SOME ASPECTS OF THE BIOLOGY, POPULATION DYNAMICS AND ECONOMIC STATUS OF *WISEANA CERVINATA* (WALKER) (HEPIALIDAE : LEPIDOPTERA)

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INTRODUCTION

Entomology, like many other biological disciplines has developed into a quantitative science in nearly all aspects of the subject. Insect ecology is no exception, and in fact, has probably received more attention recently with the rapid development of insect population dynamics, the emergence of synecological studies, and the challenge such studies offer to statisticians and mathematicians. There is also a growing awareness of the significance and limitations of the environment in which insects play an important role. Searching questions are now being asked concerning the effect of insects and their control on man's existence (see Report of Environmental Pollution by the U.S.A. President's Science Advisory Committee 1965). The only universally meaningful way to attempt to answer these questions and to co-ordinate the work involved is, firstly, to quantify or measure the environmental parameters involved and, secondly, by their rational manipulation towards intelligent goals. The former is aptly described by Chant (1964) in relation to insect control, and the latter by Geier (1966).

With the current specific emphasis on costs of food production in New Zealand, insect ecological studies with an economic basis should be directed towards the provision of urgently required knowledge to help answer the following questions.

1. How much harm or benefit is brought about by both the direct and indirect actions of insects?
2. What are the various courses of action available to minimise the benefit of insects?
3. What are the costs involved in pursuing these aims?

The theme of this thesis is based on this ecological-economic cost benefit philosophy. Not only have various quantitative entomological tools been used, but economic principles have been included in a conceptual framework to study the ecology and economic status of the Wiseana cervinata (Walk.) complex in New Zealand. This pest and Costelytra zealandica (Wh.) are considered the two most important insect pests in New Zealand. As pastural farming has been, and will remain, the basis of this country's economic structure for some time, damage caused by these pests is of national and farm significance. This conclusion, together with recent political stimulus, prompted the demand for wider and urgent research on the control of porina and the associated costs.

Studies in porina population dynamics had been initiated as early as 1966 (Pottinger, 1967) but an epidemic population in 1967, coupled with the phasing out of D.D.T., increased the need for alternative control measures and greater understanding of the insect's behaviour.

Because of the urgency to obtain a practical and cheap method of porina control, and the preliminary nature of this

study, a broad based quantitative approach was used to develop meaningful but limited life tables. It was decided that such an approach would be best for a univoltine species and in view of the limited aims of the thesis it was not considered essential to develop complete and detailed life tables or to explore in depth all behavioural aspects of the insect. Instead, effort was concentrated into the study of those aspects which had some direct bearing on the practical and economic evaluation of the pest.

It was thought that porina was amenable to ecological studies using life table methods. Except for the egg and juvenile larval stages it has reasonably large larval and adult stages and is relatively easy to sample. Areas for study are not difficult to find, but the insect does have the disadvantage (for life table work) of being univoltine. This could be advantageous in that there are no overlapping populations.

The project briefly outlined below was designed to investigate the effect of porina populations on farm production and to study some aspects of the insect's ecology.

1. Development of sampling techniques for use in life table and other ecological studies.
2. (a) The study of the life cycle and natural history of the pest.
   (b) The development of life tables.
   (c) Economic assessment of the pest.
3. (a) Determination of the 'key mortality factors' regulating porina populations.

(b) The practical testing of 'key mortality factors' as a means of control.

4. The development of mathematical models leading to predictive equations and simulation studies.

CHAPTER 1

STUDY APPROACH AND TACTICS USED

The approach

In this thesis an ecological approach was used in an attempt to understand the regulatory processes involved in single insect species populations.

An insect pest is defined subjectively as "any insect causing displeasure to man". Economic entomology is thus defined as the work carried out on an insect pest population with the ultimate aim of reducing, maintaining, or managing that population below economic damaging threshold levels by the manipulation of various natural or artificial regulatory mechanisms responsible for pest population fluctuations.

For many years economic entomology both in New Zealand and overseas was concerned mainly with the testing and use of insecticides. The emphasis centred around the use of practical palliatives (Glen, 1951). The approach to pest control had long been the widespread acceptance of the concept of "100 percent mortality by poisons" (Ullyett, 1951).

Perhaps the greatest stimulus towards the development of a new approach was:

1. A need for better understanding of the effects of pesticides and biological agents on pest population fluctuations.
2. An equal need for meaningful ecological knowledge to clarify the various "a priori" arguments expounded by population theorists.

The need to know more about and explain pest population fluctuations has resulted in the development of a specialized type of entomology called population dynamics; this has particular applicability to economic entomology. It is debatable whether the authors of the various population theories actually contributed much to the tactics (Chant, 1964) involved in the study of population dynamics. They showed instead, that lack of adequate field data was possibly the sole reason why the concepts developed, and their practical application, were either biologically oversimplified or unrealistic. The conclusions reached were mostly no better than the basic assumptions (Harcourt, 1969) and the arguments at times became merely exercises in semantics. Nevertheless, some contribution to constructive entomological thinking stems from a basic assumption common to all population theorists, namely, that insect population levels do change and are probably controlled at some time by some factor in the whole ecosystem (Lawson, 1958).

This truism, although broad and functionally meaningless, is nevertheless very helpful in initiating a particular and more useful way of thinking in the minds of economic entomologists. Essentially their aim should be to find out,

using a scientific "a posteriori" approach, just which part or parts of the pest's ecosystem are important regulatory factors. It can be assumed that any factor within the pest ecosystem, be it density dependent or independent, biotic or abiotic, can act as a controlling mechanism at some time, in some place, on some pest populations. The implication behind this almost naive way of thinking is that in order to study and develop control measures for insect pests entomologists should approach the problem broadly! The pest should be viewed not as an isolated entomological phenomenon but as a product of its environment, including all major elements both biotic and abiotic. There seems to be a remarkable agreement on this principle (at least by implication) by nearly all major workers overseas, e.g. Morris (1963); Geier (1966); Pickett et al. (1946); Huffaker (1958); Harcourt (1969); Paradis and Le Roux (1964); Varley and Gradwell (1970) and Le Roux (1964a).

Although there appears to be agreement concerning the basic approach, the weight of opinion has had comparatively little influence on the approach used in present day economic entomology, especially in New Zealand. In a few places overseas, remarkable achievements have been made using the ecological approach, e.g. with spruce bud worm, Choristoneura fumiferana (Clem.) in Canada. In other countries, however, many talk about the necessity of trying to study the entire ecosystem but do little about it. Le Roux (1964a), Beirne (1962) and Chant (1964) have all noted this verbal hypocrisy and suggested various reasons for it. Both Beirne (1962) and Le Roux (1964a) suggested that the workers concerned

believed that the inherent complexity of pest population studies in relation to the whole ecosystem was so great as to make such studies impracticable. Furthermore, Le Roux (1964a) stated that a number of workers thought the time and manpower required for such fundamental studies was a limiting factor. However, he contended that these and other beliefs concerning logistics were erroneous. A further reason why economic entomologists did not attempt the apparently complex ecosystem studies was the tradition of most specialists not to favour the community or team idea in research (Chant, 1964). This isolationist attitude tends to be self destroying, especially when studying insect pests which live in a very broad and complex ecosystem not made up of insect pest problems alone.

The study of major pests may well demand a team approach, or, at the very least, a broad way of thinking by economic entomologists. This broad approach is most applicable to New Zealand's pest problems, particularly in farming. Essentially the New Zealand farm is an ecosystem, facets of which are utilized by the farmer to maximize production of food-stuffs. In such a multi-factor system, insect pests are only one aspect which has to be contended with and manipulated in relation to others. To enable the making of rational decisions within this pastoral farm system, understanding of the population dynamics and economics of insect pests is essential.

Furthermore, no one has really determined whether or not insects significantly affect overall farm profitability. Without this type of knowledge, decisions involving economics

of damage control cannot be made.

Aims and tactics

The discussion so far has centred around an approach to insect pest research, already well developed overseas, to show how it could be applied to the study of New Zealand insect pasture pests. The approach, although simple to understand, is seemingly difficult to apply in the field as a review of literature on overseas integrated control shows (Pickett, et al. 1946). It seems that the major barriers in studying insect population regulatory factors are:

1. Gathering the complex data required.
2. The way in which it should be gathered.
3. The analysis of the results obtained.

Part of the above problem is often aggravated by the aims of different workers.

There are three, and possibly more, aims an economic entomologist can have prior to initiating the actual study.

1. He may aim to detect 'key mortality factors' (Morris, 1957) in an "a posteriori" manner by fundamental long term population dynamic studies.

This implies a mostly academic outlook not too concerned with economic considerations. This aim is fundamentally sound, logical, and wholly creditable but, because of the time factor, is really more suited to the Class III and IV phytophagous insects as classified by Chant (1964).

2. He may have a more short term aim but still along the same basic lines as above, namely, of finding, relatively quickly, some mortality factor which, although not necessarily proven to be a 'key mortality factor', can nevertheless be more or less immediately applied to lessen the adverse effects of insect pest depradations.

This aim would be suited to the Class II pests described by Chant (1964) and to many types of integrated control studies. It is really a combination of an "a posteriori" and "a priori" approach.

3. Some entomologists have a more pragmatic view but again along basically similar lines as the previous aims Their outlook is closely aligned with thoughts concerning economic choice. Before initiating a detailed pest population study some attempt is made to assess just how much damage is caused by that pest. Following this damage evaluation, the data for a number of "pests" can then be critically examined, a decision made concerning research fund allocation, and further intensive studies later initiated on the most serious pest, to determine both long and short term controls. In practice, determination of economic damage parameters and the study of population mortalities should be contemporaneous, at least in the initial study period. Thereafter it is theoretically possible that the whole study is terminated if the economic data suggest another pest is more important. This type of outlook is most useful for studying Class I insects (Chant, 1964) and especially if the research area covers the habitat of a number of supposedly important insect pests.

It must be stressed that all the above aims embrace a common approach, namely the quantitative study of pest population fluctuations. The essential differences between them being

1. the practical necessity of discovering immediate control measures even if they are only short term palliatives;
2. the need for economic decisions concerning scarce research funds.

Once the basic study approach is accepted and the aim carefully considered, the next step concerns field tactics or the execution of a plan to obtain the information required. Generally, once an ecological approach has been decided upon the tactics follow; namely the development of sampling techniques and life tables. To show how life tables fit into research tactics the remainder of this review will take the form of a proposed pest research plan, based upon the third aim described previously.

Varley and Gradwell (1970) have already proposed a broad but limited research plan for the field study of insect populations. An amplification of their plan more applicable to a study of New Zealand agricultural pests could read as follows.

Stage 1

1. Identification of the insect concerned and a study of its life cycle and natural history.

2. Development of sampling and extraction techniques suitable for population enumeration.

3. The recording of census counts from which life tables can be derived.

4. The definition of economic damage parameters, and an assessment of the extent of population distribution and their densities. Surveys, which are a form of census count, are useful at this stage.

5. Analysis of economic data, together with provisional analysis of life table results gathered so far. It should be possible to determine at least a suspected 'key mortality factor' which could then be studied and field tested in the hope of providing a short term control measure.

The time involved for this stage of the plan would be approximately three to four years or at least three to four complete generations of the insect being studied.

Stage 2

1. Further gathering of census data and development of predictive mathematical population models.

2. The development of mathematically simulated ecosystems using computer techniques, with the aim of simulating situations which maximize agricultural production by minimizing the effect of the pest by various means.

3. The field testing of the knowledge obtained from both the predictive models and the simulated systems, with the aim of assessing the biological reality of both the original data and its subsequent analysis.

This plan, as outlined, looks overly simple and could be considered naive to experienced entomologists. There is the usual over-riding disadvantage if such an extensive plan is adopted, namely, that adequate research funds are seldom available. There is also the presumption that it can be executed in a practical manner. To the best of this author's knowledge, no published attempt has been made to detail a similar plan which is practical and which embodies both short and long term objectives. This would suggest that the plan as outlined is not applicable to modern economic entomological research, and that the general approach is more important. However, in spite of possible oversimplifications, the plan has advantages.

1. It assigns priority of study on the basis of an economic hierarchy of pest dominance in the agricultural ecosystem or 'agroecosystem'. Research personnel and facilities can thus be allocated on a rational basis and concentrated where needed.

2. The plan emphasizes the need to think beyond conventional bonds of pesticide use and even biological control, when attempting to solve problems dealing with pest control.

3. It stresses the need for the team approach and relegates the entomologist to just one member involved (albeit, perhaps the co-ordinating one) in the project.

4. The plan is flexible in that it can be used for studying chemical, biological and integrated types of control in such a manner as to allow comparisons between all these aspects of essentially the same problem. This would apply particularly to the gathering and subsequent analysis of results from insecticide trials which are usually conducted in a notoriously single-minded manner.

5. Attention is focused on the importance of the return to field conditions to test conclusions and mathematical models for biological meaning.

This thesis is an example of how such a plan could be applied to almost any insect study in New Zealand.

In the following sections it is proposed to review briefly the parts involved with Stage 1 of the research plan, emphasizing work carried out overseas and in New Zealand but highlighting those features having important implications in this thesis. For completeness some aspects of Stage 2 will also be discussed.

Insect identification

One of the earliest forms of entomological research was species identification and the study of life cycles. The early entomological literature contains many examples of this qualitative taxonomic work (Hudson, 1928). Mostly

the work consisted of written descriptions of morphological characters. Generally the descriptions were reasonably accurate, although in some species excessive variation caused confusion both to the taxonomist and later the population ecologist. For example, some Wiseana species are physiologically variable, to the extent that they are still causing confusion (Dumbleton, 1966 and Dugdale, 1969). The importance of correct identification prior to the commencement of any population dynamics study cannot be overstressed. It is especially important, if an entomologist is dealing with a number of insect populations having rather similar ecological niches (Pottinger and Le Roux, 1971).

This problem of insect identification is not great in agricultural ecosystems (agroecosystems) particularly in large monocultures such as forests, crops and some types of New Zealand pasture. Usually these large agroecosystems contain a few common or major damaging species (pests) and numerous relatively rare or minor species (Le Roux, 1964a). In New Zealand there are about six pasture pests considered of major significance. In any particular area, however, usually only one predominates. The fact, however, that there is considerable variation within some Wiseana species (Dumbleton, 1966) emphasizes the importance of careful taxonomic work in the initial stages of any ecological study carried out over a wide area.

Faulty pest identification must mean faulty sampling, no matter how precise. Misinterpretation of census data inevitably follows.

A good field taxonomist can also materially assist in

the interpretation of mortality factors, especially if parasites or predators are involved. He could also help define the pest's geographical boundaries. The economic entomologist needs this type of information to help determine the pest's economic importance as well as to assist in the interpretation of mortality data, especially if the latter is obtained from different areas.

Natural history

Having correctly identified the insect pest, detailed knowledge on its life cycle and general ecology is required for the following.

1. To help design suitable techniques for later census counts.

2. To determine the correct timing for sampling various stages of the pest's life cycle.

Prior to all pest population studies, bionomic information can be obtained from published literature (Morris, 1963 and Pottinger, 1964).

The following details are required to assist organisation and interpretation of life table information.

1. Adult flight behaviour.
2. Adult longevity and fecundity.
3. Oviposition behaviour.
4. Number of instars and duration of each stage.
5. Physical ecology of early stages, i.e. egg, and juvenile larval stages.

6. General behaviour of instars, e.g. habitat preference and host preference.

7. Identification of parasites, predators and pathogens.

8. Observations of climatic and geographical variations.

Once the entomologist has obtained this knowledge and has had at least some time in the field making his own observations, the next step is consideration and execution of sampling procedures.

Sampling insect populations

Many books both in part and whole have been devoted to the principles and methods of this very wide subject, (Cochran, 1953; Allee *et al.*, 1949; Andrewartha and Birch 1954; Odum, 1954; Southwood, 1966). To keep within the limits of the approach and the aims of this thesis the following dissertation will be confined to those aspects concerned with the development of life tables and economic assessment of pest damage.

Population sampling programmes have been designed for many different purposes ranging from extensive surveys assessing provincial damage to intensive population dynamics studies on a small plot or two. This distinction, although useful insofar as determination of sampling design is concerned, is by no means categorical. The basic principles regarding frequency distribution, major sources of variance and optimal sample size and number are applicable to both

types of programmes. For example the results obtained from the intensive sampling of Choristoneura fumiferana were equally useful in designing sequential sampling plans to assist surveys of hundreds of square miles of forest (Morris, 1955).

In his comprehensive review on sampling insect populations, Morris (1960) also proposed a number of criteria concerning definition of objectives with respect to the type of intensive or extensive census count required. He stressed that sampling in itself has no intrinsic value but is merely an entomological tool. Nevertheless, workers involved in economic insect pest studies usually have two objectives in mind requiring different types of census counts; namely the detection of 'key mortality factors' and/or assessment of damage. It is preferable if the sampling methods are applicable to both as it is better work efficiency. For example the Canadian School of Insect Population Dynamics has suggested (and used) a 10 per cent standard error of the mean as being a statistically acceptable level of precision for measuring insect populations. A similar statistical criterion could be used for determining economic damage, as well as for distribution surveys. In practice this might be difficult to achieve, especially if dissimilar sampling methods have to be used. In fact, Morris (1955) has stated that, "trial and error play(ed) a much larger part in the development of the (sampling) techniques than might be supposed" (from his presentation). This is not surprising, considering the range and variety of environments in which

insect pests can exist. Nevertheless certain basic sampling principles must be considered. These are best described in a flow type diagram (Fig. 1). In practice the order as shown is not necessarily binding. In fact, in many projects various steps are inapplicable. To observe how various workers developed specific sampling techniques for different environments, the following authors merit study. Morris (1955) for forest insects; Harcourt (1961, 1962) for horticultural insects; Le Roux and Reimer (1959) for orchard pests; and Strickland (1961) for crop pests.

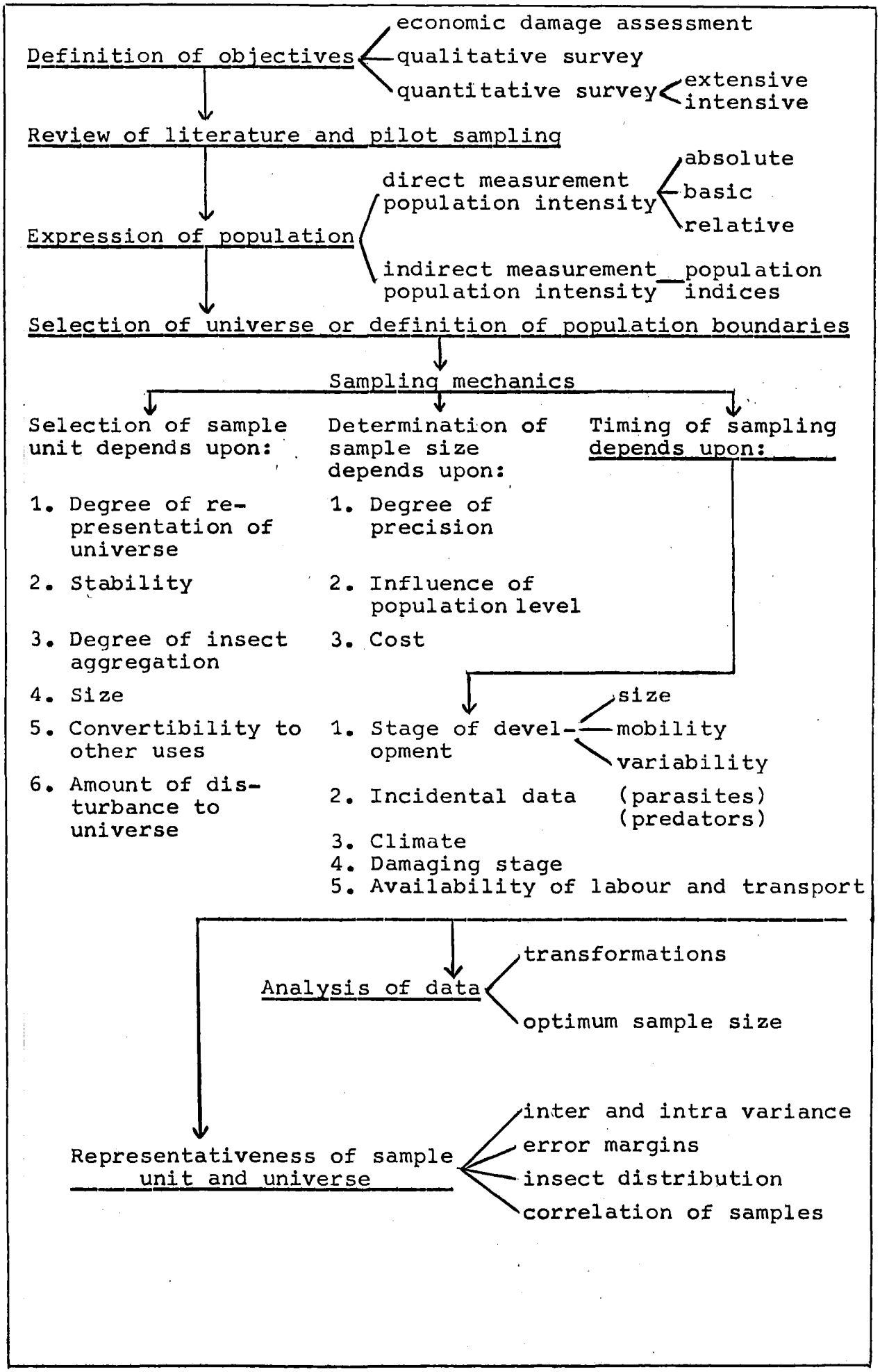
Pottinger (1967) has summarized most of the sampling criterion incorporated in the above studies. Details on extensive survey type sampling are covered by Cochran (1953) and Hanson et al. (1953).

Life tables

Once sampling techniques have been developed and tested, which is sometimes a difficult and lengthy task especially with highly aggregated populations, the taking of systematic census counts follows. Although pest control objectives differ, it is helpful to consider that distribution surveys as well as life tables are forms of census counts and hence subject directly or indirectly to certain principles common to all pest control programmes. For example, no control measures should be undertaken against a pest unless it is known to be actually present and in sufficient numbers to cause economic loss.

