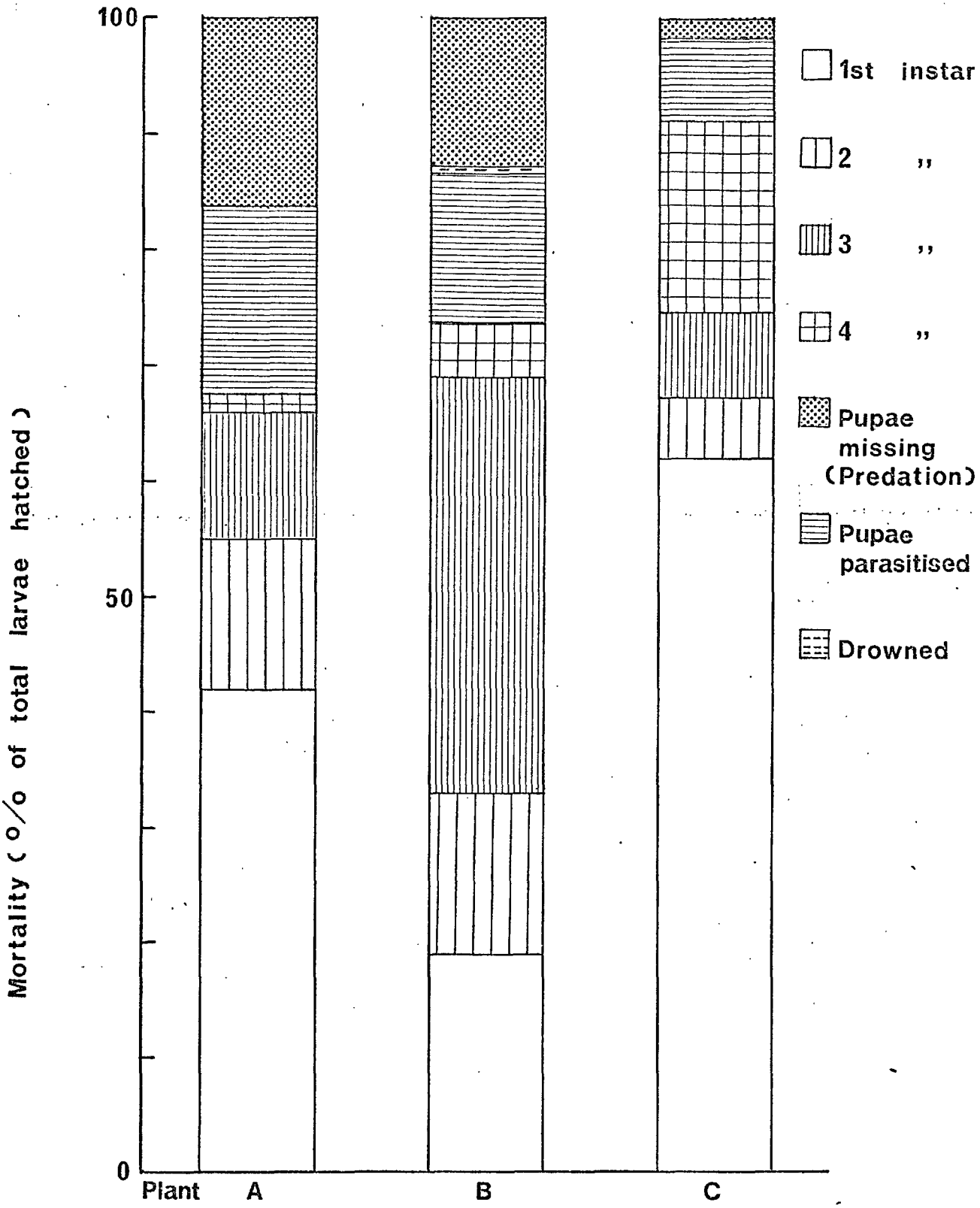


Fig.51.b. Field experiment 3. Effects of excluding birds. Mortality.

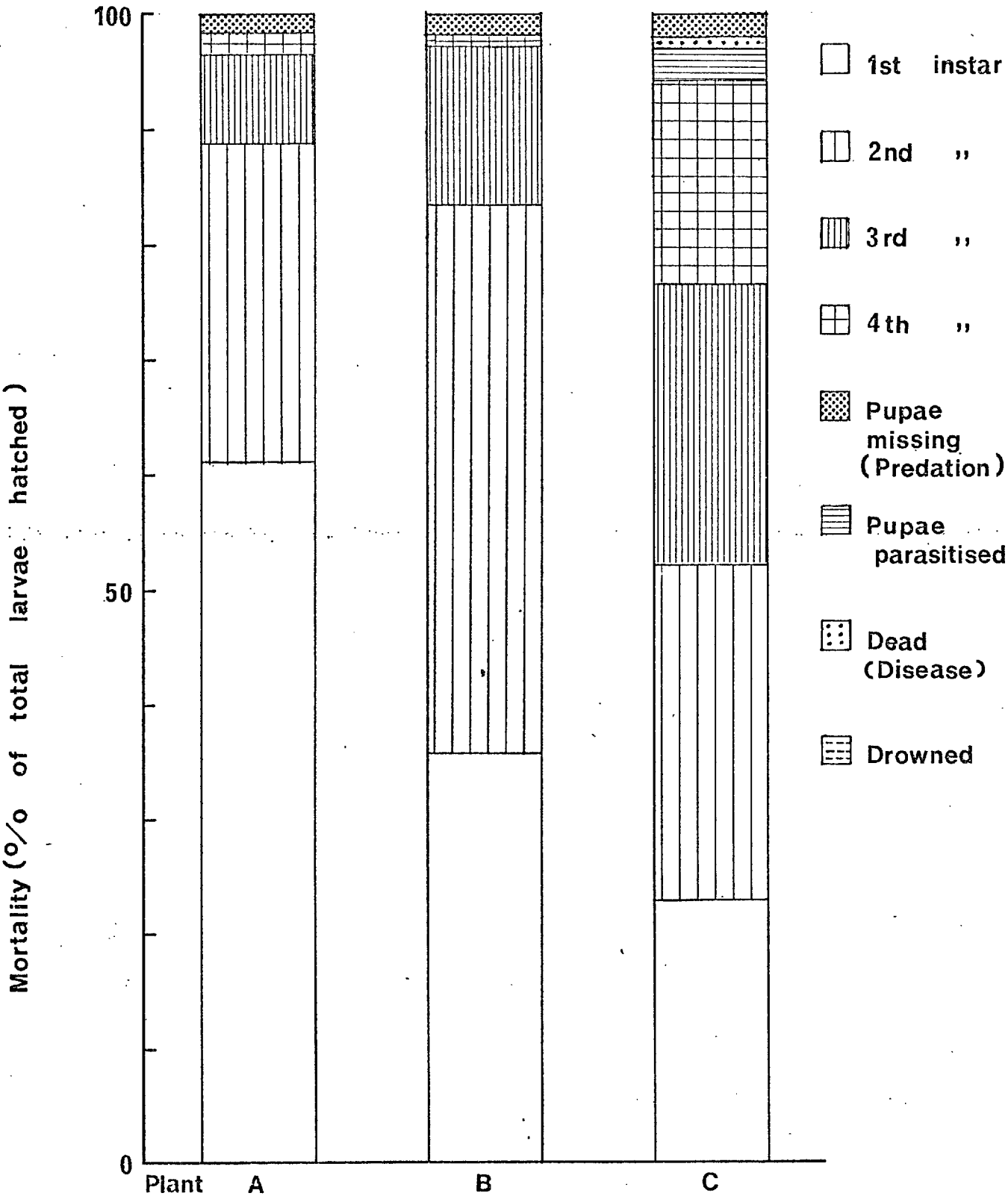


Fig.51.c. Field experiment 3. Effects of excluding soil predators. Mortality.

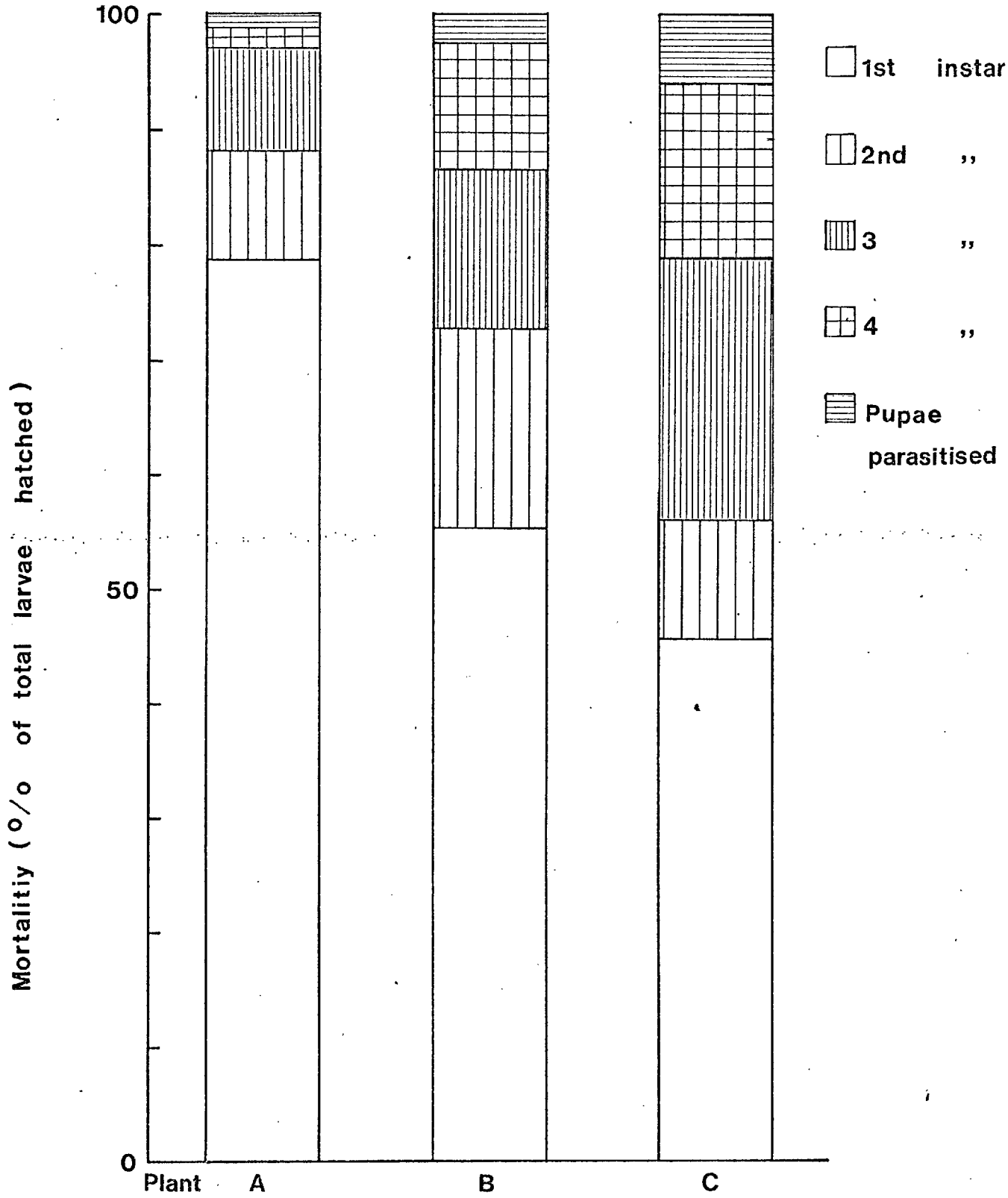


Fig. 51. d. Field experiment 3. Effects of exposure to all mortality factors. Mortality.

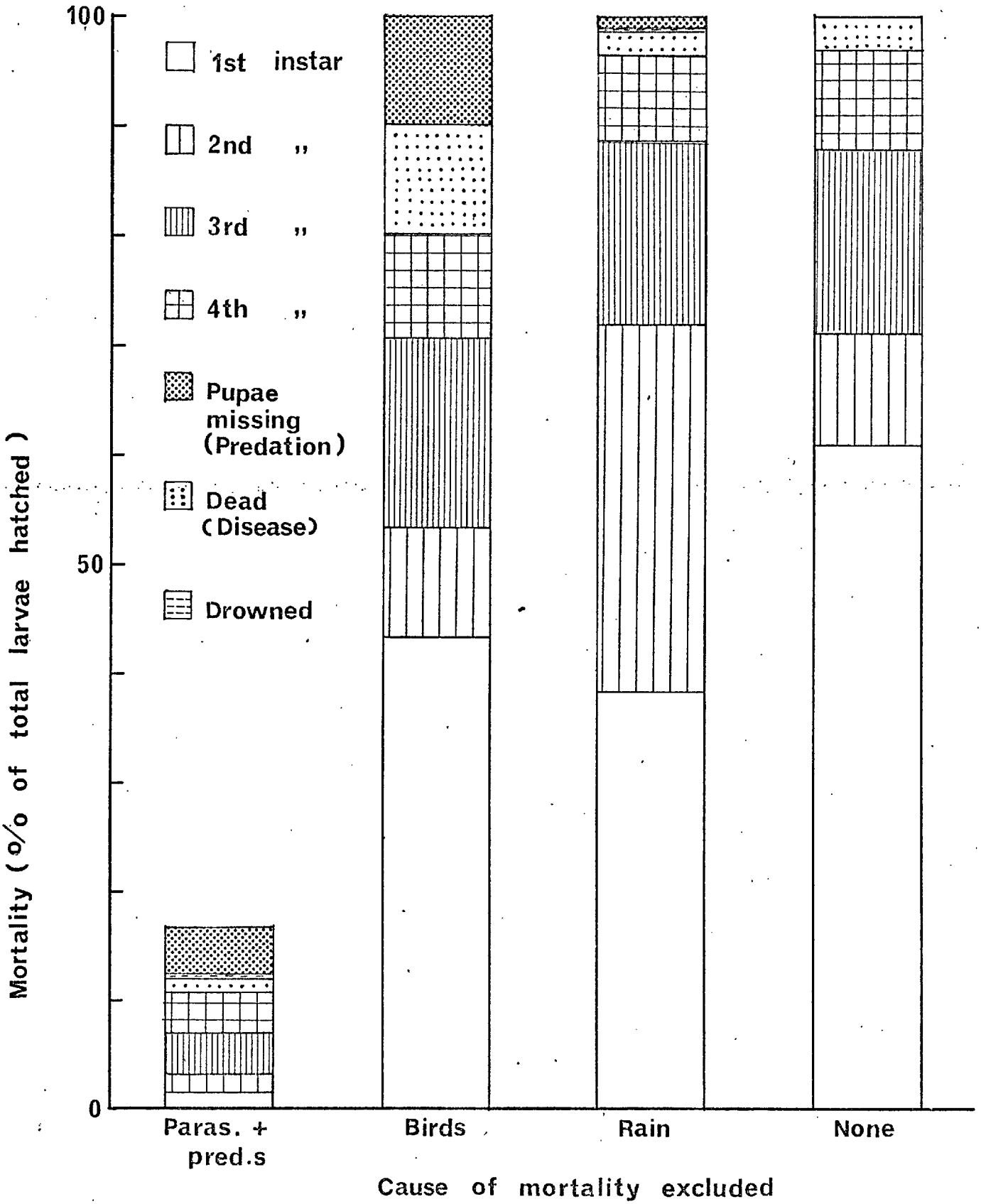


Fig. 50. e. Field Experiment 2. Effects of excluding different factors or none. Survival.

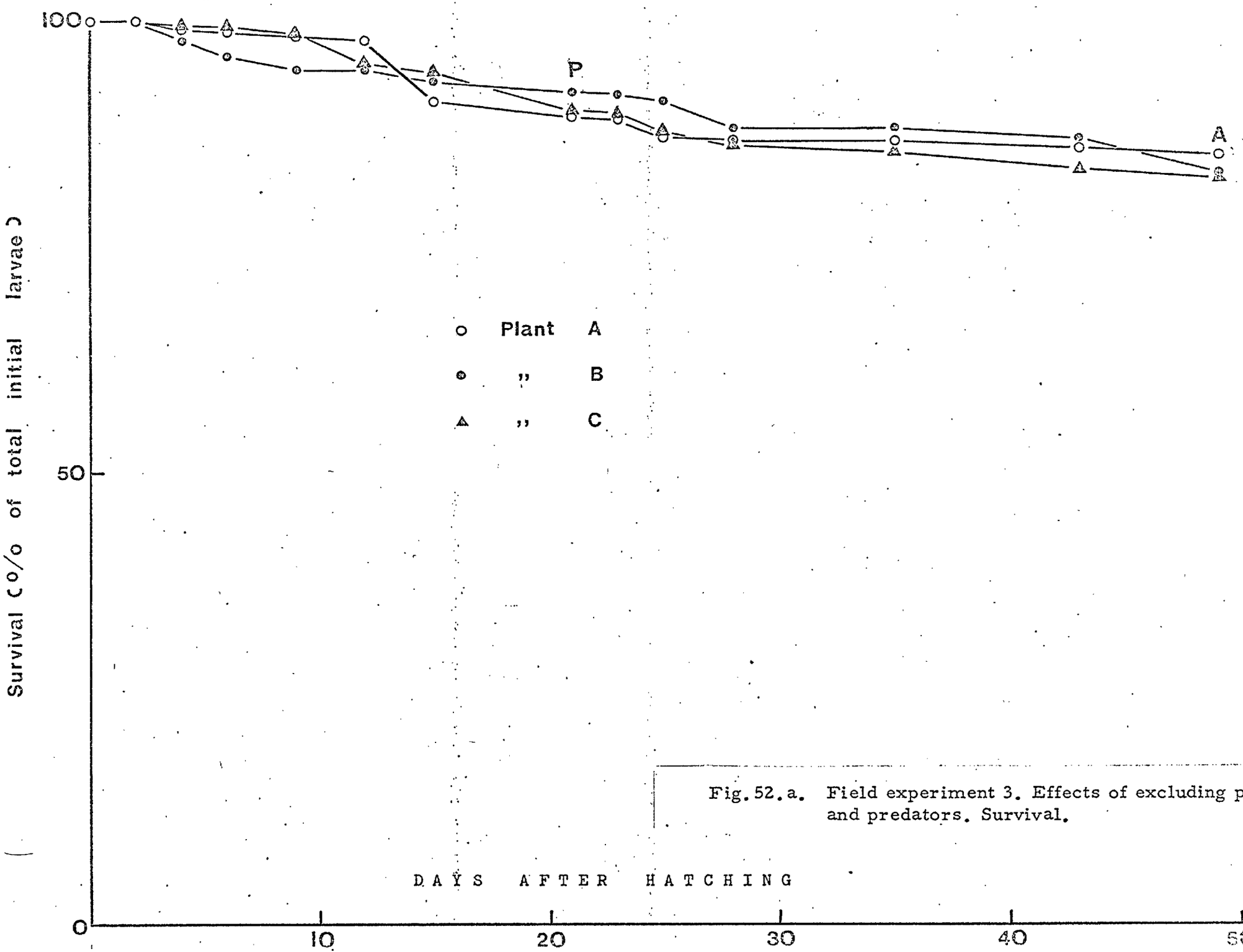


Fig. 52. a. Field experiment 3. Effects of excluding parasites and predators. Survival.

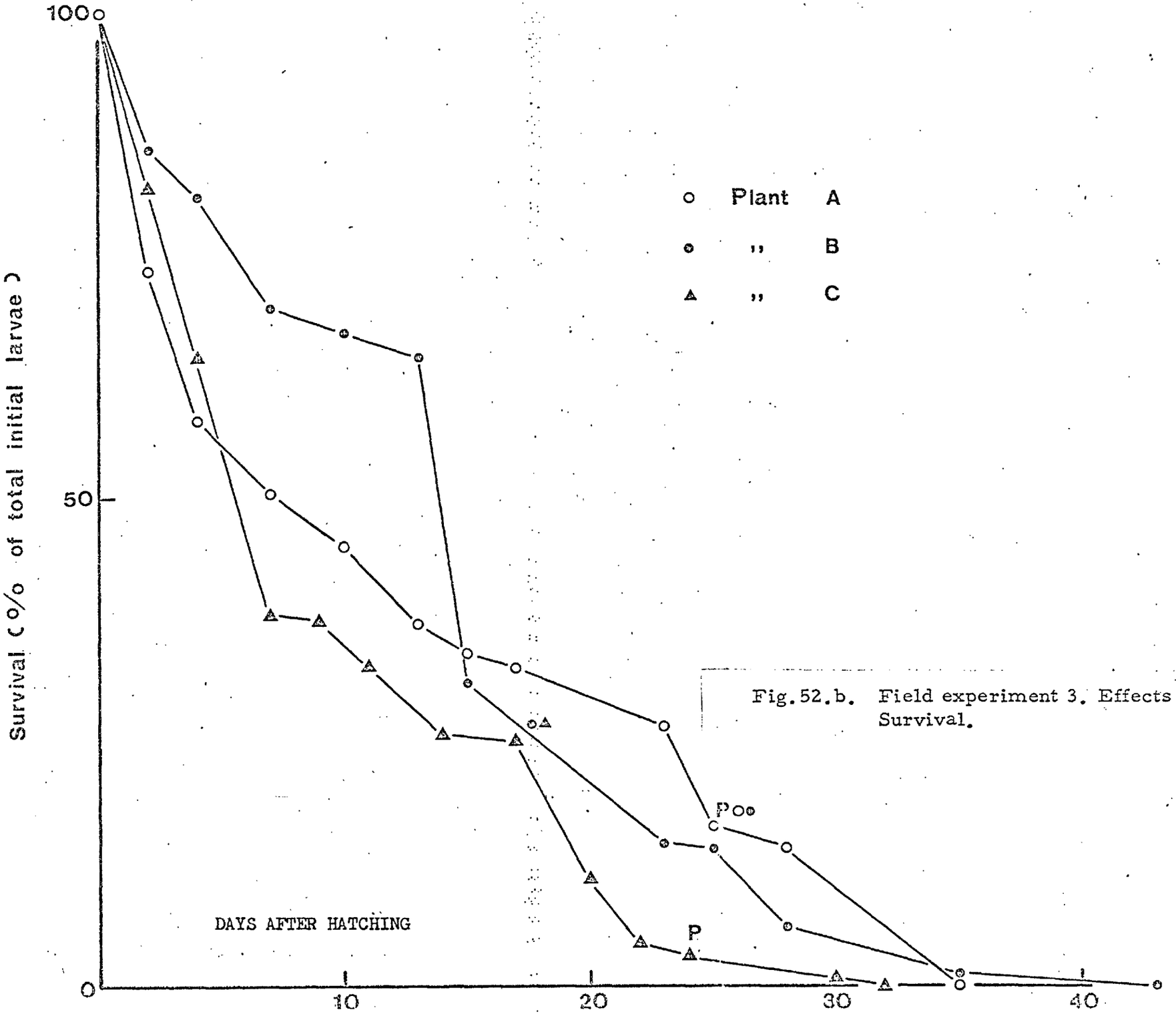


Fig.52.b. Field experiment 3. Effects of excluding birds. Survival.

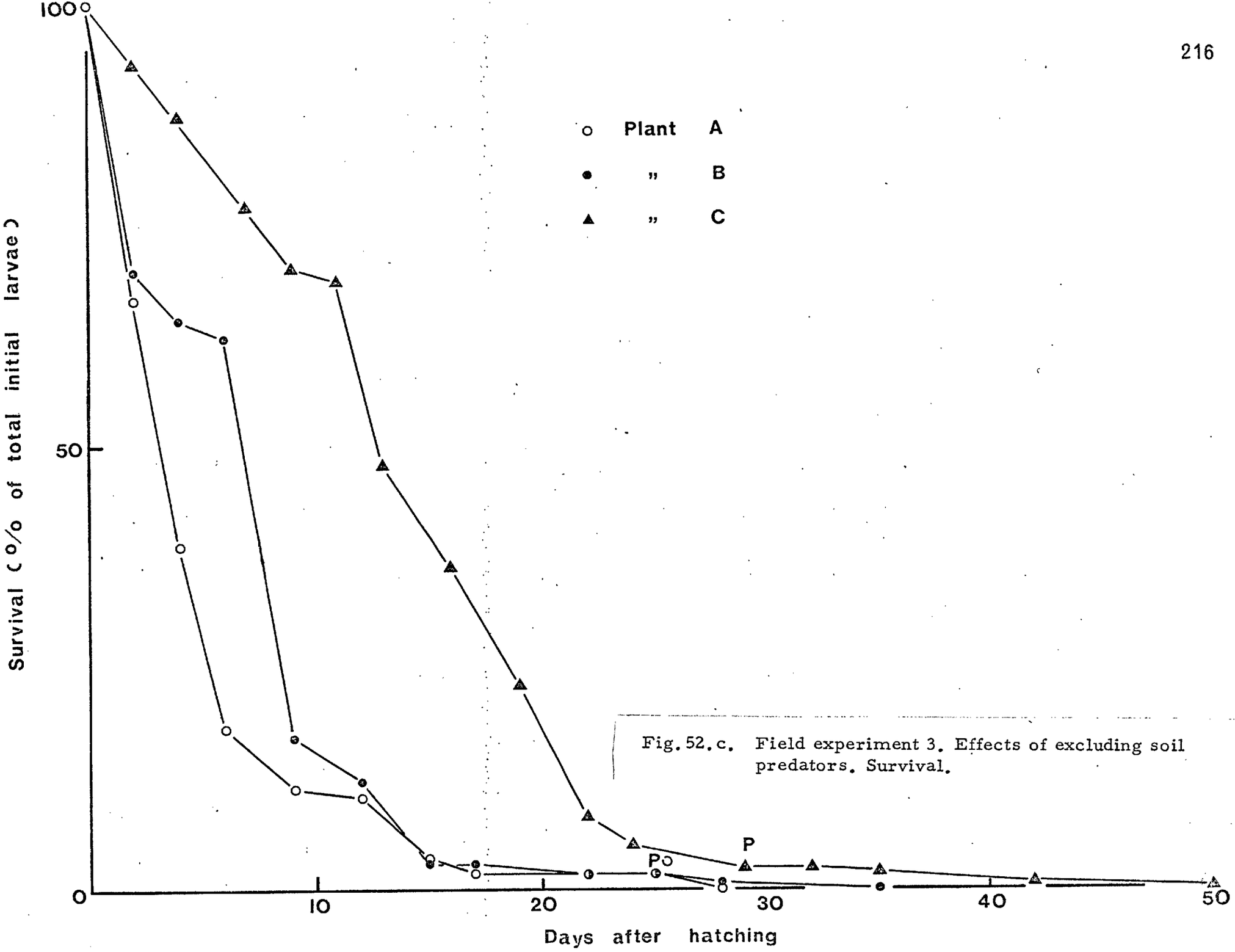


Fig. 52. c. Field experiment 3. Effects of excluding soil predators. Survival.

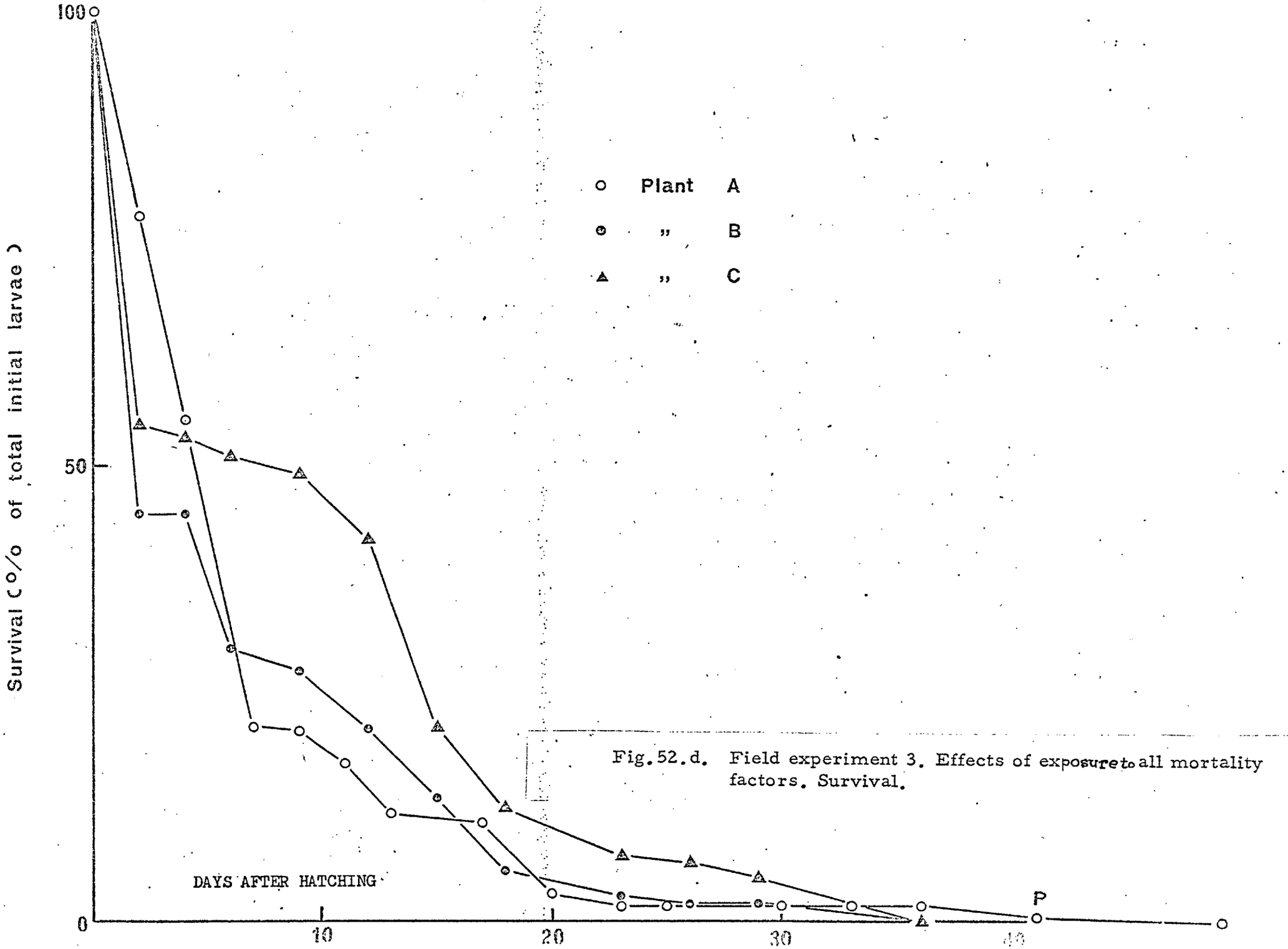


Fig.52.d. Field experiment 3. Effects of exposure to all mortality factors. Survival.

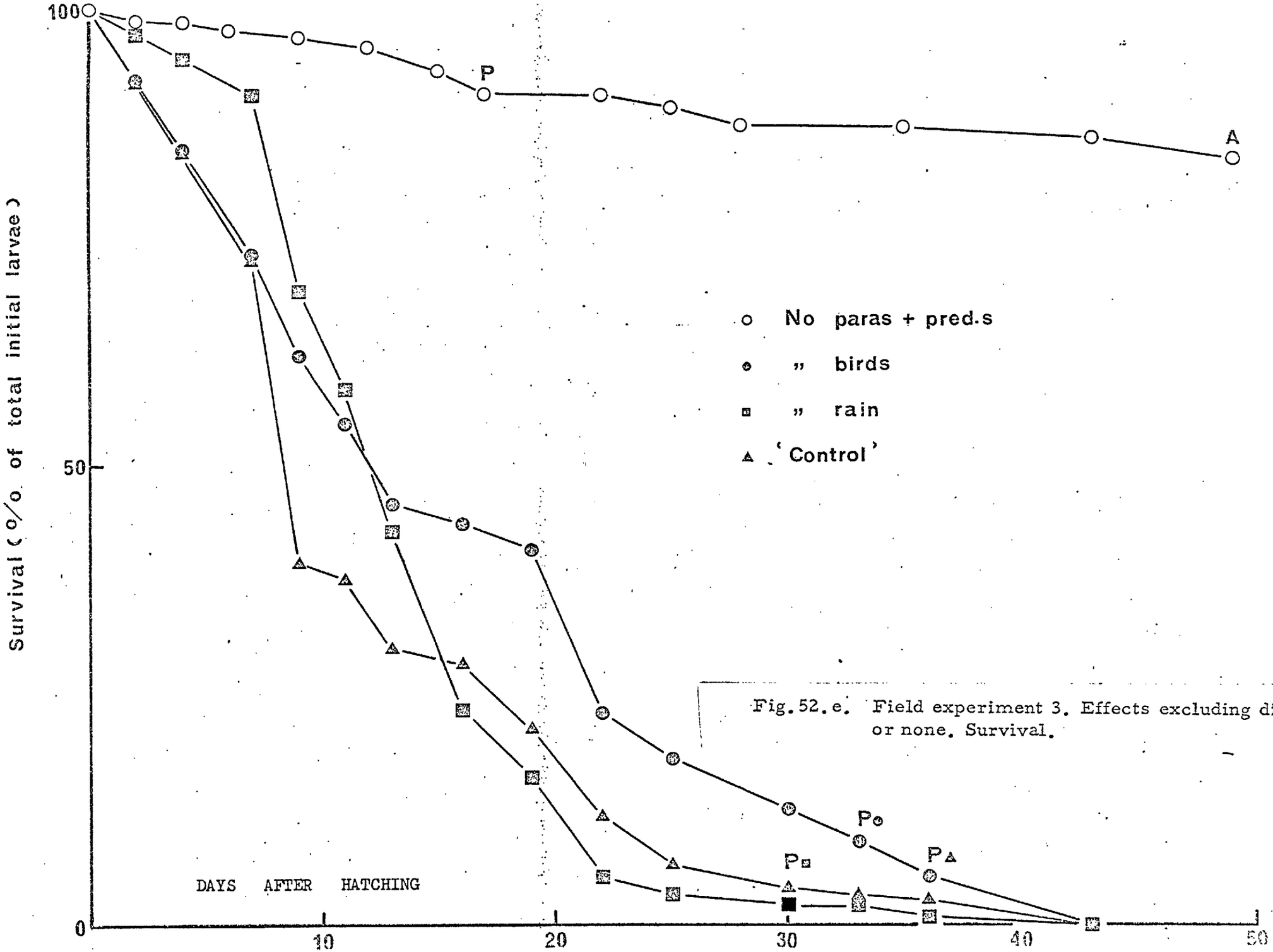


Fig.52.e. Field experiment 3. Effects excluding different factors or none. Survival.

present experiment increased with the instar, so the highest instar mortality ('real') of 6.2% was observed in the 'pupae'. Some 'disappeared' and others died from what seemed to be a disease.

Overall, 83.3% of the newly hatched larvae survived to the adult stage; therefore the results differ from those of Experiments 1 and 2 in which about 50% of the initial larvae became adults.

Effects of excluding birds.

Table 10.6.2. - Plants protected from birds. Mortality in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	519	225	43.4	43.4	0.0
Larvae II	294	52	17.7	10.0	0.0
Larvae III	242	90	37.2	17.3	0.0
Larvae IV	152	49	32.2	9.4	0.0
Pupae	103	103	100.0	19.9	100.0
Adults	0	-	-	-	-
Total	519	519		100.0	

From Table 10.6.2 and Figs 51 and 52 it can be seen that mortalities occurred in all the stages. The 'mean apparent mortalities' in the different larval instars were not significantly different from each other but they were highly significant from that of the pupal stage ($F = 7.17$; $P < 0.01$).

The most important features of these results were the mortality of the first instar which was the highest of all the instars

(43.4% of 'real' mortality), the similarity in the losses of the other instars, and the 100% mortality of the 'pupae'.

The 100% mortality of the 'pupae' confirms the results of Experiments 1 and 2 although in those a few pupae produced adults.

Effects of excluding soil predators.

Table 10.6.3. - Plants protected from soil predators. Mortality in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	379	145	38.3	38.3	0.0
Larvae II	234	128	54.7	33.8	0.0
Larvae III	106	63	59.4	16.6	0.0
Larvae IV	43	30	69.8	7.9	0.0
Pupae	13	13	100.0	3.4	100.0
Adults	0	-	-	-	-
Total	379	379		100.0	

From Table 10.6.3 and Figs 51 and 52 it can be seen that mortalities occurred throughout all the developmental stages. The 'mean apparent mortalities' in the different instars had highly significant differences ($F = 7.33$; $P < 0.01$).

The most notable aspects of the results were the high losses of the first two instars which accounted for 72.1% of the 'real' mortality, also some mortality in the third and fourth instars, and the 'pupae' suffered 100% mortality.

Effects of all causes of mortality (Control).

Table 10.6.4. - Plants fully exposed (Controls). Mortality in successive instars (total of 3 replicates).

Instar	Initial No.	No. dead	Apparent mortality (%)	Real mortality (%)	Indispensable mortality (%)
Larvae I	481	293	60.9	60.9	-
Larvae II	181	50	26.6	10.4	-
Larvae III	138	79	57.2	16.4	-
Larvae IV	59	44	74.6	9.1	-
Pupae	15	15	100.0	3.1	100.0
Adults	0	-	-	-	-
Total	481	481		100.0	

From Table 10.6.4 and Figs 51 and 52 it can be seen that mortalities occurred in all stages. There were highly significant differences between the 'mean apparent mortalities' in the different instars ($F = 11.21$; $P < 0.01$).

The most notable features of the results were the large loss of the first instar (60.9% of the 'real' mortality). Some losses also occurred in the other larval instars, and the mortality of the 'pupae' was 100%.

This 100% pupal mortality can be considered comparable to that of the same treatment (Control) in Experiments 1 and 2, except than in those experiments a very few pupae survived to the adult stage.

Table 10.6.5. - Field Experiment 3. Mortality in different instars.

First instar

Treatment	Total initial No.	No. dead	Apparent mortality (%)
No PP	826	12	1.5
No Birds	519	225	43.4
No S.P.	379	145	38.3
Control	481	293	60.9
F = 7.00; P < 0.05			

Second instar

Total initial No.	No. dead	Apparent mortality (%)
814	15	1.8
294	52	17.7
234	128	54.7
188	50	26.6
F = 17.07; P < 0.01		

Third instar

Total initial No.	No. dead	Apparent mortality (%)
799	28	3.5
242	90	37.2
106	63	59.4
138	79	57.2
F = 14.44; P < 0.01		

Fourth instar

Treatment	Total initial No.	No. dead	Apparent mortality (%)
No PP	771	32	4.2
No Birds	152	49	32.2
No S.P.	43	30	69.8
Control	59	44	74.6
F = 8.80; P < 0.05			

Pupae

Total initial No.	No. dead	Apparent mortality (%)
739	51	6.9
103	103	100.0
13	13	100.0
15	15	100.0
F = 2187; P < 0.001		

Table 10.6.6. - Field Experiment 3. Real and Indispensable mortalities during development of P. xylostella populations (Aug - Oct. 1970).

	Real mortality			
	Cause of mortality excluded			
Instar	All natural enemies	Birds	Rain	None
Larvae I	1.5	43.4	38.3	60.9
Larvae II	1.8	10.0	33.8	10.4
Larvae III	3.4	17.3	16.6	16.4
Larvae IV	3.9	9.4	7.9	9.1
Pupae	6.2	19.9	3.4	3.1
Total mortality	16.7	100.0	100.0	100.0

	Indispensable mortality			
	Cause of mortality excluded			
Instar	All natural enemies	Birds	Rain	None
Larvae I	1.2	0.0	0.0	0.0
Larvae II	1.5	0.0	0.0	0.0
Larvae III	3.0	0.0	0.0	0.0
Larvae IV	3.6	0.0	0.0	0.0
Pupae	6.9	100.0	100.0	100.0
Total mortality	-	-	-	-

Table 10.6.7. - Effects of different mortality factors on each instar (based on % Apparent mortality).

Instar	Birds	Soil Predators	All parasites + predators
	Control-No Birds	Control-No S P	Control-No P P
Larvae I	17.5	22.6	59.4
Larvae II	8.9	-28.1	24.8
Larvae III	20.0	- 2.2	53.7
Larvae IV	42.4	4.8	70.4
Pupae	0.0	0.0	93.1
Total (Real mortality)	0.0	0.0	83.3

Table 10.6.8. - Causes of 'pupal' mortality.

Treatment	No. entering prepupal stage	No. killed by parasites	No. disappeared (predation?)	No. killed by disease	No. drowned	No. adults
No PP	739	0	39	10	2	688
No Birds	103	57	46	0	0	0
No SP	13	6	1	1	5	0
Control	15	15	0	0	0	0

10.6.3. Discussion.

When all parasites and predators were excluded from the field populations of P. xylostella, larval mortality, although highest in the replicate with the highest density, was not directly related to the density as regards the other replicates. The mortality was in general very low.

A similar examination to those in Experiments 1 and 2 can be attempted in order to identify the most important factors affecting the population at this time of the year (Aug-Oct 1970).

The data are summarized in Tables 10.6.5 to 10.6.8 and the significances are indicated.

Table 10.6.6 shows the overall 'real' and 'indispensable' mortalities of each instar in each treatment.

The most important feature of the results was that, as well as in Experiments 1 and 2, protection from all parasites and predators greatly decreased developmental mortality ('real' mortality) to a very low level of 16.7% (Table 10.6.6) compared with total (100%) in the other, exposed treatments. The first instar mortality in all treatments except 'No Parasites and Predators' (Table 10.6.6) was high, ranging from 38.3% to 60.9%; the mortality in the first instar in the populations protected from all parasites and predators was only 1.5%.

Total 'real' mortalities during the first three instars in the three exposed treatments ranged from 70.7% in 'No Birds' to 88.7% in 'No Soil Predators', to 87.7% in the 'Controls'. This seems to be an indication that in this experiment soil predators were not important at all in killing P. xylostella larvae.

As well as in Experiments 1 and 2, pupal mortality was crucial and total in the exposed populations, as indicated by the figures for 'indispensable' mortality (Table 10.6.6).

Causes of pupal mortality are given in Table 10.6.8. Thus, in the fully exposed plants (Controls) all the 'pupae' were killed by parasites, therefore differing from Experiments 1 and 2 in which some pupae were probably taken by predators, and some survived to the adult stage.

Again as in Experiments 1 and 2, there was very small mortality of 'pupae' in the 'No Parasites and Predators' populations. About 1.3% of the initial 'pupae' were killed by diseases, and about 5.5% were missing, probably fallen and lost in the ground, one pupa out of 739 was drowned in a water-pocket on a leaf.

In the 'No Birds' treatments about 55% of the 'pupae' were killed by parasitism and the rest were presumably eaten by predators.

In the 'No Soil Predators' treatment 46% of the initial 'pupae' were lost due to parasites, 7.5% were killed by what seems to be a disease, a further 7.5% was drowned in water-pockets on the leaf-surface, and 39% was assumed taken by predators.

The total pupal mortality in the 'No Birds' treatment is similar to that in experiment 1, but different to Experiment 2.

Summarizing it can be said that in general the results confirm the results of previous experiments.

As in Experiment 2, the mortalities of the larval stages were more distributed between the two first instars (in the Experiment 1 they were concentrated in the first instar), and there was some mortality during the third and fourth instars as in Experiment 2 and in contrast to Experiment 1. Therefore a similar interpretation

can be applied in the present experiment, i.e. that the late instars mortality may be a consequence of the decrease of tempe rature (overall means: Aug 15.9°C; Sept 14.1°C; Fig 53) which increases the developmental rate of the insects and thus the larvae are for a longer time available to natural enemies; also by becoming sluggish they are more easily attacked by predators and parasites.

The 'pupa ' as in Experiments 1 and 2, was the most susceptible stage. In contrast to Experiment 2, no treatment (except 'No Parasites and Predators') produced any adults.

Finally from Table 10.6.7 it can be seen that in all the stages the parasites and predators (except birds) were the most important mortality factors, although in the fourth instar the birds may also have had some effect.

10.7. DISCUSSION.

Table 10.7.1 shows in a summarized form the mortality of the larvae and pupae of P. xylostella on Brussels Sprouts under field conditions.

Table 10.7.1 - Mortality of P. xylostella field populations.

	Mortality			
Treatment	Exp. 1	Exp. 2	Exp. 3	Mean
No P.P.	46.9	51.2	16.7	38.3
No Birds	100.0	99.5	100.0	99.8
No Rain	100.0	99.8	-	99.9
No S.P.	-	-	100.0	100.0
Control	98.9	99.8	100.0	99.6

From Table 10.7.1 and Figs 47e, 49e and 51e, it can be seen that the mean mortality of larvae and pupae of P. xylostella under field conditions is almost total (99.6% in the 'Control' populations).

The effect of each factor can be estimated or determined by the difference with relation to the total mortality. However in the present investigation the mortality of the 'Control' populations was slightly lower than on those populations which have been isolated from birds, rain, or soil predators, and although the difference is insignificant it suggests that when all the factors act together on the populations of P. xylostella they may interfere with each other so as to allow a small proportion of the population to survive and produce a new generation. Similarly it suggests that when one of the factors is removed the other or others are left in more favourable conditions to cause mortality and therefore the mortality appears to be higher in those populations which were isolated from one factor than on the 'Control' populations.

Effect of bird predation.

When the mortality of the 'Control' populations (99.6%) is subtracted from that on the populations isolated from the attack of birds (99.8%), the difference (0.2%) is insignificant. Therefore birds can be discounted on this evidence as being significant causes of mortality. It could even be that by eating other insects, they eat some parasites and predators and so could decrease the effect of the latter on the populations of P. xylostella. It can be seen from Fig 47e that the first instar 'real' mortality in Experiment 1 was in agreement with the above suggestion : much higher in the populations isolated from birds than in those exposed to them, but Figs 49e and 51e suggest that this did not happen in the two other experiments where mortality ('real') was slightly higher when the birds were allowed access to the plants. Figs 47e and 49e indicate that the second instar mortality was higher when the birds were excluded, so agreeing with the proposed suggestion. In the third instar the mortality was slightly higher in the populations excluded from birds in Experiment 1 (Fig 47e), but much lower in the two others (Figs 49e and 51e) suggesting that birds may be important predators during this instar. In the fourth instar there was no mortality in Experiment 1 (Fig 47e); in the second experiment (Fig 49e) mortality of the fourth instar was much higher in the 'Controls'. The cause is unknown. More survived to the fourth instar than in previous experiments so a predator may have 'seen' them more readily. It is, therefore, possible that in this case birds did prey on them.

In the pupal stage the mortalities were 100% or virtually so in all three experiments (Figs 47e, 49e and 51e). About half the pupae were parasitised and half were presumably taken by

predators, whether protected or unprotected from birds, except in the 'controls' of the Experiment 3, where all the pupae were parasitised.

Effects of soil predators.

Only in Experiment 3 were soil predators specifically excluded. In this experiment when the mortality of the 'Control' populations (99.6%) is subtracted from that on the populations isolated from soil predators (100.0%), the difference (0.4%) is insignificant so soil predators were entirely ineffective in these conditions. However, the results should be again considered in terms of mortalities in successive instars. In the first instar (Fig 51e) there was a lower mortality ('real') in the populations protected from soil predators than in the 'Controls', which may suggest that such predators were possibly eating recently hatched larvae; but from Fig 51 e it can be seen that in the second instar the 'Control' populations suffered less than one third the mortality ('real') of that of the larvae protected from soil predators. In the third instar the mortalities of the populations protected or fully exposed ('Controls') against soil predators were similar suggesting that the soil predators were unimportant at this stage. The fourth instar 'real' mortality was similar in both protected and unprotected populations (Fig 51e) but the 'apparent' mortality was much greater in the 'No Soil Predators' populations and no doubt represented a major source of population mortality. The cause is unknown but certainly the results could be interpreted as soil predators being unimportant in reducing the populations of P. xylostella at this stage.

In the 'pupa' (Fig 51e) the situation was similar to that when birds were excluded, that is the mortality was 100% in both

'Control' and 'No Soil Predators' populations. In the populations protected from soil predators about half the mortality was caused by parasites and about half by flying predators (with a low proportion drowned in water-pockets or killed by diseases), while in the 'Control' populations all the pupae were killed by parasites. Perhaps the dieldrin killed the parasites, which are known to be highly susceptible to this chemical.

Effect of parasites.

When the overall % mortality during the larval and pupal stages of the fully exposed populations (99.6%) is subtracted from that of the populations isolated from all parasites and predators (38.3%), the difference (61.3%) can be considered as the mortality caused by parasites and predators.

The parasites of P. xylostella, and especially Nythobia eurocerophaga Horstm. and N. neocerophaga Horstm. (the most common parasites in the present investigation), do not kill the host until pre-pupation or pupation; therefore their effect as a mortality factor can be considered as limited to those stages ('pupa').

Effects of rainfall.

When the overall mortality of the fully exposed ('Controls') populations (99.6%) is subtracted from that of the populations isolated from rainfall (99.9%), the difference is insignificant, implying no effect of rainfall. However the results should be again considered in relation to the different experiments and stages. Thus in Experiment 1 (Fig 47e) exclusion of rain actually increased mortality of first instar larvae compared with the rain-exposed 'Controls', but in Experiment 2 there was, conversely, lower mortality when the rain was excluded. In the second instar the mortality in Experiment

1 (Fig 47e) was smaller in the populations protected from rain than in the 'Controls', implying a possible effect of rain on this larval stage, however, in Experiment 2, rain-protected and unprotected populations suffered similar mortality (Fig 49e). In the third instar, Experiment 1 had similar mortalities in the populations isolated from rain and in the fully exposed 'Controls' (Fig 47e), but in Experiment 2 there was greater mortality in 'No Rain' populations than in those exposed to rain ('Controls') (Fig 49e). In Experiment 1 there was no mortality in the fourth instar (Fig 47e), and in Experiment 2 the mortalities were similar in both treatments, protected and unprotected from rain.

In the pupal stage in Experiment 1 (Fig 47e) there were similar mortalities whether the populations were excluded or exposed to rainfall, but in Experiment 2 the mortality was greater in the rain-protected population than in the fully exposed 'Controls' (Fig 49e). In both cases parasites and predators were more important.

Effects of other factors.

The overall mortality (38.3%) still occurring in those populations protected from parasites and predators can be regarded as caused by the combined effect (in variable proportion) of climate (mainly temperature), host plant condition, density of larvae (especially in the first instar), and failure of the recently hatched larvae to eat. In general it can be considered as the 'early instars' mortality since it is higher in the early instars (Fig 47, 49 and 51).

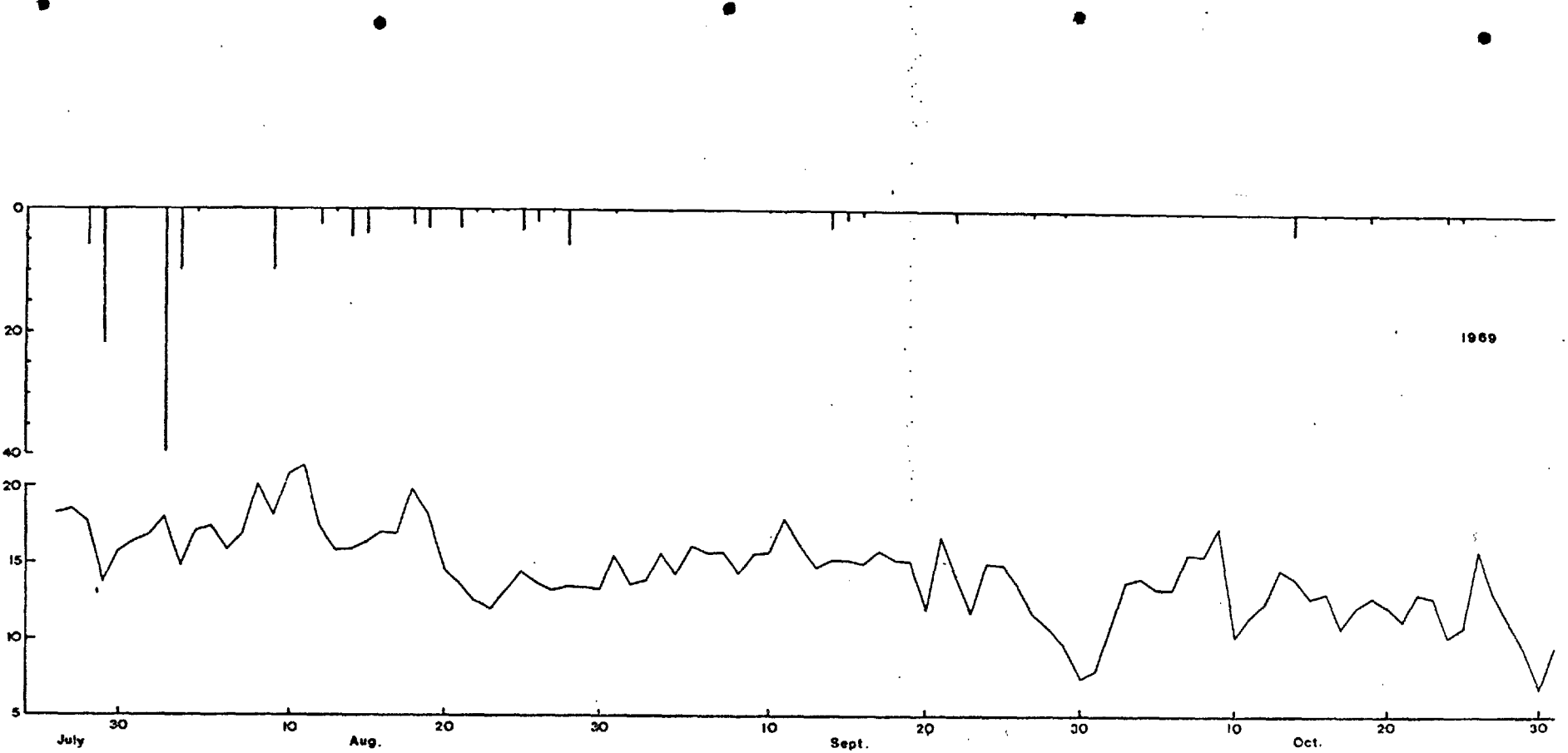


Fig. 53. Total rainfall (mm) and mean (max. -min. /2) temperature (°C).