The former is concerned with precise enumeration of the

Fig. I Suggested steps in the form of a flow diagram for a sampling programme for the study of insect pest populations



pest during its damaging period and if possible, prediction in enough time for control. The latter involves the study of economic damage parameters as well as actual insect counts.

In general, survey type census counts are usually carried out to determine population densities of spatially discreet pests and to assess the extent of damage. Usually these surveys are specialized forms of insect counts requiring specific sampling techniques and differing for each insect surveyed.

An important type of census count is that taken to develop life tables. This entomological tool is a device adopted by Morris and Miller (1954) from life table concepts applied elsewhere (Cole, 1957). Life tables, as used by Morris and Miller, record in a systematic fashion those facts basic to the age distribution of insect mortality. A life table in other words "keeps the books on insect death and survival." Hence, where life tables differ from other census counts is in their temporal continuity and fundamental usefulness for helping to predict pest population levels.

Aims of life tables

Life tables were developed to obtain the following knowledge.

1. The amount of mortality occurring within and between pest generations.
2. The amount of significant variable mortality occurring over this period.

3. The effect of variable environmental factors on survival.

This fundamental information is the foundation of insect population dynamics generally, and more specifically is used to develop predictive systems for insect damage.

General structure of life tables

Deevey (1947) has said that "a life table is a concise summary of certain vital statistics of a population", obtained by either of the following.

1. Periodic census counts of the same population throughout a generation but not necessarily of the same individuals or

2. Counts of the same individuals.

The latter is more desirable but has limited application in insect studies. In fact, the structure of insect life tables differs considerably from those developed for mammals, in the following ways.

1. There is greater emphasis on the cause of mortality than the order of dying.

2. Major insect stages, viz. eggs, larval instars, pupae and adults are used, rather than equal age intervals

3. Actual population figures are used to show the changes in population density from generation to generation.

4. The periodic sampling of the same population throughout a generation is used rather than counting the same individuals.

5. The concept of mortality is broadened to include apparent mortalities caused by the following.

(a) Unequal sex ratios.

(b) Loss of fecundity due to reduced female body size, and mating behaviour.

(c) Premature deaths of females.

6. The concept of an index of population trend (I) as devised by Balch and Bird (1944) is used as a quick and simple method of determining population changes between generations.

Detailed structure of life tables

The clearest and most detailed example of life table structure is given by Pottinger (1967) for L. blancardella Fabr. Harcourt (1969) also gives the detailed structure of a life table for the third generation of the diamond-black moth P. maculipennis Curt. In both examples, explanation of the various columns is given, although Pottinger gives more detail with regard to adult migration and expression of the index of population trend. This vital index is calculated from egg counts sampled in one generation and compared with the previous. The other fundamental term used is the constant mortality rate (C.M.R.) which is used as the base upon which the importance of variable mortalities is assessed. This type of analysis, however, can only be carried out when a number

of tables have been developed.

To develop meaningful life tables a thorough knowledge of the insect life history is required. This assists the following.

1. The evaluation of the statistical and biological significance of the results.

2. Enables all stages of the insect population to be sampled at the correct time.

3. Assists development of the correct mechanical sampling techniques.

The analysis of life table data

Interpretation of mortality

Most economic entomologists in the past have expressed mortality figures as percentages, assuming that high percentage mortalities indicate important mortalities and vice versa. This assumption, although of limited usefulness for such comparative work as insecticide trials, is at best misleading in population dynamics and at the worst, quite erroneous. Morris (1957) in his now classic article on the interpretation of mortality data, has written that, "it is only after very careful interpretation that mortality data (can) begin to serve a useful purpose by helping us to understand the fascinating problem of animal numbers".

He then goes on to discuss at some length the interpretation of life table measurements, his objective being the explanation of temporal and spatial population changes. His article has been summarized by Pottinger (1967). Briefly,

what both authors attempted to show is the importance of variable and sometimes small insect mortalities on the index of population trend or generation change, and the measurement of the variability around the C.M.R. The two types of variable mortality were discussed, one being sequential mortality which has important economic control implications, and the other contemporaneous mortality which has more direct bearing on actual generation changes.

Key mortality factors

Morris (1959) introduced the term "key factor" for mortality factors which cause a variable mortality and appear to be significantly responsible for the observed changes in population densities in successive generations. Key mortality factors can best be found and understood by using a series of life tables, for at least a rise and fall of a pest infestation. Temporal and spatial replication is essential. The former is sometimes lacking. Varley and Gradwell (1970) have stressed the importance of temporal continuity and criticized Morris's work on Choristoneura fumiferana in this respect. Morris (1963) did, in fact, concede in his study that, "it may be profitable to study intensively on a few plots the age specific survivals and mortality factors that determine temporal population changes."

In the initial analysis for key mortality factors, both Morris (1959) and Watt (1963) made use of the index of population trend (I) and the survival ratios of each age interval, by assuming I as a dependent variable of the supposedly independent survival components and combining all

in a single linear correlation. Varley and Gradwell (1970) have criticized this approach on both biological and mathematical grounds. They preferred the more biologically meaningful approach of formulating independent sub-models for each age interval and later combining these in such a way as to show the effect of age interval changes on generation numbers. They also suggested that the initial stage of the analysis could even be visual, using graphs of k values rather than a complicated regression technique. Nevertheless both methods are probably acceptable to most economic entomologists, provided the predictive value of the key mortality factor was field tested and found to have practical implications. It is relatively immaterial when considering the complexity of the pest's ecosystem, whether the key factor is a statistical or truly causal relationship. This applies particularly in the early stages of a pest control programme, where some palliative control measure is urgently required regardless of sound statistical proof. For all long term population studies, however, the causal biological relationship must be aimed for, if full understanding and accurate prediction of population changes is to be achieved.

Whichever method of analysis is used, both have limitations which must be fully realised. The essentially statistical method used by Morris (1959) and Watt (1963), by definition, must produce a formula of some description. However, the production of that formula is no indication of a causal relationship.

On the other hand it would be impossible, at least in the early stages, to measure all variables in the ecosystem which

influence pest populations. Therefore the success of the sub-model method of Varley and Gradwell (1970) will depend upon operative chosen variables. The onus of choosing the most important variable thus rests on certain "hunches" or inspired guesses by the entomologist. The dangers of this are obvious.

The advantages and disadvantages of the use of life tables

Advantages

The results of life table studies on pest populations can have practical application in the following ways.

1. Feedback of information on economic damage thresholds of a pest.

2. The information obtained may be very useful for improving integrated pest management practices

The basic and most important use of life tables, however, is centred around the fact that insect population numbers change from generation to generation and that economic entomologists must be able to predict these changes. Life tables provide the conceptual framework around which this can be done. Furthermore, the structure of life tables demands that entomologists work in a disciplined scientifically inductive manner and discard pre-conceived ideas on what causes population changes. This type of work pattern helps negate any tendencies towards 'ad hoc' pest control research.

Life tables can be used to compare various types of

pest environments in order to determine economic damage differences. For example, the host plant, soil and climatic differences acting upon a widely distributed pest, such as grass grub in New Zealand, can really only be scientifically evaluated and understood by developing a number of spatially replicated life tables. The economic significance of variable temporal and spatial survival is obvious.

Finally, in addition to determining pest population regulatory mechanisms, the development of life tables presupposes prior accumulation of knowledge on the natural history and instar behaviour. This information when used with mortality data is the only way to 'pest management', as described by Geier (1966). Without this knowledge, future pest control measures will be at best palliative, and at worst environmentally destructive.

Disadvantages

Many entomologists have been, and still are, apprehensive when contemplating both long and short term, broad based ecological approaches to control pest populations. Le Roux (1964b) and others have supplied reasons for this attitude, which is centred around the complexity of ecological studies and problems of logistics. In practice, life table development does have certain logistic disadvantages, particularly if the study areas are widely separated or are difficult to reach. Univoltine pests markedly increase the time required to gather meaningful mortality data, while the study of univoltine subterranean insects further complicates the issue.

Nevertheless, considering the vast amount of "ad hoc"

entomological research carried out to date and comparing the effort with the relatively meagre and mostly ecologically void information acquired (Geier and Clark, 1961) life table work is more valuable. The fact that excellent life table studies have already been carried out, albeit at times well organized and hence costly, with outstanding success, corroborates Le Roux's (1964) ecological and logistic contentions.

Lastly, life tables have an unfortunate disadvantage, mainly brought about by human impatience. By definition life table studies are essentially long term. On the other hand, political pressures often dictate that a means of controlling pests be found quickly. It is thought that adherence to life table study methods could result in reduced appropriation of research funds if no answer is immediately forthcoming. This attitude is, of course, extremely short-sighted and scientifically disheartening. Many administrators do not realize that life table studies can quickly provide knowledge within two or three years, that can be used in a practical control programme. The work by Le Roux *et al.* (1963) on *Spilonota ocellana* (D. and S.) is a good example. Generally the attitude can be overcome by a careful compromise between long term research and short term needs for palliatives, in which life tables can serve the dual purpose. This present study is an example of this type of compromise.

Examples of life table studies

Perhaps the best known example of the ecological life table approach is the Green River Valley project in New Brunswick, initiated by Morris and co-workers in 1944-45 on the spruce budworm. This study showed how climatic conditions affected spruce budworm epidemics and the influence of chemical control. This and other valuable information on spruce budworm epidemic population dynamics, biology, behaviour and natural history have been published in a memoir of the Entomological Society of Canada (Morris, 1963) and is a very useful practical reference for other workers contemplating using life tables.

Although the Green River Valley project was the first serious attempt at understanding pest population changes, there have been relatively few similar studies since. The project was initiated in 1945 and since then only about 20 other insect populations have been studied using the multi-factor approach (Harcourt, 1969). The "universe" of these projects ranged from orchards to rice paddies and bogs and included many horticultural crops. Some of these studies provided information which proved of immediate benefit (Le Roux et al. 1963) while other more long term studies pointed to potentially important key mortality factors. For example, of eleven Canadian insect populations studied three were regulated by climatic key factors, and six were regulated by parasitic or predatious key factors (Anon, 1969). The practical application of the information obtained from such studies has already been mentioned. Of more importance,

however, is the potential manipulation of pest populations made possible by recognition of key factors. This type of control used with other appropriate ecological knowledge should help solve problems already employing many nonsensical unenlightened and environmental polluting methods and must have profound implications for pest control of the future.

The future

The study of pest populations does not necessarily end with the development of life tables and determination of key factors. As emphasized elsewhere, life tables are merely entomological tools used for quantifying certain environmental factors significantly influencing pest populations. One of the fundamental aims of economic entomologists is to be able to predict pest outbreaks. Therefore the future of pest population dynamics centres around the development of predictive mathematical models and computer simulation. The aim of using such mathematical techniques is the expression, in a dynamic and wholly quantitative manner, of the insect's complete ecosystem and the controlling forces involved.

It is accepted that the insect's environment is very complex, and that to quantify and understand it, mathematical techniques must be used. Without mathematics we can scarcely begin to think about entities that have more than a few variables. Biological mathematical models are really mathematical statements that make biological sense. Based on life table data and associated key factor analysis they can be used to facilitate the following.

1. Predict pest population density at least one generation in advance and probably more.

2. Assess the degree of interaction of mortality factors within and between stages of a pest species and determine their effects on population trend.

3. Help to develop and test pest control tactics which could lead to new strategical concepts for pest control.

This last point refers mainly to computer simulation as a very useful adjunct to pest population research. It is one way of handling and testing environmental measurements without undue cost. Using the large modern computers now available, both hypothetical and real situations pertaining to insect control and the economics thereof, can be simulated and numerous variables tested without moving out of the laboratory. Watt (1964) has called this type of computer experimentation, "strategy evaluation simulation". The techniques, although new to entomology, have already played important roles in such diverse areas as rocket design, urban and airport traffic control. The fundamental importance of computer experimentation is that it is a self-teaching device. By starting with a programme of simple mathematical models and comparing discrepancies between the real and model system, a more biologically meaningful model is finally evolved. Thus clarification and fuller understanding of a particular biological phenomenon can be achieved with a minimum amount of further field experimentation.

It is obvious how the application of this technique to test population theories could bring them to a new conceptual strength. Its application to economic entomology and the determination of optimum control measures is also challenging and stimulating.

One of the main problems, however, is lack of adequate and precise field information. Watt (1964) nevertheless developed a computer programme and using what he termed, "scanty data" simulated insect pest population fluctuations and then evaluated various pest control strategies and the economics involved. Another well known example of this futuristic economic entomology is the predator model developed by Holling (1963 and 1964). He showed, by using "computer feedback", that this type of study yielded extensive knowledge on how certain population regulatory mechanisms worked.

Generally, however, such examples are rare and unfortunately it will be some years before enough of the right sort of information is obtained for this type of research to have any real influence on pest control strategy.

ECONOMIC ASSESSMENT OF INSECT DAMAGE

Chant (1964) has defined insect pests as any insect causing displeasure to man. This definition is subjective and unscientific, as no relative idea of actual harm is implied. Almost all insects at some time could be "pests". It is, however, a fact that insects compete with man for food, transmit disease and destroy property. It is also a fact that very little quantitative data on the amount of loss has

been published other than on one or two major insect pests such as malaria transmitting mosquitos and locusts. This is rather surprising when damage estimates should be mandatory for the following reasons.

1. When faced with the prospect of loss from insect damage the modern producer needs to know whether the potential loss will be larger than the cost of control and approximately the difference. This applies particularly to New Zealand farming where escalating costs of food production are seriously reducing profit margins.

2. Entomological research funds in New Zealand and elsewhere are nearly always limited. This means decisions on research priorities are always necessary. The only rational way of assessing these is to have some form of economic assessment for a number of insect pests within a research area. This would enable costly entomological studies to be carried out in order of importance. Chant (1964) implied this research fund allocation concept when he stated that the first step in evolving the solution to an insect problem is, "recognition and assessment of the importance of the problem".

There are very few good examples of insect pest assessments in the literature. A singularly good one is by Bullen (1966) on locusts and grasshoppers. In his paper he shows how a knowledge of food consumption of the desert locust, Schistoceria gregaria (L.) was obtained and related to such things as fluctuations in population size, type of food, time

of defoliation, food preferences and the effects these have on the human economy. A crop vulnerability index (C.V.I.) was developed which represented the relative change in profitability of a particular crop in a defined area when locust damage occurred. C.V.I. values for cotton damaged by the locust were plotted on a map of India and Pakistan using "degree squares" as the geographical unit. The maps were then used to define areas where intense local control was essential and to aid control planning. This type of damage assessment, or any other, is lacking in New Zealand even for the major pests, such as grassgrub and porina. What little damage assessment has been carried out has usually been parochial and based on a limited number of measurements (Kelsey, 1970).

Even during the detailed study of the population dynamics of the spruce budworm Morris (1963) failed to show conclusively the potential or actual damage, both spatial and temporal, on either individually owned forests or on the national economy.

Much of the paucity of economic damage information has been due in the past to the widespread use of cheap and effective insecticides such as D.D.T. In recent years, however, rigid residual standards in foodstuffs have been legislated. This, plus pollution problems, now makes it imperative that the economics of pest management, chemical or otherwise, be fully known.

The importance of sound economic assessments of pest damage is well illustrated in a country like New Zealand which spends approximately one per cent of the Gross National Product on all forms of research and only about $80 - $100 thousand annually on pasture pest research. This money is

supposed to cover research for a number of pasture pests. These would include grassgrub (Costelytra zealandica) Tasmanian grassgrub (Aphodius howitti Hope), porina (Wiseana spp.), Argentine stem weevil (Hyperodies bonariensis Kusch.) black beetle (Heteronychus arator (F.), soldier fly (Inopus rubriceps (Macq.) and white fringed weevil (Graphognathus leucoloma Boh.) to mention a few. These insects all cause various amounts of damage but other than limited measurements on damage caused by grassgrub (Kelsey, 1970) and Argentine stem weevil (Pottinger, 1961) no-one knows the real effect these "pests" have on farming profitability or the national economy. In other words, the economic entomologist could not decide, on a cost/benefit basis, which insects warrant his limited time and energy. In practice the decision is made for him by administrators who are sometimes influenced by political pressures.

It is disappointing that short term conservative research policies are still common in a number of entomological research institutions today. In many cases decisions on research policy are made subjectively rather than by an inductive process. To overcome this it is suggested that more consideration be given to Chant's (1964) three point plan which provides a conceptual framework for solving insect problems.

1. Recognition and assessment of the importance of problem.

2. Development of a quick and effective palliative to prevent damage.

3. Solution of the problem through long term research on population dynamics.

Pest research in New Zealand appears to have missed the first stage, become mired in the second and is only just entering the third.

In conclusion, there appears to be a necessity, especially in New Zealand, for a more balanced pest research policy consisting of economic assessments of damage coupled with studies on mortality data, and much less palliative insecticide research. It is only after the former types of knowledge are collected and collated for a number of pests that future pest control research can be scientifically administrated in New Zealand.

CHAPTER 2

REVIEW OF THE LITERATURE ON PORINA

The classification of *Wiseana* spp. is as follows.

Order Lepidoptera
Family Hepialidae
Genus *Wiseana* (syn. = *Porina*, *Oxycanus*)

Probably the first detailed record of a species of the genus *Wiseana* in New Zealand was made by Quail (1900), who gave some information on what was known at the time as *Porina cervinata* and *Porina umbraculata*. He recorded that eggs of *P. cervinata* took approximately 22-30 days to hatch under normal laboratory conditions.

Since this early record, the literature on the ecology of this supposedly important pasture pest is meagre. Of the 40 papers published up till 1966, only 14 were along either taxonomic or general ecological lines (Table 1). The remainder dealt almost wholly with insecticide trials. This indicates the unbalanced research carried out up till that time.

In fairness, however, it was probable that all insect damaged pasture in New Zealand, and particularly in Canterbury

Table 1 A summary of the literature on the genus Wiseana in New Zealand

Subject matter				
Mainly chemical testing and recommendations		Mainly ecological (ecol.) bionomic (bio.) economic (eco.) taxonomic (tax.) identification (iden.)		
Author	Year	Author	Specific subject matter	Year
		Quail	tax.	1900
		Cockayne	iden.	1915
		Miller	bio.	1929
		Gourlay	ecol.	1930
Greenall	1940			
Dumbleton et.al.	1941			
Dumbleton et.al.	1941			
Dumbleton	1943			
Anon	1943			
Dumbleton et.al.	1944			
		Dumbleton	ecol.	1945
		Dick	ecol.	1945
Bates	1946			
Dumbleton et.al.	1948			
Sydenham	1948			
Kelsey et.al.	1949	Dumbleton	ecol.	1949
Kelsey et.al.	1950			
Kelsey	1950			
Doull	1951	Doull	iden.	1951
Kelsey	1953			
Kelsey	1955			
Kelsey	1959			
		Cottier	bio.	1962
		Gaskin	ecol.	1963
Helson	1964	Taylor		1964
Kelsey	1964			
Kelsey	1965	Eyles	ecol.	1965
Arthur et.al.	1965			
Christie	1965			

Cont.

Table 1 cont.

Mainly chemical testing and recommendations		Mainly ecological (ecol.) bionomic (bio.) economic (eco.) taxonomic (tax.) identification (iden.)		
Author	Year	Author	Specific subject matter	Year
Cassels	1966	Arthur	ecol.	1966
Kelsey	1966	Eyles	ecol.	1966
Lowe	1966			
Perrott	1966			
Patterson	1966			
Taylor	1966			
		Waller	bio.	1967
Maclean	1968	Pottinger	ecol. bio.	1968
Rough	1968	Power	bio.	1968
Allen	1968	Rastrick et.al.	eco.	1968
		Waller	ecol.	1968
		Waller	ecol.	1968
		Waller	tax.	1968
		McLaren & Crump	eco.	1969
		Harris	ecol.	1969
		French	ecol.	1969
		Fenemore et.al.	ecol.	1969
Taylor	1970	Esson	ecol.	1970
Upritchard	1970	Perrott	bio.	1970
		Helson	ecol.	1970
		Wood	ecol.	1970
		Moore	ecol.	1972
		Kelly	ecol.	1971

and Otago, was generally attributed to "the grass grub", Costelytra zealandica then known as Odontria zealandica. From about 1940 onwards more farmers learned to distinguish between the two pests and considered their relative importance (Dumbleton and Dick, 1941a).

It was also at this time (supposedly under farmer group pressure) that entomologists were asked to investigate a situation that was now beginning to noticeably affect farmer livelihood. This resulted in an example of palliative pest research, i.e., the use of chemicals to provide a quick answer to a pressing problem (Dumbleton and Dick, 1941a,b, and 1944). The first paper by Dumbleton and Dick (1941a) showed that "Paris green" applied in various forms was effective against porina populations. The second paper by Dumbleton and Dick (1941b) although essentially similar to the first did contain what later proved to be very significant ecological observations. They found,

1. that larvae moult approximately eight-nine times during their life history.

2. that up to 20 per cent of a population did not feed for several days over any given period.

They deduced that the latter was responsible for the incomplete destruction of a population treated with"Paris green". Mortality, brought about by larval overcrowding was also discussed, together with other possible population mortality factors such as flooding. Larval head width measurements were given which indicated an exponential growth phase during

February, March and April in Canterbury.

The third and final paper in this series (Dumbleton and Dick, 1944) contained some very important ecological information. If a research programme had been developed at this stage, based on the field of inquiry initiated by Dumbleton and Dick in 1940 it could have, in effect, pre-dated the present study. Indeed, the heading of some sections of these papers ("Seasonal Variations in Population Density") implies a population dynamics philosophy. The authors, in fact, supply population density measurements which show a larval mortality of up to 80 per cent over the Autumn-Winter period. They thought that this mortality was brought about by factors such as starvation at the higher densities, together with adverse climatic conditions, predators, parasites and diseases.

In the latter part of the paper a very clear and mostly accurate picture of some aspects of porina ecology is given. The authors believed that porina populations probably required a two-three year period to reach an economically damaging status. They therefore recommended that pasture be chemically treated in the second year of noticeable damage, working on the assumption that a serious infestation developed from the preceding light one. They emphasized the importance of pasture management as having a controlling influence on juvenile larval survival. They also considered that the cover, provided by crops of ryegrass and clover shut up for seed in early spring, provided a more favourable microclimate for juvenile larval survival than close grazed pasture. After detailing a very interesting example of different grazing

management systems resulting in two markedly distinct infestation levels in the one paddock, they concluded this particular section by stating

"It is the conditions following the laying of eggs, say in October/November until January, that are critical in determining caterpillar mortality".