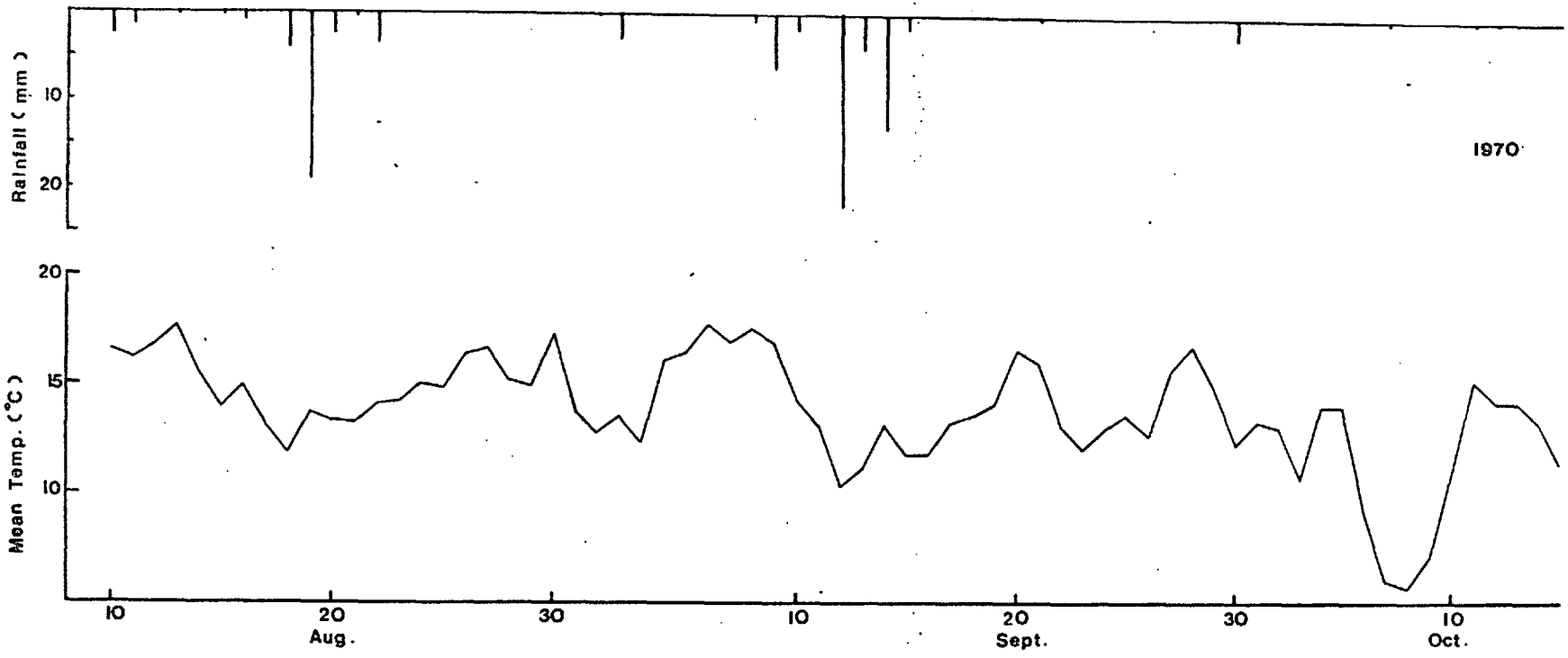


Fig. 54. Total rainfall (mm) and mean (max.-min./2) temperature(°C).

10.8. LIFE-TABLES.

10.8.1. Introduction.

Results of the field experiments described above indicate factors responsible for the mortality of larval and pupal populations of P. xylostella. However, with the use of life-tables it is possible to summarize the data and compare them, especially when analysing the relative effects of those factors regulating the populations during different periods of time. The importance of life-tables is discussed by Southwood (1966) when he points out that 'the construction of a number of life-tables is vital to the description and understanding of the population dynamics of a species ... '. In the present work the data are not entirely suitable for life-table analysis but this was done as an exercise to show what could be obtained by such a study that was not apparent from the raw data.

10.8.2. Materials and methods.

The data analysed were limited to those obtained from the unprotected ('Control') populations in the field experiments above described, and from those protected against all parasites and predators. These provided two extremely contrasting situations.

In order to determine the potential rate of increase of the populations under field conditions, life and 'fertility' tables were constructed for the populations protected from all parasites and predators and for the fully exposed ('Controls') populations.

The method used to develop the life-table was that in which the survival of a cohort is followed at close intervals throughout its existence (second method in Deevey, 1947). The method used to construct the actual table was similar to that

given by Harcourt (1969) although some modifications were introduced because of differences in conditions. For example, the sample unit was a whole Brussels Sprouts plant, plants were artifically infested, there was no immigration, and the mortality was recorded every two or three days. The data obtained were, therefore, more reliable than sampling from the natural population since the survivorship was measured in the same cohort every time and there were no complications from immigrants.

The pivotal age (x) in the life-tables is given in days although for comparison between treatments or experiments they are related to the different instars, hence the extra column 'stage'. The initial numbers of eggs were not directly counted but assumed to be the same as the initial numbers of larvae because the egg mortality is normally small as usually found in laboratory populations. Harcourt (1969) also found less than 1% egg mortality in field populations.

For the 'fertility tables' the numbers of females (lx) was assumed to be half the total numbers of individuals reaching the adult stage because laboratory experiments gave a ratio of male to female of 1 : 1.26. The longevity of the females was assumed to be 15 days (about the mean for males and females bred in the laboratory). The number of living females born per female per day (mx) was taken from the laboratory pattern of daily oviposition, assuming a sex ratio 50 : 50.

The headings of the columns of the life-tables are those given by Deevey (1947), Morris (1963) and Southwood (1966). Also 'fertility' tables were constructed following the pattern suggested by Southwood (1966), and 'stable-age distribution tables' as indicated in Andrewartha & Birch (1954).

The following are the headings and their meanings; for more details on their calculation, the original references above quoted should be consulted.

Life-tables:

x The pivotal age (or age interval) in units of time (days).

l_x The number of individuals alive at the beginning of age interval x.

d_x The number of individuals dying during the age interval x.

L_x The number of Individuals alive between age x and $x+1$.

T_x The total number of animal x age units beyond the age x.

e_x The expectation of life remaining for individuals of age x.

$100\ q_x$ The mortality rate per age interval (per 100 individuals alive at x).

Fertility tables:

l_x The number of females alive at the beginning of age x (as a proportion of 1).

m_x The number of living females born per female during the age x.

Ro The net reproductive rate (the number of times a population will multiply per generation).

T The mean duration of a generation.

r_m The intrinsic (or innate) rate of natural increase (the maximal rate of increase when the population is growing in an unlimited environment and the age distribution has become stable).

Stable-age distribution table:

L_x The number of individuals alive between age x and $x + 1$ (as a proportion of one).

β The birth rate (number of females born during a certain interval of time in a stable population).

$100\beta L_x e^{-r_m(x+1)}$ The distribution of the population (as a percentage).

Results.

Appendix-Tables 10.8.1 to 10.8.23 are the 'budgets' or life-tables, the 'fertility' tables, and the 'stable-age distribution' tables, for each individual cohort (plant) and for the total population on each of the three seasons studied.

Tables 10.8.2 and 10.8.3 are the 'budgets' prepared for K-factor analysis for the same populations and years.

Discussion.

The r values summarized from Appendix-Tables 10.8.1 to 10.8.23 and Fig A6 are given in Table 10.8.1.

Table 10.8.1. - r values.

Experiment	Natural enemies excluded	Fully exposed ('Controls')
1	0.077	0.027
2	0.074	-0.044
3	0.085	0.000

Although they are subject to serious limitations because laboratory data were used to assess aspects of fertility, the values are useful for comparison rather than as absolute values. Thus it can be seen that in most circumstances except when there was complete protection from natural enemies the values were very small (0.027 and 0.000) or negative (-0.044) indicating in the case of the very small values a very small potential for increase (0.027) or none at all (0.000) from generation to generation and in the case of negative values, evidence that the population was dying out. This explains the observed field situation whereby P. xylostella is usually scarce and at Silwood Park during the period of the experiments was probably non-existent as a natural population. Clearly there are large mortalities due to natural enemies culminating in the virtually 100% parasite/predator mortality in the pre-pupal/pupal stage.

The K values estimates (Tables 10.8.2 and 10.8.3) are also based on not entirely valid procedures since the generations studied were not successive. Again however they are a useful exercise, complementing the raw data obtained already. In particular they indicate a surprisingly important component of mortality during the second instar (Figs 55; 56 and 57), i.e. they suggest that mortality in the second instar is more closely related to total mortality in the generation than is any other factor. This may be spurious but, nevertheless, requires further study since it could be crucial, in some circumstances in terms of pest outbreaks, for example a low value of second instar mortality in one generation could lead to an outbreak in the next.

Table 10.8.2. - 'Budget' table for key factor analysis.
(Fully exposed plants ('Controls')).

	'Generations'					
	1		2		3	
	No.	Log$_e$K	No.	Log$_e$K	No.	Log$_e$K
Eggs	93	1.96848	501	2.69984	481	2.68215
Larvae I	93	1.96848	501	2.69984	481	2.68215
K1 Predators, intra-specific competition		0.34523		0.27659		0.40799
Larvae II	42	1.62325	265	2.42325	188	2.27416
K2 Predators, intra-specific competition		0.28083		0.45477		0.13428
Larvae III	22	1.34242	93	1.96848	138	2.13988
K3 predators		0.11197		0.11928		0.36903
Larvae VI	17	1.23045	17	1.23045	59	1.77085
K4 predators		0.00000		0.62839		0.59476
Prepupae and pupae	17	1.23045	4	0.60206	15	1.17609
K5 parasites		0.38535		0.30103		
	7	0.84510	2	0.30103	15	1.17609
K6 predators		0.84510		0.30103		0.00000
Adults	1	0.00000	1	0.00000	0	--
K total mortality		1.96848		2.08109		1.68215

Table 10.8.3. - 'Budget' table for key factor analysis.

(Plants protected from all natural enemies)

	'Generations'					
	1		2		3	
	No.	Log x K	No.	Log x K	No.	Log x K
Eggs	337	2.52763	402	2.60423	826	2.91698
Larvae I	337	2.52763	402	2.60423	826	2.91698
K1 Predators, intra-specific competition		0.18324		0.04432		0.06557
Larvae II	221	2.34439	363	2.55991	814	2.91062
K2 Predators, intra-specific competition		0.07488		0.11587		0.00807
Larvae III	186	2.26951	278	2.44404	799	2.90255
K3 Predators		0.01424		0.05310		0.01550
Larvae IV	180	2.25527	246	2.39094	771	2.88705
K4 Predators		0.00000		0.03301		0.01841
Pre-pupae + pupae	180	2.25527	228	2.35793	739	2.86864
K5 Disappearance		0.00242		0.01158		0.02354
	179	2.25285	222	2.34635	700	2.84510
K6 Disease		0.00000		0.03672		0.00625
			204	2.30963	690	2.83885
K7 Drowning		0.00000		0.01737		0.00126
Adults	179	2.25285	196	2.29226	688	2.83759
K total mortality		0.27478		0.31197		0.13870

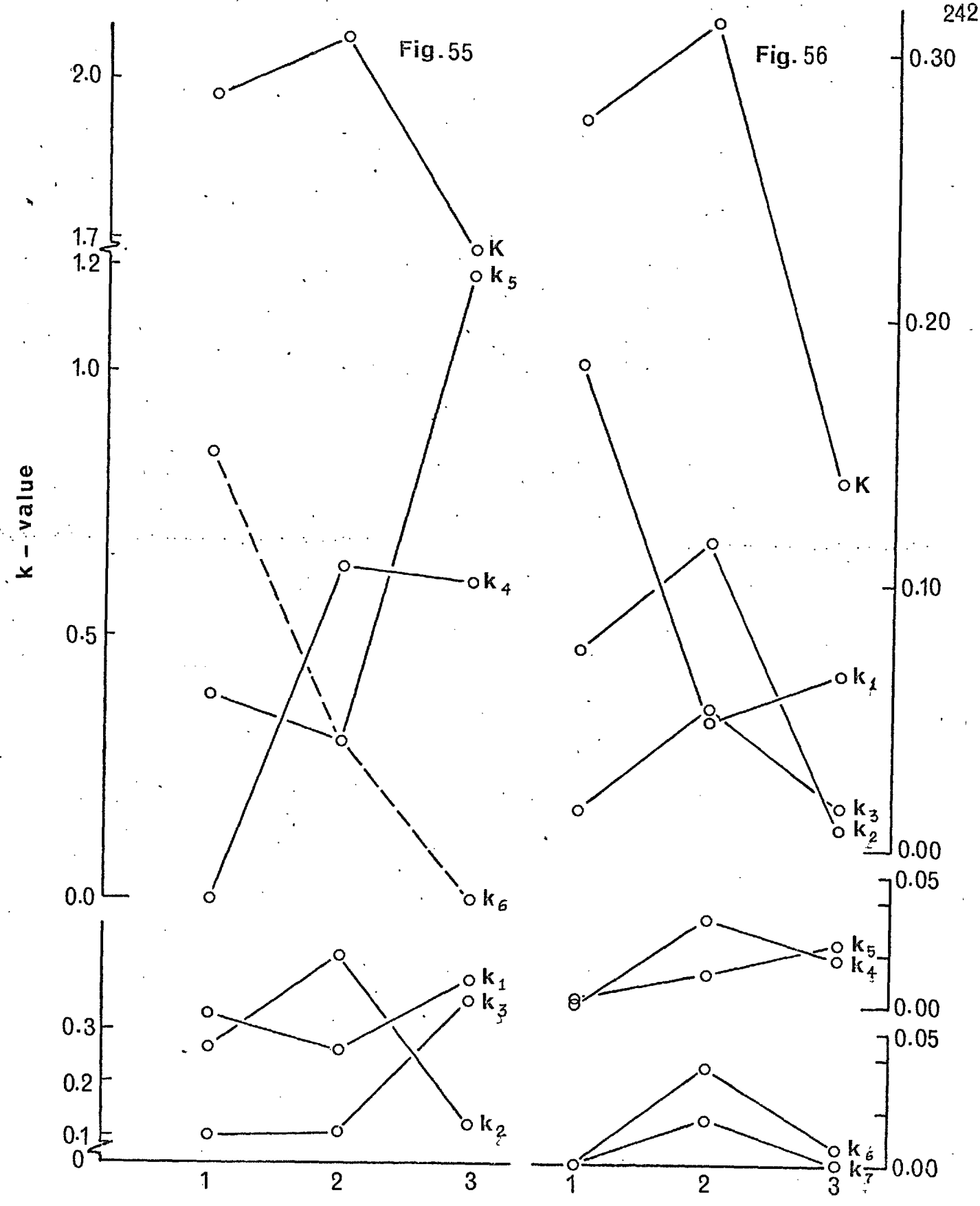


Fig. 55. Recognition of K factors by visual correlation. Fully exposed plants (Controls).

Fig. 56. Recognition of K factors by visual correlation. lants rotected from all natural enemies.

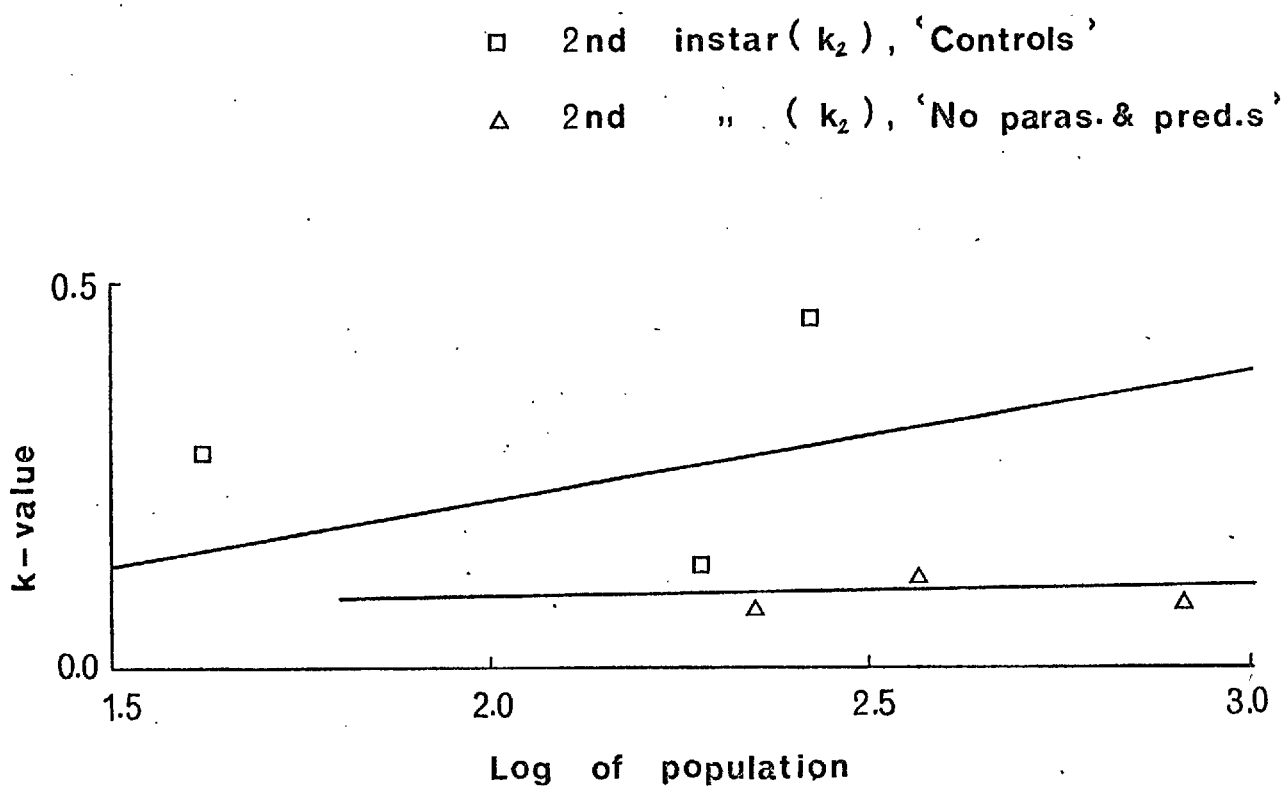


Fig. 57. Recognition of density dependence.

11. DISCUSSION

There are two main approaches to the study of the dynamics of populations in animals, particularly insects (Varley & Gradwell, 1970). One is the extensive study approach, in which a species is studied over a large area although relatively few samples per year are taken in any given place because the limitations of time. The other is the intensive study approach, in which a species is studied in a relatively small area, sometimes limited to a few plants. Therefore, sampling is done frequently in the same place and the life history of every cohort can, in theory, be followed in detail.

In the latter conditions the main factors influencing the populations change can be more accurately determined and the conclusions can be more adequately interpreted. This latter approach was attempted in the present investigations in order to analyse the effect of mortality factors acting on P. xylostella populations.

P. xylostella populations, as well as those of any other organism, fluctuate constantly. These fluctuations depend on a number of different factors acting on the individuals, which are collectively known as their 'environment.'

The environment includes very broadly speaking, biotic and abiotic factors; therefore it is also constantly changing. Since it includes abiotic factors such as temperature, radiation, etc., it tends to be different under different geographical places and since it includes biotic factors such as food plant conditions, parasites, predators, competitors, etc., it also tends to be different from season to season, and finally since for each individual it includes other individuals of the same species it tends to be different from population to population (within the same locality and time).

11.1 LABORATORY POPULATIONS.

Intra-specific interactions are perhaps best observable in the laboratory in which all environmental conditions can be made constant except the insect subject to the study.

P. xylostella populations are subject to the effects of density in a predictable way whereby there is higher mortality at higher densities, i.e. directly density dependent mortality. However, in the present work, mortality was most noticeable during the early instars, particularly in the first instar. This seems partially due to the mining behaviour of the larvae at this stage, for example when a mining larva is about to meet another mine it goes out and starts a new mine in a different place. In that way it avoids overcrowding and over-exploitation of the host plant. However during that period of time in which the larvae are out of the mine they may be subjected to several mortality factors such as predators or rain, or even the wind may blow them off the plants. The same can be said for the second and early third instar larvae.

The host plant condition plays a similarly important role in the survival of P. xylostella as demonstrated in laboratory conditions. For example if the leaf tissue is not tender enough, as may happen in certain circumstances, the young larvae, especially those recently hatched, will find difficulty in biting the leaf surface and in establishing a feeding place. If the time taken before succeeding in piercing a feeding hole is very long the young larvae may die of exhaustion and/or inanition.

There is also a very important aspect of the mortality of P. xylostella in relation to the density and it is the effect of isolated larvae. For example when a moth lays a single egg on a leaf, or when by any other circumstances a larva is born isolated, its behaviour differs from those born in small groups. The first manifestation is a tendency to mine near the egg in contrast to the larvae in groups which tend to

move away from the group before starting to eat the leaf. The isolated larva behaviour may be a form of defence against natural enemies and climate, that is by getting into the mine quickly the larva is protected from extrinsic mortality causes. The behaviour of the larvae in groups may be interpreted as a means of avoiding deterioration of the leaf tissue in order to save it for the larvae hatching later on. Another important characteristic of the isolated larvae is susceptibility to death before eating or moulting to the second instar when the leaf tissue is not very tender. This may suggest that mutual stimulation is useful in encouraging larvae to bite the leaf surface. This stimulation must be by sensory stimuli, such as tactile, odour or any other chemosensorial stimuli.

After the gallery-making period the larvae feed on the leaf surface making window-type holes and adopting a distribution on the plants which is very dispersed (random) and sometimes becomes overdispersed (regular). This even distribution is not only on the plants but also on each leaf and seems to be achieved by a type of spacing-out mechanism involving sudden wriggling movements when disturbed by another larva. The final effect is a spaced distribution which seemingly helps to make a better utilization of the resources, mainly food and space, and avoids all the effects of overcrowding such as contamination, over-exploitation of resources, and also limits the effects of predators by being dispersed and sometimes by a sort of alarm system caused when a larva tries to escape and disturbs others which in turn will wriggle away or fall from the plant on threads and so on.

11.2. FIELD POPULATIONS.

Populations of P. xylostella under field conditions are subjected to a number of different mortality factors which are interacting and affect each other as well as P. xylostella. Those factors are responsible for the regulation of the populations and hence for the greater or smaller importance of the species as a pest. It is sometimes difficult to isolate the actual effect of each factor; for example temperature will affect

the rate of development of P. xylostella and also that of its predators and parasites and the rate of growth of the host plants; therefore it is difficult to assess the direct effect of temperature alone. Nevertheless, estimates of the effects of single factors are normally obtained by isolating one or more factors. This 'exclusion' technique is a valuable ecological tool in studies of field mortality and was used in the present investigation to assess the importance of bird predation, soil predators, other predators, parasites and rainfall, which apart from temperature and food are probably the most important natural factors regulating the populations of P. xylostella under field conditions.

11.2.1. Early instar mortality (up to 3rd instar).

The'early instar mortality' is induced by a series of mortality factors which act with particular emphasis during the egg, first and second larval instar, but also may include early third instar.

In the egg the most common cause of mortality is 'reduced viability' and this includes infertility of the females which may lay eggs without being fertilized (or even copulated), it also includes the overall effects of other environmental factors such as temperature and humidity, or incidental predation. However, no parasite or specific predator of the eggs has been recorded from field populations of P. xylostella.

The larvae of P. xylostella are susceptible to intraspecific competition, as demonstrated in laboratory conditions, especially during the first and second instars. This competition is mainly for space since there was always plenty of food. The competition is at the beginning expressed by the longer distance travelled by the recently hatched larvae between the egg and the first feeding place, and later by a change of mining-place induced by the presence of other mines; this change of mining-place before the normal time exposes the first instar larvae to external factors which may cause a high mortality.

In the early stages and mainly during the first instar the larvae are likely to be susceptible to the general conditions of the host plant, especially to the toughness of the leaf tissue, which is given firstly by the plant species and variety, and is later influenced by other factors such as rainfall or irrigation, temperature, relative humidity, solar radiation, etc. Unfortunately such effects of the host plant were not demonstrated very successfully in the present work perhaps because it was difficult to simulate different plant conditions in laboratory-grown plants.

The early as well as the older larvae are subjected to the effects of climate in general, i.e. temperature has a marked effect on the rate of development of the larvae. Rainfall had little effect in the present experiments since the amount of rain and especially the intensity was small. However, when present in considerable amounts, as has occurred in certain regions (Harcourt 1963a, 1969), it may seemingly cause great mortality.

Although parasites attack the larvae in all stages (Hardy, 1938) they do not kill the host until it is inside the cocoon (e.g. Nythobia, spp., the most common parasites) or less often when the larva is full grown (e.g. Apanteles plutellae). Thus, they do not cause any mortality in the early instars.

Finally there is the effect of predators which, although normally non-specific, seems to be the main single cause of mortality during this early instar period.

Despite all the mortality factors acting upon the early instar larvae of P. xylostella the overall effects of predators ('real' mortality) was about 40% of the total initial larvae. Unfortunately the range of species concerned was not successfully determined.

11.2.2. Later instar mortality

Parasites;

Parasites are quoted as being of great importance in the regulation

of populations of P. xylostella in many countries (Delucchi et al., 1954; Thompson, 1964). Hardy (1938) quoted from the world literature 43 parasites (40 Ichneumonoidea and 3 Chalcidoidea) of which at least four were reared or recorded by him in Great Britain. He also found twoIchneumonoidea apparently not previously recorded as parasites of P. xylostella. Thompson (1946) recorded from the world literature, 59 species parasitising P. xylostella. In England there are several parasites of P. xylostella of which Hardy (1938) quotes at least six species (some of the groups have been taxonomically reviewed later). The most common are Nythobia spp. mainly N. eucerophaga Horstm. and N. neocerophaga Horstm. At least one of the parasitic species can survive on an alternative host during the winter when no larva of P. xylostella exists in the field as quoted by van Emden (1965) who cites an unpublished record by O.W. Richards of Horogenes (Nythobia) fenestralis overwintering on Swammerdamia lutarea (Haworth) (Lepidoptera:Iponomeutidae) on hawthorn. Nythobia spp. attack the larvae in all instars although preferably in second and third instars, but actually kill the host after cocoon formation. This means that they are not an important factor in regulating the actual larval population which is the economically-important stage but in the present investigation they were responsible, together with predators, for the reduction virtually to zero of the pupal population, therefore eliminating, or at least drastically lessening, any possibility of further infestation.

Birds.

In general birds were unimportant as predators of P.xylostella, although under special circumstances, for example during outbreaks of the insect, they may eat larvae and/or pupae (Ormerod, 1892).

Soil predators.

In the area of the present investigation the most common and likely soil predators were Carabids, but in the experiment in which they were excluded their effect was insignificant when considering the overall mortality of the field populations.

Other predators.

There is a group of predators, other than birds and soil predators which are an important cause of mortality during all the stages but particularly in the early instars when they may be considered as the main single factor killing the larvae. For example, different species of spiders were seen eating larvae from the early second to late third instar; larvae of Chrysopa sp. were seen devouring third and early fourth instar larvae. They are also especially important during the pre-pupal and pupal stages when they, together with the parasites, kill most if not all the individuals so that practically no pupae become adult. Therefore, on their action depends whether there will be a next generation and if so whether the numbers of individuals will be high or low.

Other mortality causes.

There are some other causes of mortality which were insignificant in the present experiments but which may not be so in other circumstances. The most notable is a disease which makes the late fourth instar larvae, the prepupae and the pupae collapse. The symptoms are similar to those described by Ullyett (1947) for an un-named bacterial diseasein South Africa.

11.3. GENERAL REMARKS.

In general it can be said that the behaviour of the young larvae of P. xylostella causes high mortality if abundant and also induces their early and even distribution. This minimises over exploitation of the host plant or of any particular part of it. In the early instar there may be some mortality due to intra-specific competition, this mortality is, therefore, directly density dependent and beneficial at high densities, when it eliminates the surplus population which will compete for the resources and eventually give as a result, weaker, less fecund or otherwise less normal adults to produce a new generation.

The texture of the leaf tissue may also be important for the survival of the early instar larvae, especially those isolated.

Attacking all the stages there are natural enemies, mainly predators, which in the present investigation decimated the populations and eventually led to virtually no adult to start a new generation. This may be the normal situation in the South of England since P. xylostella does not normally occur as an important pest in that region.

Mortality in the second instar may be important in the survival of the generation.

Mortality in the later stages especially in the pupae is detrimental because on it depends the survival, if any, for the next generation.

The causes of mortality in the different stages of P.xylostella normally interact in such a way that their individual effects supplement each other. This interaction results in an overlapping of instar-mortalities, for example, when there is little mortality of the eggs, there will be high mortality in the first instar larvae, if that mortality fails to kill many of these larvae, the mortality of the second instar will drastically reduce the population; if however there is little second instar mortality, the mortality in the third instar will be high, and so on up to the pupae, in such a way that the high mortality in one instar will compensate for any low mortality in previous instars.

From the applied point of view it can be said that a way of maintaining the populations of P. xylostella at the lowest level possible may be achieved by the use of resistant plant varieties. This seems feasible if plants could be developed which make entry difficult for the newly hatched larvae. Another way is by maintaining a high level of natural enemies by creating favourable conditions for them such as alternative hosts for parasit es, or natural vegetation, or places for predators survival. Parasites normally survive throughout the winter on alternative hosts which feed on non-agricultural plants. The presence of alternative hosts in uncultivated land may be one of the reasons for the low populations of P. xylostella in places like Silwood Park. In contrast, places subjected to intensive agriculture are generally kept clean of wild vegetation which may provide

shelter or food to the parasites and other natural enemies, furthermore the woods and hedges, if any, are kept to the minimum possible area and maintained very trimmed to facilitate agricultural practices. This lack of alternative hosts for parasites, together with the use of insecticides which also kill parasites may contribute to the increase of P. xylostella populations.

In places with enough rainfall, a possible means of reducing the populations of P. xylostella may be achieved by planting in the season when the rains will coincide with the early instar larvae. Rainfall may also deter the moths from flying and therefore laying eggs. Overhead irrigation might be valuable.

In places with marked changes in temperature with the seasons (temperate regions), the decline in temperature affects the rate of development by increasing the time necessary to reach the adult stage, thus by planting late season varieties the larval populations will be exposed for longer time, allowing biotic and abiotic factors to act upon them.

The planting time might also be used to avoid coincidence of the susceptible stage of the crops with the adult immigrations in those countries subjected to them.

In all cases the economics of the crop will probably be the most important aspect from the applied point of view, therefore, in some circumstances the use of insecticides will be inevitable; in such cases however the integrated control approach ought to be adopted in order to increase the favourable effects and diminish the well known bad effects of pesticide use, especially insecticide-resistance which has already become widespread in tropical and sub-tropical populations of P. xylostella.

12. SUMMARY

The lengths of the different instars, the behaviour and the larval dispersion of Plutella xylostella (L.) (Plutellidae:Lepidoptera) were studied on potted cabbage plants at different densities of populations in constant environment rooms at 20°C, 44-52% relative humidity (in 'day time') and 16 hours of light per 24 hours period. Experimental populations were also studied in the field.;

In the laboratory, the lengths of the different instars were found to be: Eggs 3.2 days; First instar 3.7 days; Second instar 3.1 days, Third instar 3.2 days; Fourth instar 2.8 days; Pre-pupa 1.3 days; Pupa 7.0 days; and adult 17.1 days. The mean number of eggs laid per female was 246.4.

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 that pupal length and weight, and adult weight were inversely correlated with larval density.

Older larvae tend to keep near to each other but maintain 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 seems to be beneficial especially for escaping of natural enemies or avoidance of other competitors either of the same or different species.

Under laboratory conditions the eggs generally suffered little or no mortality. The larvae seem to be subjected to mortality from intra-specific competition, especially the early (first and second) instars. This early intra-specific competition seems to cause directly density dependent mortality. However, an isolated larva may also die unless the conditions are very favourable, for example the leaf tissue is very tender. Older larvae suffered very little mortality and pupal mortality was virtually zero in laboratory or protected conditions.

The dispersion of the laboratory populations is at the beginning highly aggregated; then the larvae start to move on the leaves and become randomly, and sometimes regularly distributed; then, before pupation, they tend to aggregate again. However, this latter tendency to aggregate for pupation is perhaps related to the restricted environment of the cages since it did not happen in the field populations.

Mortality and dispersion of P. xylostella was studied under field conditions, during Summer and Autumn 1969-70. Plants of Brussels Sprouts were artificially infested, and caged to protect the insects from different and separate mortality factors, namely - parasites, birds, soil predators, other small predators, and rainfall; plants were also left unprotected and so were fully exposed to all mortality factors.

The early instar larvae were mostly killed by predators which also were the main cause of mortality of the older larvae. Parasites together with predators played an important role in killing virtually all individuals that survived to become pre-pupae or pupae. Rain, birds, and soil predators were insignificant as mortality factors, although rain may cause some mortality in the early instars. In the absence of natural enemies there was some possible mortality due to intraspecific competition. The effect of host plant condition (leaf texture) might be important as suggested by preliminary laboratory experiments.

The dispersion of larvae was similar to those in laboratory conditions i.e. highly aggregated at the beginning, then they distributed on the leaves to reach a random (sometime regular) distribution. Under field conditions there was no aggregation before pupation as in the laboratory and it is

interpreted as due to the much greater number of suitable places on each plant (20 to 70 leaves crinkled leaves, most of them 100 or more cm^2 in area, compared with 4 to 7 rather smooth leaves, most of them 100 or less cm^2 in the laboratory experiments) where the larvae can find sites to construct their cocoons.

Finally, it is concluded that by manipulating plant characteristics such as tenderness of leaves, together with cultural practices such as planting time and encouragement of natural enemies by protection of their habitat, the need for more severe measures of control could be decreased in places where P. xylostella is a regular pest.

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15. APPENDICES

15.1. APPENDIX 1. BEHAVIOUR OF THE LARVAE

A.1 BEHAVIOUR OF RECENTLY HATCHED LARVAE

A.1.1. Single larva from egg within a batch.

One young cabbage plant was placed in a cage with several P. xylostella adults for about three days. From the plant a leaf was chosen which bore a group of sixty eggs in an area of about 3.5 cm^2 (Fig A.1).

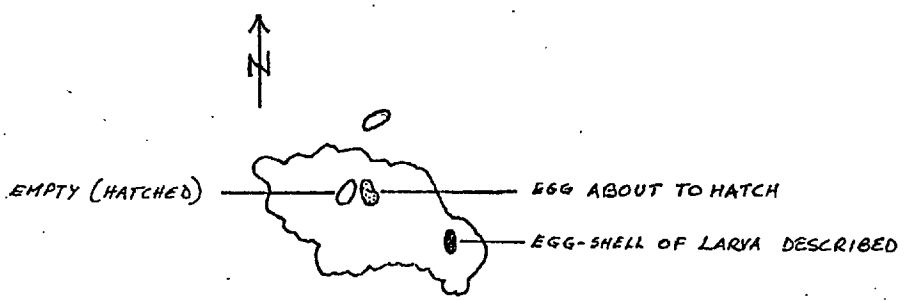


Fig.A.1. Eggs. Grouped and isolated.

The eggs were observed under a dissecting microscope and the behaviour of one larva was recorded:

First five minutes (0-5 min.). After eating its way out of the chorion the larva crawled over the other eggs in the group. It then stopped and started to move the head from side to side, as is normally done when spinning silk. Then it crawled 2 mm away from the area of the 60-eggs group, stopped and moved the head slowly from side to side above the leaf surface, not as when spinning but seemingly sensing an impression of the environment, visually or chemosensorily. After crawling to about 2 mm from the isolated egg (top in Fig. A.1) it turned back and crawled again over the batch of eggs, moving the head in the sensing-type movement. Then it went to the only other egg about to hatch (Fig A.1), stopped there, made the sensing movement for two or three seconds and then crawled onto its own egg shell and then to the left ('East') edge of the batch where it stopped for a moment, turned back, crawling again over its own egg shell to the 'North' edge of the batch. Again it stopped for two or three seconds and while doing the sensing movements it turned down to the 'South-West' edge, crawled over the edging line of eggs and went to the 'South' edge.

5 - 10 minutes. From the 'South' edge it went away from the batch and wandered for about 10 seconds, then went back to the 'South-East' side of the batch, crawled over its own egg shell and went towards the previously hatched egg (Fig A.1) and then to the 'North-West' edge of the batch. Then, making sensing movements, it took the 'South-West' direction and went out of the batch for about five seconds. Then it returned to the 'South-East' side of the batch and crawled to the 'North' and out of the batch again. It crawled about 3 mm, stopped, made the sensing movements for two or three seconds and went about 10 mm northwards, stopped again, wandered for a few

seconds and continued crawling northwards up to the edge of the leaf where it stopped and, with half its body in the air moved the head and thorax from side to side.

10 - 15 minutes. After about 5 to 7 seconds of moving the head and thorax in the air it turned back and went to the lower surface of the leaf, stopped about 1 mm from the edge, then started to crawl again. When examined after 2 hours it had probably been feeding for most of this time.

A.1.2. Single larva from egg separated from batch.

One egg was laid about 2 mm separated from the main 60-eggs group from which the larva previously described had hatched. The larva in the isolated egg hatched exactly fifteen minutes later. Its behaviour was recorded as follows:

First five minutes (0 - 5 min.). After getting out of the egg shell the larva started to crawl towards the batch of eggs which was separated from it by about the length of the larval body. When the larva met the eggs it probed on them by moving the head in a spinning-like movement; then it moved on and put the prothoraxic legs on one of the eggs and remained there for about two minutes making the 'spinning' movements all over the same egg. After that it placed all the thoraxic legs on the egg and continued with the 'spinning' movements. Then it crawled over the egg and moved to the next egg where it started the same process of probing first and then making the 'spinning' movements.

5 - 10 minutes. The larva moved to the next egg and then to an egg about to hatch and to the empty shell where it started the spinning movement but stopped quickly, then it moved to the next egg. Six minutes after hatching, the larva stopped all movements and became motionless. After one minute it started to move slowly again; about 20 seconds later it crawled quickly onto the batch, and then crawled, making the sensing-type movements at the same time, for about three minutes.

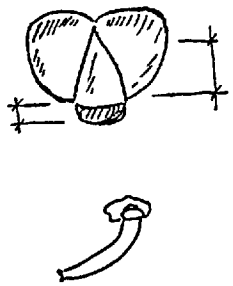
10 - 15 minutes. The larva stopped, turned back and went to the egg which was about to hatch (Fig A.1), stood on it and then started to 'spin' but on the next egg. After one minute it crawled away and went to the egg shell of the previously described larva, stepped on it and made 'spinning' movements for about 30 seconds, then went to the edge of the batch where it stopped and 'span' on the 'East' edging line of eggs. After about two minutes it turned back and crawled through the edge of the batch. Then it came onto the batch and went to the egg about to hatch, stood by the side of that egg with the head on the next egg.

15 - 20 minutes. After about one minute in that position, the larva raised the head and thorax and moved them in the air as if sensing the environment. Then it crawled in a 'North-West' direction and then to the 'South-West', always making spinning-type movements. The larva went on to the 'South-West' edge of the batch where it stopped and remained 'spinning' for about 30 seconds. After that it tried to crawl out of the batch, but after having half its body out of the batch it returned and went southwards.

20 - 25 minutes. The larva stopped and tried unsuccessfully to bite one egg (probably it was approaching the stage of hunger and the urge to bite in order to eat), then it crawled in 'North-East' direction, stopped and made the sensing movements in the air, finally it crawled out of the batch and went to the 'North'; later changed again to 'North-East' direction. At about 5 mm distance from the batch it stopped and started to move the head from side to side (not in the air). The whole sequence took only one minute. Then it went to a depression on the leaf surface and put the head in that depression, stayed there for about two minutes, took the head out and started to 'spin' on one egg near the depression. Afterwards it moved away and went to the batch, taking about 30 seconds to go through the batch ('NE' to 'SE' direction) and out of it again. Then turned back and stepped onto the 'South' side of the batch where it made the sensing movements for a short time.

25 - 30 minutes. A cut was made with a scalpel on the leaf,very near the batch of eggs to see whether the larva could be stimulated to go to that part of the leaf. The larva (still on the batch) went in 'South-West' direction and then in 'North-West' direction. Then, probably at this moment the larva perceived the odour of the leaf recently cut, turned back and went straight to the part of the leaf that has been cut and, with most of its body on the batch of eggs, tried to eat the fresh-cut edge of the leaf; all this sequence took about 30 seconds. One and a half minute later the larva crawled away and onto the cut edge where it tried to eat. One minute later it went onto the upper leaf surface, crawled for about 5 seconds and made the sensing-type movement without trying to bite. It kept doing that for about five minutes.

A.2



A.3

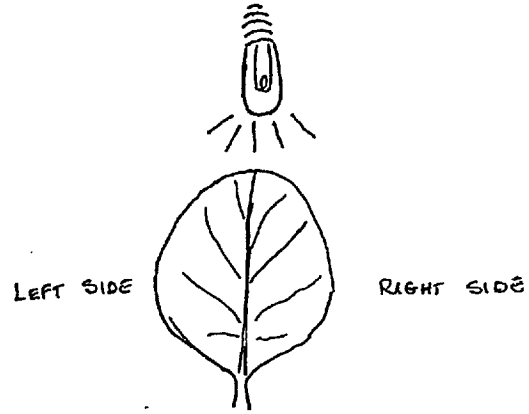


Fig. A. 2. Head of 1st instar larva, and head of first instar larva in hole.

Fig. A. 3. Cabbage leaf with light from one side.

A. 1. 3. Group of larvae within a batch.

Eight larvae recently hatched were placed on a leaf and pushed together with a paint brush into a single 'tangled' group. The leaf was receiving more light from one side than the other (Fig. A. 3).

First five minutes (0-5 min.). Immediately the larvae were placed together they started to struggle in order to free themselves. Not all moved at the same time, but usually when one moved these stimulated others. After three minutes one larva (larva A) got free and crawled towards the lighted side of the leaf. About one minute later, another larva (larva B) got free but instead of crawling away it remained outside the group without moving. The rest was still moving but not struggling.

5 - 10 minutes. Larva A crawled out and went to the lower surface of the leaf. Two minutes later larva B started to make the sensing-type movements and to crawl slowly towards the left side of the leaf (and towards the less lighted area).

10-15 minutes. A third larva (larva C) started to crawl out and also went to the left side of the leaf (also the less lighted area). Another larva (larva D) got free and started to crawl towards the lighted area of the leaf; it was followed by larva C which moved from the opposite side. Larva D went to the lower surface of the leaf on the lighted side. The rest of the larvae in the group had remained almost motionless. About two minutes later larva B turned back and crawled towards the lighted side of the leaf; one minute later larva C followed it. Then both went to the lower surface of the leaf. The remaining group was still very quiet, making very slow almost imperceptible rocking movements.

At this time the larvae on the lower surface would not be observed.

15 - 20 minutes. First only the slow rocking movements from the group of larvae could be noticed. Two minutes after the beginning of the period one larva (larva E) started to struggle and to make its way out.

20 - 25 minutes. Larva E was still struggling but almost free. Seven minutes after it started to struggle, larva E got free from the group although it was held up by a thread of silk in one proleg. The rest of the larvae in the group were moving slowly.

25 - 30 minutes. The three larvae in the group were moving slowly; one minute later they started to move faster, three minutes later another larva (larva F) started to struggle to get free, but was tangled by silk. Larva E was motionless.

30 - 40 minutes. Larva F got free from the group and crawled to the left side of the leaf, then started to make sensing-type movements. Two minutes later it started to crawl again towards the left side of the leaf (and towards the lighted area). Larva E still was in the same place making sensing-type movements. The remaining two larvae were moving slowly. Two minutes later larva E went to the less lighted area of the leaf and after two minutes crawling it turned to the left side of the leaf. The remaining two larvae were struggling but their bodies were tied with silk. Larva E turned around and crawled towards the lighted area of the leaf, then turned back again and went to the less lighted area of the leaf on the right side.

40 - 60 minutes. Larva E went to the edge of the leaf and then to the lower surface. After three minutes one of the two larvae still tangled together (Larva G) started to get out. One minute later it succeeded and crawled very fast to the left side of the leaf. The remaining larva (larva H) started to move very slowly. Two minutes later larva G crawled very fast to the far end of the leaf on the left; after about three minutes larva G slowed down and stopped at the left edge of the leaf. Larva H was still moving slowly. Larva G went to the lower surface of the leaf. Three minutes later larva H started to move fast and kept doing that for about five minutes when it stopped and stayed motionless.

Two hours. Larva H was dead, perhaps from exhaustion. The leaf was turned upside down and all the other seven larvae were seen to be feeding in holes in the lower surface. Two larvae were side by side head to tail (Fig A.4.a) with another larva about 2mm distant. In another place two larvae were feeding in the same hole (Fig A.4.b). The other larvae were feeding on the leaf separated of each other.



Fig.A.4. Pairs of first instar larvae : head-to-tail and two heads in a hole.

A.2. BEHAVIOUR OF THE DIFFERENT STAGES OF THE LARVA.

Two recently hatched larvae were placed very close to each other on the upper surface of disc 1 and two others in disx 10 (Fig 6.a). They were observed regularly and their behaviour was recorded. The observations were numbered successively, and as they were not made at regular intervals, the time after the first observation is given in brackets. For convenience those larvae in disc 1 will be referred to as A and B, and those in disc 10 as C and D. All the larvae were on the upper surface unless otherwise stated; similarly

the feeding holes made were the window-type holes unless otherwise stated. A graphical summarized representation of the behaviour is given in Fig A.5 (= Fig 10).

The behaviour of larvae A and B will be described first.

1. (00 minutes). Starting the experiment by placing the larvae on discs and arranging the discs and cages. The two larvae A and B were put on the leaf 5 mm apart.

2. (15 min.). Larva A not visible. Replaced by A'.
Larvae A' and B moved to 3 mm apart.

3. (22 min). Larva A' started to make a hole near a thick vein in quadrat 4. Larva B was wandering in quadrat 14. They were 16 mm separated.

4. (2 hours 06 min.). Larva A' was wandering in the top centre quadrat 2). Larva B not visible.

5. (2h 47 min.). Larva A' was still in the centre (same place as before). Larva B was wandering in 'North-West' direction (Fig 6.b.). Both larvae 16 mm separated.

6. (18h. 0 min.). Larva A' is dead. Larva B is starting a hole in quadrat 1 at 7 mm from larva A'.

7. (22 h. 0 min.). Larva B abandoned the hole and was wandering 'southwards'.

8. (24h. 0 min.) Larva B was motionless in quadrat 5. The original larva A re-appeared inside a long mine started in quadrat 14 and going up to quadrat 9 (see Fig A. 5). This mine was burrowed almost alongside the border of the leaf disc, the larva had obviously avoided going directly to the border of the disc probably because it was deterred by the damaged leaf tissue after the disc has been cut (see Fig A. 5).

9. (30h. 40 min). Larva B was dead. Larva A (inside gallery) avoided a rather thick vein and went to the border of the leaf disc, then turned back and alongside the border.

10. (32h 0 min.). Larva A went through its own previously made gallery.

11. (42h. 40 min.). Larva A during the night went out of the mine in disc 1 and moved to disc 2 where it made a short mine in quadrat 14 and from there it went to quadrat 13 where it made a gallery running into quadrat 9.

12. (50h. 0 min.). Larva A went out of the gallery (which finished in quadrat 9) and was wandering in quadrat 13.

13. (55h. 30 min.). Larva A went to the lower surface of the leaf and was resting on a thick vein (quadrat 10).

14. (66h. 50 min.). During the night larva A (still in lower surface) went to quadrat 9 where it moulted into the second instar. From there it went to quadrat 10 where it was feeding with the head in a hole near a thick vein.

15. (72h. 0 min.). Larva A continued the hole into a short gallery (started and finished in quadrat 10) in 'North' direction and alongside a thick vein. Then it went out of the gallery to quadrat 12

where it made a hole.

16. (74h. 45 min.). Larva A still in the same quadrat 12 (lower surface), the hole increased in size (about 3 x 1 mm), but stopped before a thick vein.

17. (116 h. 45 min.). During the night and following day larva A went to quadrat 13 (lower surface) and made first a small sized hole (about 1 mm diameter) then moved a little 'northwards' and made a big window type hole in a C shape. From there it went to disc 4 and made a small hole (less than 1 mm diameter) in quadrat 12. Then it went to the lower surface of disc 6 where it ate two big window-type holes in quadrats 2 and 3 respectively, then went to quadrat 12 and was eating very close to the edge; from there it went to quadrat 6 where it unsuccessfully bit the leaf tissue, and returned to eat in the same hole in quadrat 12.

18. (138h. 15 min.). During the night larva A remained on the same quadrat 12 (lower surface of disc 6) and moulted to the third instar. Then went to quadrat 3 where it made a hole about 3 x 1 mm, and was eating in a bigger hole between quadrat 3 and 7.

19. (140 h. 55 min.). Larva A increased the size of the hole which was extending from quadrat 7 to quadrat 11. The larva went from quadrat 11 to 9 and then to 13 where it was wandering. Then it went to disc 8 and 10 respectively, and in disc 10 it went from quadrat 9 to 5. Then to quadrats 1, 2 and 3, then it went to the lower surface to quadrats 3, 7, 11 and 14 successively. All the time it crawled, it moved the head from side to side (spinning-type movement).

20. (145 h. 10 min.). Larva A moved from disc 10 to discs 9, 7, and 5 respectively. In the lower surface of disc 5 the larva was eating

on the edge of quadrat 12 on a hole about 1 mm wide and about 12 mm long, which was started in quadrat 16. In the same disc 5 (lower surface) larva C was eating a hole about 7 x 3 mm in quadrat 2. Despite two third-instar larvae in the same disc there was no sign of interference between them; they were, however, widely separated.

21. (162 h. 15 min.). During the night Larva A moved to the lower surface of disc 7 and made a small hole (about 1 mm diameter) in the lower surface of quadrat 12 near the border, then moved a little southwards and made a big hole about 5 x 4 mm. From there it went up to the top of the disc where it ate a hole through the edge between quadrats 2 and 3.

22. (167 h. 10 min.). Larva A moved to the upper surface and continued to eat in the same place between quadrats 2 and 3 but now the hole (through the leaf disc 7) is bigger.

23. (166 h. 40 min.). During the night larva A went to quadrat 10 in the lower surface of disc 7 and stayed there until it moulted into fourth instar. The larva had moulted recently because it was still motionless and with skin very pale in colour.

24. (189 h. 45 min.). Larva A moved to quadrat 6, lower surface of disc 7 and was feeding in a hole about 4 mm diameter. In the upper surface of disc 7, larva D was eating through the leaf a big hole about 5 x 10 mm (between quadrats 2 and 3) on the North edge of the leaf disc (that hole was started by larva A). The two larvae were eating without interfering with each other, even when they were relatively close.

25. (210 h. 40 min.). Larva A moved during the night from disc 7 to disc 10 and it was on the upper surface (quadrat 16) but the head and thorax were on quadrat 13 of disc 8 were it was feeding in a big hole (about 7 mm diameter) through the leaf.

26. (218 h. 40 min.). Larva A moved to disc 4, lower surface, and was eating a hole through the leaf in quadrat 8. In the same disc 4 was larva C (in quadrat 10, lower surface) which had eaten about one quarter of that disc. The two larvae were eating separately without interference. More than half of the leaf disc was still uneaten.

27. (235 h. 20 min.). Larva A remained during the night, on the lower surface of disc 4. It was now eating in quadrat 11, and had eaten through almost half the disc. Larva C during the night finished feeding in window-type holes in almost all the lower half of the leaf disc 4, then moved away (to disc 3, quadrats 3 and 5). It probably moved away under the interference or disturbance of larva A, and to a certain extent due to lack of space to feed.

28. (237 h. 40 min.). Larva A was motionless in quadrat 2 in the lower surface of disc 4.

29. (258 h. 20 min.). During the night larva A went out of disc 4 and crawled onto the lid of the cage and pupated there (on the muslin covering the central hole of the lid).

The behaviour of larvae C and D, which were placed in the same cage but on disc 10 is described below. Little interference occurred between these two larvae and those placed in disc 1 (see Observation 27 of larva A).

1. (00 minutes). Starting experiment. Larva C and D placed on leaf disc 10, 2 mm separated.

2. (15 min.). Both larvae went 'southwards', larva C to the right and larva D to the left. 8 mm separated.

3. (22 min.). Both larvae continued wandering 'southwards'. Larva C in quadrat 16. Larva D not seen.

4. (2 hours 06 min.). Larva C was trying to bite the leaf tissue in quadrat 12. Larva D still missing.

5. (2h. 27 min.). Larva C succeeded in making a hole in quadrat 12, exactly 1.5 mm from the edge of the disc. The larva had its head in the hole. When disturbed it pulled its head out of the hole, stayed motionless for a moment and then continued eating but on the edge of the hole. Larva D appeared in quadrat 15 (lower surface) with half the body inside a mine 1 mm from the sand.

6. (18 h. 0 min.). During the night, larva C made a gallery 4 mm long in quadrat 12 (going to quadrat 8), and still about 1.5 mm from the edge of the disc. Larva D finished a gallery 1 mm long in quadrat 15 and then went up to quadrat 10 and was inside a gallery 1 mm long (from 'South' to 'North').

7. (22 h. 0 min.). Larva C had made its gallery (see Observation 6) 1 mm longer and was about 1 mm from the edge of the disc. Larva D had not moved from the previous position.

8. (24 h. 0 min). Larva-C gallery (5 mm long) arrived at quadrat 8 and was about 0.5 mm from the edge of the disc. Larva-D gallery changed direction and was going completely to the left.

9. (30 h. 40 min.). The gallery of larva C touched the edge of the leaf disc and followed it for about 1 mm, then as it approached a vein it changed to the left (towards centre of the disc). Larva D went out of the gallery in quadrat 10 and crawled 'southwards'.