Therein lies the thesis for this present study.

The final part of this section in their paper briefly relates the authors' first thoughts about the influence of rainfall and evaporation on surface dwelling larval mortality, using as an example an outbreak of porina in Canterbury in 1937. Soil type and fertiliser effects were also discussed, but more in relation to their direct effect on pasture production than on larval mortality.

Following this period during which mainly chemical investigations were carried out, two papers were published dealing solely with ecological aspects of what was then known as Oxycanus spp. These two papers (Dumbleton, 1945 and Dick, 1945) have been the only meaningful ecological and biological studies on porina published up until the 1970's.

Dick (1945) observed moth emergence, mating, flight and oviposition of Wiseana cervinata. Using light traps, he noted an apparent relationship between evening weather conditions, moth flight and emergence. Wind speed and soil temperatures were considered the most significant factors. Flight commenced about 7 p.m. with a brief male flight followed by a longer female one. Egg deposition commenced soon after mating and usually quite close to the point of eclosion.

As the female laid eggs and became lighter, longer and higher flights became possible. It was thought that moths could fly considerable distances after laying a number of eggs. It was, however, found that the majority of female moths did not seem to migrate out of the field in which they emerged. This corroborated an earlier observation by Dumbleton and Dick (1941b) concerning small, insignificant populations building up to damaging ones after two-three seasons.

Dumbleton (1945) gave very useful information on egg incubation periods, together with the effects of varying physical conditions on both egg and juvenile larval stages. He also confirmed Dick's (1945) observations on eclosion, adult emergence and flight and noted that peak moth flights and later larval damage occurred earlier in the North Island than in the South Island. He calculated the upper lethal constant temperature for eggs to be about 25°C and below 29°C, the lower lethal constant temperature being 6.5°C. He observed that eggs developed most rapidly and with least mortality in a saturated atmosphere. This, in effect, quantified an earlier important observation concerning field conditions during egg laying (Dumbleton and Dick, 1944).

Following this section Dumbleton (1945) dealt with various parasites and pathogens of porina. Two tachinid flies, Hexamera alcis (Walk.) and Cerosomyia usitata (Hutt.) are described in some detail together with the fungal pathogens Metarrhizium anisopliae (Metchn.)

The final section summarises Dumbleton's earlier statements on those field conditions affecting eggs and juvenile larvae

and substantiates these using some climatic measurements. He maintained that existing parasites and diseases were not significant mortality factors controlling population fluctuations. He assumed, quite rightly, that larger larvae were well protected from climatic variations but deduced that egg and juvenile larvae still on the soil surface were more subject to adverse microclimatic conditions, soil moisture and humidity at the soil surface. He argued that if a causal relationship existed between soil moisture and egg/larval mortality, there should be a correlation between the rainfall/evaporation ratio for November and subsequent porina abundance. The data presented does seem to indicate a possible relationship but it is not of sufficient precision or abundance for confident analysis. Nevertheless, the relationship is very credible. He concluded that in years when conditions are not generally favourable for epidemics, the presence or absence of field infestations was probably due to three reasons.

1. A porina population sufficiently high to infest the field.

2. Local conditions of favourable soil moisture due to high rainfall and low temperature/evaporation ratios.

3. Adequate plant cover which influences temperature/evaporation ratios and which permits a greater part of the potential increase of the population to be realised.

These concluding statements from Dumbleton marked the

end of a brief era of quantitative porina ecology. Soon after, D.D.T. was introduced into New Zealand and was being used extensively by 1950 (Hoy, 1953). The effect this had on entomological research in New Zealand was, in retrospect, diversionary. The main emphasis in pasture pest research was now placed on testing organo-chlorine insecticides, in particular, B.H.C. and D.D.T. This shift in emphasis is well illustrated by studying the list of publications from 1949 to 1966 in Table 1. Over this period there were 18 publications on chemical trials with little or no ecological information given. In comparison, there were eight papers published dealing with ecological, economical or taxonomic subjects.

Perusal of the literature on chemical control of porina from 1947-1966 shows how D.D.T. rapidly became known as the panacea for porina control, surpassing all previous compounds in effectiveness and cost.

D.D.T. was first tried experimentally against porina prior to 1950 (Dumbleton et al., 1948). Following this was a large number of papers all supplying results on rates, methods of application and formulations of D.D.T. and B.H.C. for control of porina (Kelsey et al., 1950a; Kelsey, 1950b; Doull, 1951a and b; Kelsey, 1953, 1955 and 1959).

Towards the latter stages of 1966 there was a gradual change of emphasis to testing the newer organo-phosphate chemicals (Helson et al., 1964; Kelsey, 1964 and 1965; Arthur and Cassels, 1965; and Christie, 1965). During the whole period research on porina ecology was virtually ignored. A few ecological observations were published in the above papers but it was merely reiteration of earlier work by

Dumbleton (1945), Dick (1945) and Greenall (1940).

The only significant ecological work carried out during the period consisted of a study by Dumbleton (1949) on a gregarine parasite of porina, work by Gaskin (1964) on light trapping of adults and their later identicication, some ecological observations by Taylor (1964) on aspects of larval behaviour and finally a survey by Arthur (1966) carried out to assess the porina problem in Southland.

Taylor (1964), although realising the influence that spring conditions and summer drought had on both species determination and larval survival, had little hope for any significant porina control by farm management factors. He thought that more use could be made of resistant or tolerant grass species.

The survey by Arthur (1966) although helping to define the porina problem really only shows the importance of climate and pasture growth. He found that even though most farmers surveyed considered they had a porina problem, 19 out of 25 were running 10-14 ewe equivalents/ha and only applying insecticide when visible damage was apparent. It was implied that under a Southland climate, farmers could still run up to 14 ewe equivalents/ha even with a considerable amount of porina damage.

Towards the end of 1966 the possible withdrawal of D.D.T. was first discussed. Following this, a number of papers were published on control of porina using organo-phosphate compounds. The work consisted mainly of small plot insecticide testing using various types of pasture yield measurements (Cassels, 1966; Taylor, 1966; and Patterson, 1966) and/or

larvae counts (Perrott, 1966; Patterson, 1966; Lowe, 1966; and Kelsey and Read, 1966). Various organo-phosphate compounds such as trichlorfon, fenitrothion, and diazinon were all evaluted using D.D.T. in a prill formulation as the standard. These chemicals became recognised as being reasonably effective against porina larvae, albeit at much higher cost and with a need for greater frequency of application.

Up to and including the year 1966 porina research was characterized by chemical control investigations and a lack of research policy. This is exemplified by the spasmodic appearance of only 14 papers published since 1900 on ecological and related subjects, compared with 27 on almost wholly insecticide work. Furthermore, for an insect pest which was considered "second in importance to grassgrub" as early as the 1940's (Dumbleton and Dick, 1941a) the basic ecological knowledge necessary for long term control was absent. In the opinion of the author much research on porina, chemical or otherwise, was apparently initiated by some political stimulus. For example, the prohibition of dust formulations of D.D.T. in 1964 and its complete prohibition in 1970 led to a rapid rate of increase in research on organo-phosphate controls.

During the winter of 1967 there was much publicity over epidemic populations ("The Press" 1.7.67) and a demand by Federated Farmer groups for more research, notwithstanding the fact that epidemic porina populations had been recorded at least eight times since 1930, Kelsey (pers. comm.). In 1967, however, the withdrawal of all forms of D.D.T. was being

discussed together with the fact that alternative control measures would have to be found. Although the emphasis was again placed mainly on chemical alternatives some demands were made by various Federated Farmers' groups for fuller investigations into ecological aspects of porina. It is interesting to note that published literature thereafter until 1971, does indicate some shift in research policy (Table 1).

Perhaps the most ecologically significant paper of the post 1967 period, for porina as well as other New Zealand insect pasture pests, was published by Pottinger (1967). He outlined the sort of research which should have taken place in the past on porina and most certainly should in the future. The approach he suggested was long term, quantitative, inductive ecological research based initially on sound sampling techniques followed by the development of life tables. He maintained that research should be aimed at finding out the significant mortalities of porina populations in various areas and over rising and falling populations. This type of research is essentially long term, in some ways laborious and costly particularly for a subterranean insect, but wholly logical. Such research could easily be carried out in conjunction with more short term work having more immediate practical application

The ecological approach was accepted for this study but little or no notice was taken of it elsewhere in New Zealand entomological research institutions, other than for grassgrub research in the Field Research Station of the Department of Agriculture. Although the ecological approach had been used overseas by entomologists in Canada prior to

1967 and was shown to have applications in New Zealand in early 1967 (Pottinger, 1967), porina research from 1967 onwards was still fragmentary.

The subjects studied ranged from egg and larval handling techniques (Waller, 1968a); unsuccessful methods of easily obtaining counts of field larval populations (Waller and Satory, 1968); larval feeding studies (Harris, 1969); to attempts at determining the economic status of porina damage (Rastrick and Upritchard, 1968; McLaren and Crump, 1969). Sampling techniques (French, 1969), taxonomy (Dumbleton, 1966), and flight behaviour in relation to ionic changes due to movement of weather systems (Helson and Penman, 1970) were also studied during this period. Although the subject matter covered a wide field, contributions to the understanding of the pest's population dynamics were again noticeably lacking. There were exceptions, however. Esson (1970) using a complex time lapse photographic technique, attempted to study larval feeding behaviour, but with limited success. He was able to show that larval feeding tended to be sporadic and was influenced positively by rain and negatively by frosts. Of more ecological importance was work carried out by Fenemore and Allen (1969) on egg and juvenile larval mortalities. They found that high mortality occurred in the juvenile larval stages and confirmed earlier work by Dumbleton (1945) who showed that a high level of humidity was required for maximum larval survival and egg hatch in the field. They also suggested that excessively wet conditions at this stage could be just as detrimental as dry. They were unable to give any conclusive evidence to show that long pasture

was more favoured for oviposition than short.

The authors did not attempt to interpret their results in relation to overall population mortality. Although stressing that high mortality does occur in the early stages of the life cycle they did not consider the possible effect of this mortality on overall generation fluctuations.

The other noteworthy feature of the period between 1967-1971 was the reduction in chemical work compared to the 1950-66 period as indicated by the number of publications (Table 1). From 1968-70 only five papers dealing with insecticide work were published. These dealt with the effects of late flying species on spring pasture (Allen, 1968) and the testing of likely new insecticides (Upritchard, 1970) together with further evaluation of the now standard recommended chemicals for porina control. Taylor (1970), Rough (1968) and Waller (1968b) reviewed the chemical work up to 1967 and stressed the larval behavioural problems associated with chemical work, in particular the transient nature of organophosphates and the effect of climatic factors on larval emergence. Soon after this a plea was made by Perrott (1970) for a standard method of recording chemical trial results to help overcome some of the difficulties of interpretation mentioned by Waller (1968b).

From 1970 onwards there was a gradual decline in the volume of ecological research on porina, as indicated by the number of publications during the 1970-72 period. There are a number of reasons for this situation. Two consecutive drought years in Canterbury reduced the general severity of porina attack in the province. This, coupled with greater emphasis on grassgrub attack, and a trend towards

diversification away from pastoral farming, reduced the numbers of workers on porina ecology and population dynamics. Thus research on porina is again entering a stage similar to that which occurred during the D.D.T. era, namely a sense of complacency, especially in the farming community, due to the following reasons.

1. The availability of three reasonably effective insecticides, i.e. Fenitrothion, Diazinon, Trichlorphon.

2. No porina epidemic has been experienced since 1967.

3. The present attitude of many farmers (particularly in Canterbury, Otago and Southland) who now consider that porina is no longer a problem.

4. An over-emphasis on grassgrub damage. This impression was underlined at a recent meeting of the Canterbury Federated Farmers in August 1971, called to review pasture pest research carried out since 1967. The 'porina problem' was neither discussed nor mentioned, other than a statement to say that porina was now "not considered a problem."

In summary, this chronological review of the literature on porina has revealed still persistent trends in pasture pest research which need reorganising.

1. There is still a certain lack of co-ordination when planning entomological research and this is preventing a specific wholehearted co-ordinated

attempt to fully understand porina population dynamics.

2. There is no balanced entomological research policy to include the gathering and interpretation of information on the economics of damage thresholds.

3. Not enough consideration has been given to the implications inherent in certain publications on porina by Dumbleton (1945) and Pottinger (1967).

In conclusion, it could be stated that much information on porina ecology and the understanding of its population dynamics would have been available today if work initiate by Dumbleton in 1945 had thereafter been planned and executed using the principles suggested by Morris (1955) and reiterated by Pottinger (1967) with more direct application to New Zealand pasture pest research.

CHAPTER 3

SOME ASPECTS OF THE ECOLOGY OF PORINA

IDENTIFICATION OF PORINA

In recent years, the identification of species within the genus Wiseana has become a confused issue. Both Dumbleton (1966) and Gaskin (1964) considered that W. cervinata (Walk.), W. umbraculata (Guen.), W. signata (Walk.)., W. despecta (Walk.), W. jocosa (Meyr.), W. copularis (Meyr.) and W. mimica (Philp.) are discrete species. Dugdale (1969), while agreeing that there were certain physiological differences came to the conclusion that there were only three distinct species of Wiseana and that one, W. cervinata, was a "complex", consisting of variations embodying hereto considered true species, i.e. W. cervinata = jocosa = despecta = copularis = mimica. Esson (pers. comm.) remained undecided, but acknowledged the fact that there was indeed considerable variation and hybridisation, which was apparent in adult physiology.

The larvae were even more difficult to classify. Length and general size have been used by some workers as a dubious means to classify larvae which have developed from early or late flying adult forms.

The current concensus is that there are three distinct Wiseana species, viz. W. cervinata, W. umbraculata and W. signata. W. cervinata is considered to consist of a number of temporally separated variations or races which occasionally genetically mix, both chronologically and spatially, to form a continuous but fluctuating common gene pool (Dugdale, pers. comm.).

There are undesirable ecological disadvantages arising from these conclusions, namely the risk of misinterpretation of ecological data in areas where species hybridisation is prominent. This could have repercussions when forecasting periods of maximum damage and the type and amount of damage. For example, the larvae from the so-called 'late flying species', W. despecta, has been described by Allan (1968) as causing serious pasture damage in spring "in some areas". On the other hand, the 'early flying species', W. cervinata, causes maximum damage in mid-winter over a very wide area. It could be argued that the larvae of these two supposedly different species, present at different times of the year, consumed different amounts of pasture green matter. It could also be argued that these two "species' are merely races of one true species adapting to variable climatic conditions, e.g. summer drought (Taylor, 1964). If so, ecological knowledge obtained from one should mostly apply to the other, particularly when dealing with such things as larval feeding behaviour. Thus, although the conclusion stated by Dugdale (1969), that Wiseana cervinata is indeed a "complex", could lead to ecological complications, the problem is not insurmountable. A rather similar problem was encountered by

Pottinger and Le Roux (1971) with Lithocolletis blancardella (Fabr.). In this case careful taxonomic work overcame it.

For the present study the advice of a field taxonomist would have been valuable. However, it was not considered essential as it was assumed from the available literature (Dumbleton, 1966; and Dugdale, 1969) that the species under study was W. cervinata and variations could be expected. Nevertheless interpretation of some of the results in this thesis may be challenged on taxonomic grounds. This really stresses the need for the initial advice of a field taxonomist when studying the ecology of physiologically variable insect pests. It also stresses the necessity of carefully defining a population of the study insect (see pages 107 & 108).

Specimens of moths collected over the study period (1968-1971) are held at Invermay Agricultural Research Centre while larval specimens gathered during life table sampling at Hindon and elsewhere in Canterbury and Otago are preserved at the Department of Scientific and Industrial Research, Lincoln. These specimens are available for inspection if required.

GENERAL ECOLOGY

Introduction

Although the life cycle of porina was known in general and certain other ecological aspects known in some detail, further ecological knowledge was required to assist in the development of sampling techniques and interpretation of life tables. Information was required on such things as

1. Moth flight behaviour
2. Egg deposition
3. Moth fecundity

It was also observed very early in the project that high mortality occurred in the egg and juvenile larval stages. This was followed by a hypothesis that these age intervals could be 'key' age intervals affecting population fluctuations. They certainly warranted more detailed investigation, particularly from the point of view of porina control. Confirmation of work by Dumbleton (1945) on the subject was also thought desirable.

FLIGHT BEHAVIOUR OF MOTHS

This subject was studied from two different but complementary views.

1. A detailed field study of moth flight behaviour, oviposition and fecundity.

2. An extensive study of moth flight behaviour with the aim of predicting on a national basis times of peak larval damage.

Method 1

To obtain semi-quantitative moth counts, baffle traps were used. These traps were built of fly screen mesh (3.2 mm square) attached to a framework of 13 mm diameter reinforcing steel. Each trap consisted of four arms, each pointing towards one of the cardinal points of the compass (Plates 1 and 2). Each trap was implanted around four triangular plywood funnels which fitted closely to the

boundaries of each sector (Plate 2).

Moths striking the mesh and falling were trapped in a container placed under each funnel. The majority of moths, however, clung to the wire mesh and were easily counted (Plates 3 and 4).

A total of eighteen traps were used. There were three different heights, i.e. 1.8 m, .9 m, and .2 m, each replicated six times.

The traps were erected in random positions over paddocks shut up for clover seed. The paddocks were situated at Yaldhurst (6.5 km N.W. of Christchurch) and Ladbrooks (16 km S.E. of Christchurch). The paddocks contained high numbers of pupae which were sampled in September and October ($21/m^2$ at Yaldhurst and $11/m^2$ at Ladbrooks).

Beginning in early October all traps were examined almost every evening between 7 p.m. and 11 p.m. Moths trapped in each sector, either clinging to the mesh (Plates 3 and 4) or found in the funnel containers, were counted and sexed. This procedure was carried out sometimes three to four times each evening depending on weather conditions.

All trapped female moths were preserved in alcohol in the first study (1968-69) and dry, in individual bottles, in the second study (1969-70). During inspection of the traps any females found on the pasture and just emerged from the pupal case were collected. The eggs from all females were later counted to determine moth fecundity.

Some weather readings were taken most evenings. These consisted of wind speed and direction taken .5 m above sward height using hand held anemometers for the first

study and later automatic wind recorders. Maximum and minimum air and ground temperatures, rainfall and occasionally relative humidity, were also measured. General weather observations such as cloud cover, moonlight intensity and occurrence of frost were recorded.

Method 2

Several light traps (Plate 5) designed and described by Helson (1970) were set up in various areas of the South Island.

The total number of moths, both male and female, caught in these traps between 7 p.m. - 11 p.m. were recorded each night. Traps were set up at,

1. Invermay Agricultural Research Centre
2. Hindon Lands and Survey Block (460 m a.s.l.)
3. Tara Hills Research Station (480 m a.s.l.)
4. Tara Hills Research Station (780 m a.s.l.)

Results from traps situated elsewhere were also used in the final analysis.

The light traps at Tara Hills and Hindon were controlled by automatic switching gear (Plate 6) as daily readings from these areas were impossible because of problems of accessibility. The rather complex electrical gear automatically switched on the light of one of seven light traps, each night.

The seven traps were installed together. "Vapona" strips in the tray of each trap killed all moths, which were collected and counted once a week. A photograph of the general trap layout at Tara Hills plus the switching gear is

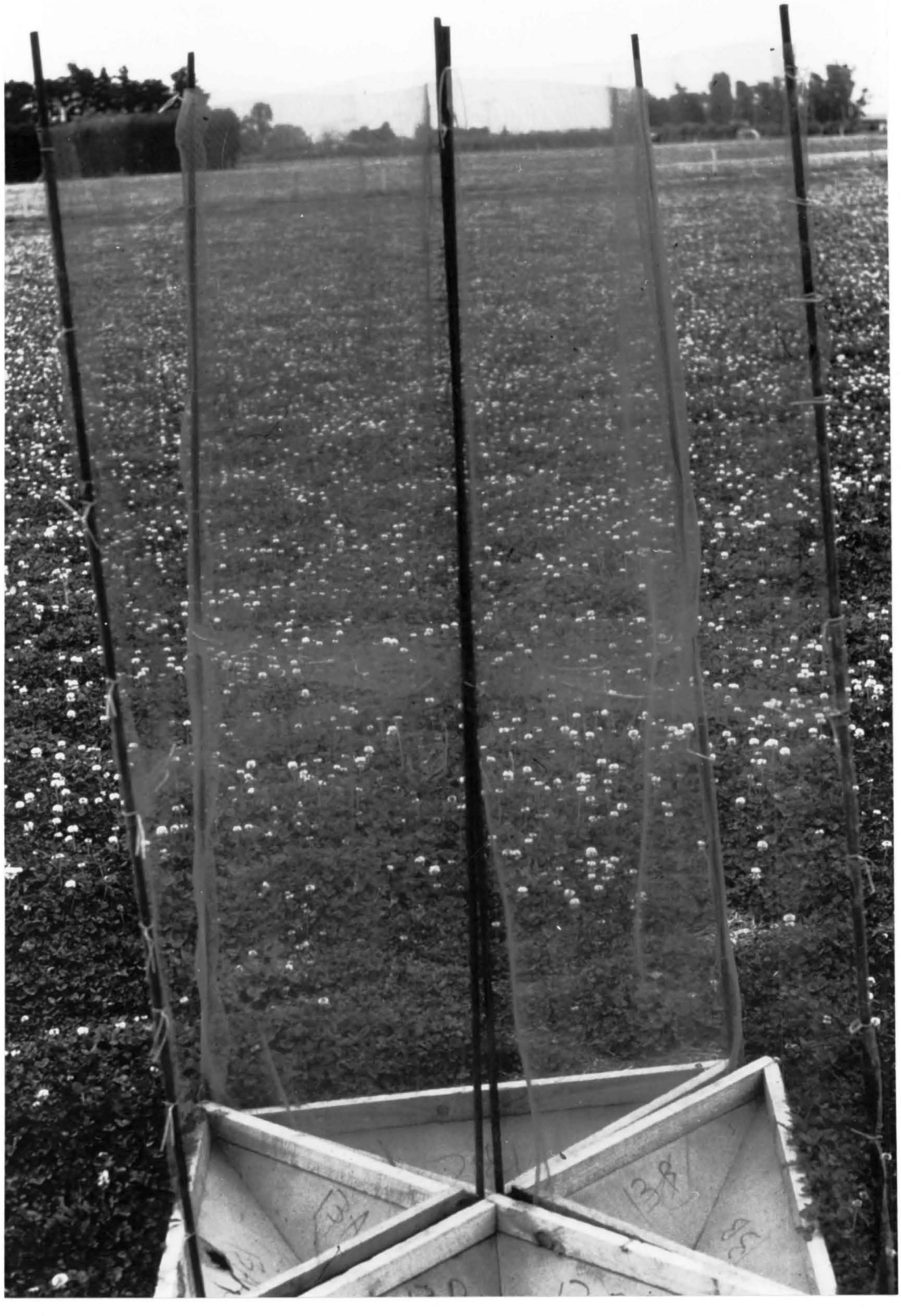


Plate 1 Baffle trap (1.8m high) used in moth flight experiments at Ladbrooks and Yaldhurst.

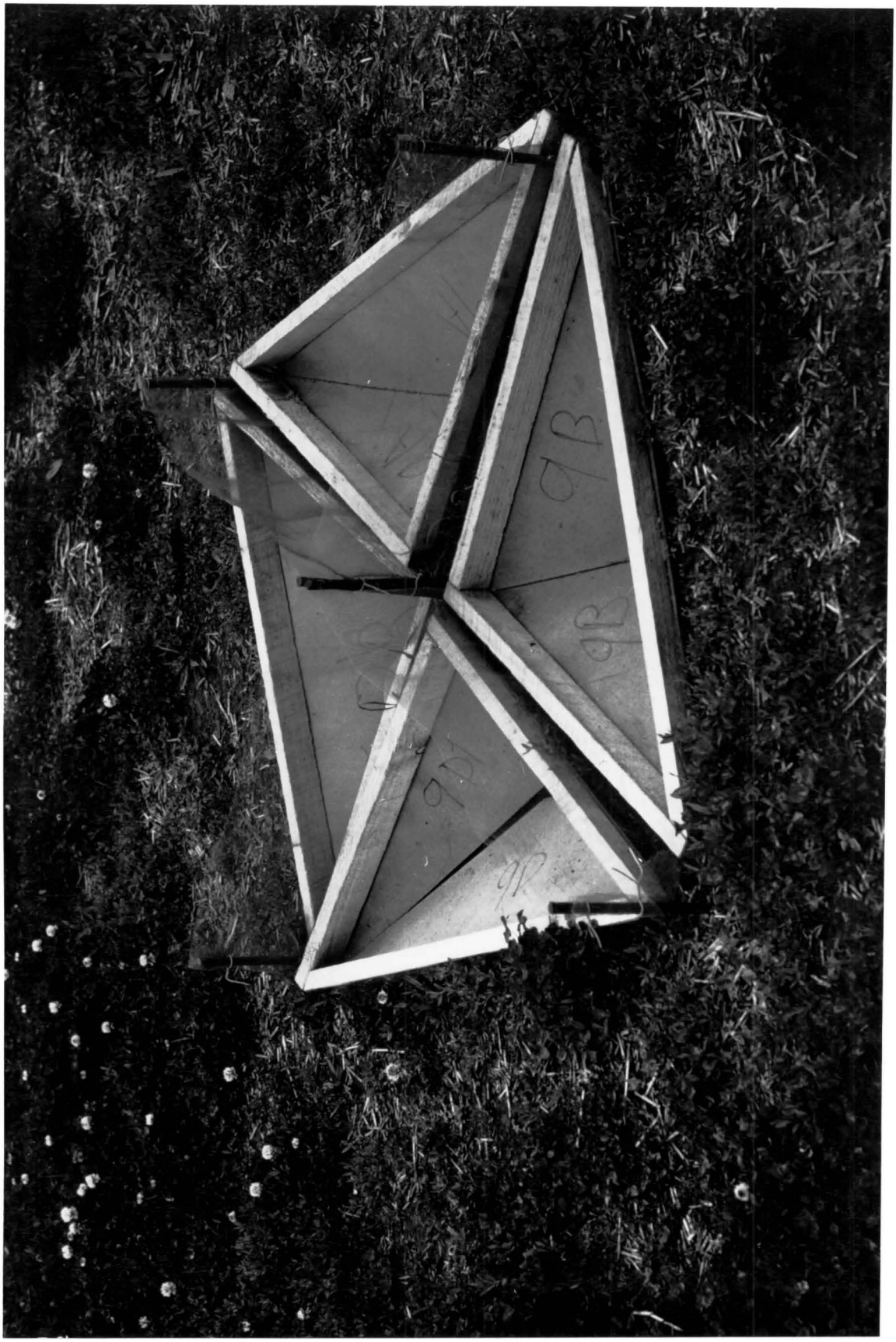


Plate 2 Baffle trap (.15m high) used in moth flight experiments at Ladbrooks and Yaldhurst.

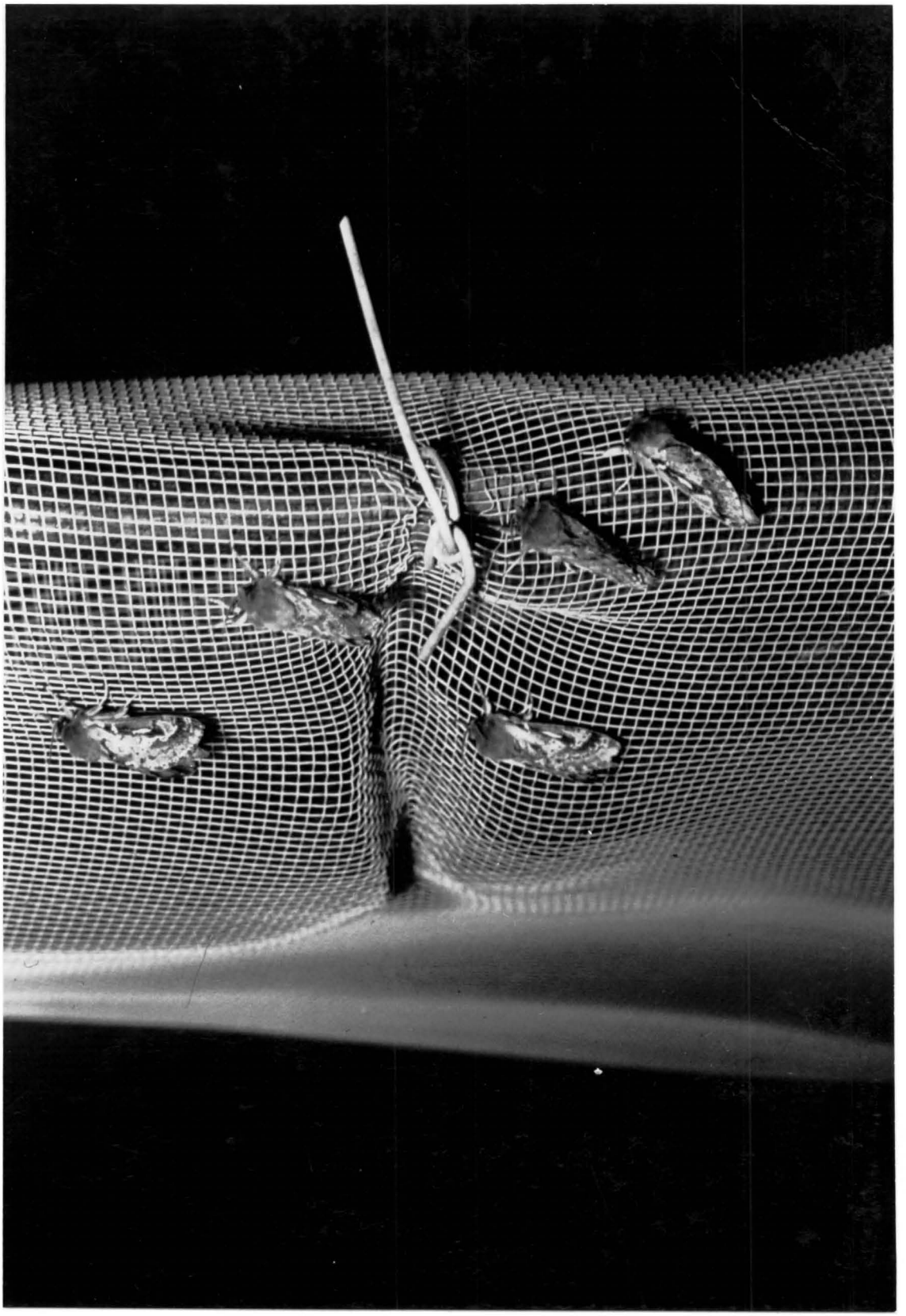


Plate 3 Porina moths clinging to the mesh on a baffle trap used in the moth flight experiments at Ladbrooks and Yaldhurst.

Plate 4 Close up view of a male porina moth clinging to the mesh on a baffle trap used in the moth flight experiments at Ladbrooks and Yaldhurst.

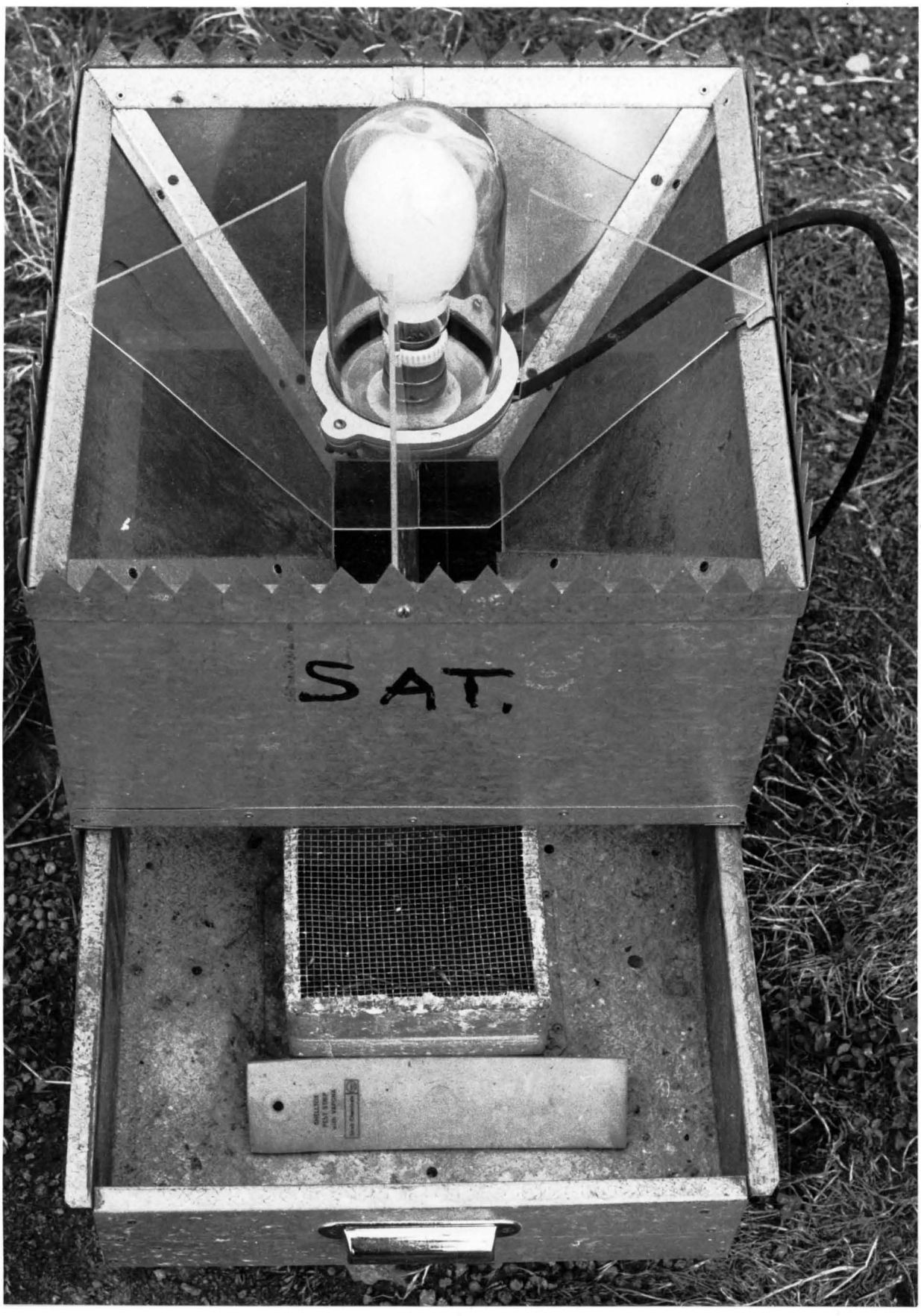


Plate 5 Light trap (Helson type) used to determine time of occurrence of peak moth flights.

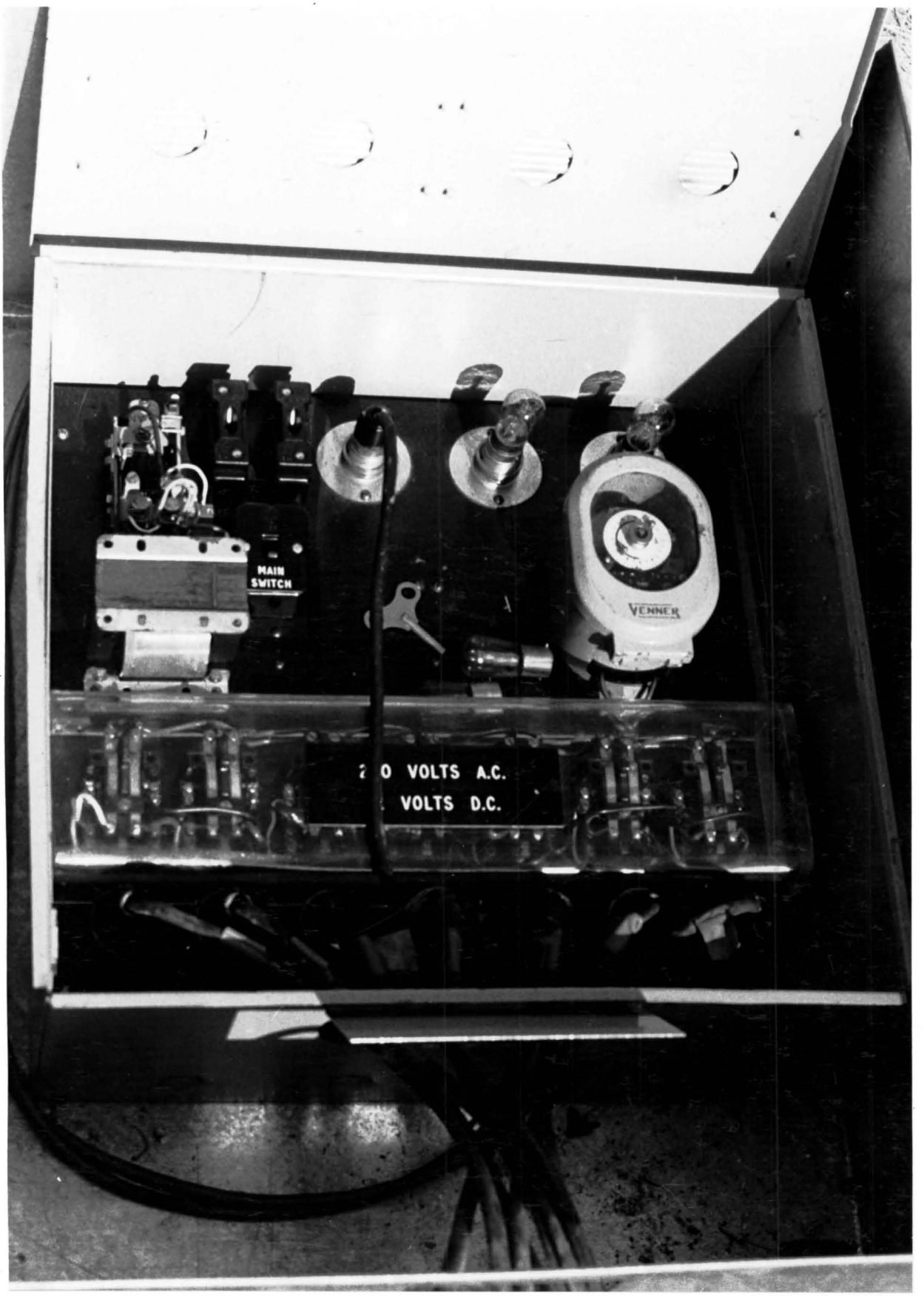


Plate 6 Detailed view of automatic switching gear used at Tara Hills and Hindon for the light trap experiments.

Plate 7 View of the 240v diesel generating unit (left) and automatic switching gear (right) used to operate a set of light traps at Tara Hills and Hindon.

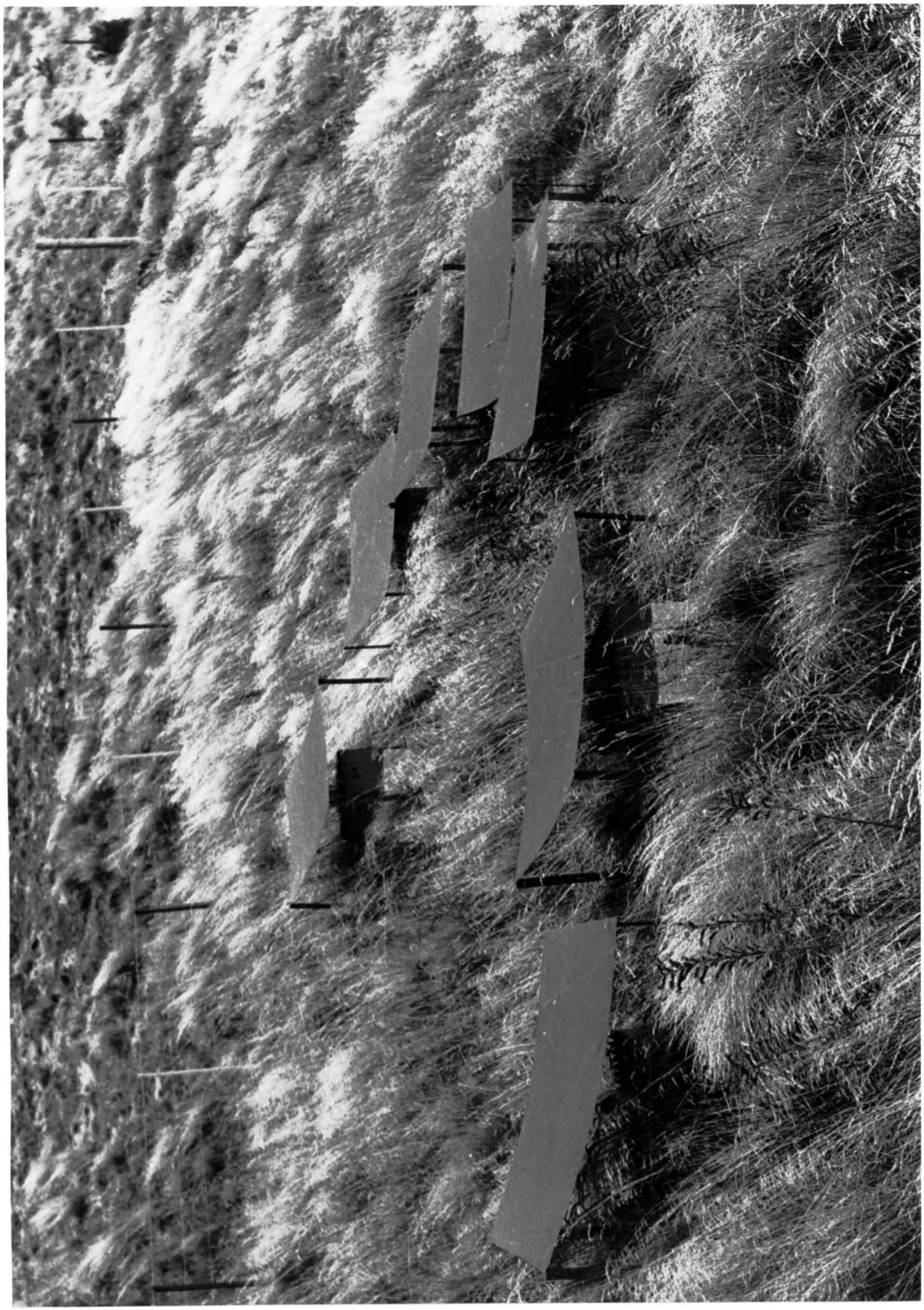


Plate 8 General view of light trap layout at Tara Hills.