10. (32 h. 0 min.). Larva C and D were in the same position as in the previous observation.

11. (42 h. 40 min.). Larva C continued during the night, making its gallery to the left, then just before reaching a vein, it turned back 'southwards' and slightly to the right. Then a fraction of a mm before meeting its own gallery it made a hole and went out of the mine to quadrat 7 where it was in a mine the length of the larva body. Larva D was inside a mine about 4 mm long (going 'South-West') in quadrat 13.

12. (50 h. 0 min.). Larva C continued burrowing the mine from quadrat 7 to quadrat 6 (and as something rather unusual it ate through a vein). Larva D continued its gallery 'southwards' to near a thick vein, then turned back and continued it 'northwards' and to the right, always in quadrat 13.

13. (55 h. 30 min.). Larva C went out of the mine and crawled to quadrat 10 where it was eating with the head in a hole. Larva D also went out of the mine and crawled to the lower surface, quadrat 10, where it was feeding with the head in a hole.

14. (66 h. 50 min.). During the night, larva C went out of the mine and to quadrat 16, where it made a mine (about half its body length). Larva D crawled to the upper surface and was wandering in quadrat 11.

15. (72 h. 0 min.). Larva C was still in the same mine (quadrat 16). Larva D crawled from disc 10 to quadrat 15 of disc 8 where it stayed and moulted into the second instar, then started to make a hole in the leaf.

16. (74 h. 45 min.). Larva C moved out from its previous gallery and was making a hole between the previous gallery and the edge of the disc. Larva D made a hole about 1 mm diameter in quadrat 15 of disc 8.

17. (116 h. 45 min.). During the night and following day larva C went to the lower surface of disc 8 where it made a long hole alongside the edge from quadrat 9 to 5, then went to quadrat 3 and made a small hole about 1 mm long, then went 'southwards' and made a big irregular hole about 6 mm long in quadrat 7. Then it went to disc 6 where it made a gallery about 4 mm long, that gallery finished about 1 mm before a thick vein and the larva went out to quadrat 13 where it stopped. Larva D (in disc 8) moved about 1 mm and made another hole (1 mm diameter) then went over to the lower surface to quadrat 10 where it made a big hole (about 5 x 5 mm) then moved to quadrat 6 where it was wandering.

18. (138 h. 15 min.). Larva C, during the night, moulted into the third instar while at quadrat 13 of disc 6. Then it placed half its body on quadrat 12 of disc 8 (where it was eating on the edge). Then it crawled through quadrat 12 of disc 8, then to quadrat 9 and over to the lower surface where it went from quadrat 9 to quadrat 12 and moved over to disc 6 (quadrat 9, upper surface), then to quadrats 12, 8, 4 and to the lower surface where it started to eat in a hole (previously made by larva A) between quadrats 3 and 7. Larva D stayed in quadrat 6 (lower surface of disc 8) and during the night moulted into the third instar. Then moved to quadrat 2 and went to disc 10 and made a hole in the lower sur-

face of quadrat 8.

19. (140h. 55 min.). Larva C went from disc 6 to discs 4, 2 and 1. It was standing in disc 1 (quadrat 8, lower surface) but eating on the edge of quadrat 5, disc 3. Larva D went from disc 10 to 8 and back again to disc 10 where it went to make a hole in the lower surface of quadrat 4 very near the edge of the disc.

20. (145 h. 10 min.). Larva C went from disc 1 to disc 6 where it made a hole (about 3 mm diameter) on the lower surface of quadrat 2, very near the edge. At the same time larva A was in this disc but no interference occurred between the two larvae. Larva D moved from disc 10 to disc 1 where it was eating on the edge of quadrat 12 (continuing a hole previously started by larva C on the lower surface).

21. (162 h. 15 min.). Larva C, during the night, went to the lower surface of disc 9 and made a hole on the edge between quadrats 9 and 13, then left a small gap and went 'northwards' making a big irregular hole alongside the edge between quadrats 9 and 5 (in quadrat 5 it stopped where a vein was across). Then it moved to quadrat 2 and made a big hole also on the edge of the disc, it kept eating 'southwards' to quadrats 1 and 5 where it was restrained by a vein. Larva D, during the night went from disc 1 to the lower surface of disc 2 (quadrat 11) where it moulted and then moved to quadrat 7 and stayed there motionless for about 2 hours.

22. (167 h. 10 min.). Larva C went from disc 9 to disc 10 and then to the upper surface of disc 8 and crawling from quadrat 11 to quadrat 6. Larva D (still in lower surface of disc 2) made a big hole between quadrats 8 and 12.

23. (186 h. 40 min.). Larva C went from disc 8 to the lower surface of disc 10 where, during the night, it moulted into fourth instar in quadrat 9, then went to quadrat 3 where it made a hole on the edge. Larva D, during the night, went from disc 2 to 5 (lower surface) where it made a big hole in quadrat 12 by widening a long narrow hole previously made by larva A. That hole was limited by two jointed veins and by the edge of the disc, but was continued alongside the edge as a very narrow hole (1 mm wide, 11 mm long).

24. (189 h. 45 min.). Larva C went to disc 7 and widened a hole to quadrat 6 (about 4 x 5 mm). Larva D moved from disc 5 to the lower surface of disc 7 where it was eating through the leaf in quadrat 3 (continuing a hole started by another larva).

25. (210 h. 40 min.). Larva C went from disc 7 to disc 4 and made a big hole in the lower surface of quadrat 3. Larva D from disc 7 went to the lower surface of disc 3 and was eating on the edge of quadrat 9.

26. (218 h. 40 min.). Larva C was in disc 4 eating a hole in the lower surface of quadrat 10 (it had eaten more than 1/4 of the disc since the morning). In the same disc was larva A, but no interference was noticed even when a lot of the leaf tissue had already been eaten. Larva D went from disc 7 to disc 5 where it made a hole in 5 and ate through the edge (about 2 mm wide) of quadrat 5, 9 and 13.

27. (235 h. 20 min.). During the night, larva C finished eating most of the leaf tissue in the lower surface of disc 4 (actually most of quadrats 9, 10, 13 and 14) and moved to disc 3 because of interference with larva A which was eating the whole tissue. Larva C

was then eating through the tissue from quadrats 9 to 5 of disc 4. Larva D went from disc 5 to disc 9 and made there a big hole (about 4 mm diameter) in quadrat 14 (upper surface).

28. (237 h. 40 min.). Larva C was eating through in quadrat 5 of disc 3 (lower surface). Larva D in disc 9 moved to quadrat 8 (lower surface) and made a hole about 2.5 mm diameter.

29. (258 h. 20 min.). Larva C and D went out to pupate on the lid of the plastic cage.

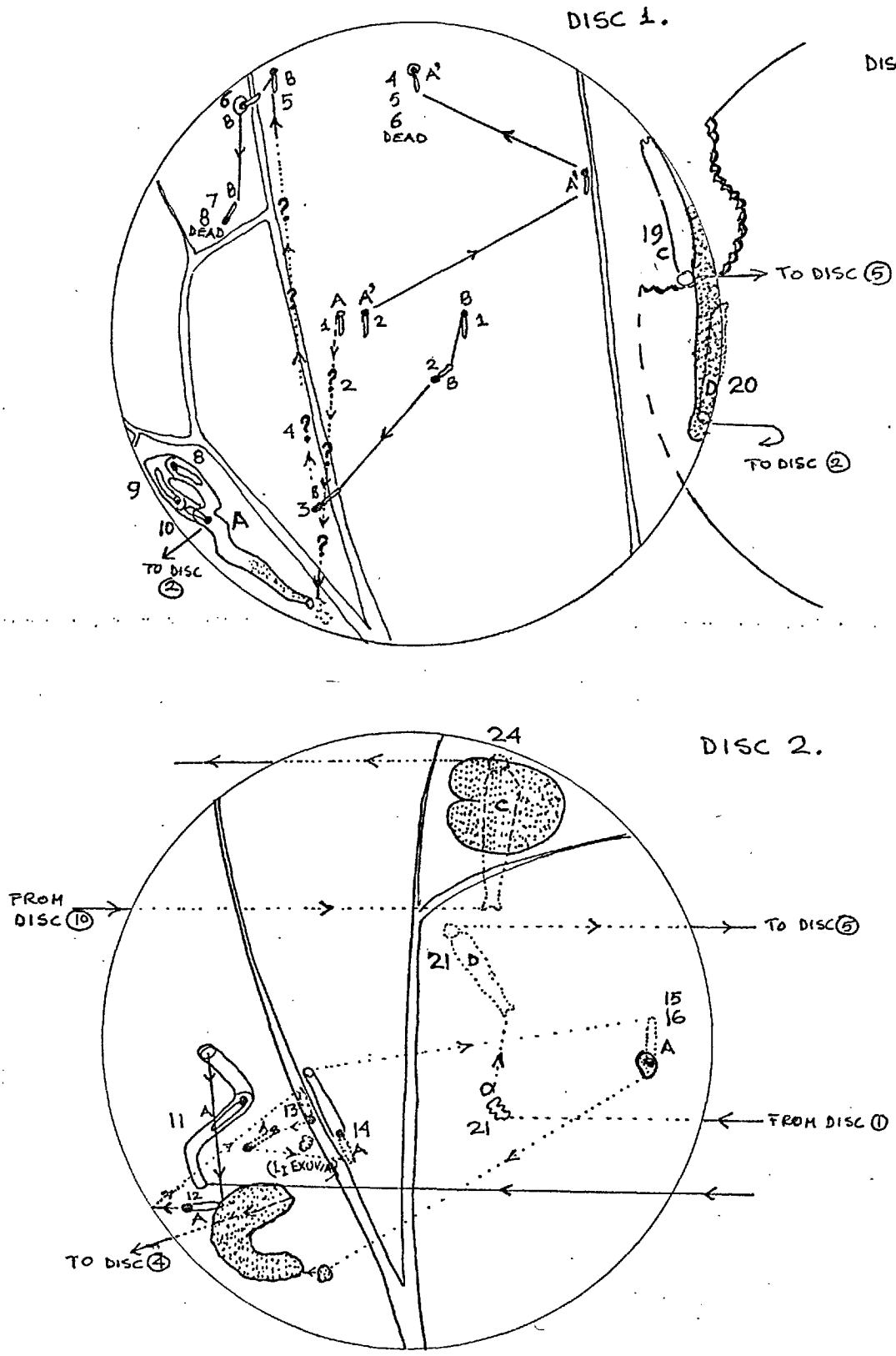
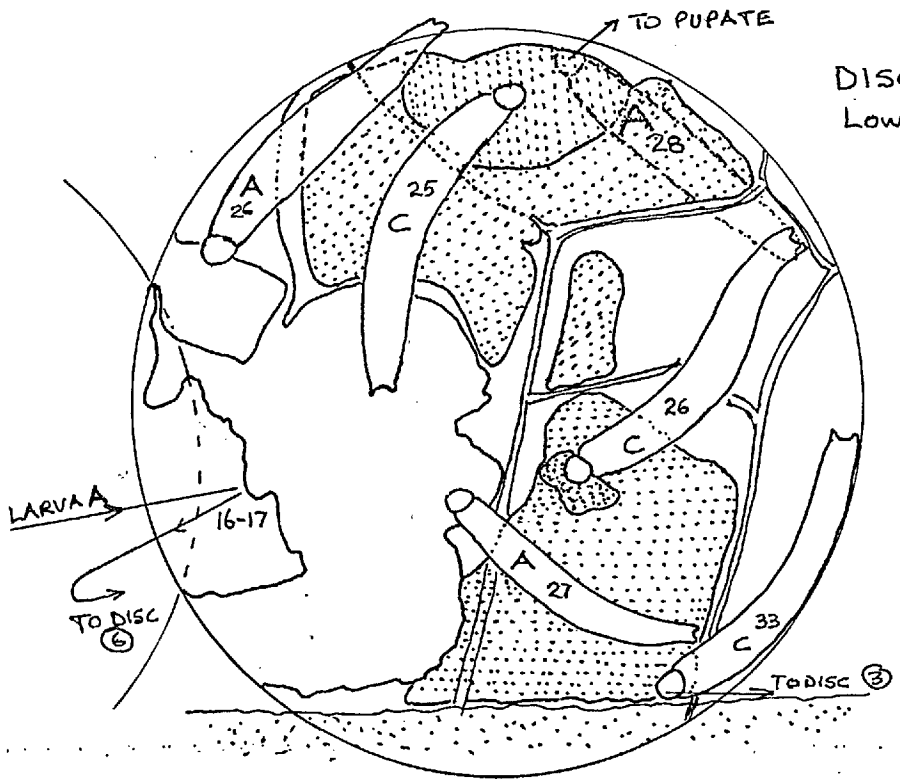
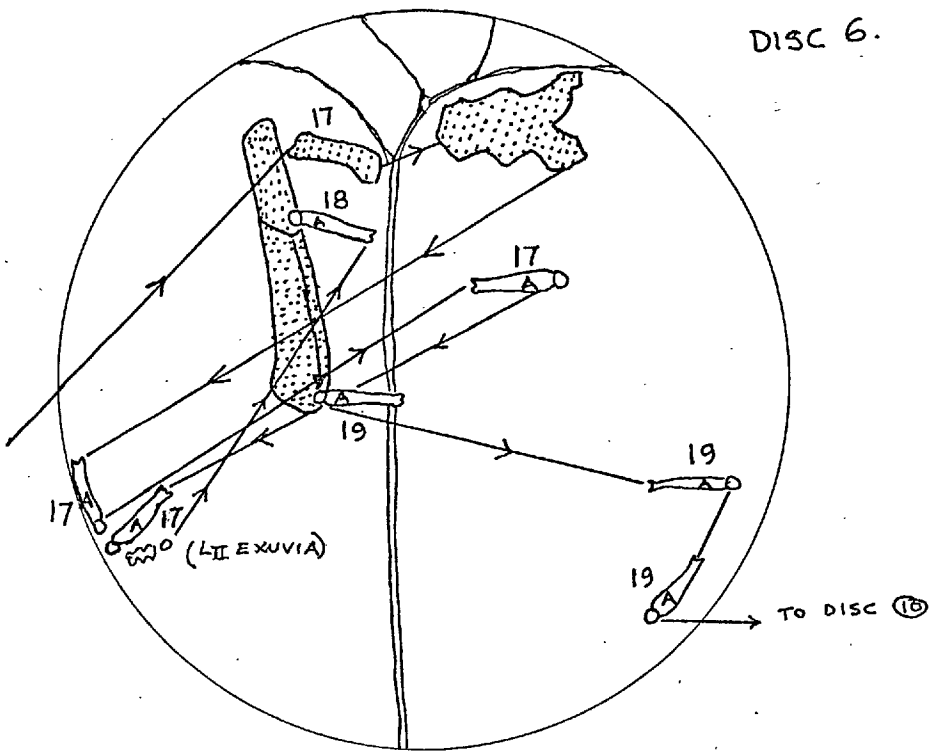


Fig. A. 5. (= Fig. 10). Behaviour of P. xylostella larvae.

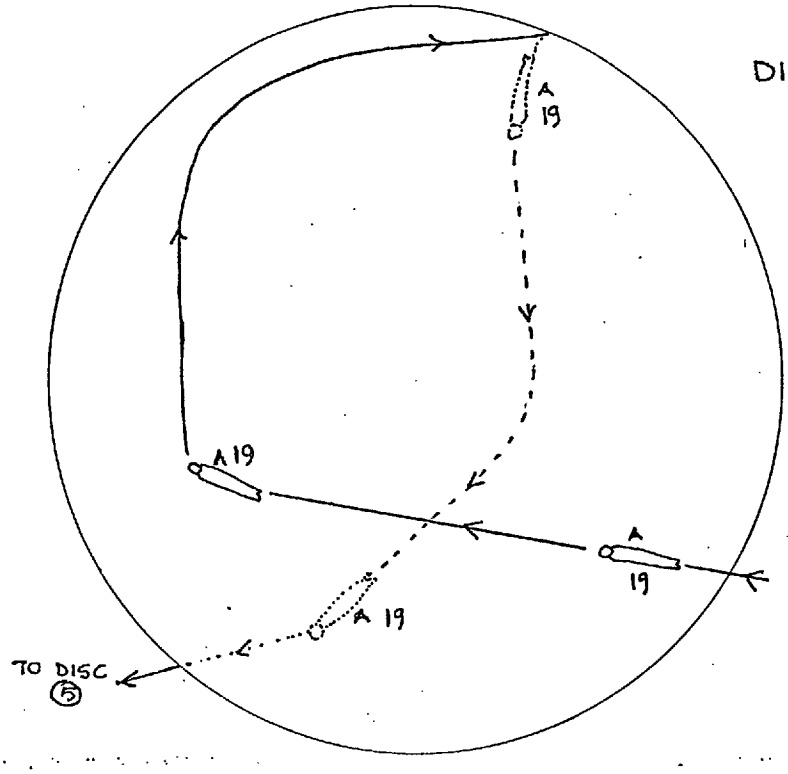


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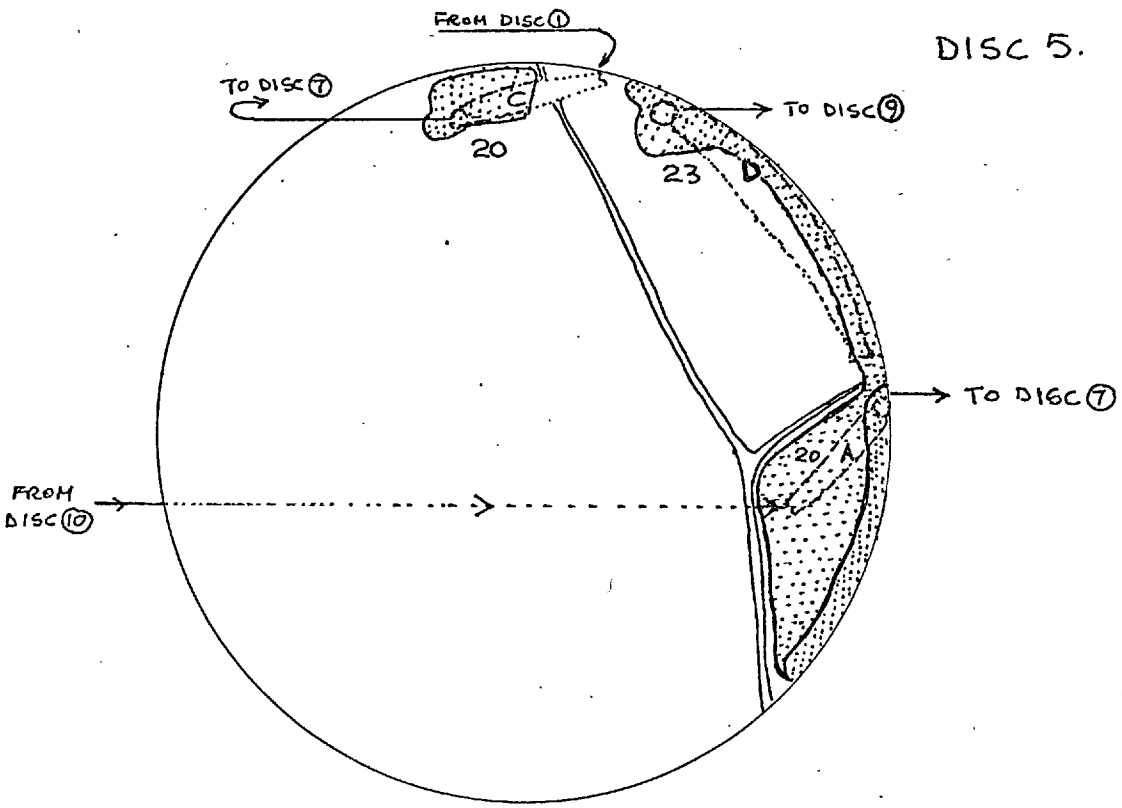


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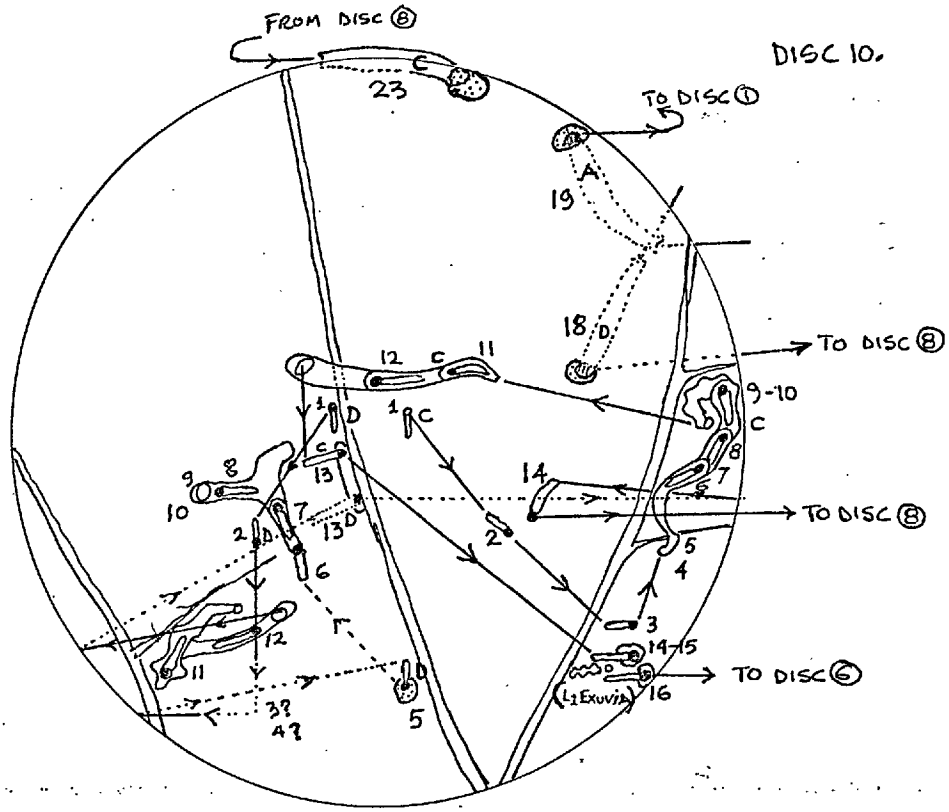
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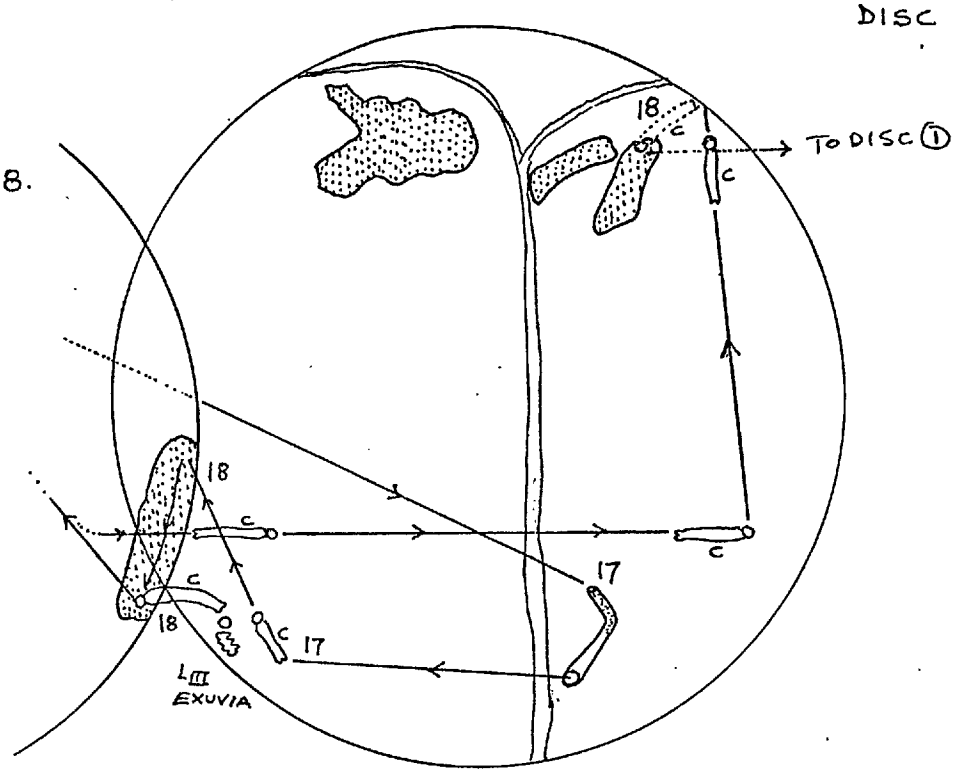
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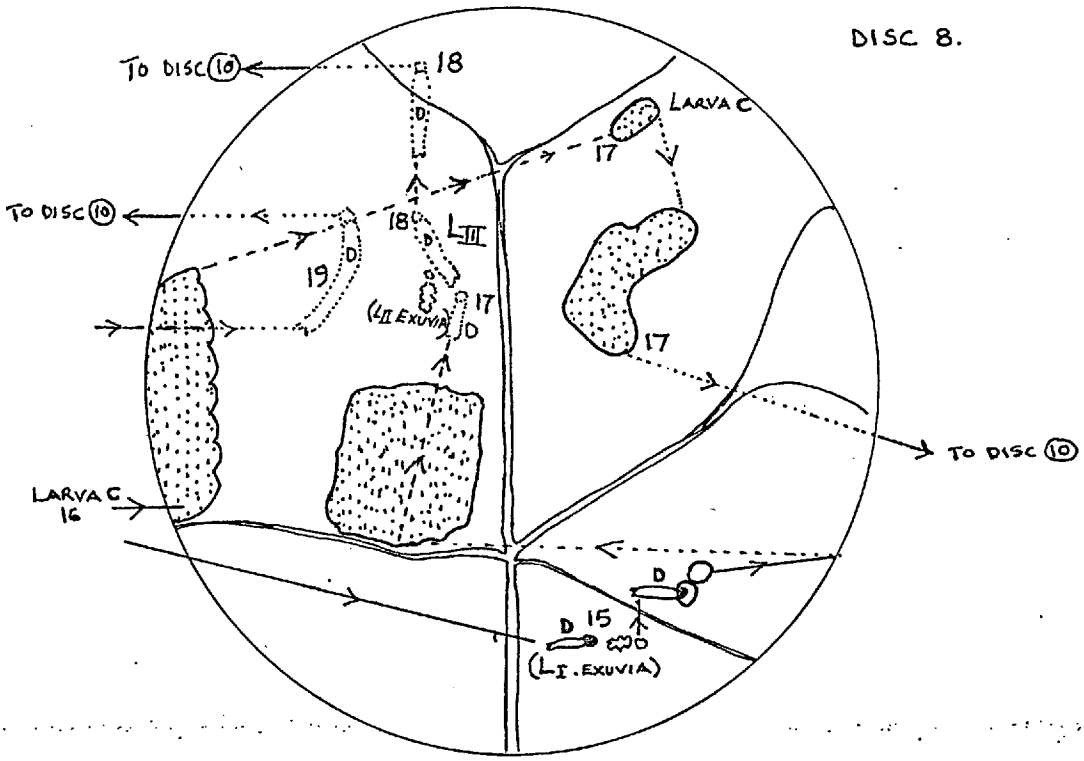


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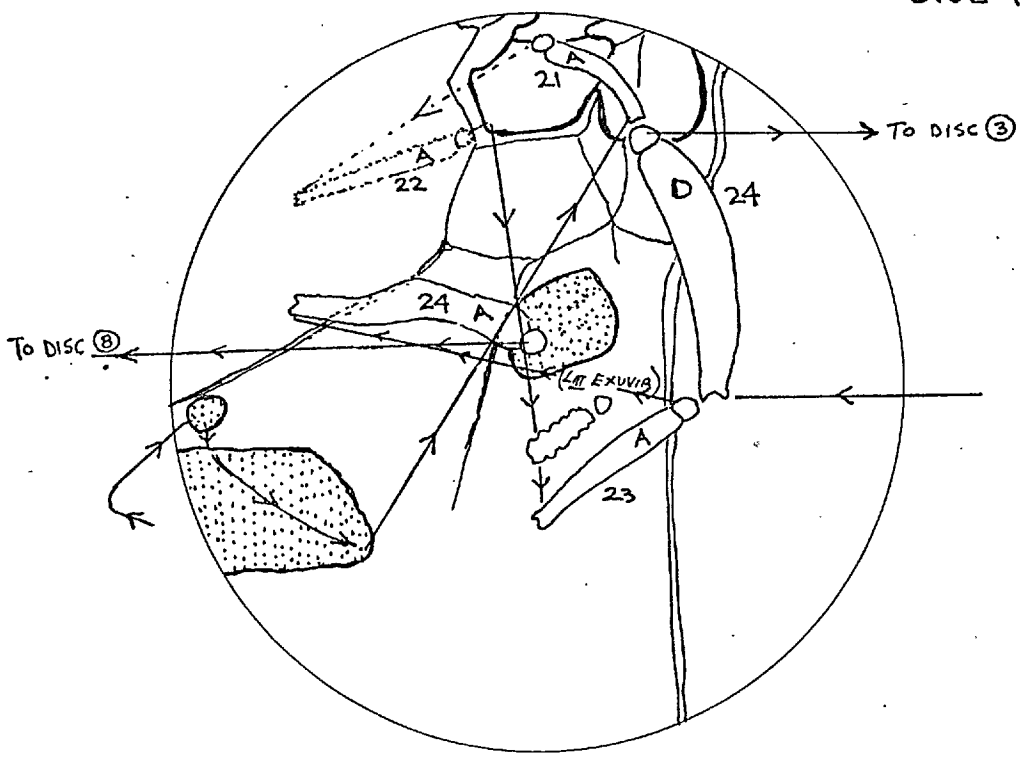


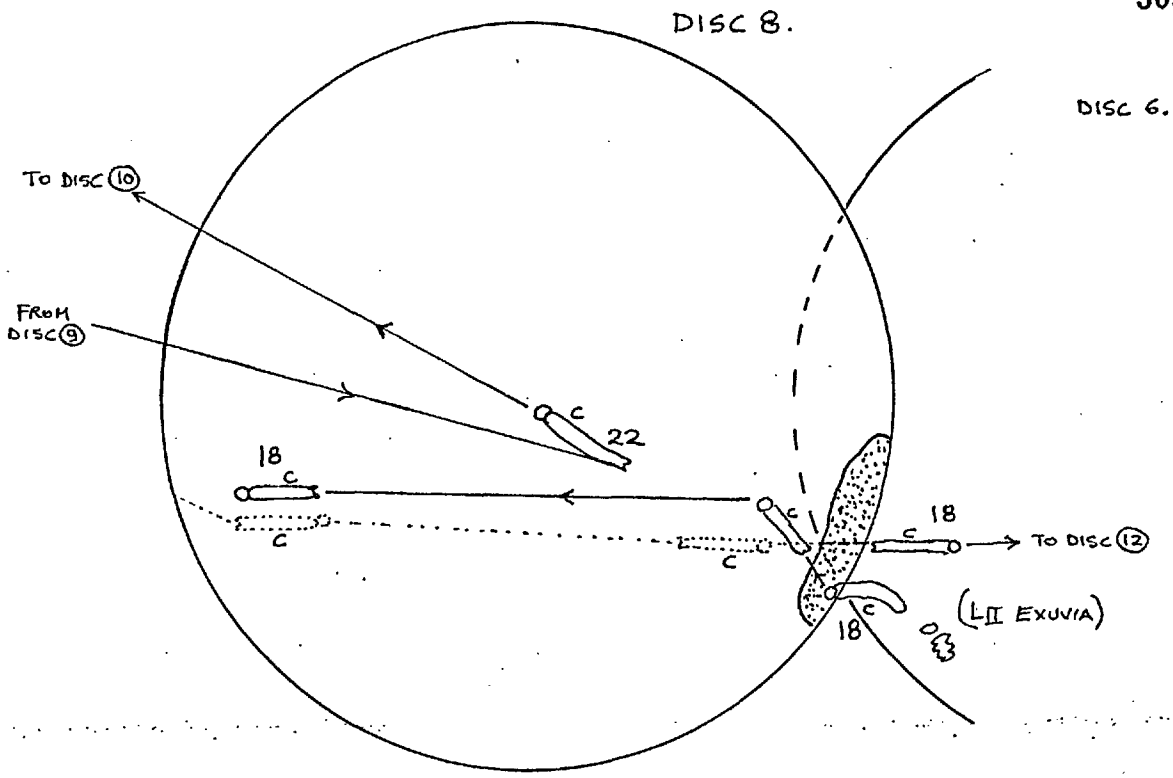
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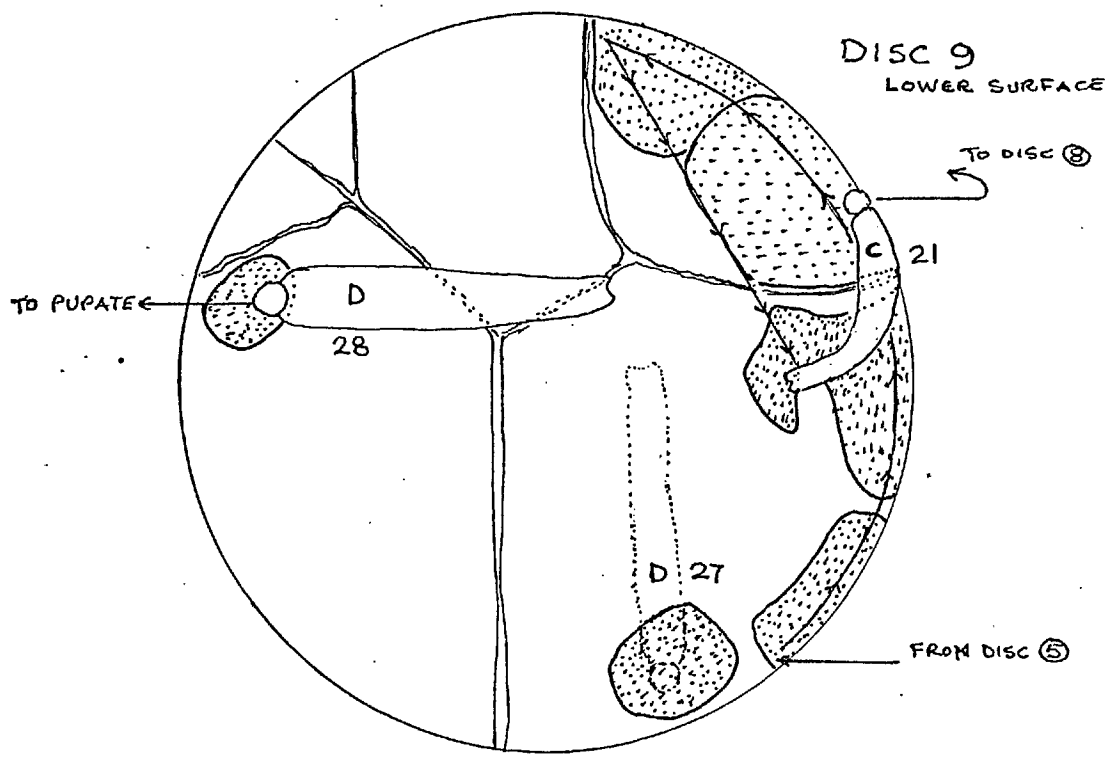
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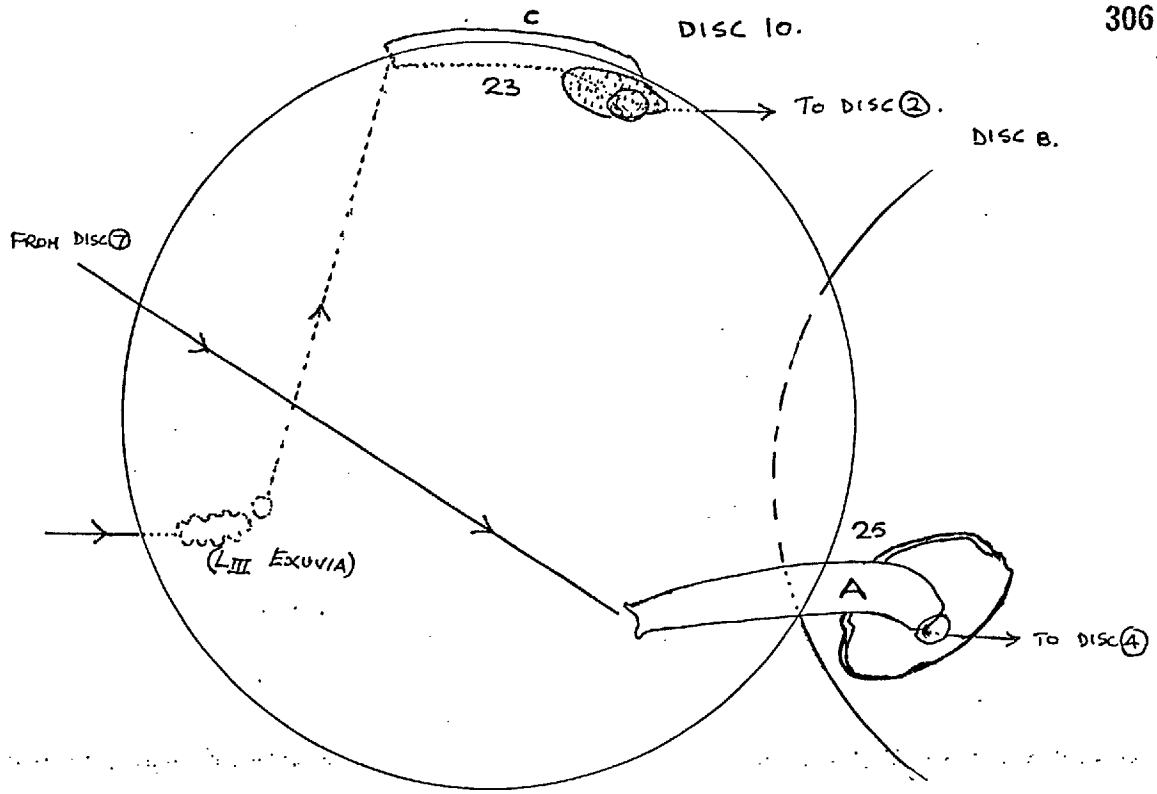

TO DISC (10)
18
D
LARVA C
17
TO DISC (10)
18
LIII
19
D
(LII EXUVIA)
17
D
17
TO DISC (10)
LARVA C
16
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(LI. EXUVIA)

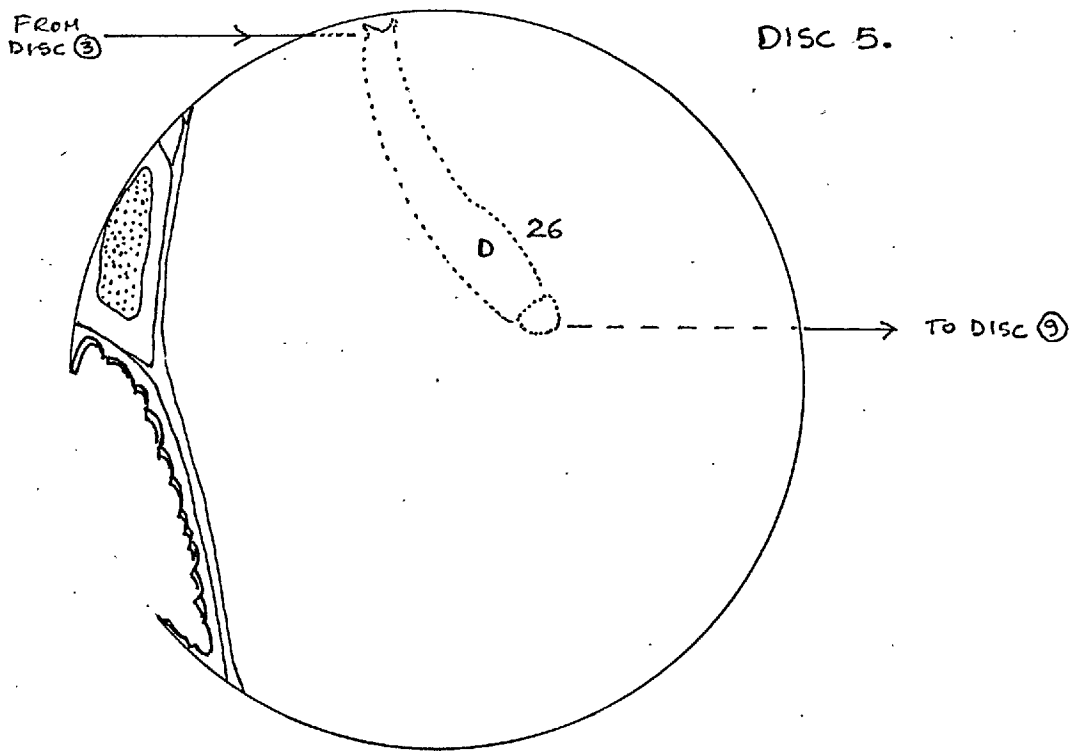
DISC 7.


A
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TO DISC (3)
A
22
D
24
24
A
TO DISC (8)
(LII EXUVIA)
D
A
23

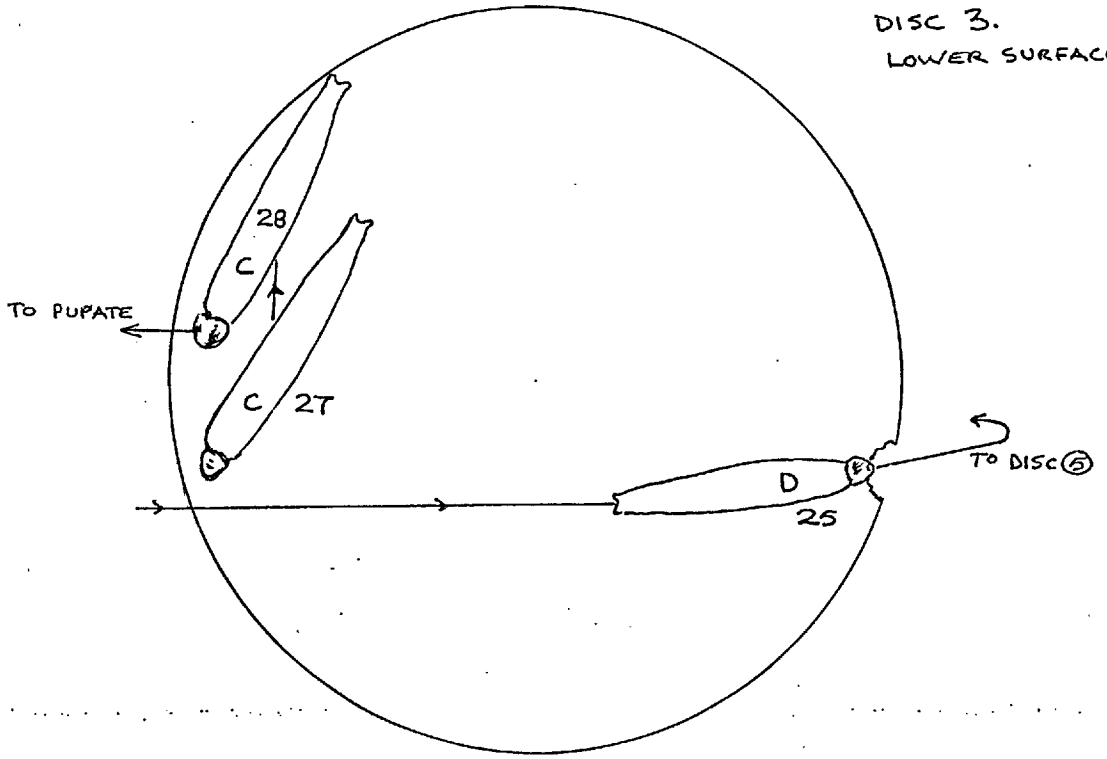

DISC 8.
DISC 6.
TO DISC (10)
FROM DISC (9)
C
22
18
C
C
C
C
C
18
C
TO DISC (12)
C
18
(LII EXUVIA)


DISC 9
LOWER SURFACE
TO DISC (8)
C
21
TO PUPATE
D
28
D
27
FROM DISC (5)

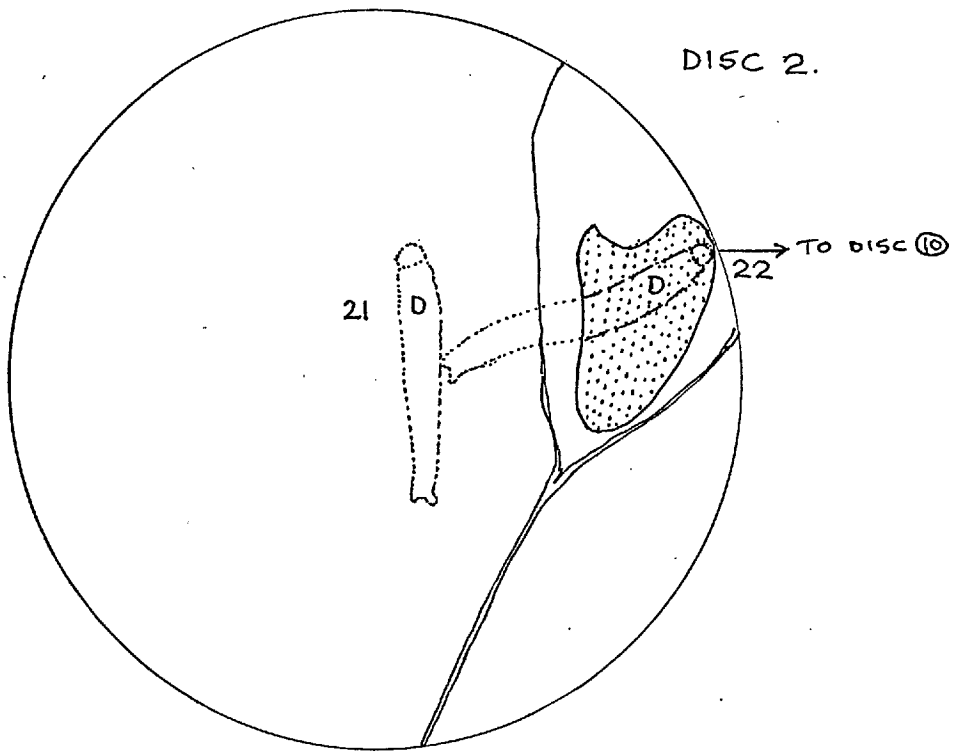

C
DISC 10.
23
To DISC ②.
DISC B.
FROM DISC ⑦
25
A
(LIII EXUVIA)
TO DISC ④


FROM DISC ③
DISC 5.
26
D
TO DISC ⑨

DISC 3.
LOWER SURFACE



DISC 2.



15.2 1. Dispersion and distribution parameters

Table 9.11.1. Dispersion of P. xylostella. Changes with age at medium density.

a. - Exp 1. Plant A. 116 larvae / plant.

Date	Morisita's index	$s^2/\bar{x}$	Fit to Poisson distribution (chi-square test)	Fit to Negative binomial (Chi-square test)	K3	Lloyd's mean crowding
			Alternative	Alternative		
(Eggs) 15-I-69	4.429	4.552	P < .001	P < .001	0.292*	-
(Larvae) 19	1.410	1.425	.005>P>.001	.20>P>.10	2.170	1.513
22	0.840	0.834	.20>P>.10	-	-	-
23	1.744	1.637	.10>P>.05	.95>P>.90	1.346	1.494
24	1.957	1.810	P<.001	.02>P>.01	1.200	1.555
25	1.241	1.171	.005>P>.001	.005>P>.001	3.095	0.945
26	1.072	1.052	.70>P>.50	.50>P>.30	14.807	0.772
27	0.943	0.962	.30>P>.25	-	-	-
28	0.679	0.812	.30>P>.25	-	-	-
29	0.955	0.972	.50>P>.30	-	-	-
30	0.962	0.978	.80>P>.75	-	-	-
31	1.147	1.082	.20>P>.10	.10>P>.25	9.591	0.621
1-II-69	0.278	0.633	P<.001	-	-	-
2	1.280	1.124	.50>P>.30	.30>P>.25	4.928	0.537
3	2.279	1.530	.010>P>.005	.30>P>.25	0.769	0.966
4	0.762	0.897	.70>P>.50	-	-	-
(>50% Pupae) 5-II-69	0.762	0.897	.70>P>.50	-	-	-

* Moment estimate of K (= Bliss & Fisher (1953) K1 index)

Table 9.11.2.

b. Exp. 1. Plant B. 180 larvae/plant.

Date	Morsita's index	$S^2/\bar{x}$	Fit to Poisson distribution (chi-square test) alternative	Fit to Negative binomial (chi-square test) alternative	K3	Lloyd's mean crowding
(Eggs) 15-I-69	10.791	10.616	P<.001	.75>P>.70	0.057	18.192
(Larvae)						
19	1.415	1.389	.050>P>.025	.30>P>.25	2.643	1.292
22	1.413	1.615	.010>P>.005	.30>P>.25	2.411	2.103
23	1.598	1.663	P<.001	.050>P>.025	1.723	1.751
24	1.429	1.406	.050>P>.025	.50>P>.30	2.319	1.354
25	1.415	1.389	.050>P>.025	-	-	-
26	1.272	1.238	.75>P>.70	.80>P>.75	3.573	1.120
27	1.414	1.362	.02>P>.01	.02>P>.01	3.484	1.126
28	1.227	1.196	.25>P>.20	.50>P>.30	4.535	1.057
29	0.888	0.925	.70>P>.50	-	-	-
30	0.919	0.944	.75>P>.70	-	-	-
31	0.709	0.798	.10>P>.05	-	-	-
1-II-69	0.511	0.670	.025>P>.020	-	-	-
2	0.622	0.843	.20>P>.10	-	-	-
3	2.182	1.586	.010>P>.005	.50>P>.30	0.831	1.102
4	1.544	1.255	.25>P>.20	.50>P>.30	1.780	0.739
(>50% Pupae)						
5-II-69	1.707	1.331	.050>P>.025	.20>P>.10	1.197	0.868

Table 9.11.3.
c. - Exp. 2. Plant A. 123 larvae/plant.

Date	Morisita's index	$S^2/\bar{x}$	Fit to Poisson distribution (chi-square test) alternative	Fit to Negative binomial (chi-square test) alternative	K3	Lloyd's mean crowding
(Eggs) 15-II-69	3.929	5.844	P<.001	.050>P>.025	0.199	9.907
(Larvae) 20-II-69	2.733	3.742	P<.001	.25>P>.20	0.731	3.728
24	0.959	0.960	.980>P>.975			
25	1.441	11.284	P<.001	P<.001	2.258*	
26	0.996	0.996	.70>P>.50			
27	0.960	0.957	.75>P>.70			
28	0.988	0.987	.050>P>.025			
1-III-69	1.364	1.377	.050>P>.025	.20>P>.10	3.280	1.354
2	1.033	1.030	.90>P>.80	.90>P>.80	50.058	0.918
3	1.089	1.075	.70>P>.50	.50>P>.30	13.786	0.912
4	0.502	0.685	.10>P>.05			
(>50% pupae)	0.557	0.770	.20>P>.10			
5						
6	0.557	0.770				
7	0.923	0.962	.10>P>.05			
8	0.756	0.883	.25>P>.20			
9	0.972	0.986	.50>P>.30			
			.30>P>.25			

Table 9.11.4.
d. - Exp. 2. Plant B. 126 larvae/plant

Date	Morisita's index	$S^2 / \bar{x}$	Fit to Poisson distribution (chi-Square test) alternative	Fit to Negative binomial (chi-square test) alternative	K3	Lloyd's mean crowdin
(Eggs) 15-II-69	9.912	16.956	P<.001	.50>P>.30	0.064	29.669
(Larvae) 20	2.901	4.772	P<.001	.70>P>.50	0.463	6.225
24	1.396	1.729	.010>P>.005	.005>P>.001	3.408	2.365
25	1.541	2.012	P<.001	.005>P>.001	2.829	2.517
26	1.773	2.178	.02>P>.01	.25>P>.20	1.754	2.380
27	1.113	1.116	.95>P>.90	.70>P>.50	8.821*	
28	0.860	0.806	.02>P>.01			
1-III-69	0.841	0.770	.20>P>.10			
2	0.669	0.611	.005>P>.001			
3	0.557	0.514	P<.001			
4	0.561	0.596	.005>P>.001			
(>50% pupae) 5	0.511	0.635	.025>P>.020			
6	0.774	0.889	.50>P>.30			
7	0.736	0.878	.20>P>.10			
8	0.912	0.964	.50>P>.30			

* Moment estimate of K (Bliss & Fisher (1953) K1 index)

Table 9.115 Dispersion of P. xylostella. Changes with age and with density

a. - Exp. 3. Plant A. 24 larvae / plant.

Date	Morisita's index	$S^2 / \bar{x}$	Fit to Poisson distribution (Chi-square test)	Fit to Negative binomial (Chi-square test)	K3	Lloyd's mean crowdin
			alternative	alternative		
(hatching larvae)						
20-III-69	7.420	3.344	P<.001	.975>P>.950	0.149	2.895
22	2.319	1.481	.050>P>.025	.70>P>.50	0.620	0.980
24	1.623	1.228	.50>P>.30	.75>P>.70	1.513	0.623
26	0.928	0.974	.010>P>.005			
28	1.435	1.154	.10>P>.05	Insufficient degrees of freedom	1.791	0.567
30	1.385	1.128	.70>P>.50	.50>P>.30	3.528	0.449
1-IV-69	0.337	0.800	.20>P>.10			
3	0.374	0.821	.25>P>.20			
(pupae)						
5-IV-69	0.418	0.843	.30>P>.25			

Table 9.11.6.
b. Exp. 3. Plant B. 266 larvae/plant.