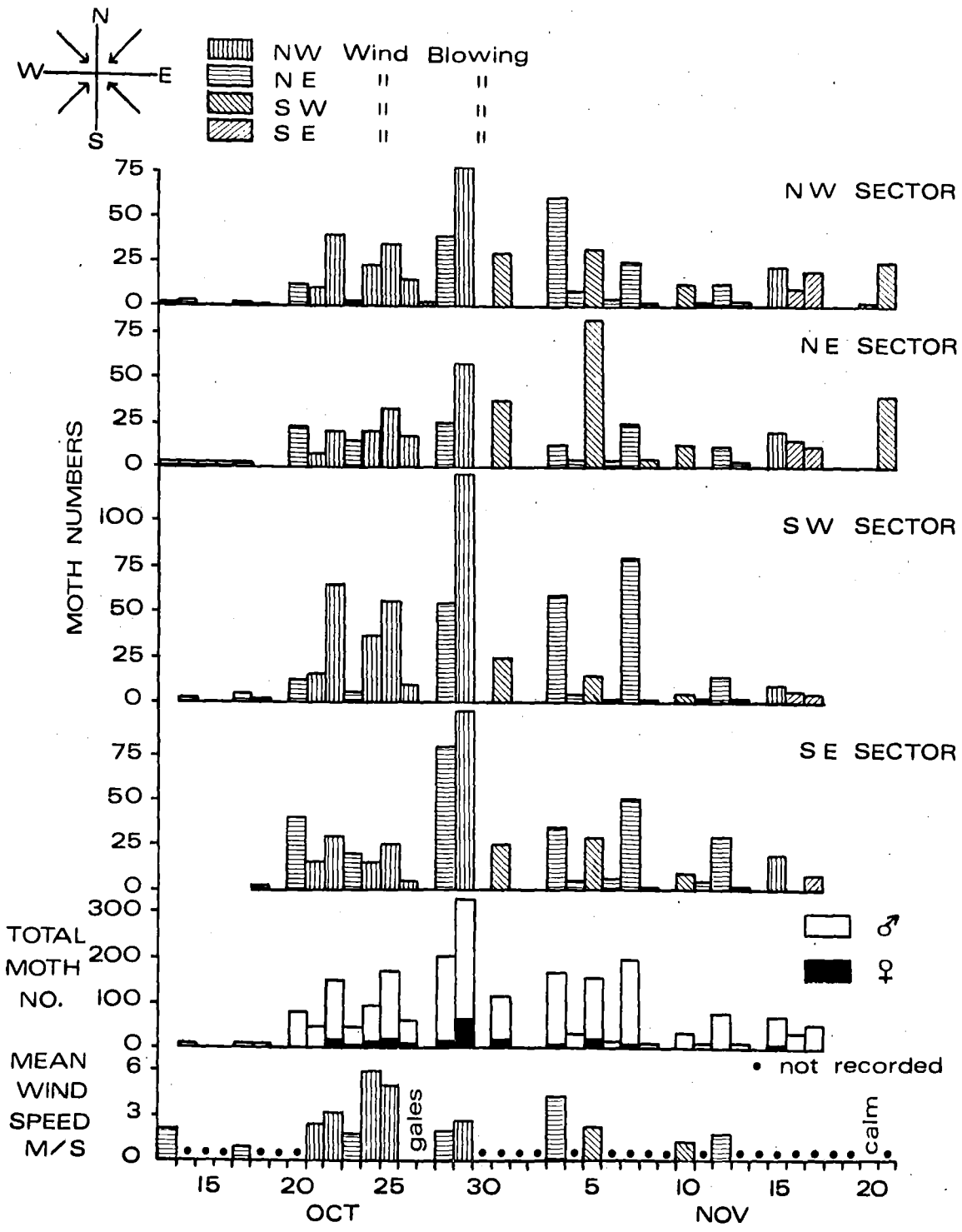


FIG. 2

The effect of wind speed and direction on the number of moths flying and their direction of flight at Yaldhurst during the spring of 1968.

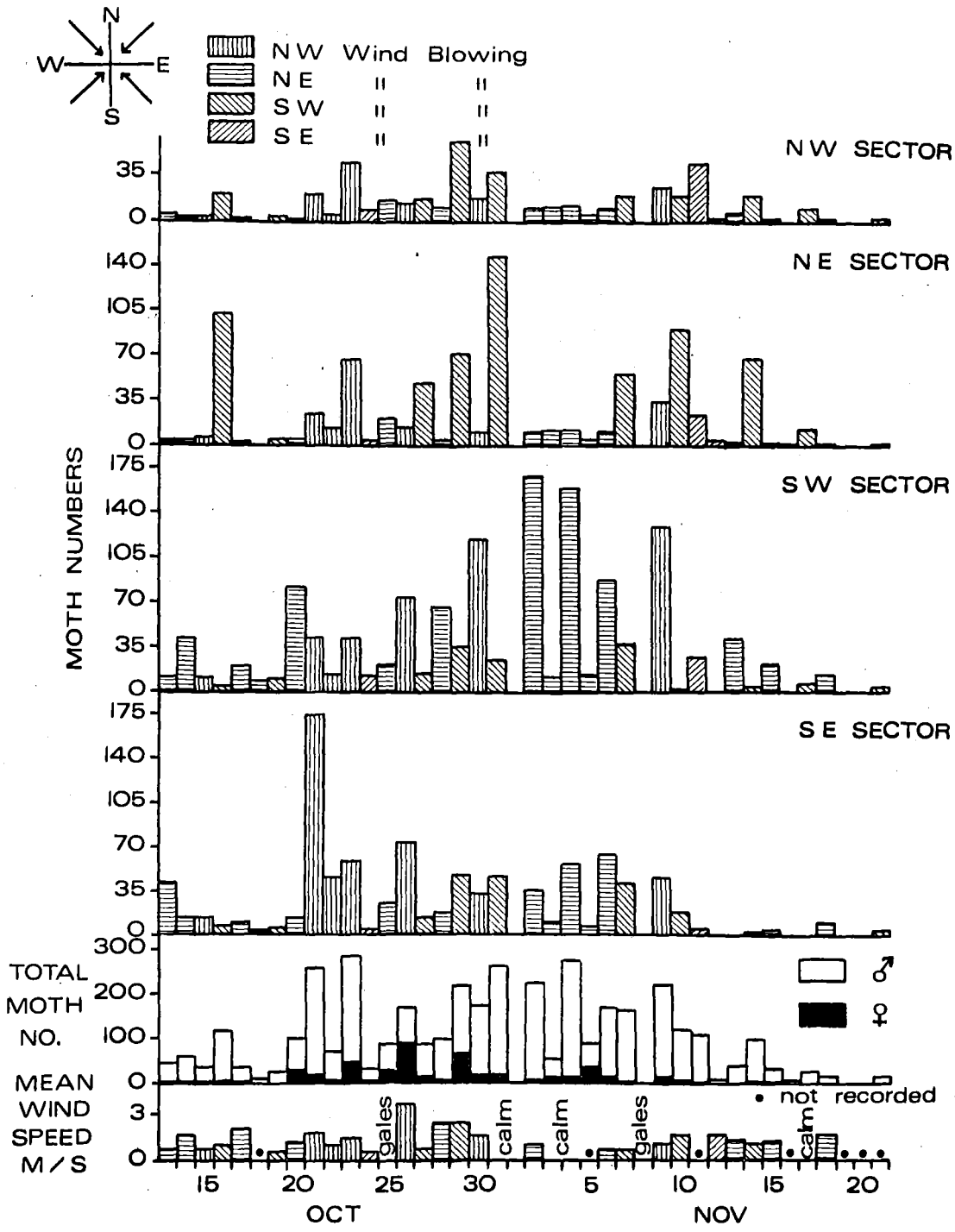


FIG. 3

The effect of wind speed and direction on the number of moths flying and their direction of flight at Ladbrooks during the spring of 1969.

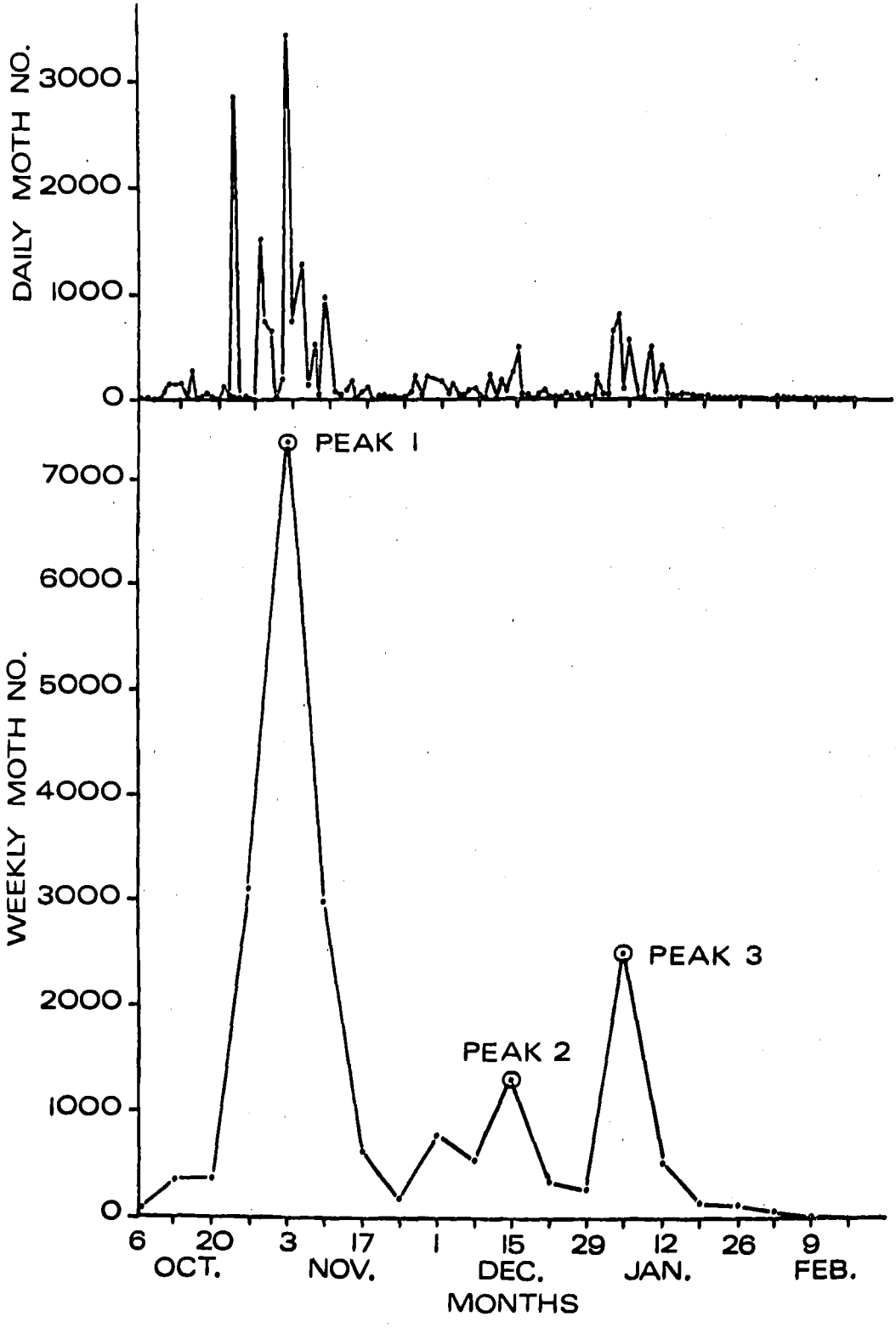
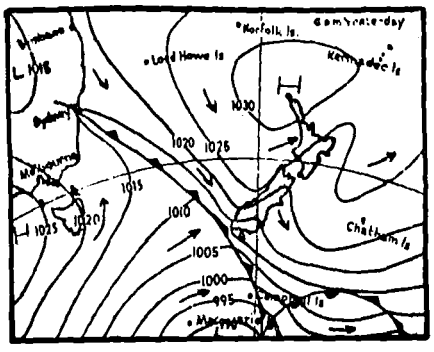
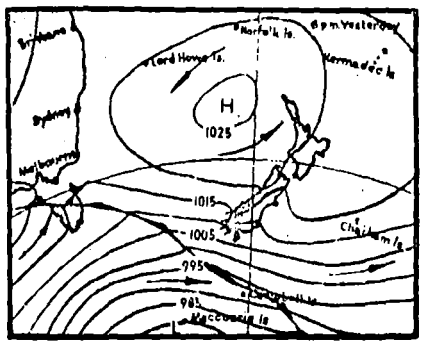


FIG. 4

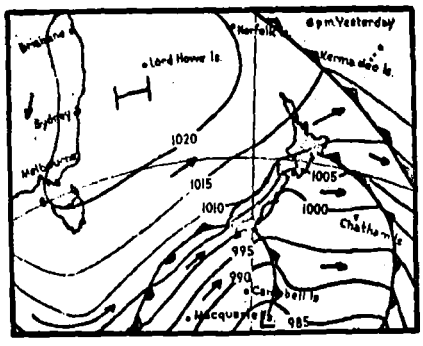
Invermay light trap results 1969/70 exemplifying the bulking of daily light trap catches into weekly intervals.



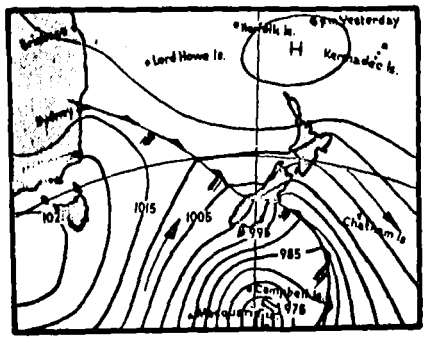
16·10·'69



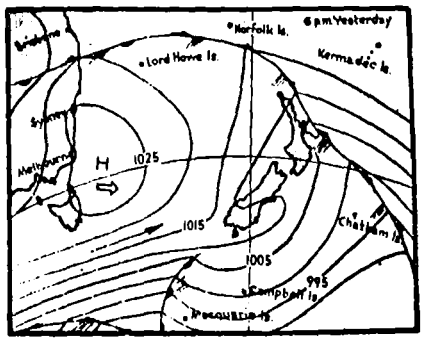
21·10·'69



25·10·'69



27·10·'69



28·10·'69

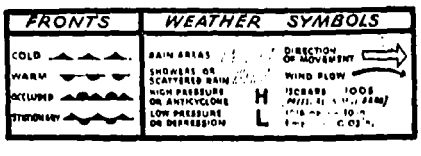
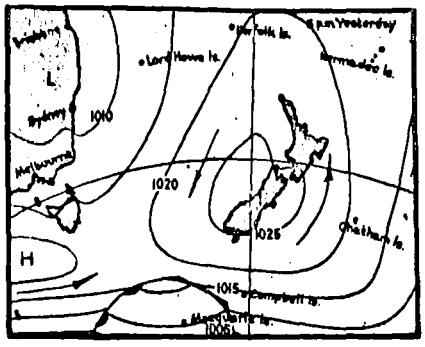


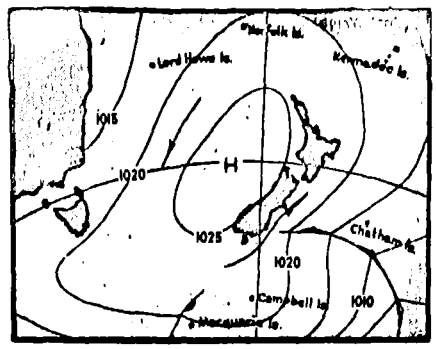
FIG. 5

New Zealand synoptic weather maps showing movement of characteristic weather systems.

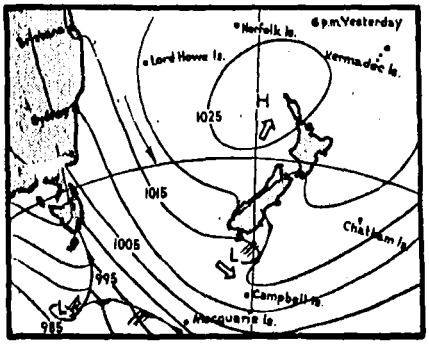
Contd.



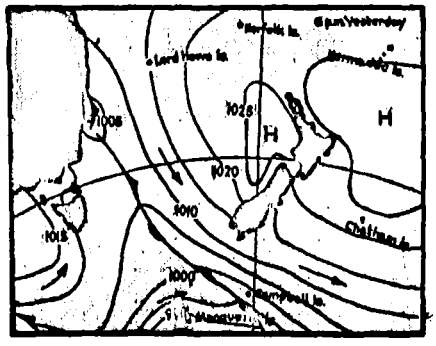
3·11·'69



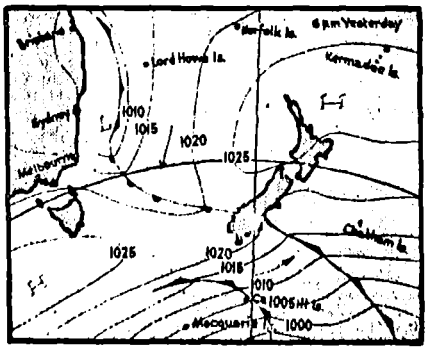
4·11·'69



6·11·'69



7·11·'69



8·11·'69

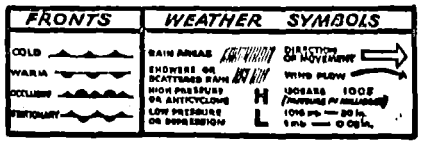


FIG. 5 contd.

New Zealand synoptic weather maps showing movement of characteristic weather systems.

Table 2 Estimated dates on which peak moth flights occur at various localities in New Zealand

Occurrence of Peak 1 (Mean Date)		
Makara	11 Oct.	± 8
Wairakei	19 Oct.	± 8
Winchmore	24 Oct.	± 8
Alexandra	24 Oct.	± 14
Manatuke	28 Oct.	± 8
Lauder	28 Oct.	± 14
Ruakura	28 Oct.	± 10
Tara Hills A *	29 Oct.	± 9
Tara Hills B **	31 Oct.	± 9
Roxburgh	31 Oct.	± 14
Invermay	3 Nov.	± 8
Hindon	8 Nov.	± 9
Stratford	17 Nov.	± 12

Occurrence of Peak 2 (Mean Date)		
Alexandra	7 Nov.	± 18
Makara	13 Nov.	± 10
Wairakei	17 Nov.	± 11
Hindon	2 Dec.	± 13
Tara Hills B **	4 Dec.	± 11
Lauder	9 Dec.	± 18
Stratford	14 Dec.	± 15
Tara Hills A *	14 Dec.	± 11
Ruakura	14 Dec.	± 15
Invermay	21 Dec.	± 10
Roxburgh	22 Dec.	-
Winchmore	26 Jan.	± 10
Manatuke	1 Feb.	± 10

Occurrence of Peak 3 (Mean Date)		
Alexandra	10 Dec.	± 26
Wairakei	17 Dec.	± 15
Hindon	6 Jan.	± 18
Tara Hills B **	8 Jan.	± 17
Invermay	11 Jan.	± 15
Tara Hills A *	11 Jan.	± 17
Lauder	27 Jan.	± 26
Ruakura	10 Feb.	± 21
Stratford	11 Feb.	± 26
Makara	19 Feb.	± 15

Footnote * = 480 m A.S.L. ± = 95% confidence limits

** = 700 m A.S.L.

Table 3 Differences in weeks between peak flight periods for each race from all localities

Locality	Race 1	Race 2	Race 3
INVERMAY	53	50.5	54
	52	54.5	53
	53	54	53
	49	48	49
	55	55	55
HINDON	53.5	53	51.5
	50	50	49.5
	52	53.5	54
WINCHMORE	52	51	-
	52	54	-
	51.5	51	-
	51.5	52.5	-
	51.5	50	-
MAKARA	55	56.5	41
	48	47.5	54
	53	52	52
	51	56	54.5
	51	49	49.5
	52	50	-
MANATUKE	53	51	-
	53	54	-
	51	54.5	-
	49	49	-
	-	51	-
	-	52	-
RUAKURA	51	51	52
	54	-	-
STRATFORD	54	54	-
TARA HILLS A	52	51	50
	54	55	54
	48	49	49
	58	55	54
TARA HILLS B	51	51	51
	52	52	52
	52	51	54
	53	54	51
WAIRAKEI	51	49	50
	51	54.5	54
	53	51	49
	52	-	56
	54.5	-	50

Locality	Race 1	Race 2	Race 3
ROXBURGH	52	52	-
ALEXANDRA	53	53	54
LAUDER	54	54	50

Summary

Race	Number of Samples	$\bar{x}$	95% c.l.
1	42	52.26	± .15
2	41	52.09	± .71
3	29	51.72	± 1.1

shown in Plates 6, 7 and 8.

Results from Method 1

Moth counts from Yaldhurst and Ladbrooks are presented in Figures 2 and 3 respectively, together with wind speed and direction.

Results and methods of analysis from Method 2

Daily counts of moths of all male and female Wiseana species were added together each week for each district to produce a graph as seen in Figure 4. The peak flight period over a week was then determined by eye. The daily catches for the "peak week" were then re-examined and the highest evening's count for that week was taken as the actual date of peak flight. Using these dates the time, in weeks, between the corresponding peak in the following year was determined (Table 3). The difference in days between succeeding peaks in the one season was also determined. The mean dates of appearance were estimated for each peak in a number of districts and 95 per cent confidence limits calculated. These dates are given in Table 2. To determine whether there were real differences between light trap sites three ANOVA were applied to each of the three sets of figures. A statistically significant difference ($P < .05$) was found in each case. This indicated that the respective peaks occurred at a significantly different date at each light trap site. To calculate the 95 per cent confidence limits for each date, Bartlett's test for variance homogeneity (Sokal and Rohlf, 1969) was applied to determine whether

a common variance could be used for each set of figures. It was found that a common variance was applicable for peaks one and two but not three. Because P $\doteq$ .1, however, a common variance was assumed for the third peak.

Discussion on moth flight behaviour

The results of the above experiments corroborated in general the work of both Dumbleton (1945) and Dick (1945). The following conclusions were reached from the information presented in Figures 2 and 3 and observations.

1. Male moths tended to fly upwind, depending on wind speeds but only succeeded at low wind speeds of less than approximately 3 metres per second (m.p.s.) measured .5 m above ground level. It is important to note, however, that this was not the real wind speed in the moth's flying zone. The sward causes drag which decreases wind speed just above sward height. According to Geiger (1965) a "power law" must be applied to determine the actual wind speed at heights other than those measured. The law can be approximated from the assumption that wind speed is in the same ratio as the fourth root of the heights at which they were measured.

2. The height of sustained flight across a clover crop about .14 m high varied with wind speed but was seldom below .15 m. The flight zone of most moths, both male and female, was between .3 m and 1 m. Some moths, however, were observed to fly as high as 12 m or more.

3. The number of moths trapped decreased with increasing wind speeds.

4. In either season the majority of moths were trapped between the 20 - 28 October.

5. The data from both sites corroborated Dick's (1945) published work on the factors influencing moth emergence, time of emergence and actual eclosion. However, his contention that strong winds somehow retarded eclosion was not observed. Although fewer moths were trapped during very windy periods, this was thought due to the moth's physical inability to fly under such turbulent conditions. Trends revealed in this study suggest that strong winds (greater than 3 m.p.s. measured at .5 m) could prevent emigration from a given paddock and inhibit the mating pattern.

6. By studying the weather maps presented in Figure 5 and the results given in Figure 3, it can be seen that large moth flights tend to occur as a depression plus its associated cold front approaches the country from the south. In fact, it was possible to predict the evenings when a large moth flight would occur. This was done by studying the daily weather maps any time between early October and mid November and judging when calm N.W. conditions would prevail preceding a cold front.

Discussion on mating behaviour

It became obvious that the characteristic flight behaviour of the male moth has developed to facilitate mating. The fact that males have emerged and are flying before females, ensures a daily high male/female ratio. The zig zag upwind male flight, makes for easy detection of the

Plate 9-1 Female porina moth ovipositing approximately twenty minutes after mating which occurred soon after eclosion.
Note: Plates 9-2, 9-3, 9-4 show further oviposition by the same moth shown above.