Date	Morisita's index	$S^2 / \bar{x}$	Fit to Poisson distribution (Chi-square test) alternative	Fit to Negative binomial (Chi-square test) alternative	K3	Lloyd's mean crowding
(hatching larvae)						
20-III-69	2.268	6.334	P<.001	.005>P>.001	0.724	9.897
22	2.071	4.197	P<.001	.20>P>.10	1.137	5.550
24	2.362	4.633	P<.001	.25>P>.20	1.045	5.167
26	1.856	2.712	P<.001	P<.001	2.078	2.939
28	1.318	1.469	.10>P>.05	.02>P>.01	3.460	1.893
30	1.017	1.025	.010>P>.005	.005>P>.001	206.633	1.460
1-IV-69	0.703	0.576	.010>P>.005			
3	0.903	0.873	.50>P>.30			
5	0.794	0.733	.10>P>.05			
7	1.014	1.015	.25>P>.20	.20>P>.10	69.160*	
(pupae)						
9-IV-69	0.776	0.769	.70>P>.50			

* Moment estimate of K (Bliss & Fisher (1953) K1 index)

Table 9.11.7.
c. Exp. 3. Plant C. 420 larvae/plant.

Date	Morisita's index	$S^2 / \bar{x}$	Fit to Poisson distribution (Chi-square test) alternative	Fit to Negative binomial (Chi-square test) alternative	K3	Lloyd's mean crowding
(hatching larvae)						
20-III-69	1.512	4.406	P<.001	.50>P>.30	2.170	9.587
22	1.248	2.117	P<.001	.25>P>.20	3.727	5.648
24	1.304	2.151	.005>P>.001	.50>P>.30	3.111	4.940
26	1.154	1.395	.20>P>.10	.20>P>.10	7.301	2.896
28	1.506	2.212	P<.001	.02>P>.01	2.241	3.435
30	1.067	1.152	.70>P>.50	.70>P>.50	18.216	2.390
1-IV-69	0.920	0.829	.050>P>.025			
3	1.142	1.305	.50>P>.30	.30>P>.25	5.509	2.522
5	1.555	1.977	.050>P>.025	.20>P>.10	2.069	2.596
7	1.553	1.921	P<.001	P<.001	3.290	2.160
(pupae)						
9-IV-69	1.787	2.199	P<.001	.005>P>.001	2.267	2.184

9.11.8.

Table Dispersion of P. xylostella. Changes with age and with density.

a. Exp. 4. Plant A. 10 larvae / plant.

Date	Morisita's index	$S^2/\bar{x}$	Fit to Poisson distribution (Chi-square test) alternative	Fit to Negative binomial (Chi-square test) alternative	K3	Lloyd's mean crowding
(larvae)						
25-IV-69	32.000	4.532	P<.001	.50>P>.30	3.539*	
26	32.000	4.532	P<.001	.50>P>.30	3.539*	
28	7.111	1.696	.02>P>.01	.70>P>.50	0.156	0.927
30	14.667	2.079	.005>P>.001	.70>P>.50	0.055	1.745
2-V-69	1.778	1.089	.70>P>.50	Insufficient degress of freedom	1.446	0.211
5	3.556	1.291	.10>P>.05	"	0.336	0.496
7	0.000	0.911	Insufficient degrees of freedom			
9	0.000	0.924	"			
11	3.810	1.213	.25>P>.20	Insufficient degrees of freedom	0.359	0.331

* Moment estimate of K (Bliss & Fisher (1953) K1 index).

Table 9.11.9.

b. Exp. 4. Plant B. 188 larvae/plant.

Date	Morisita's index	$S^2/\bar{x}$	Fit to Poisson distribution (Chi-square test) alternative	Fit to Negative binomial (Chi-square test) alternative	K3	Lloyd's mean crowding
(larvae)						
30-IV-69	1.519	1.729	.005>P>.001	.25>P>.20	1.978	2.108
2-V-69	1.395	1.455	.050>P>.025	.10>P>.05	2.214	1.670
5	1.252	1.266	.50>P>.30	.70>P>.50	4.640	1.094
7	1.320	1.283	.50>P>.30	.90>P>.80	3.356	1.152
9	0.901	0.922	.70>P>.50			
11	0.821	0.852	.010>P>.005			
13	0.942	0.955	.10>P>.05			
15	0.942	0.955	.10>P>.05			

c. Exp. 4. Plant C. 550 larvae / plant.

(larvae)						
25-IV-69	27.739	183.432	P<.001	.10>P>.05	0.037*	
26	52.031	355.636	P<.001	.50>P>.30	0.015	466.277
28	14.991	25.215	P<.001	.050>P>.025	0.071*	
30	1.537	1.633	.050>P>.025	.20>P>.10	2.697	1.611
2-V-69	1.292	1.255	.20>P>.10	.25>P>.20	2.751	1.193
5	2.637	1.269	.80>P>.75	Insufficient degrees of freedom	0.648	0.445

* Moment estimate of K (Bliss & Fisher (1953) K1 index)

Table 9.11.10.
e. Exp. 5. Plant A. 130 larvae/plant.

Date	Morisita's index	$S^2/\bar{x}$	Fit to Poisson distribution (Chi-square test) alternative	Fit to Negative binomial (Chi-square test) alternative	K 3	Lloyd's mean crowding
(larvae)						
3-VI-69	7.967	12.376	P<.001	P<.001	0.143*	
4	7.967	12.376	P<.001	P<.001	0.143*	
5	4.297	5.668	P<.001	.20>P>.10	0.175	9.481
6	2.457	3.287	P<.001	.95>P>.90	0.742	3.669
7	2.129	2.700	P<.001	.70>P>.50	0.945	3.087
8	1.389	1.542	.050>P>.025	.50>P>.30	3.220	1.818
9	2.053	2.378	P<.001	.50>P>.30	1.143	2.446
10	0.938	0.918	.010>P>.005			
11	0.926	0.904	.50> P>.30			
12	0.963	0.960	.70>P>.50			
13	0.707	0.640	.050>P>.025			
14	0.859	0.829	.50>P>.30			
15	1.037	1.047	.050>P>.025	.02>P>.01	40.022	1.295
16	1.414	1.477	.02>P>.01	.20>P>.10	2.659	1.583
(pupae)						
17-VI-69	1.786	1.931	.010>P>.005	.50>P>.30	1.624	1.910

* Moment estimate of K (Bliss & Fisher (1953) K1 index)

Table 9.11.11. Dispersion of P. xylostella. Changes with age and density.

a. Field Exp. 1. No parasites and predators. (3 plants. 337 larvae)

Date	Morisita's index	$S^2/\bar{x}$	Fit to Poisson distribution (Chi-square test) alternative	Fit to Negative binomial (Chi-square test) alternative	K3	Lloyd's mean crowdin
3-VIII-69	11.134	35.648	P< .001	.50>P>.30	0.079	46.054
5	4.429	9.121	P< .001	.50>P>.30	0.247	11.888
7	3.232	4.951	P< .001	.50>P>.30	0.641	4.517
10	2.769	3.833	P< .001	.30>P>.25	0.664	4.000
12	2.486	3.288	P< .001	.50>P>.30	0.630	3.971
16	2.316	2.934	P< .001	.80>P>.75	0.738	3.451
18	2.514	3.185	P< .001	.90>P>.80	0.712	3.462
20	2.464	3.106	P< .001	.30>P>.25	0.900	3.031
25	2.125	2.628	P< .001	.20>P>.10	1.106	2.749

Table 9.11.12.
b. Field Exp. 2 No parasites and predators. (3 plants. 402 larvae)

Date	Morisita's index	$S^2 / \bar{x}$	Fit to Poisson distribution (Chi-square test) alternative	Fit to Negative bi nomial (Chi-square test) alternative	K3	Lloyd's mean crowding
12-IX-69	21.461	62.039	$P < .001$	$.70 > P > .50$	0.029	104.946
14	20.350	51.829	$P < .001$	$.02 > P > .01$	0.071	39.459
16	19.290	43.313	$P < .001$	$.50 > P > .30$	0.080	30.995
19	7.869	13.861	$P < .001$	$.50 > P > .30$	0.197	11.338
23	7.191	11.318	$P < .001$	$.25 > P > .20$	0.286	7.479
28	2.217	2.764	$P < .001$	$.90 > P > .80$	0.733	3.422
30	2.200	2.543	$P < .001$	$.10 > P > .05$	0.853	2.790
2-X-69	1.955	2.232	$P < .001$	$.75 > P > .70$	0.928	2.678
4	1.989	2.244	$P < .001$	$.10 > P > .05$	0.732	2.971
7	1.953	2.187	$P < .001$	$.30 > P > .25$	0.937	2.572
9	2.577	2.920	$P < .001$	$.50 > P > .30$	0.630	3.148
11	2.319	2.604	$P < .001$	$.025 > P > .020$	0.800	2.734
15	2.413	2.697	$P < .001$	$.50 > P > .30$	0.712	2.885

Table 9.11.13.

c. Field Exp. 3. No parasites and predators. (3 plants. 826 larvae)

Date	Morisita's index	$S^2/\bar{x}$	Fit to Poisson distribution (Chi-square test) alternative	Fit to Negative binomial (Chi-square test) alternative	K3	Lloyd's mean crowding
24-VIII-70	10.216	105.972	P< .001	.02>P>.01	0.118	105.969
26	8.429	101.911	P< .001	.90>P>.80	0.111	133.568
28	4.490	51.443	P< .001	.050>P>.025	0.187	90.159
30	3.523	35.386	P< .001	.70>P>.50	0.245	68.230
2-IX-70	3.147	29.700	P< .011	.70>P>.50	0.350	50.741
5	3.481	34.180	P< .001	.995>P>.990	0.369	48.842
8	2.759	23.863	P< .001	.95>P>.90	0.444	41.599
10	2.507	20.087	P< .001	.75>P>.70	0.450	40.139
15	2.751	22.075	P< .001	.30>P>.25	0.405	41.101
18	2.628	21.803	P< .001	.20>P>.10	0.438	41.313

15.2.2. Life-Tables, etc.

Appendix-Table 10.8.1. - Life-tables. 'Control'. Exp. I.

Plant A.

x	stage	lx	dx	Lx	Tx	ex	100 qx
0-3	Eggs	40	0	40.0	82.0	2.05	0.0
8	Larvae I	40	25	27.5	42.0	1.05	62.5
13	Larvae II	15	10	10.0	14.5	0.97	66.7
18	Larvae III	5	4	3.0	4.5	0.90	80.0
22	Larvae IV	1	0	1.0	1.5	1.50	0.0
43	Pre-pupae and pupae	1	1	0.5	0.5	0.50	100.0
	Adults	0	0				

Plant B

0 - 3	Eggs	35	0	35.0	82.5	2.36	0.0
8	Larvae I	35	21	24.0	47.5	1.36	60.0
13	Larvae II	14	8	10.0	23.0	1.64	57.1
18	Larvae III	6	1	5.5	13.0	2.17	16.7
22	Larvae IV	5	0	5.0	7.5	1.50	0.0
43	Pp + pupae	5	5	2.5	2.5	0.50	100.0
	Adults	0					

Appendix-Table 10.8.2. - Life-table. 'Control' C. Exp. 1.

x	stage	lx	dx	Lx	Tx	ex	100 qx
0 - 3	Eggs	18	0	18.0	74.0	4.11	0.0
8	Larvae I	18	5	15.5	56.0	3.11	27.8
13	Larvae II	13	2	12.0	40.5	3.12	23.1
18	Larvae III	11	0	11.0	28.5	2.59	0.0
22	Larvae IV	11	0	11.0	17.5	1.59	0.0
43	Pp + pupae	11	10	6.0	6.5	0.59	90.9
	Adults	1	0	0.5	0.5	0.59	0.0

Fertility table.

						r = 0.02			r = 0.03	
x	lx	mx	lxmx	xlxmx	3-rx	e^{3-rx}	e^{3-rx}lxmx	3-rx	e^{3-rx}lxmx	e^{3-rx}lxmx
0	1.000									
44	0.028	21.8	0.610	26.84	2.12	8.33	5.08	1.68	5.37	3.28
45	.028	20.7	.580	26.10	2.10	8.17	4.74	1.65	5.21	3.02
46	.028	21.0	.588	27.05	2.08	8.00	4.70	1.62	5.05	2.97
47	.028	17.1	.479	22.51	2.06	7.85	3.76	1.59	4.90	2.35
48	.028	15.4	.431	20.69	2.04	7.69	3.31	1.56	4.76	2.05
49	.028	8.2	.230	11.27	2.02	7.54	1.73	1.53	4.62	1.06
50	.028	7.4	.202	10.10	2.00	7.39	1.49	1.50	4.48	0.90
51	.028	4.3	.120	6.12	1.98	7.24	0.87	1.47	4.35	0.52
52	.028	3.2	.090	4.68	1.96	7.10	0.64	1.44	4.22	0.38
53	.028	2.1	.059	3.13	1.94	6.96	0.41	1.41	4.10	0.24
54	.028	1.3	.036	1.94	1.92	6.82	0.25	1.38	3.97	0.14
55	.028	0.5	.014	0.77	1.90	6.69	0.09	1.35	3.86	0.05
57	.028	0.1	.003	0.17	1.86	6.42	0.02	1.29	3.63	0.01
59	.028	0.1	.003	0.18	1.82	6.17	0.02	1.23	3.42	0.01
		Ro =	3.445	161.55			27.11			~~16.98~~ 16.98

$T = \frac{161.55}{3.445} = 46.894$ $\quad r = \frac{\log e\ Ro}{T} = 0.026$ $\quad \sum e^{3-rx}lxmx = 20.09$

$r = 0.0269 = \underline{0.027}$

Appendix-Table 10.8.3. - Life-table. 'Control' (Total). Exp. 1.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0 - 3	Eggs	93	0	93.0	238.5	2.56	0.0
8	Larvae I	93	51	67.5	145.5	1.56	54.8
13	Larvae II	42	20	32.0	78.0	1.86	47.6
18	Larvae III	22	5	19.5	46.0	2.09	22.7
22	Larvae IV	17	0	17.0	26.5	1.56	0.0
43	Pp + pupae	17	16	9.0	9.5	0.56	94.1
	Adults	1		0.5	0.5	0.50	0.0

Fertility table

					r = -0.008			r = -0.009		
x	lx	mx	lxmx	xlxmx	-rx	e^{-rx}	e^{-rx}lxmx	-rx	e^{-rx}	e^{-rx}lxmx
0	1.000									
44	0.005	21.8	0.109	4.80	0.35	1.42	0.15	0.40	1.49	0.26
45	.005	20.7	.104	4.68	0.36	1.43	.15	.41	1.51	.16
46	.005	21.0	.105	4.83	0.37	1.45	.15	.41	1.51	.16
47	.005	17.1	.086	4.04	0.38	1.46	.13	.42	1.52	.13
48	.005	15.4	.077	3.70	0.38	1.46	.11	.43	1.54	.12
49	.005	8.2	.041	2.01	0.39	1.48	.06	.44	1.55	.06
50	.005	7.4	.037	1.85	0.40	1.49	.06	.45	1.57	.06
51	.005	4.3	.022	1.12	0.41	1.51	.03	.46	1.58	.03
52	.005	3.2	.016	0.83	0.42	1.52	.02	.47	1.60	.03
53	.005	2.1	.011	0.58	0.42	1.52	.02	.48	1.62	.02
54	.005	1.3	.007	0.38	0.43	1.54	.01	.49	1.63	.01
55	.005	0.5	.003	0.17	0.44	1.55	.00	.50	1.65	.00
57	.005	0.1	.001	0.06	0.46	1.58	.00	.51	1.67	.00
59	.005	0.1	.001	0.06	0.47	1.60	.00	.53	1.70	.00
	Ro =		0.620	35.31			0.89			1.04

$T = 56.952$ $r = -0.0084$ $\sum e^{-rx}lxmx = 1$ $r = -0.00863 = \underline{-0.0087}$

Appendix - Table 10.8.4. - Stable-age distribution table. 'Control' (Total) Exp. 1.

Stage	x	lx	rm(x+1)	$e^{-rm(x+1)}$	$Lxe^{-rm(x+1)}$	$100\beta Lx\, e^{-rm(x+1)}$
Eggs	0	1.0000	-0.0087	1.00913	1.00913	38.48
Larvae I	1	.7258	-0.0174	1.01755	0.73854	28.16
Larvae II	2	.3441	-0.0261	1.0266	0.35325	13.47
Larvae III	3	.2097	-0.0348	1.0349	0.21702	8.28
Larvae IV	4	.1828	-0.0435	1.0446	0.19095	7.28
Pp + pupae	5	.0968	-0.0552	1.0536	0.10199	3.89
Adults	6	.0108	-0.0609	1.0627	0.01148	0.44
				$1/\beta$ =	2.62236	
				β =	0.38143	

Appendix-Table 10.8.5. - Life-table. 'No parasites and predators' A. Exp. 1

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-3	Eggs	63	0	63.0	354.5	5.63	0.0
8	Larvae I	63	11	57.5	291.5	4.63	17.5
13	Larvae II	52	0	52.0	234.0	4.50	0.0
18	Larvae III	52	0	52.0	182.0	3.50	0.0
22	Larvae IV	52	0	52.0	130.0	2.50	0.0
43	Pp + pupae	52	0	52.0	78.0	1.50	0.0
	Adults	52		26	26	0.50	0.0

Fertility table.

						r = 0.08			r = 0.09	
x	lx	mx	lxmx	xlxmx	6-rx	e^{6-rx}	e^{6-rx}lxmx	6-rx	e^{6-rx}	e^{6-rx}lxmx
0	1.000									
44	0.413	21.8	9.003	396.13	2.48	11.94	107.50	2.04	7.69	69.23
45	.413	20.7	8.549	384.71	2.40	11.02	94.21	1.95	7.03	60.10
46	.413	21.0	8.673	398.96	2.32	10.17	88.20	1.86	6.43	55.77
47	.413	17.1	7.062	331.91	2.24	9.39	66.31	1.77	5.87	41.45
48	.413	15.4	6.360	305.28	2.16	8.67	55.14	1.68	5.37	34.15
49	.413	8.2	3.387	165.96	2.08	8.00	27.10	1.59	4.90	16.60
50	.413	7.4	3.056	152.80	2.00	7.39	22.58	1.50	4.48	13.69
51	.413	4.3	1.776	90.58	1.92	6.82	12.11	1.41	4.10	7.28
52	.413	3.2	1.322	68.74	1.84	6.30	8.33	1.32	3.74	4.94
53	.413	2.1	0.867	45.95	1.76	5.81	5.04	1.23	3.42	2.97
54	.413	1.3	0.537	29.00	1.68	5.37	2.88	1.14	3.13	1.68
55	.413	0.5	0.207	11.39	1.60	4.95	1.02	1.05	2.86	0.59
57	.413	0.1	0.041	2.34	1.44	4.22	0.17	0.87	2.39	0.10
59	.413	0.1	0.041	2.42	1.28	3.60	0.15	0.69	1.99	0.09
	Ro =		50.881	2386.17			490.74			308.64

T = 46.897 r = 0.084 $\sum e^{6-rx}$lx mx = 403.43 r = 0.0848 = <u>0.085</u>

Appendix-Table 10.8.6. - Life-table. 'No parasites and predators' B. Exp. 1.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-3	Eggs	166	0	166.0	681.0	4.10	0.0
8	Larvae I	166	70	131.0	515.0	3.10	421.7
13	Larvae II	96	9	91.5	384.0	4.00	93.8
18	Larvae III	87	4	85.0	292.5	3.36	46.0
22	Larvae IV	83	0	83.0	207.5	2.50	0.0
43	Pp + pupae	83	0	83.0	124.5	1.50	0.0
	Adults	83		41.5	41.5	0.50	0.0

Fertility table.

x	lx	mx	lxmx	xlxmx	5-rx	r = 0.07 e^{5-rx}	e^{5-rx} lxmx	5-rx	r=0.08 e^{5-rx}	e^{5-rx} lxmx
0	1.000									
44	0.250	21.8	5.450	239.80	1.92	6.82	37.17	1.48	4.39	23.93
45	.250	20.7	5.175	232.88	1.85	6.36	32.91	1.40	4.06	21.01
46	.250	21.0	5.250	241.50	1.78	5.93	31.13	1.32	3.74	19.64
47	.250	17.1	4.275	200.93	1.71	5.53	23.64	1.24	3.46	14.79
48	.250	15.4	3.850	184.80	1.64	5.16	19.87	1.16	3.19	12.28
49	.250	8.2	2.050	100.45	1.57	4.81	9.86	1.08	2.94	6.03
50	.250	7.4	1.850	92.50	1.50	4.48	8.29	1.00	2.72	5.03
51	.250	4.3	1.075	54.83	1.43	4.18	4.49	0.92	2.51	2.70
52	.250	3.2	0.800	41.60	1.36	3.90	3.12	0.84	2.32	1.86
53	.250	2.1	0.525	27.83	1.29	3.63	1.91	0.75	2.14	1.12
54	.250	1.3	0.325	17.55	1.22	3.39	1.10	0.68	1.97	0.64
55	.250	0.5	0.125	6.88	1.15	3.16	0.40	0.60	1.82	0.23
57	.250	0.1	0.025	1.43	1.01	2.75	0.07	0.44	1.55	0.04
59	.250	0.1	0.025	1.48	0.87	2.39	0.06	0.28	1.32	0.03
		Ro	=30.800	1444.46			174.02			85.40

T = 46.898 r = 0.073

$\sum e^{5-rx}$ lxmx = 148.413 r = 0.0729 = 0.073

Appendix-Table 10.8.7 - Life-table. 'No parasites and predators' C. Exp. 1.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-3	Eggs	108	0	108.0	416.0	3.85	0.0
8	Larvae I	108	35	90.5	308.0	2.85	32.4
13	Larvae II	73	26	60.0	217.5	2.98	35.6
18	Larvae III	47	2	46.0	157.5	3.35	4.3
22	Larvae IV	45	0	45.0	111.5	2.48	0.0
43	Pp + pupae	45	1	44.5	66.5	1.48	2.2
	Adults	44		22.0	22.0	0.50	0.0

Fertility table.

						r = 0.06		r=0.07		
x	lx	mx	lxmx	xlxmx	5-rx	e^{5-rx}	e^{5-rx} lxmx	5-rx	e^{5-rx}	e^{5-rx} lxmx
0	1.000									
44	0.204	21.8	4.447	195.67	2.36	10.61	47.18	1.92	6.82	30.33
45	.204	20.7	4.223	190.04	2.30	9.97	42.10	1.85	6.36	26.86
46	.204	21.0	4.284	197.06	2.24	9.39	40.23	1.78	5.93	25.40
47	.204	17.1	3.488	163.94	2.18	8.85	30.87	1.71	5.53	19.29
48	.204	15.4	3.142	150.82	2.12	8.33	26.17	1.64	5.16	16.21
49	.204	8.2	1.673	81.98	2.06	7.85	13.13	1.57	4.81	8.05
50	.204	7.4	1.510	75.50	2.00	7.39	11.16	1.50	4.48	6.76
51	.204	4.3	0.877	44.73	1.94	6.96	6.10	1.43	4.18	3.67
52	.204	3.2	0.653	33.96	1.88	6.55	4.28	1.36	3.90	2.55
53	.204	2.1	0.428	22.68	1.82	6.17	2.64	1.29	3.63	1.55
54	.204	1.3	0.265	14.31	1.76	5.81	1.54	1.22	3.39	0.90
55	.204	0.5	0.102	5.61	1.70	5.47	0.56	1.15	3.16	0.32
57	.204	0.1	0.020	1.14	1.58	4.86	0.10	1.01	2.75	0.06
59	.204	0.1	0.020	1.18	1.46	4.31	0.09	0.87	2.39	0.05
		Ro=	25.132	1178.62			226.15			142.00

T = 46.897 r = 0.0687

$\sum e^{5-rx}$ lxmx = 148.413 r = 0.0692 = 0.069

Appendix-Table 10.8.8. - Life-Table. 'No parasites and predators' Total. Exp. 1

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-3	Eggs	337	0	337.0	1451.5	4.31	0.0
8	Larvae I	337	156	279.0	1114.5	2.96	41.4
13	Larvae II	221	35	203.5	835.5	3.78	15.8
18	Larvae III	186	6	183.0	632.0	3.40	3.2
22	Larvae IV	180	0	180.0	449.0	2.49	0.0
43	Pp + pupae	180	1	179.5	269.0	1.49	0.6
	Adults	179		89.5	89.5	0.50	0.0

Fertility table.

x	lx	mx	lxmx	xlxmx	r=0.07 e^{5-rx} lxmx	r=0.08 e^{5-rx} lxmx
0	1.000					
44	0.266	21.8	5.799	255.16	39.55	25.46
45	.266	20.7	5.506	247.77	35.02	22.35
46	.266	21.0	5.586	256.96	33.12	20.89
47	.266	17.1	4.549	213.80	25.16	15.74
48	.266	15.4	4.096	196.61	21.14	13.07
49	.266	8.2	2.181	106.87	10.49	6.41
50	.266	7.4	1.968	98.40	8.82	5.35
51	.266	4.3	1.144	58.34	4.78	2.87
52	.266	3.2	0.851	44.25	3.32	1.97
53	.266	2.1	0.559	29.63	2.03	1.20
54	.266	1.3	0.346	18.68	1.17	0.68
55	.266	0.5	0.133	7.32	0.42	0.24
57	.266	0.1	0.027	1.54	0.07	0.04
59	.266	0.1	0.027	1.59	0.06	0.04
		Ro =	32.772	1536.92	185.15	116.31

T = 46.897 r = 0.074

$\sum e^{5-rx}$ lxmx = 148.413 r = 0.0769 = 0.077

Appendix-Table 10.8.9 - Stable-age distribution table. 'No parasites and predators' Total. Exp. 1.

Stage	x	lx	rm(x+1)	$e^{-rm(x+1)}$	$Lx\, e^{-rm(x+1)}$	$100\beta\, Lxe^{-rm(x+1)}$
Eggs	0	1.0000	0.077	.92539	.92593	29.05
Larvae I	1	.7401	0.154	.85690	.63419	19.90
Larvae II	2	.5398	0.231	.79635	.42841	13.44
Larvae III	3	.4854	0.308	.73529	.35691	11.20
Larvae IV	4	.4775	0.385	.68027	.32483	10.19
Pp + pupae	5	.4761	0.462	.62933	.29962	9.40
Adults	6	.4748	0.539	.58343	.27701	8.69

$1/\beta$ = 3.18690

β = 0.31378

Appendix-Table 10.8.10 - Life-table. 'Control' A. Exp. 2.