Plate 9-2 25 minutes after eclosion.

Plate 9-3 35 minutes after eclosion.

Plate 9-4 45 minutes after eclosion.

female sex attractant, which is probably liberated prior to mating. The characteristic lifting of the female abdomen and the consequent mobbing by a large number of males (up to 20 per female have been counted) was often observed. If the wind was too strong, however, the male flight behaviour pattern was disrupted and became non directional. As a consequence many females emerged and were not mated. Heavy rainfall and sometimes even heavy dew during the evening inhibited flight. These factors caused moth wings to either stick together or become entangled in foliage. If there was too much wind and/or wet weather during evenings over the flight period, the amount of oviposition and the number of matings was reduced. The evening weather pattern during the flight period could therefore be a variable mortality factor influencing generation fluctuations. Very detailed life tables would be required to prove this.

Discussion on oviposition behaviour

Plates 9 (1-4) show the sequence of egg laying by the same moth over a 30 minute period (approximately). This egg laying behaviour affords a partial explanation of why the larval distribution pattern tends to be aggregated. It explains why some very high individual counts of larvae were obtained in the present study, e.g. up to 3,250 m^2. The fact that up to 50 per cent of all eggs were laid within a short distance of the eclosion site confirmed the early observations of Dumbleton (1945) regarding the buildup of populations.

Dick (1945) claimed that he did not observe females laying eggs while flying. Such a phenomenon was observed during this study. This would explain why there were elements of randomness in larval distribution patterns which were generally aggregated.

Some observational evidence for oviposition preference was obtained by this author when studying the environmental factors influencing egg and larval mortality but it was never a distinct characteristic of the species. Considering the original rather open tussock habitat of members of the genus Wiseana it would be unusual if some oviposition preference had not developed. The benefit to egg and juvenile larval survival is obvious as oviposition under cover would protect these stages from exposure and dessication.

Discussion on migration

This important behaviour was not studied directly but much can be inferred from observations and the information presented in Figures 2 and 3. The fact that both male and female moths try to fly upwind close to the ground, suggests that the majority of females would not emigrate from a field under windy conditions if there were physical barriers such as gorse hedges. This was observed to be the case at Yaldhurst in 1968 during a perimeter check of the paddock when no noticeable moth emigration occurred from the parent site. Even during peak flight periods no moths were observed flying into adjacent lucerne and ploughed paddocks. This particular season was characterised by strong winds which occurred nearly every evening over the peak flight period.

This meant that little emigration took place and that the majority of eggs were laid within the paddock boundaries. Redistribution of the population within the paddock probably occurred as there would be a general move away from previously damaged areas which, by this time, would have sparse cover. There would be a tendency for eggs to be deposited in areas which had reasonable cover - an obvious survival mechanism.

Similar observations concerning migration were made in 1969 at Ladbrooks where the N.E. boundary was protected by a high gorse hedge. On the other side was an irrigated, dense grass seed crop about .9 m high. Numerous checks with a sweep net during evenings of dense moth flights and strong N.E. winds (between 3 and 5 m.p.s.) showed very little emigration. Later, sampling for larvae confirmed this. On the other hand, on calm nights some moths were observed in a light beam to be flying approximately 10-12 m high. If they maintained this height for about a quarter of an hour and drifted with the wind (at say 1-3 m.p.s.) then theoretically they could cover a distance of 900-2,700 m. Many would probably be carried further. Such individuals would initiate new populations provided suitable conditions prevailed thereafter for egg and surface dwelling larval survival. It was concluded that dispersal was a rather haphazard and chancy procedure, considering the vulnerability of the egg and juvenile larval stages and the generally indeterminate random flight of the female moth.

It was also concluded that emigration is a highly variable apparent mortality which could affect generation

fluctuations, particularly in exposed windy areas.

Discussion on provincial flight patterns and appearance of peak flights

The use of light traps as quantitative tools for ecological work are highly suspect as shown by Kelly (1971). Nevertheless, arrangement of the information in the manner already described on page 73 and the results presented in Tables 2 and 3 led to the following conclusions.

1. There is a statistically significant difference between the site means for dates of occurrence for each of the three peaks (Table 2).

2. Ranking the means shows that in general the appearance of the first peak (in the North Island) is earlier than in the South Island, although this is by no means categorical. Geographical and altitudinal differences confuse the trend, e.g. Tara Hills B at 780 m a.s.l.

3. There is some evidence to show that in perennially droughty areas such as Tara Hills and Alexandra, the second and third peaks occurred much closer to the first peak, particularly in those areas usually suffering early summer drought, e.g. Alexandra. The second or third peaks occurred much later in areas usually having late summer or autumn droughts, e.g. Winchmore and Roxburgh. The peaks occurring in more temperate and wetter areas such as Ruakura and Manutuke were relatively well spaced.

There is an ecological advantage in correct timing of peak flights (= peak egg laying), to allow time for

larvae to begin tunnelling to survive later drought periods. Natural selection has no doubt caused development of the appropriate race for the district. This natural selection of a more persistent and hence better adapted local race also helps explain why there is so much apparent intra-specific variation in one supposedly pure species.

4. Although more measurements would be preferable, enough information has been obtained to determine times of peak flights in various districts in New Zealand. These results given in Table 2 should prove useful to time control measures aimed at the egg or surface dwelling larval stage. This is discussed more fully on page 271.

5. It can be seen in Table 3 that the mean of the annual period between each corresponding peak (= race) is very close to 52 weeks. The 95 per cent confidence limits show that there is little variation around these means. Furthermore, from Table 2 it can be seen that, in all cases bar Alexandra, the times of occurrence of the three peaks at each site do not overlap. This would suggest that they are, in fact, real biological entities not created by data manipulation. Whether each peak consists of different species or merely depicts the occurrence of the variations or races of the one species, is not certain. It is likely, however, that the second peak consists mainly of W. umbraculata, the other two peaks consisting of the early and late flying races, respectively, of the W. cervinata complex.

The information presented in Table 3 also indicates the

possibility of an annual cycle in the time of peak occurrence. Thus, if the peak occurred early one year, it was later the following. There is probably some genetic compensating factor to ensure that peak flights occur within a certain mean time period regardless of climatic variations. This type of survival mechanism would ensure that eggs are generally laid at the most appropriate time.

For example, in dry regions, the eggs would be laid well before the onset of drought after temperatures had risen sufficiently for optimum egg maturation.

DETERMINATION OF MOTH FECUNDITY

Method

Fecundity was determined using moths captured during the baffle trap experiments. The female moths were collected in three ways.

1. From baffle traps.
2. At eclosion prior to oviposition.
3. Around household lights.

Each moth was isolated when collected. In the 1968 season they were preserved in alcohol, later dissected and their eggs counted manually. Great difficulty was experienced separating individual eggs from the egg mass and this caused counting problems.

In the 1969 and 1970 seasons each trapped moth was placed in a glass jar and allowed to lay her eggs. A small glass jar 3.8 cm in diameter and 6 cm high, with a screw top,

was used in preference to anything larger. The smaller volume seemed to increase the relative humidity brought about by the presence of the moth. This facilitated egg laying (Pottinger pers. comm.). All the eggs were laid within two - three days after which the moth died. Using this technique the eggs were easily and accurately counted by an electronic egg counting machine.

Results from moth fecundity studies

The egg counts for each of three different annual flights are given in Table 4. Differences between localities are indicated and the environment of the moth when captured, viz. whether they had been attracted to lights (lights), just emerged from pupae (ground), or taken from baffle traps (traps).

Discussion of moth fecundity studies

There was considerable variation in fecundity (Table 4). The species is, however, unusually fecund having an average of 1,297 eggs per female over the three year study period. This is almost double that for the related species Onocopera intricata. A lower average figure calculated by Dick (1945) was no doubt due to a very high larval population in his study area which, due to reduced food availability, would have produced less fecund moths. The egg counts presented in Table 4 were obtained from moths collected from light infestations in highly productive pastures on heavy soil types.

The influence of adverse weather conditions, particularly wind, on generation survival can be seen from a comparison

Table 4 The fecundity of moths caught in various situations at Prebbleton and Ladbrooks over a three year period

	1968		1969		
	Ladbrooks		Prebbleton	Ladbrooks	
	Traps	Ground	Lights	Traps	Ground
$\bar{x}$	646	1123	762	1165	1069
95% c.l.	±72.5	±108	±134	±236	±99
max.	2124	2039	1417	2214	1830
min.	30	121	32	10	34
% S.E.	5.7%	4.9%	9.0%	10.3%	4.7%
no. females	137	62	33	29	10

	1970		
	Prebbleton	Ladbrooks	
	Lights	Traps	Ground
$\bar{x}$	809	1396	1699
95% c.l.	±140	±184	±149
max.	1084	2484	2109
min.	569	603	1096
% S.E.	8.8%	6.7%	4.5%
no. females	7	21	15

Key

Traps = caught in baffle traps
Ground = caught just after ecolsion and mating, but prior to oviposition
Lights = caught after flying to a light source

Table 5 Mean wind speed in metres per second (m.p.s.) measured ·5m above ground level during large moth flights

1968 seasonal mean = 3.1 ± 1.01 m.p.s.

1969				
	Time			
Date	7-8pm	8-9pm	9-10pm	10-11pm
18/10	1.9	1.8	1.3	1.0
20/10	3.3	3.6	3.6	3.6
21/10	1.6	1.3	1.2	1.2
22/10	.7	.7	.7	.5
23/10	2.9	3.9	5.2	2.7
2/11	2.2	1.7	1.6	1.7
3/11	2.1	1.5	1.9	1.8
7/11	2.4	1.9	1.2	1.0

Seasonal mean = 1.9 ±.39 m.p.s.

1970				
	Time			
Date	7-8pm	8-9pm	9-10pm	10-11pm
12/10	2.9	1.7	1.5	.7
16/10	4.0	1.7	1.2	.7
20/10	1.1	.9	1.7	1.7
27/10	1.9	3.3	7.3	4.9

Seasonal mean = 2.3 ±.94 m.p.s.

of the 'trap' and 'ground' egg counts (Table 4). In 1968, strong winds (greater than 3 m.p.s.) were experienced most evenings just after sunset (Table 5). Thus, in this study area, the female moths laid approximately 50 per cent (646 vs. 1,123) of their eggs before flying.

When the females attempted to fly it was initially a 'grasshopper type' flight consisting of a sudden takeoff into the wind to a height of 1 - 1.5 m, followed by an equally swift descent back into the cover of the sward. In the instances observed the distance travelled was about 10 - 15 m. Very few female moths were observed in sustained flight. This only happened during lulls in the wind. The airborne moths were rapidly carried away as the wind speed increased.

On the other hand, the 1969 flight season was characterised by generally low wind speeds (less than 2 m.p.s.) in the evenings (Table 5). Consequently, female moths became airborne with heavier egg loads. The fecundity data for 1969 indicates this, viz. 1,165 vs. 1,069 (Table 4).

In comparison, the 1970 season was somewhere between the previous two. For example, during the early evening of 16.10.70 when there was a large moth emergence, a strong wind was blowing (4.0 m.p.s.) (Table 5). On the other hand, on 20.10.70 when there was another large moth flight, calm N.W. conditions prevailed. These weather vagaries explain why, overall, the difference between the trap and egg counts for the 1970 season was somewhere between the two previous seasons.

To summarise, in 1968 43 per cent of the eggs were deposited within the boundaries of the parent population before dispersal flights occurred. Furthermore, there was only a slight chance that the remainder were laid outside the boundaries of the parent site.

In 1969, however, female moths could have become airborne and emigrated with their full egg complement. In 1970 only 18 per cent of the eggs were laid prior to flight.

It was concluded that dispersal is affected by wind speed during the evenings of the flight period.

For future use in life table studies it was also concluded that 1,123 would be a reasonable assumption of the mean egg fecundity for each generation. Bec use of the limited nature of the proposed life table study and problems of site accessibility during the short flight period, a mean egg fecundity based on the limited information available was the only practical solution. It was realised, however, that using this mean figure for every generation was biologically incorrect, as even the limited results presented in Table 4 show the variable nature of moth fecundity. This could be a significant variable mortality, and have important ecological implications. The higher the larval population the lower the fecundity due to the previous lack of larval food. The lighter weight moths would therefore be more capable of flight. This would enable them to disperse to more favourable areas away from the severely damaged and exposed parent site. On the other hand, with less dense larval population, a more fecund and heavier moth would be formed. This would cause a larger number of eggs to be laid on the parent site to biologically 'capitalise'

on the relatively undamaged and hence protected sward. In either case wind would influence the trend, but the hypothesis does explain why severely damaged porina swards very seldom harbour larval populations the following year.

THE PHYSICAL ECOLOGY OF EGGS

Introduction

From early observations and reading of available literature it was deduced that the surface dwelling stages were very susceptible to changes in temperature. Initial field studies indicated that catastrophic juvenile mortality sometimes occurred and soil temperature seemed to be one factor involved. Therefore it was thought essential that the information published by Dumbleton (1945) on the effects of temperature on the juvenile stages (page 43) be confirmed and quantified.

Method

Eggs were obtained from an ordinary funnel light trap situated at D.S.I.R., Lincoln. After the eggs were collected they were cleaned using a method described by Waller (1968a). A known number of eggs (usually 100) were placed on moist filter paper inside a covered petri dish and placed in a constant temperature oven at different temperature regimes Daily checks were carried out and dates of hatching recorded. Egg hatching under laboratory conditions was also studied. Each treatment was replicated at least five times.

The results from studies on the effect of temperature on egg incubation

The results summarised in Figure 6 show the mean number of days required for a maximum hatch under the temperatures studied. Also included on the graph is similar information published by Dumbleton (1945). A simple linear regression was then calculated.

Table 6 gives the mean egg fertilities obtained from the above experiments, again including information given by Dumbleton (1945).

Figure 7 shows the amount of accumulated heat energy expressed as "degree days" required to produce the maximum egg hatch at the given mean temperature. The "degree day" index was calculated by multiplying each mean temperature by the respective number of days required to achieve maximum egg hatch. These figures were plotted against the respective mean temperature.

The calculated lineal regression lines are also included in Figures 6 and 7.

Discussion on the effect of temperature on egg incubation

A statistically significant relationship ($P < .01$) was found between time and the temperature required for egg development (Fig. 6). The relationship appears to be biologically meaningful as the calculated upper threshold temperature (Y), when $X = 0$ is approximately 25°C. This figure is nearly within the range calculated by Dumbleton (1945) viz. 25°C - 29°C. The lower threshold temperature although more difficult to determine from a regression line is approximately 10-11°C.

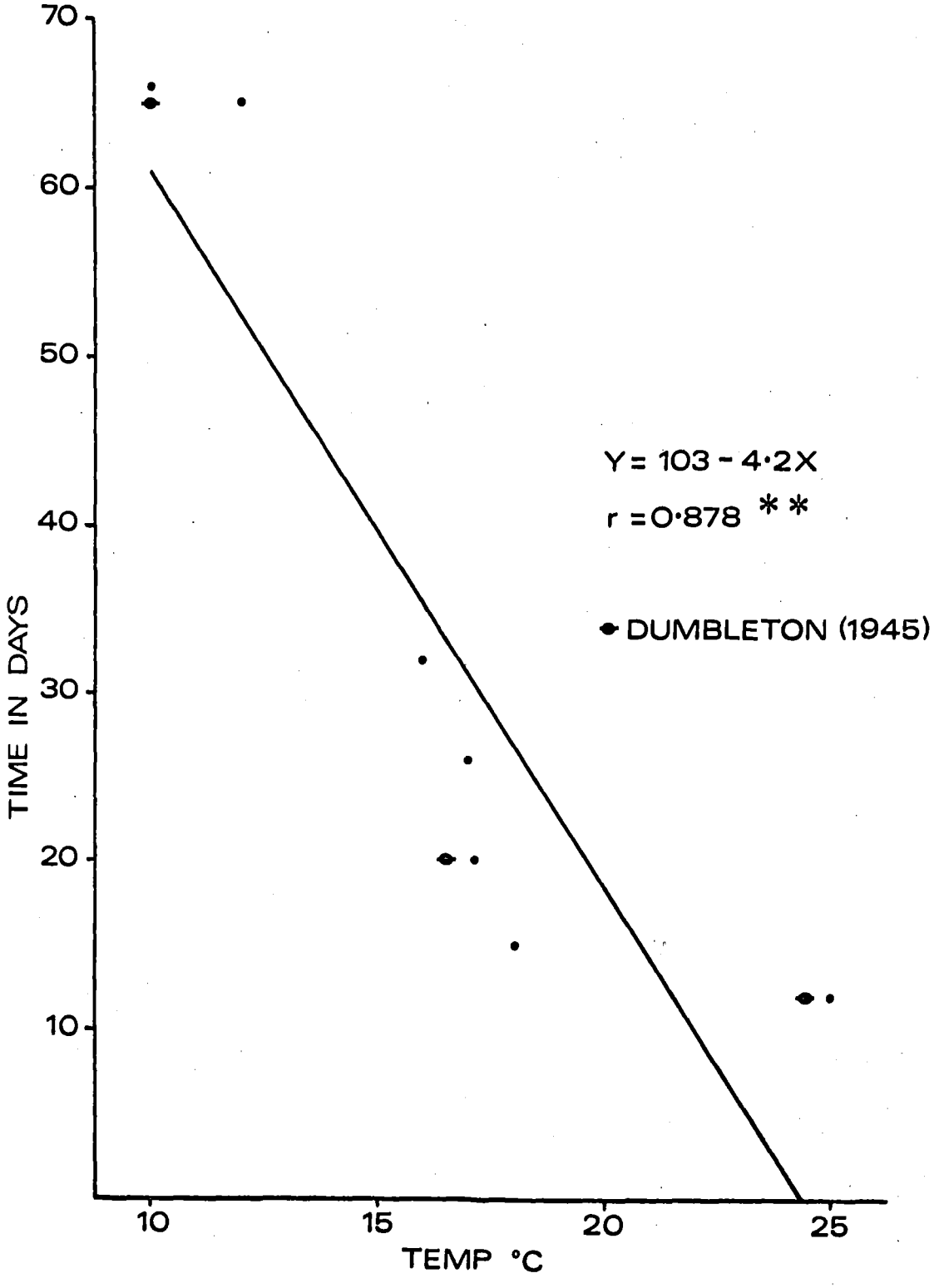


FIG. 6

The effect of different mean temperatures on the period required for egg incubation in a moist environment.

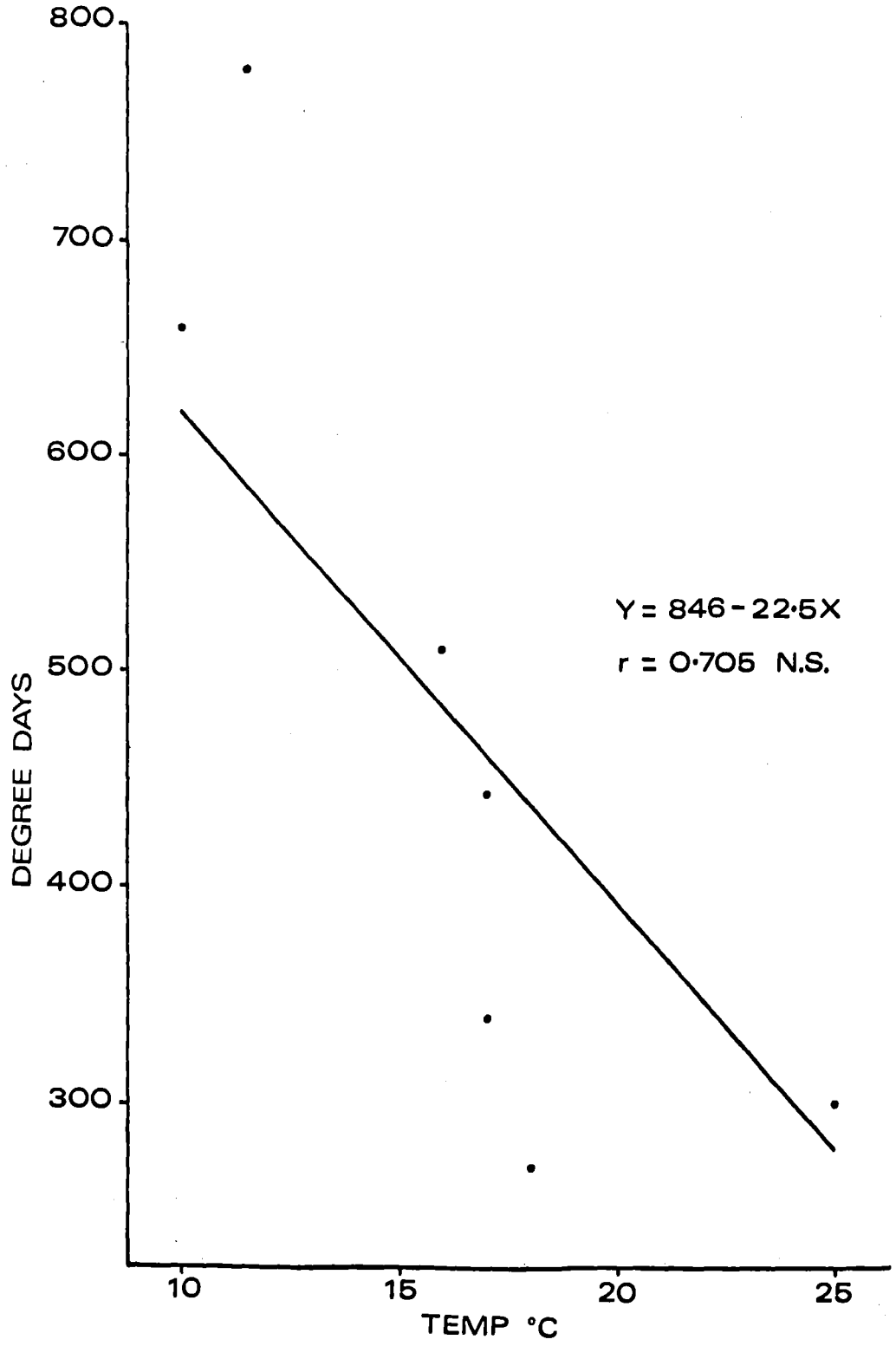


FIG. 7

The correlation of "degree days" with mean temperature.

Table 6 Fertility of eggs collected from light traps and subjected to various temperature regimes

Incubation conditions	% Fertility														
Laboratory	10.5	22.5	49.5	100	76.1	25.1									
Constant environment oven at 12°C	100	100	94	96	99	77	61	75	77	77					
Constant environment oven at 16°C	66	58	68	60	63	70	81								
Constant environment oven at 17°C	100	99	100	100	100	79	97	88	67	91					
Constant environment oven at 18°C	100	96	85	97	98	81	66	82	77	78	43	41	41	43	45

Data from Dumbleton (1945)

70-100% RH 18°C	98.4	98.0	59.0												
Variable humidity 25°C	98.7	98.7	26.7	98.6	98.7	100	100								
Constant environment oven at 16°C	51.2														
Constant environment oven at 10°C	98.6														

Although no statistically significant relationship was found between degree days and temperature (Figure 7) the r value of .705 was sufficiently high to suggest some slight relationship. Further corroboration was obtained when a comparison of the heat energy accumulation in various districts was made with the information given in Figure 7.

The district heat accumulation expressed in "degree days" was calculated from daily maximum and minimum data, using a computer programme developed by Baskerville and Emin (1969). The district "degree days" index was calculated from October 20 (the date estimated as the mean for occurrence of peak flights in Canterbury) to late November (the estimated time of hatching calculated from the peak flight date). This figure compared favourably with the "degree days" index calculated from Figure 7, based on a mean temperature for the October - November period. For example, the mean temperature for Lincoln between late October and late November over a number of seasons was approximately $11^{o}C \pm 1^{o}$. Approximately 600 "degree days" would be required to achieve egg hatching at this temperature (Figure 7). The mean "degree day" index for the period October 20 to November 20 for Lincoln and Christchurch using computed daily maximum and minimum temperatures over three seasons was 650 ± 23 and 641 ± 19 respectively.

This information could be used to predict when the majority of eggs will hatch in a given district, using the time of occurrence of peak moth flights (Table 2) as the base time.

No attempt was made to check whether eggs were more

susceptible to dessication in the latter stages of their development. As Dumbleton's (1945) other work on egg physical ecology was shown to be mostly correct it was assumed he was also correct in the other aspects.

SURFACE DWELLING LARVAL BEHAVIOUR

Introduction

Newly emerged larvae are very frail and appear very susceptible to high temperatures and dessication. As it has been observed that moths do not have a well-developed oviposition preference, newly hatched larvae must have some ability to seek shelter. Larval movement is also important when considering sampling programmes, particularly if initial larval population movement results in clumped distribution patterns.

Methods used to determine direction of movement of surface dwelling larvae

A number of newly hatched larvae were placed in the centre of a 50 cm x 40 cm oval area of concentrated light shone onto a flat sheet of white paper. The light source was placed at a slight angle to the surface, giving a light intensity gradient. The illuminated area was divided up into four sectors. When each larva reached the edge of the illuminated area, the sector in which it was in was noted.

Method used to determine the distance travelled by surface dwelling larvae

Newly hatched larvae were placed on various types of surfaces and their movement traced with a pencil. This line

was later measured. The time was recorded. Larvae were observed until they became immobile or time became limiting. Three types of surface were used.

1. Plain paper surface
2. Dry sand sprinkled on paper
3. Wet sand sprinkled on paper

Results from studies to determine direction of movement and distance travelled by surface dwelling larvae

Figure 8 and Table 7 respectively detail the distance and direction of travel. The results obtained from the experiments to determine distance travelled were bulked together to make analysis more biologically meaningful as in the field variable terrain would be commonly encountered by larvae.

Discussion on direction of movement and distance travelled by surface dwelling larvae

A statistically significant relationship was obtained between distance travelled and time ($P < .01$). This lineal relationship obtained under laboratory conditions illustrates what probably happens in the field. After hatching, the highly vulnerable surface dwelling larvae must rapidly find shelter or die. Figure 8 indicates that their searching potential is considerable. The distance they are capable of travelling in a short time would be more than adequate for them to find shelter in most pasture environments as the distance to shelter would only be a matter of a few centimetres, particularly if the eggs were laid in relatively dense cover. Moreover, the eggs being oval and hard would be deflected by upright vegetation, particularly grass, to the

soil surface and usually close to the base of the plant. This area offers the optimum microclimate with regard to both moisture and temperature. Broad leaved plants with the leaves close to, or touching, the soil surface and well tillered grasses provide the best microclimate, e.g. clovers (Trifolium spp.) and storksbill (Erodium spp.), cocksfoot (Dactylis glomerata L.) and established ryegrass (Lolium perenne L.).

The moist, cool environment under surface organic debris is also an ideal cover and partially explains why severe porina infestations can occur in hay crops or grass seed crops in which litter is left lying after the farming operations.

The potential mobility of the larvae would allow them to change sites if necessary, if local plant cover started to die or was removed by grazing. If this occurs larvae would tend to move towards more dense pasture and this would result in a clumped distribution pattern. If various soil types occurred in the one paddock this effect would be compounded, as many larvae would tend to move to heavier (hence moister) soil types within a paddock.

It was concluded that newly hatched larvae are negatively phototrophic (Table 7). This behaviour would compel larvae to travel away from light. This would eventually direct them to the favourable dark microclimate existing under plants or organic debris.

The above laboratory findings have been confirmed in the field. Generally, larvae do not change sites unless compelled to by diminishing plant cover and increased temperatures due to heavy stock grazing and/or dry weather. A gradual change

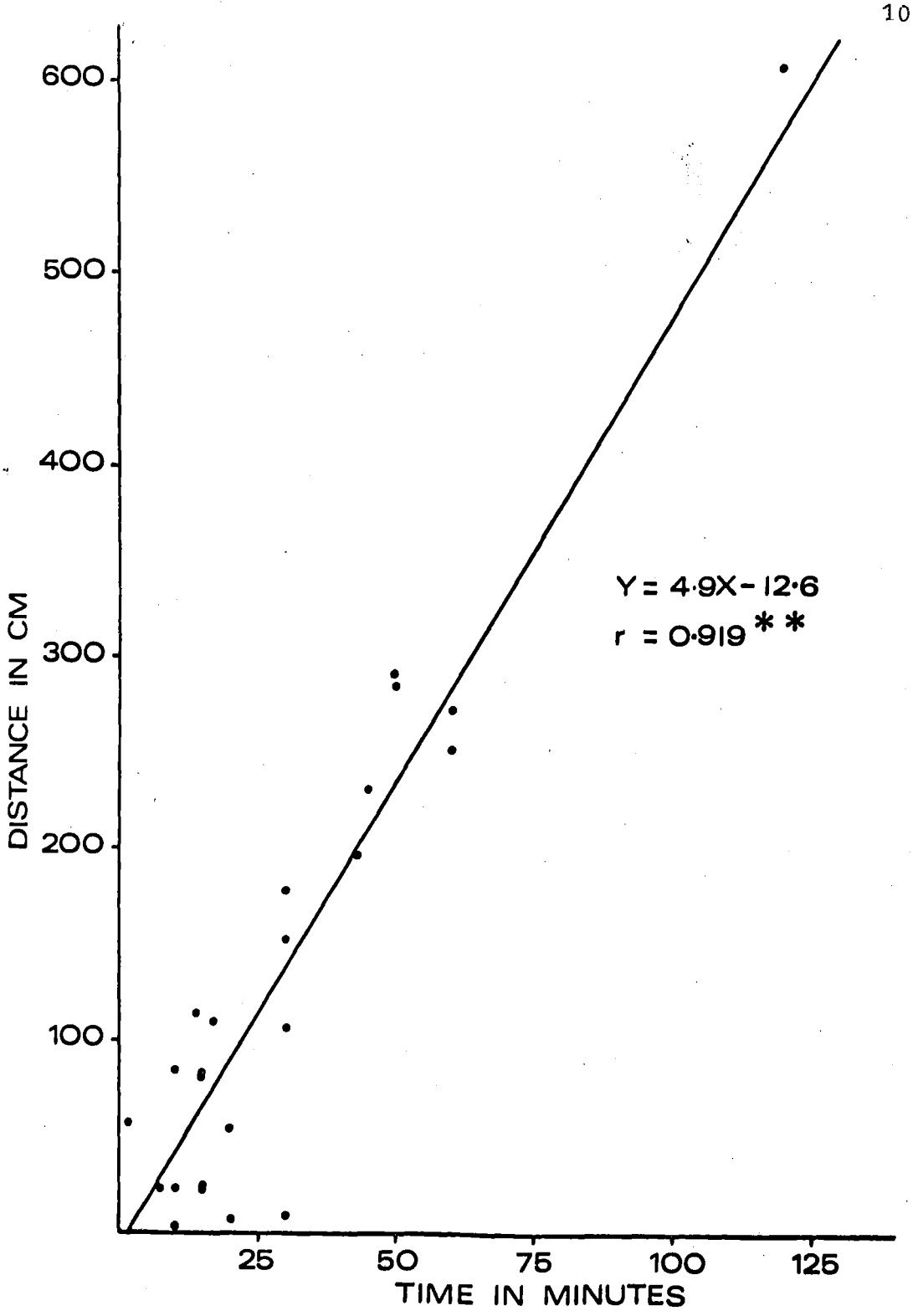


FIG. 8

The relationship between time and the distance travelled by surface dwelling larvae.

Table 7 Dispersion of juvenile larvae away from a light source to differently lit zones.

	No. of larvae in each zone			
Exp	A	B	C	D
1	0	7	3	9
2	0	6	3	6
3	0	6	8	7
	0	19	14	22

Key

A = area closest to light source

B = left side of the zone midway between light source and shade

C = right side of the zone midway between light source and shade

D = furthest zone away from the light source

towards unfavourable conditions, however, can be partially compensated for by increased webbing. Webbing is produced from a spinneret situated close to the mouth parts. It is characteristically carried out by surface dwelling larvae once a favourable shelter has been reached. In many cases a small crack in the soil surface is webbed over. This helps to ensure a constant and favourable microclimate and probably prevents predator attacks. Abrupt removal of cover, however, would still cause high mortality even though the larvae were well webbed. Likewise, with the onset of a severe and widespread drought.

SUMMARY AND CONCLUSIONS FROM STUDIES ON SOME ASPECTS OF THE ECOLOGY OF PORINA

An investigation into some aspects of the natural history of porina has shown that when the life cycle ends a large aerodynamically inefficient female adult emerges and lays a number of her eggs, more or less randomly in the immediate area of eclosion.

Flight is influenced by weather conditions such as wind speed and the movement of weather systems.

The eggs hatch into highly mobile, negatively phototrophic, surface dwelling larvae, which need to actively seek out favourable microclimates beneath and within pasture plants, in order to survive. Survival of both eggs and surface dwelling larvae depends upon the microclimate remaining favourable during the months of November and December.

The upper lethal constant temperature for eggs is between 25°C - 29°C. Larvae succumb at somewhat higher temperatures.

From the data presented it was concluded that:

1. The species Wiseana cervinata consists of a number of variable races with, however, a common gene pool. This is exemplified by differences in adult physiology and time of occurrence of peak flights.

2. Both male and female moths after eclosion tend to fly into the wind provided it is below 2 m.p.s. measured at .5 m above ground level.

3. Males are more vigorous fliers and aggressively seek out females, which, after mating, lay a variable number (0 - 50 per cent) of their eggs within the boundaries of the parent population. The female moths then become more efficient fliers and a number can be carried considerable distances.

4. Wind speed during the evenings, when moths emerge and fly, plays an important role in determing,

(a) the efficiency of males seeking out females;

(b) the number of eggs laid within the parent population boundaries;

(c) the amount and extent of dispersal.

5. Peak flights tend to occur earlier in the North Island than in the South. There appears to be a natural selection towards the occurrence of peak flights to ensure that larvae reach the protected tunnelling stage before seasonal drought periods.

6. Both the egg and newly hatched larvae require moist, cool conditions to ensure maximum survival. The larvae upon hatching, actively seek out favourable microclimates.

7. The significance of egg and surface dwelling larval mortality on generation survival is stressed. These stages appear to be very susceptible to adverse environmental conditions, causing high mortality. Although this occurs normally, any factor which worsens the situation must be important by both reducing damage caused by later larvae and influencing generation fluctuations.

CHAPTER 4

DEVELOPMENT OF SAMPLING TECHNIQUES

Introduction

Morris (1960) has stated that "sampling itself has no intrinsic value in studying population dymanics", and "trial and error play a large part in development of the techniques involved". This study was no exception even though porina has been studied for at least 30 years by many workers and it would be expected that their first job would have been the development of suitable sampling techniques. These workers were involved mainly in studying short term effects of insecticides on larvae, but even so no attempt was made to develop and assess sampling techniques for other stages of the life cycle. Even such things as sampling accuracy and error margins were inadequately defined, while comparative studies on sampling techniques for various stages, sampling variance of high and low levels of populations, costs of sampling and types of population distributions are virtually non-existent.

Moreover, meaningful sampling parameters obtained from insecticide trials are meagre. Throughout the history of insecticide trials few attempts have been made to determine initial populations, sampling patterns, or the effect of

declining plot populations on sampling accuracy. All these experiments have been purely short term, small area, chemical comparisons. They have many inherent limitations. Generally the results are of little use for long term population dynamic studies. Basically, the only useful sampling information obtained from previous trial work was the fact that a number of square spade samples (usually 10 per plot) replicated 3-10 times per treatment, gave what was considered reasonable statistical precision. The sampling technique used was the removal of a volume of soil with a surface area varying from .02m^2 to .09m^2 both taken to a depth of .2 m. This basic technique with minor modifications has remained the only sure method of sampling the subterranean larval stages.

Definition of population

A definition of the term population was essential to define the scope of this study. Many definitions have been proposed, e.g. Cole (1957); Thompson (1956); Andrewartha and Birch (1954); Nicholson (1954); Milne (1957); Solomon (1949); Glen (1954); Odum (1954); and Pottinger and Le Roux (1971). The disadvantages and advantages of the application of these definitions to population dynamic studies has been summarised by Pottinger and Le Roux (1971). They composed their own version by combining parts of Glen's (1954) and Cole's (1957) definitions. They defined a population as "a defined basic taxonomic unit of the ecosystem having meaningful properties that can be estimated and described, such as birth rate, death rate, sex ratio and age structure".

This definition, however, does not adequately stress the temporal nature of insect groups, nor does it show that a fluctuating but common gene pool can result in different taxonomic units in space without any significant ecological or behavioural changes. Various porina populations which occur throughout New Zealand provide good examples of variable adult physiology, e.g. colouration. The larvae of these apparently different races of the one species are morphologically and behaviourally indistinguishable.

For the purpose of this study a more specific definition of a population was propounded. A single species population was defined as, "A basic taxonomic unit of a spatially and temporally defined ecosystem having meaningful properties such as birth rate, death rate, sex ratio and age structure, that can be estimated and described".

In this study the basic taxonomic unit was Wiseana cervinata (Walk.). The populations studied were those confined within improved and homogenous pasture systems in Canterbury and Otago. Therefore, unless otherwise stated, paddock fences marked the spatial boundaries of the populations studied in this project. The basic life table population was that confined within a .8 ha area.

Sampling objectives

Prior to commencing the development of sampling techniques, two dissimilar but somewhat complementary objectives were considered.

1. The development of life tables.
2. The economic assessment of porina damage.

The former presupposes frequent sampling to assess mortality during various stages in the life cycle. The latter is more concerned with the distribution characteristics of the damaging population over a more limited time period. In both cases a predefined accuracy is needed. This requires some precise mathematical knowledge of the variability of the population distribution pattern. This basic information is also required to determine optimum sample size and costs of sampling. In actual fact, time did not permit the pilot sampling necessary to obtain the above information. Therefore life table sampling was initially carried out using the maximum number of samples possible. As time permitted, more intensive studies on population distributions were carried out, mainly in conjunction with other studies. Later, some modification of life table sampling was made, although logistic and weather factors restricted rather than increased the sample number. Problems of labour and plot accessibility necessitated a reduction in sample number.

Nevertheless a certain amount of preliminary sampling work was carried out. This is described and discussed in approximately the order in which it occurred.

Sampling the life table study areas

Little time was spent in defining objectives, expressions of population, selection of universe and initial sampling mechanics. The objective was simply to quantitatively determine porina mortalities by measuring absolute populations as defined by Morris (1955). Being a subterranean insect, the selection of the universe was self evident. The only real

choice concerned the homogeneity and representativeness of the study areas. Soil type, topography and pasture type were important considerations.

There were two simple basic mechanics of sampling and they are described in more detail in the following sections.

1. A given area of soil was examined to sample egg and surface dwelling early larval instar populations. Funnels were used to sample eggs. Soil cores were used for the surface dwelling larvae.

2. A spade was used to remove a given volume of soil which was hand-sorted.

Later the following were determined from the analysis of results.

1. Error margins.
2. Population distribution patterns.
3. Timing of sampling.
4. Optimum sample size and number.
5. Cost of sampling.
6. Comparison of sampling techniques.

Error margins accepted for sampling life table study areas

There was little previous work available on subterranean insects to act as a guide to determine acceptable error margins of estimates of population numbers. Therefore the criterion used by the Canadian School of Insect Population Ecology was accepted. This meant trying to achieve a 10 per cent standard error of the mean for all population sampling. This decision

did not preclude the possibility that wider error margins would not suffice. Only after a large number of life tables have been developed for porina and other insects and analysed, will this problem be resolved.

Insect population distribution patterns

The study of moth flight behaviour, oviposition, larval movement and pasture damage, all indicated that larval population distributions have an aggregated or non-random characteristic. Many insect distributions can be described by a negative binomial model. Whether porina had such a distribution required proof. A decision also had to be made as to whether the distribution was skewed enough to affect sampling accuracy and the interpretation of life table data. This, and other aspects influencing porina distributions are detailed later.

Timing of sampling

The development of meaningful life tables dictates that as many age intervals as possible should be sampled. Because of the following reasons, however, a compromise was finally reached with a decision to sample at least six times over the life cycle.

1. It was impossible to determine the number of larval instars. Like many Lepidopterous species the number of larval instars varied considerably, depending upon local conditions (Perrott pers. comm.).

2. As this was a preliminary study, more emphasis

was placed on gathering the type of information urgently required for economic evaluation and practical control. Detailed life tables based on every age interval were therefore not required at this stage.

3. For this study it was decided that it was more appropriate for life table work to utilise changes in larval behaviour and seasonal weather patterns. Biologically significant time intervals were used for sample timing rather than specific age intervals.

4. There was considerable variation in larval size within a population. This made it impossible to determine clear cut times between age intervals.

5. Logistical problems made it impossible to adequately sample the widely scattered life table sites.

There are four periods in the porina life cycle which are biologically significant.

1. Egg.
2. Surface dwelling larvae.
3. Subterranean or tunnelling larvae.
4. Mobile dispersal stage.

It was finally decided to sample the following stages.

1. Egg stage.
2. Surface dwelling larvae
3. Autumn subterranean larvae.
4. Mid-winter subterranean larvae.
5. Prepupal stage.
6. Pupal stage.

As it was impossible to sample adequately the mobile moth stage, moth migration was deduced using the technique detailed by Pottinger (1967) and given on page 137.

The mechanics of sampling including cost, size and number of samples

These are virtually inter-related. To facilitate presentation, however, each of the age intervals will be briefly described and the sampling procedure for each discussed.

To clarify the discussions in the following sections concerning sample number, an outline of life table structure is given as follows. More detail can be obtained on pages 165 to 172.

There were three study areas i.e. Templeton, Winchmore and Hindon. The Templeton and Hindon study areas each consisted of six .8 ha plots (see Figures 12 and 14 on pages 167 and 169. Each plot was permanently marked out into twenty 20 m x 20 m square, subplots. The Winchmore site consisted of three plots each divided into forty 20 m x 20 m square subplots (see Figure 13 on page 168). The subplot was used as the basic area for determining the random positions of samples. Randomly paired ordinates in metres were selected and paced out beginning from a corner of each subplot. Every sample position was determined in this manner.

Initially four samples per subplot were taken giving a total number of 480 samples per study area; later the number taken was reduced to 240 per study area, for practical reasons.

Sampling the egg stage

As detailed earlier the small oval eggs about .2 mm long are randomly oviposited over the soil surface. Initially, vacuuming appeared an obvious sampling technique. Two machines were assessed, one of which was much more powerful than the other (Plates10 and 11). The machine shown in Plate 10 was an ordinary household "Electrolux" fitted with a small petrol engine which turned the fans at 8000 r.p.m. This gave an airflow of approximately 1200 c.c. per second. Nylon bags used in place of the dust catcher were used to catch the eggs. This machine was very useful for small plot work. The flexible hose and small nozzle made sampling easier in small areas.

The larger machine shown in Plate 11 consisted of a centrifugal fan .6 m in diameter connected to a 5 h.p. petrol engine reving at 5500 r.p.m. This gave an airflow of approximately 37,000 c.c. per second. Nylon bags were again used to trap the eggs. This machine was very effective for sampling large areas of about .5m^2 or more.

Both the machines were 95 - 98 per cent efficient in removing eggs from the soil surface, depending on plant cover and the thoroughness of the operator. The efficiency of both machines was tested by scattering 100 eggs over the normal sampling area used for each machine. Over ten trials, both machines picked up a mean of 97.7 per cent of the eggs with a range of $\pm$ 1.5 per cent. Both were quickly and easily operated. With the smaller machine a circular area 9 cm diameter could be sampled in about 180 seconds, while only 60 seconds was

required to sample an area of .5m^2 using the larger machine.

The disadvantage of the vacuum technique was the large amount of debris sucked up with the eggs. It was very difficult, time consuming and tedious to sort through these samples, even using Waller's (1968) technique of separating the eggs from the debris by running them down an incline. The time taken to sort through samples from the smaller machine varied between 10 and 30 minutes. Samples from the large machine sometimes took as long as 90 minutes to sort, depending upon the number of eggs to be counted.

Furthermore, the necessity of repeated egg sampling over the long flight period on three widely separated life table study areas, made this method most impracticable. On the other hand, for rapid egg sampling over a large area, this technique has merit, especially if the more powerful machine were used. It would be especially useful for sequential egg sampling, provided the sample time was carefully selected.