	Stage	lx	dx	Lx	Tx	ex	100qx
0-7	Eggs	258	0	258.0	607.0	2.35	0.0
12	Larvae I	258	131	194.5	349.0	1.35	50.8
20	Larvae II	127	47	103.5	154.5	1.22	37.0
27	Larvae III	80	72	44.0	51.0	0.64	90.0
36	Larvae IV	8	6	5.0	7.0	0.88	75.0
43	Pp+pupae	2	1	1.5	2.0	1.00	50.0
	Adults	1		0.5	0.5	0.50	0.0

Fertility table.

						r = -0.02		r=-0.03		
x	lx	mx	lxmx	xlxmx	-rx	e^{-rx}	e^{-rx}lxmx	-rx	e^{-rx}	e^{-rx}lxmx
0	1.000									
44	0.002	21.8	0.044	1.94	0.88	2.41	0.106	1.32	3.74	0.165
45	.002	20.7	.041	1.85	.90	2.46	.101	1.35	3.86	.158
46	.002	21.0	.042	1.93	.92	2.51	.105	1.38	3.97	.167
47	.002	17.1	.034	1.60	.94	2.56	.087	1.41	4.10	.139
48	.002	15.4	.031	1.49	.96	2.61	.081	1.44	4.22	.131
49	.002	8.2	.016	0.78	.98	2.66	.043	1.47	4.35	.070
50	.002	7.4	.015	0.75	1.00	2.72	.041	1.50	4.48	.067
51	.002	4.3	.009	0.46	1.02	2.77	.025	1.53	4.62	.042
52	.002	3.2	.006	0.31	1.04	2.83	.017	1.56	4.76	.029
53	.002	2.1	.004	0.21	1.06	2.89	.012	1.59	4.90	.020
54	.002	1.3	.003	0.16	1.08	2.95	.009	1.62	5.05	.015
55	.002	0.5	.001	0.06	1.10	3.00	.003	1.65	5.21	.005
57	.002	0.1	.000							
59	.002	0.1	.000							
		Ro=	0.246	11.54			0.630			1.638

T = 46.91 r = -0.0299

$\sum e^{-rx}$lxmx = 1 r = - 0.0237 = -0.024

Appendix-Table 10.8.11 - Life-table. 'Control' B. Exp. 2.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-7	Eggs	46	0	46.0	112.0	2.43	0.0
12	Larvae I	46	9	41.5	66.0	1.43	19.6
20	Larvae II	37	33	20.5	24.5	0.66	89.2
27	Larvae III	4	2	3.0	4.0	1.00	50.0
36	Larvae IV	2	2	1.0	1.0	0.50	100.0
43	Pp + pupae	0					
	Adults	0					

Life-table. Control C.

x	Stage	lx	dx	Lx	Tx	ex	1000 qx
0-7	Eggs	197	0	197.0	414.5	2.10	0.0
12	Larvae I	197	96	149.0	217.5	1.10	487.3
20	Larvae II	101	92	55.0	68.5	0.68	910.9
27	Larvae III	9	2	8.0	13.5	1.50	222.2
36	Larvae IV	7	5	4.5	5.5	0.79	714.3
43	Pp + pupae	2	2	1.0	1.0	0.50	1000.0
	Adults	0					

Appendix-Table 10.8.12. - Life-table. 'Control' (Total). Exp. 2.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-7	Eggs	501	0	501.0	1131.5	2.26	0.0
12	Larvae I	501	236	383.0	630.5	1.26	47.1
20	Larvae II	265	172	179.0	247.5	0.93	64.9
27	Larvae III	93	76	55.0	68.5	0.74	81.7
36	Larvae IV	17	13	10.5	13.5	0.79	76.5
43	Pp + pupae	4	3	2.5	3.0	0.75	75.0
	Adults	1		0.5	0.5	0.50	0.0

Fertility table.

					r=-0.04			r=-0.05		
x	lx	mx	lxmx	xlxmx	-rx	e^{-rx}	e^{-rx}lxmx	-rx	e^{-rx}	e^{-rx}lxmx
0	1.000									
44	0.001	21.8	0.022	0.968	1.76	5.81	0.13	2.20	9.03	
45	.001	20.7	.021	.945	1.80	6.05	0.13	2.25	9.49	
46	.001	21.0	.021	.945	1.84	6.30	0.13	2.30	9.97	
47	.001	17.1	.017	.799	1.88	6.55	0.11	2.35	10.50	
48	.001	15.4	.015	.720	1.92	6.82	0.10	2.40	11.02	
49	.001	8.2	.008	.392	1.96	7.10	0.06	2.45	11.59	
50	.001	7.4	.007	.350	2.00	7.39	0.05	2.50	12.19	
51	.001	4.3	.004	.204	2.04	7.69	0.03	2.55	12.81	
52	.001	3.2	.003	.156	2.08	8.00	0.02	2.60	13.46	
53	.001	2.1	.002	.106	2.12	8.33	0.02	2.65	14.17	
54	.001	1.3	.001	.054	2.16	8.67	0.01	2.70	14.88	
55	.001	0.5	.001	.055	2.20	9.03	0.01	2.75	15.64	
57	.001	0.1	.000							
59	.001	0.1	.000							
		Ro=	0.122	5.694			0.80			1.29

T = 46.67 r = -0.045

$\sum e^{-rx}$lxmx = 1 r = -0.0440 = <u>-0.044</u>

Appendix-Table 10.8.13. - Stable-age distribution table. Control(Total) Exp. 2.

Stage	x	Lx	rm(x+1)	$e^{-rm(x+1)}$	$Lx\,e^{-rm(x+1)}$	$100\beta\,Lxe^{-rm(x+1)}$
Eggs	0	1.0000	-0.044	1.5528	1.5528	52.20
Larvae I	1	.7645	-0.088	1.0921	0.83491	28.07
Larvae II	2	.3573	-0.132	1.1411	.40772	13.71
Larvae III	3	.1098	-0.176	1.1923	.13091	4.40
Larvae IV	4	.0314	-0.220	1.2460	.03912	1.32
Pp + pupae	5	.0050	-0.264	1.3020	.00651	0.22
Adults	6	.0020	-0.308	1.3620	.00272	0.09

$1/\beta$ = 2.97469

β = 0.33617

Appendix-Table 10.8.14 - Life-table. 'No parasites and predators' A. Exp. 2

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-7	Eggs	208	0	208.0	1010.0	4.86	0.0
12	Larvae I	208	25	195.5	802.0	3.86	12.0
20	Larvae II	183	43	161.5	606.5	3.31	23.5
27	Larvae III	140	2	139.0	445.0	3.18	1.4
36	Larvae IV	138	8	134.0	306.0	2.21	5.8
43	Pp+pupae	130	23	118.5	172.0	1.32	17.7
	Adults	107		53.5	53.5	0.50	0.0

Fertility table.

x	lx	mx	lxmx	xlxmx	r=0.07 e^{5-rx} lxmx	r=0.08 e^{5-rx} lxmx
0	1.000					
44	0.257	21.8	5.603	246.53	38.21	24.60
45	.257	20.7	5.320	239.40	33.84	21.60
46	.257	21.0	5.397	248.26	32.00	20.18
47	.257	17.1	4.395	206.57	24.30	15.21
48	.257	15.4	3.958	189.98	20.42	12.63
49	.257	8.2	2.107	103.24	10.13	6.19
50	.257	7.4	1.902	95.10	8.52	5.17
51	.257	4.3	1.105	56.36	4.62	2.77
52	.257	3.2	0.822	42.74	3.21	1.91
53	.257	2.1	0.540	28.62	1.96	1.16
54	.257	1.3	0.334	18.04	1.13	0.66
55	.257	0.5	0.129	7.10	0.41	0.23
57	.257	0.1	0.026	1.48	0.07	0.04
59	.257	0.1	0.026	1.53	0.06	0.03
		Ro=	31.664	1484.95	178.88	112.38

T = 46.897 r = 0.737

$\sum e^{5-rx}$ lxmx = 148.41 r = 0.0746 = 0.075

Appendix-Table 10.8.15. - Life-table. 'No parasites and predators' B. Exp. 2.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-7	Eggs	102	0	102.0	560.0	5.49	0.0
12	Larvae I	102	3	100.5	458.0	4.49	2.9
20	Larvae II	99	3	97.5	357.5	3.61	3.0
27	Larvae III	96	22	85.0	260.0	2.71	2.3
36	Larvae IV	74	2	73.0	175.0	2.36	2.7
43	Pp + pupae	72	6	69.0	102.0	1.42	8.3
	Adults	66		33.0	33.0	0.50	0.0

Fertility table.

x	lx	mx	lxmx	xlxmx	r=0.07 e^{5-rx}lxmx	r=0.08 e^{5-rx}lxmx
0	1.000					
44	0.324	21.8	7.063	310.77	48.17	31.01
45	.324	20.7	6.707	301.82	42.66	27.23
46	.324	21.0	6.804	312.98	40.35	25.45
47	.324	17.1	5.540	260.38	30.64	19.17
48	.324	15.4	4.990	239.52	25.75	15.92
49	.324	8.2	2.657	130.19	12.78	7.81
50	.324	7.4	2.398	119.90	10.74	6.52
51	.324	4.3	1.393	71.04	5.82	3.50
52	.324	3.2	1.037	53.92	4.04	2.41
53	.324	2.1	0.680	35.36	2.47	1.46
54	.324	1.3	0.421	22.73	1.43	0.83
55	.324	0.5	0.162	8.91	0.51	0.29
57	.324	0.1	0.032	1.82	0.09	0.05
59	.324	0.1	0.032	1.89	0.08	0.04
		Ro= 39.916		1871.23	225.53	141.69

T = 46.879 r = 0.0786

$\sum e^{5-rx}$lxmx = 148.41 r = 0.0792 = 0.079

Appendix-Table 10.8.16 - Life-table. 'No parasites and predators' C. Exp. 2

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-7	Eggs	92	0	92.0	348.0	3.78	0.0
12	Larvae I	92	8	88.0	256.0	2.78	8.7
20	Larvae II	84	42	63.0	168.0	2.00	50.0
27	Larvae III	42	8	38.0	105.0	2.50	19.1
36	Larvae IV	34	8	30.0	67.0	1.97	23.5
43	Pp + pupae	26	3	24.5	37.0	1.42	11.5
	Adults	23		12.5	12.5	0.50	

Fertility table.

x	lx	mx	lxmx	xlxmx	4-rx	r=0.05 e^{4-rx}	e^{4-rx}lxmx	r=0.06 4-rx	e^{4-rx}	e^{4-rx}lxmx
0	1.000									
44	0.125	21.8	2.725	119.90	1.80	6.05	16.49	1.36	3.90	10.63
45	.125	20.7	2.588	116.46	1.75	5.75	14.88	1.30	3.67	9.50
46	.125	21.0	2.625	120.75	1.79	5.47	14.36	1.24	3.46	9.08
47	.125	17.1	2.138	100.49	1.65	5.21	11.14	1.18	3.25	6.95
48	.125	15.4	1.925	92.40	1.60	4.95	9.53	1.12	3.06	5.89
49	.125	8.2	1.025	50.23	1.55	4.71	4.83	1.06	2.89	2.96
50	.125	7.4	0.925	46.25	1.50	4.48	4.14	1.00	2.72	2.52
51	.125	4.3	0.538	27.44	1.45	4.26	2.29	0.94	2.56	1.38
52	.125	3.2	0.400	20.80	1.40	4.06	1.62	0.88	2.41	0.96
53	.125	2.1	0.263	13.94	1.35	3.86	1.02	0.82	2.27	0.60
54	.125	1.3	0.163	8.80	1.30	3.67	0.60	0.76	2.14	0.35
55	.125	0.5	0.063	3.47	1.25	3.49	0.22	0.70	2.01	0.13
57	.125	0.1	0.013	0.74	1.15	3.16	0.04	0.58	1.79	0.02
59	.125	0.1	0.013	0.77	1.05	2.86	0.04	0.46	1.58	0.02
		Ro = 15.404		722.44			81.20			50.99

T = 46.90 r = 0.0583

$\sum e^{4-rx}$ lxmx = 54.60 r = 0.0562 = 0.056

Appendix-Table 10.8.17. - Life-table. 'No parasites and predators' Total. Exp. 2.

x	Stage	lx	dx	Lx	Tx	ex	100 qx
0-7	Eggs	402	0	402.0	1816.0	4.52	0.0
12	Larvae I	402	39	382.5	1414.0	3.52	9.7
20	Larvae II	363	85	320.5	1031.5	2.85	23.4
27	Larvae III	278	32	262.0	711.0	2.56	11.5
36	Larvae IV	246	18	237.0	449.0	1.83	7.3
43	Pp + pupae	228	32	212.0	212.0	0.93	14.0
	Adults	196					

Fertility table.

x	lx	mx	lxmx	xlxmx	r=0.07 $e^{5-rx}lxmx$	r=0.08 $e^{5-rx}lxmx$
0	1.000					
44	0.246	21.8	5.363	235.97	36.58	23.54
45	.246	20.7	5.092	229.14	32.39	20.67
46	.246	21.0	5.166	237.64	30.63	19.32
47	.246	17.1	4.207	197.63	23.26	14.56
48	.246	15.4	3.788	181.82	19.55	12.08
49	.246	8.2	2.017	98.83	9.70	5.93
50	.246	7.4	1.820	91.00	8.15	4.95
51	.246	4.3	1.058	53.96	4.42	2.66
52	.246	3.2	0.787	40.92	3.07	1.83
53	.246	2.1	0.517	27.40	1.88	1.11
54	.246	1.3	0.320	17.28	1.08	0.63
55	.246	0.5	0.123	6.77	0.39	0.22
57	.246	0.1	0.025	1.43	0.07	0.11
59	.246	0.1	0.025	1.48	0.06	0.08
		Ro =	30.308	1421.27	171.23	107.69

T = 46.894 r = 0.0727

$\sum e^{5-rx}$ = 148.41 r = 0.07357 = <u>0.074</u>

Appendix-Table 10.8.18 - Life-tables. 'Controls'. Exp. 3

x	Stage	lx	dx	Lx	Tx	ex	100qx
	Plant A						
0-5	Eggs	169	0	169.0	316.5	1.87	0.0
12	Larvae I	169	133	102.5	147.5	0.87	78.7
19	Larvae II	36	16	28.0	45.0	1.25	44.4
26	Larvae III	20	15	12.5	17.0	0.85	75.0
36	Larvae IV	5	3	3.5	4.5	0.90	60.0
43	Pp + pupae	2	2	1.0	1.0	0.50	100.0
	Adults	0					
	Plant B						
0-5	Eggs	161	0	161.0	383.5	2.38	0.0
12	Larvae I	161	89	116.5	222.5	1.38	55.3
19	Larvae II	72	28	58.0	106.0	1.47	38.9
26	Larvae III	44	22	33.0	48.0	1.09	50.0
36	Larvae IV	22	18	13.0	15.0	0.68	81.8
43	Pp + pupae	4	4	2.0	2.0	0.50	100.0
	Adults	0					
	Plant C						
0-5	Eggs	151	0	151.0	421.5	2.79	0.0
12	Larvae I	151	71	115.5	270.5	1.79	47.0
19	Larvae II	80	6	77.0	155.0	1.94	7.5
26	Larvae III	74	42	53.0	78.0	1.05	56.8
36	Larvae IV	32	23	20.5	25.0	0.78	71.9
43	Pp + pupae	9	9	4.5	4.5	0.50	100.0
	Adults	0					

Appendix-Table 10.8.18. (contd.)

x	Stage	lx	dx	Lx	Tx	ex	100 qx
	Total						
0-5	Eggs	481	0	481.0	1121.5	2.33	0.0
12	Larvae I	481	293	334.5	640.5	1.33	60.9
19	Larvae II	188	50	163.0	306.0	1.63	26.6
26	Larvae III	138	79	98.5	143.0	1.04	57.3
36	Larvae IV	59	44	37.0	44.5	0.75	74.6
43	Pp + pupae	15	15	7.5	7.5	0.50	100.0
	Adults	0					

Appendix-Table 10.8.19. - Life-table. 'No parasites and predators' A. Exp. 3.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-5	Eggs	225	0	225.0	1373.5	6.10	0.0
12	Larvae I	225	2	224.0	1148.5	5.10	0.9
19	Larvae II	223	2	222.0	924.5	4.15	0.9
26	Larvae III	221	16	213.0	702.5	3.18	7.2
36	Larvae IV	205	9	200.5	489.5	2.39	4.4
42	Pp + puape	196	5	193.5	289.0	1.47	2.6
	Adults	191	0	95.5	95.5	0.50	0.0

Fertility table.

x	lx	mx	lxmx	xlxmx	r= 0.08 $e^{6-rx}lxmx$	r=0.09 $e^{6-rx}lxmx$
0	1.000					
44	0.424	21.8	9.243	406.69	110.36	71.08
45	.424	20.7	8.777	394.97	96.72	61.70
46	.424	21.0	8.904	409.58	90.55	57.25
47	.424	17.1	7.250	340.75	68.08	42.56
48	.424	15.4	6.530	313.44	56.62	35.07
49	.424	8.2	3.477	170.37	27.82	17.04
50	.424	7.4	3.138	156.90	23.19	14.06
51	.424	4.3	1.823	92.97	12.43	7.47
52	.424	3.2	1.357	70.56	8.55	5.08
53	.424	2.1	0.890	47.17	5.17	3.04
54	.424	1.3	0.551	29.75	2.96	1.72
55	.424	0.5	0.212	11.66	1.05	0.61
57	.424	0.1	0.042	2.39	0.18	0.10
59	.424	0.1	0.042	2.48	0.15	0.08
		Ro =	52.536	2449.68	503.83	316.86

T = 46.629 r = 0.0850

$\sum e^{6-rx}lxmx$ = 403.43 r = 0.08537 = 0.085

Appendix-Table 10.8.20 - Life-table. 'No parasites and predators' B.Exp 3.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-5	Eggs	345	0	345.0	2002.5	5.80	0.0
12	Larvae I	345	8	341.0	1657.5	4.80	2.3
19	Larvae II	337	11	331.5	1316.5	3.91	3.3
26	Larvae III	326	4	324.0	985.0	3.02	1.2
36	Larvae IV	322	8	318.0	661.0	2.05	2.5
43	Pp + pupae	314	28	300.0	343.0	1.09	8.9
	Adults	286	0	143.0	143.0	0.50	0.0

Fertility table.

x	lx	mx	lxmx	xlxmx	r=0.08 $e^{6-rx}lxmx$	r=0.09 $e^{6-rx}lxmx$
0	1.000					
44	0.414	21.8	9.025	397.10	107.76	69.40
45	.414	20.7	8.570	385.65	94.44	60.25
46	.414	21.0	8.694	399.92	88.42	55.90
47	.414	17.1	7.079	332.71	66.47	41.55
48	.414	15.4	6.376	306.05	55.28	34.24
49	.414	8.2	3.395	166.36	27.16	16.64
50	.414	7.4	3.064	153.20	22.64	13.73
51	.414	4.3	1.780	90.78	12.14	7.30
52	.414	3.2	1.325	68.90	8.35	4.96
53	.414	2.1	0.869	46.06	5.05	2.97
54	.414	1.3	0.538	29.05	2.89	1.68
55	.414	0.5	0.207	11.39	1.02	0.59
57	.414	0.1	0.041	2.34	0.17	0.10
59	.414	0.1	0.041	2.42	0.15	0.08
		Ro=	51.004	2391.93	491.94	309.39

T = 46.897 r = 0.0838

$\sum e^{6-rx}lxmx$ = 403.43 r = 0.0848 = 0.085

Appendix-Table 10.8.21. - Life-table. 'No parasites and predators' C. Exp 3.

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-5	Eggs	256	0	256.0	1574.0	6.15	0.0
12	Larvae I	256	2	255.0	1318.0	5.15	0.8
19	Larvae II	254	2	253.0	1063.0	4.19	0.8
26	Larvae III	252	8	248.0	810.0	3.21	3.2
36	Larvae IV	244	15	236.5	562.0	2.30	6.2
43	Pp + pupae	229	18	220.0	325.5	1.42	7.9
	Adults	211	0	105.5	105.5	0.50	0.0

Fertility table.

x	lx	mx	lxmx	xlxmx	e^{6-rx}lxmx (r=0.08)	e^{6-rx}lxmx (r=0.09)
0	1.000					
44	0.412	21.8	8.982	395.21	107.25	69.07
45	.412	20.7	8.528	383.76	93.98	59.95
46	.412	21.0	8.652	397.99	87.99	55.63
47	.412	17.1	7.045	311.12	66.15	41.35
48	.412	15.4	6.345	304.56	55.01	34.07
49	.412	8.2	3.378	165.52	27.02	16.55
50	.412	7.4	3.049	152.45	22.53	13.66
51	.412	4.3	1.772	90.37	12.09	7.27
52	.412	3.2	1.318	68.54	8.30	4.93
53	.412	2.1	0.865	45.85	5.03	2.96
54	.412	1.3	0.534	28.84	2.87	1.67
55	.412	0.5	0.206	11.33	1.02	0.59
57	.412	0.1	0.041	2.34	0.17	0.10
59	.412	0.1	0.041	2.42	0.15	0.09
		Ro =	50.866	2360.30	489.56	307.89

T = 46.402 r = 0.0847

$\sum e^{6-rx}lxmx$ = 403.43 r = 0.08474 = <u>0.085</u>

Appendix-Table 10.8.22.- Life-table. 'No parasites and predators' Total. Exp 3

x	Stage	lx	dx	Lx	Tx	ex	100qx
0-5	Eggs	826	0	826.0	5050.0	6.11	0.0
12	Larvae I	826	12	820.0	4224.0	5.11	1.5
19	Larvae II	814	15	806.5	3404.0	4.18	1.8
26	Larvae III	799	28	785.0	2597.5	3.25	3.5
36	Larvae IV	771	32	755.0	1812.5	2.35	4.2
43	Pp + pupae	739	51	713.5	1057.5	1.43	6.9
	Adults	688	0	344.0	344.0	0.50	0.0

Fertility table.

x	lx	mx	lxmx	xlxmx	$e^{6-rx}lxmx$ r=0.08	$e^{6-rx}lxmx$ r=0.09
0	1.000					
44	0.416	21.8	9.069	399.04	108.28	69.74
45	.416	20.7	8.611	387.50	94.89	60.54
46	.416	21.0	8.736	401.86	88.85	56.17
47	.416	17.1	7.114	334.36	66.80	41.76
48	.416	15.4	6.406	307.49	55.54	34.40
49	.416	8.2	3.411	167.14	27.29	16.71
50	.416	7.4	3.078	153.90	22.75	13.79
51	.416	4.3	1.789	91.24	12.20	7.33
52	.416	3.2	1.331	69.21	8.39	4.98
53	.416	2.1	0.874	46.32	5.08	2.99
54	.416	1.3	0.541	29.21	2.91	1.69
55	.416	0.5	0.208	11.44	1.03	0.59
57	.416	0.1	0.042	2.39	0.18	0.10
59	.416	0.1	0.042	2.48	0.15	0.08
		R_o =	51.252	2403.58	499.39	310.87

T = 46.897 r = 0.0839

$\sum e^{6-rx}lxmx$ = 403.43 r = 0.0851 = <u>0.085</u>

Appendix-Table 10.8.23. - Stable-age distribution table. 'No parasites and predators' Total. Exp 3.

Stage	x	Lx	rm(x+1)	$e^{rm(x+1)}$	$Lx\, e^{rm(x+1)}$	$100\beta\, Lxe^{rm(x+1)}$
Eggs	0	1.0000	0.085	0.91912	.91912	19.29
Larvae I	1	.9927	0.170	.84388	.83772	17.58
Larvae II	2	.9764	0.255	.77459	.75631	15.87
Larvae III	3	.9504	0.340	.71174	.67644	14.20
Larvae IV	4	.9140	0.425	.65350	.59730	12.53
Pp + pupae	5	.8638	0.510	.60060	.51880	10.89
Adults	6	.8329	0.595	.55157	.45940	9.64

$1/\beta = 4.76509$

$\beta = 0.20986$

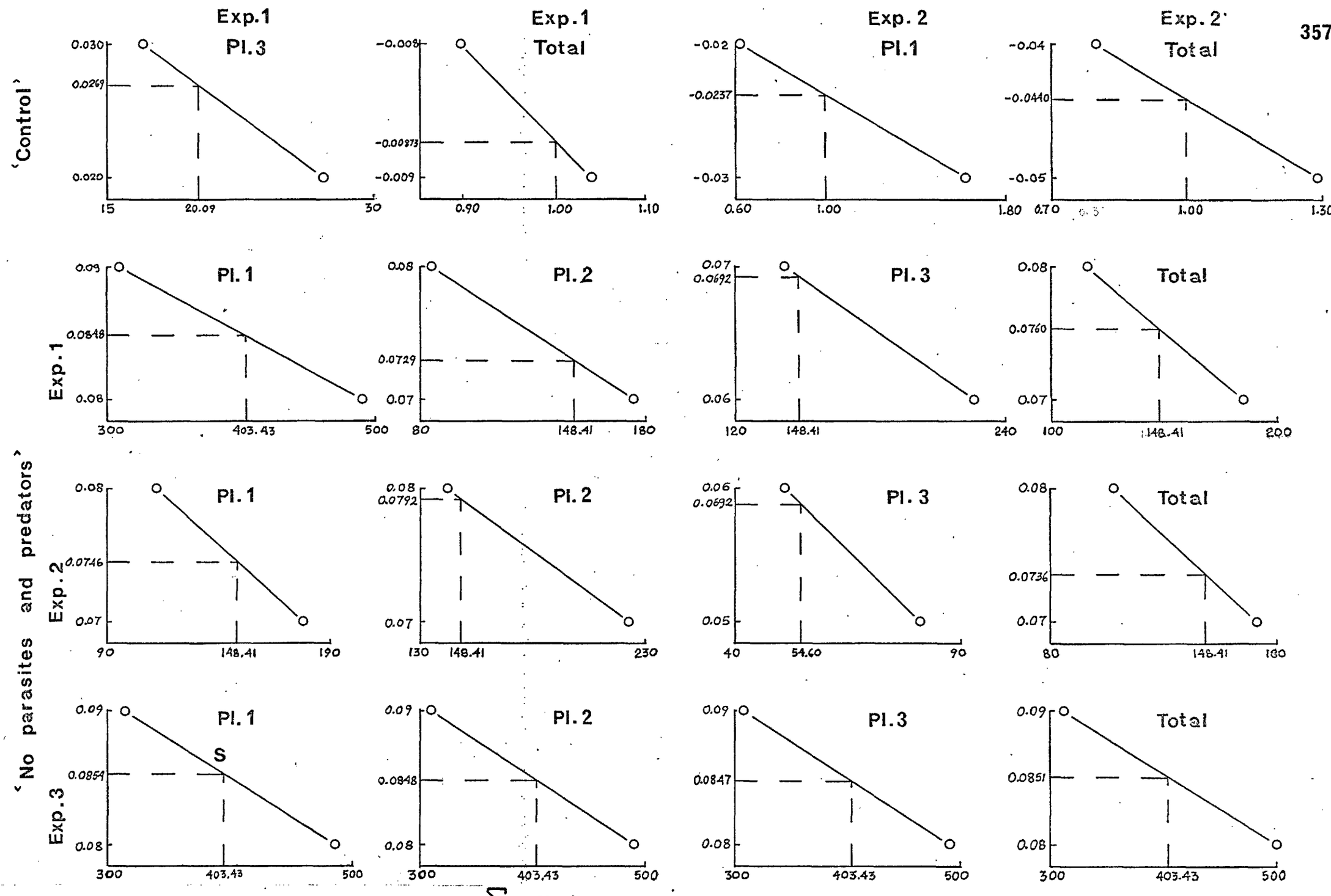


Fig.A.6. r determination by graphical method. $\sum e^{-r_x} l_x m_x$ (multiplied by e^{α}; 'α' variable in each case)