In an attempt to find a more absolute and less time consuming method the use of funnels implanted in the soil was investigated. An 11.4 cm diameter plastic funnel was placed inside a tin sleeve implanted in the ground (Plate 12). The reason this particular sized funnel was used was because it was the only cheap plastic funnel commercially available having the desired length of stem with a relatively small funnel area. A replaceable glass vial was attached to the funnel stem to catch the eggs as indicated in Plate 12. There was a small overflow hole in the funnel to allow excess rainwater to drain away. The maximum number of funnels used on each life table study area was two per subplot.

Plate 10 Vacuum machine used for sampling eggs from small plots.

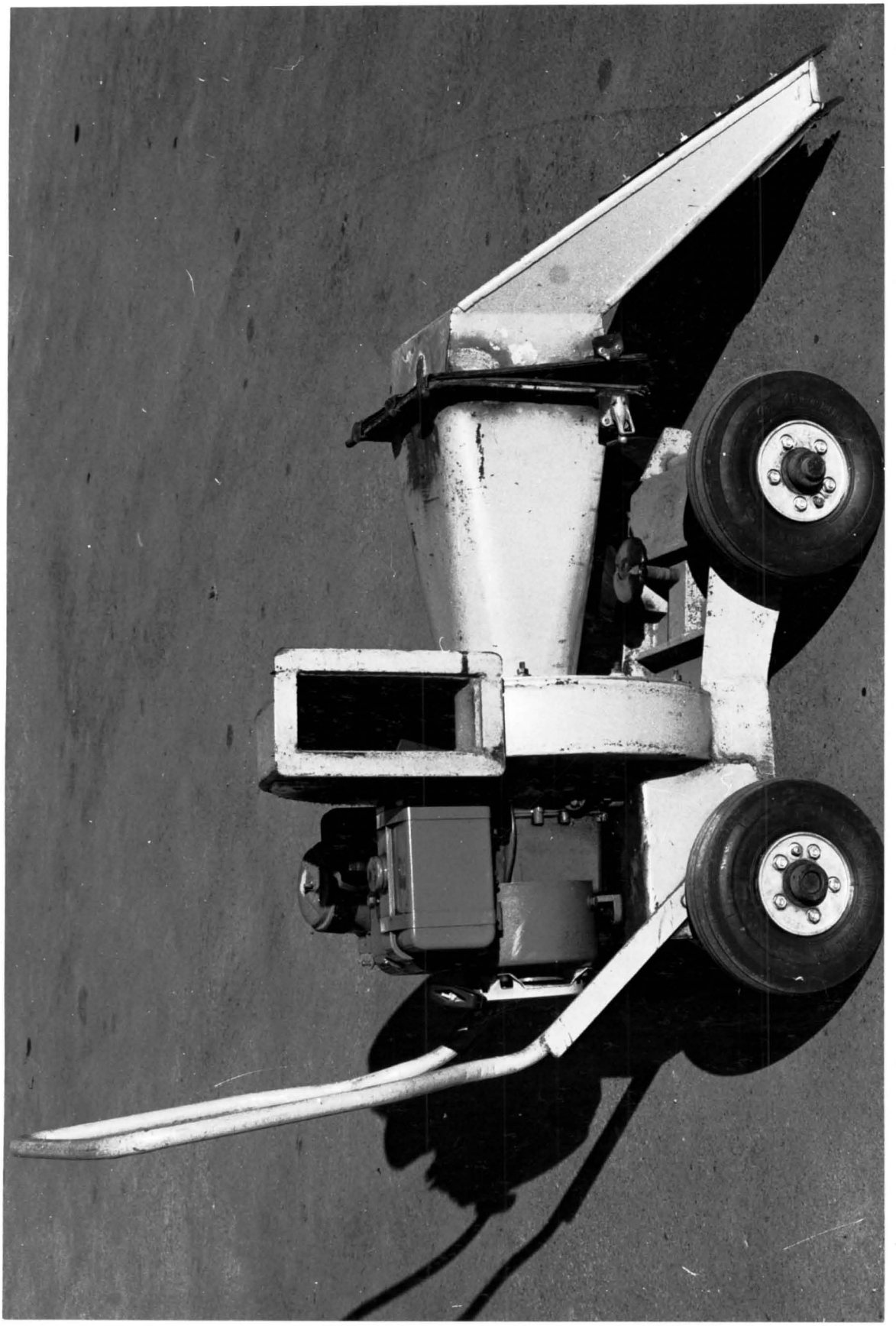


Plate 11 Vacuum machine used for sampling eggs from large areas.

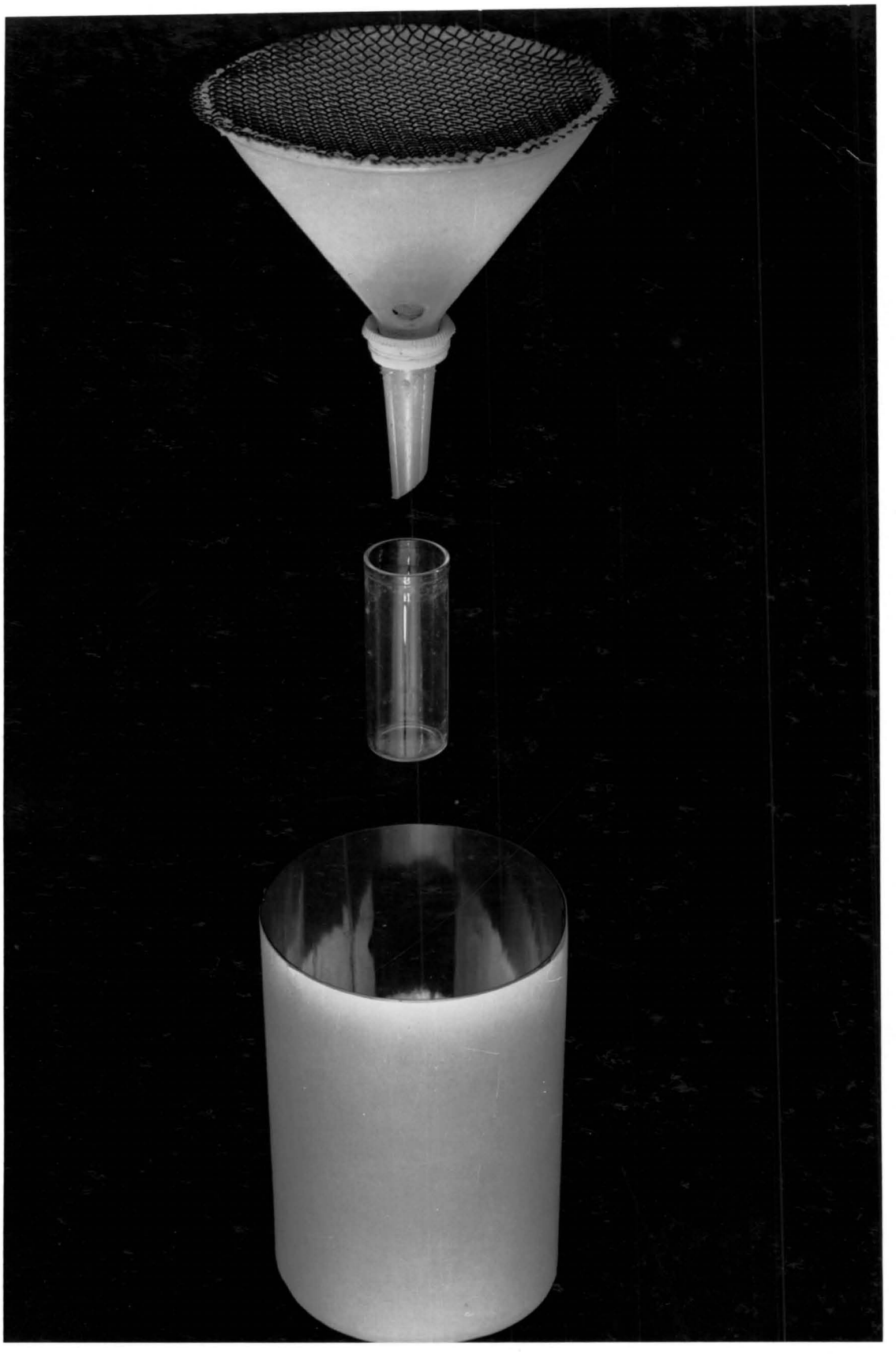


Plate 12 Plastic funnel arrangement used for sampling eggs from life table plots.

Plate 13 Soil corers 5.1cm and 7.6cm diameter used for sampling surface dwelling larvae.

Plate 14 Method of removing soil core and type of core produced when sampling for surface dwelling larvae.

Plate 15 Metal plate technique used for sampling subterranean larvae.
Note: Arrows mark tunnel entrances.

Plate 16 Enlarged view of larval tunnel entrances shown in Plate 15.

Plate 17 Pupa protruding from tunnel entrance prior to eclosion of moth.

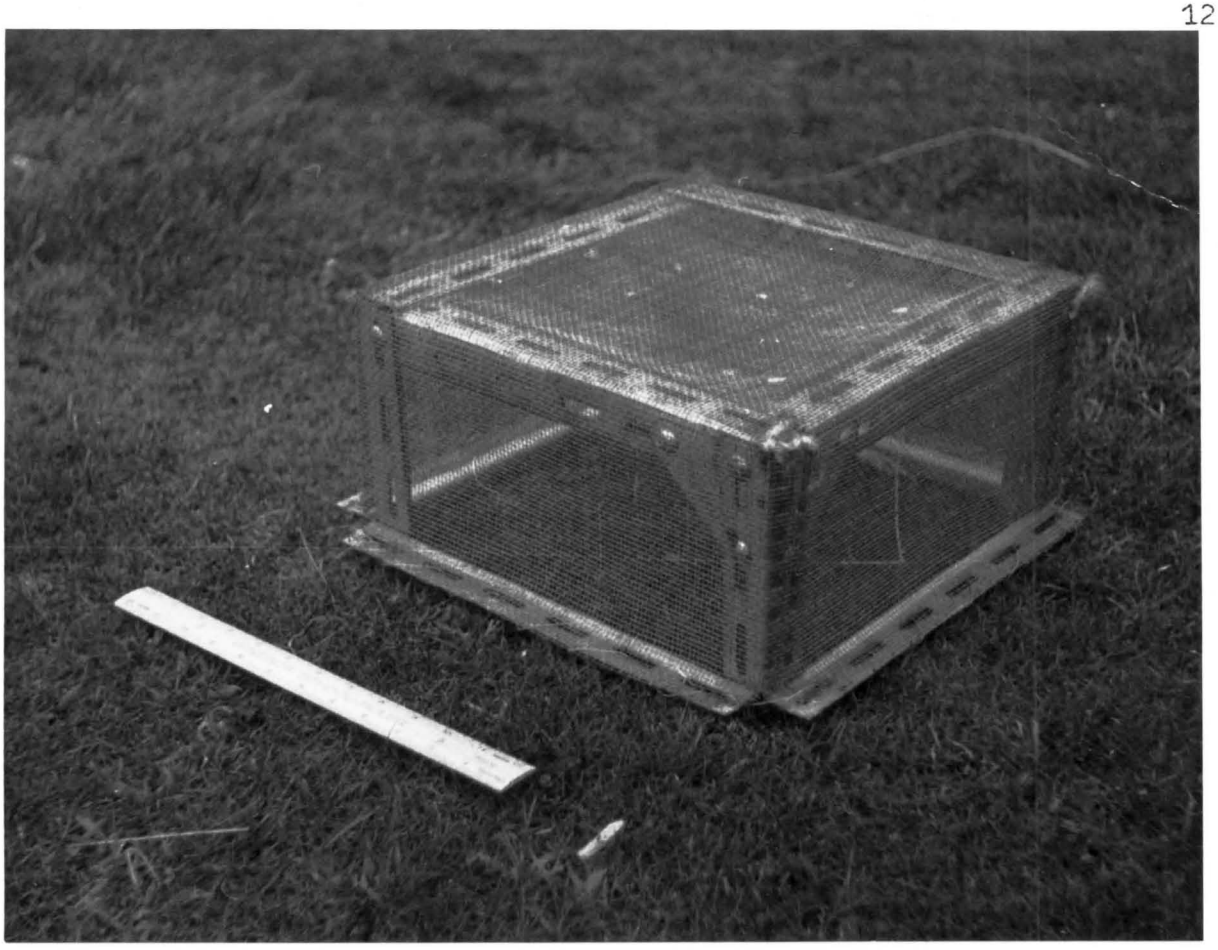


Plate 18 Cages used on the life table plots to protect exuviae from stock and wind.

After the first season's sampling (1968-69) a number of disadvantages became apparent

1. A number of female moths became trapped and laid their eggs in the funnel. This created artificially high population clumping. For example, some funnels contained over 3,000 eggs. This resulted in high standard errors and hence low accuracy (Table 8).

2. Collembola and worms sometimes became trapped in the collecting vial. They rapidly decomposed, with the result that eggs became most unpleasant to sort.

3. A certain number of funnels (up to 5 per cent) were destroyed by stock trampling. In the 1969-70 season, an eight gauge wire mesh was welded into the top of the funnels. This prevented moths from becoming trapped and to some extent reduced stock trampling effects. It did not, however, exclude Collembola or worms, which continued to be a problem.

Egg counting was carried out by tipping the vial contents onto a nylon stocking stretched over a 20 cm diameter funnel. A weak jet of water was used to gently shift the debris around which was closely examined under a well adjusted light. Porina eggs showed up as small, oval, black, shiny objects and were usually quite recognisable.

The advantage of using egg funnels was that once installed they continuously sampled eggs over the whole flight period. In order to obtain reasonable egg counts they required attention only three times a season. They also had the

advantage of being relatively cheap and easy to make.

On the other hand, counting the eggs was time consuming, tedious and at times unpleasant. Because this could cause counting errors samples were rechecked by different persons.

All life table egg counts are given in Tables 19, 20 and 21 (see pages 177, 181 & 183) together with 95 per cent confidence limits. Preliminary analysis of the egg counts showed that the percentage standard error of the mean was high in the first season but more acceptable in subsequent years once the funnels were meshed. Considering the large drop in numbers between the egg and surface dwelling larval stages plus the simplified type of life table envisaged, this egg sampling technique was considered adequate for this study. Work conducted over a number of seasons by Pottinger and Welsh (pers. comm.) indicated that a 5.1 cm diameter funnel also gave an acceptable estimate, provided the egg population did not fall below $300m^{-2}$. A similar conclusion was arrived at in this study after a comparison was made of three sample sizes using the vacuum technique (Table 9).

Sampling for surface dwelling larvae

As detailed earlier, newly hatched larvae rapidly sought well sheltered sites beneath plants and in soil cracks. Because of the high egg numbers normally encountered it was initially assumed that the juvenile larval numbers would also be high and that a small sample size would provide a reasonable population estimate. Small stainless steel cores were therefore developed with the following range of diameters - 2.5 cm, 5.1 cm, 7.6 cm, and 10.2 cm. This range of sizes was

Table 8 Egg frequencies and standard errors for each generation from Winchmore life table study area

1968-69			
No.	Frequency	No.	Frequency
0	44	413	1
1	6	499	1
2	1	556	1
3	3	560	1
4	3	677	1
5	3	811	1
6	2	825	1
7	1	848	1
8	1	1034	1
9	2	1038	1
16	1	1141	1
17	1	1363	1
24	1	1473	1
29	1	1679	1
31	1	1686	1
34	1	1722	1
25	1	1774	1
53	1	2012	1
60	1	2367	1
71	1	3600	1
84	1		
90	1		
97	1		
118	1		
123	1		
126	2		
147	1		
162	1		
176	1		
190	1		
194	1		
208	1		
215	1		
314	1		
317	1		
328	1		
358	1		
362	1		
373	1		
383	1		
398	1		

(118 samples)

$\bar{x}$ = 266.47

S.E. = 52.7

95% c.l. = ± 104.4

1969-70	
No.	Frequency
0	92
1	51
2	32
3	21
4	13
5	6
6	2
7	5
8	3
9	2
12	1
13	2
14	1
15	1
17	1
19	1
21	1
107	1

(236 samples)

$\bar{x}$ = 2.45

S.E. = .491

95% c.l. = ± .963

1970-71	
No.	Frequency
0	112
1	52
2	24
3	16
4	8
5	6
6	3
7	4
8	3
9	1
10	1
12	1
13	1
24	1
33	1
60	1
449	1

236 samples

$\bar{x}$ = 3.77

S.E. = 1.923

95% c.l. = ± 3.76

Table 9 Comparison of sample sizes for estimating the densities of porina egg populations

Date sampled: 19/11/68 - 22/11/68

Place: Winchmore life table study area

Sample sizes: 5.1 cm dia. core, 7.6 cm dia. core, 10.2 cm dia. core

Method: Motorized vacuum cleaner (see Plate 10)

Extraction: Hand sorting

Population 1

Sample size	Number of samples	$\bar{x}$	95% c.l.	% S.E.	c.v.	Number of samples required for 10% S.E.	per m^2 $\bar{x}$	per m^2 95% c.l.
5.1 cm	39	.61	± .325	26	165	272	297	± 159
7.6 cm	39	.95	± .446	23	150	225	201	± 95

Population 2

5.1 cm	60	6.9	± 1.6	11	89	79	3349	± 774
7.6 cm	59	9.11	± 1.8	10	76	59	1950	± 372
10.2 cm	59	10.03	± 2.4	12	93	86	1208	± 286

Key

Population 1 Low = approx. $< 300/m^2$

Population 2 Medium = approx. $> 300/m^2 < 2000/m^2$

Table 10 Comparison of sample sizes for estimating the densities of surface dwelling larval populations

Dates sampled: 6/1/69, 11/12/70, 16/12/70

Places: Lincoln (1), Ladbrooks (2), Ladbrooks (3)

Sample sizes: 2.5 cm dia. core, 5.1 cm dia. core, 7.6 cm dia. core, 10.2 cm dia. core

Method: Soil cores 50 mm deep

Extraction: Direct and Washing plus floatation

Population 1 (Direct extraction)

Sample size	Number of samples	$\bar{x}$	95% c.l.	% S.E.	c.v.	Av. time per sample (secs)	Number of samples required for 10% S.E.	per m^2 $\bar{x}$	per m^2 95% c.l.
5.1 cm	60	.55	± .21	19	147	-	216	265	± 105
7.6 cm	60	1.80	± .65	18	148	-	219	381	± 138
10.2 cm	60	2.56	± .66	13	96	-	92	397	± 74

Population 2 (Direct extraction)

2.5 cm	20	.25	± .23	44	200	156	400	488	± 445
5.1 cm	20	.50	± .56	53	238	360	566	244	± 254
7.6 cm	20	1.10	± .72	31	141	606	199	233	± 159

Population 3 (Direct extraction)

Sample size	Number of samples	$\sum x$	Av. time per sample (secs)	per m^2
2.5 cm	30	1	90	64.6
5.1 cm	30	0	240	-
7.6 cm	30	1	360	7.4
10.2 cm	30	8	900	32.1

contd.

Table 10 contd.

Population 3 (Washing extraction)

Sample size	Number of samples	Σx	per m^2
25.4 cm	30	0	-
50.8 cm	30	0	-
76.2 cm	30	0	-
102 cm	30	7	28.6

Key

Population 1 Medium
Population 2 Medium } see Table 9
Population 3 Low (statistical analysis meaningless)

Table 11 Comparison of sampling sizes for estimating the densities of surface dwelling larval populations

Dates sampled: 20/1/70, 2/2/70, 19/1/71

Place: Hindon life table study area

Sample sizes: 2.5 cm dia. core, 5.1 cm dia. core, 7.6 cm dia. core, 10.2 cm dia. core

Method: Soil cores 50 mm deep

Extraction: Direct and Washing plus floatation

Population 1 (Direct extraction)

Sample size	Number of samples	$\bar{x}$	95% c.l.	% S.E.	c.v.	Av. time per sample (secs)	Number of samples required for 10% S.E.	per m^2 $\bar{x}$	per m^2 95% c.l.
2.5 cm	30	.16	± .120	52	286	176	817	327	± 329
5.1 cm	30	.4	± .295	36	198	374	392	191	± 138
7.6 cm	28	.72	± .43	29	155	790	240	148	± 95

Population 1 (Washing extraction) (Sample already partially broken)

2.5 cm	30	.16	± .170	52	286	60	817	327	± 328
5.1 cm	30	1.0	± .372	18	100	140	100	477	± 180
7.6 cm	28	1.4	± .385	14	74	160	55	297	± 85

Population 2 (Direct extraction)

5.1 cm	244	.078	± .043	28	431	-	1860	38.2	± 21.1

Population 2 (Washing extraction) (Sample already partially broken)

5.1 cm	244	.143	± .051	18	280	36	784	68.9	± 24.4

contd.

Table 11 contd.

Population 3 (Direct extraction)

Sample size	Number of samples	Σx	Av. time per sample (secs)	per m^2
2.5 cm	20	0	120	-
5.1 cm	20	1	300	24.4
7.6 cm	20	2	480	22.3
10.2 cm	20	1	1320	6.4

Population 3 (Washing extraction)
(sample partially broken)

2.5 cm	20	0	60	-
5.1 cm	20	0	90	-
7.6 cm	20	1	120	11.6
10.2 cm	20	4	180	24.4

Key

Population 1 Medium)
Population 2 Low) see Table 9
Population 3 Very low) statistical analysis meaningless

Table 12 Comparison of sample sizes for estimate of the densities of autumn and winter subterranean larval populations

Date sampled: 14/5/68

Place: Russley Road, Christchurch

Sample size: 10cm x 10cm and 15cm x 15cm spade square

Method: Removal of a spade square of soil to a depth of 203-209 mm

Extraction: Direct - sample placed on sack and soil carefully sorted through by hand

Sample size	Number of samples	$\bar{x}$	95% c.l.	% S.E.	c.v.	Number of sample required for 10% S.E.	per m^2 $\bar{x}$	per m^2 95% c.l.
10 cm x 10 cm	50	2.16	.581	13	95	90	201	± 53
15 cm x 15 cm	50	1.96	.502	13	91	83	95	± 32

considered wide enough to assess sampling accuracy. The thin-walled cores were easily pushed down to a depth of 5 cm into most soil types, although some difficulty was found under very dry conditions and in the stony Lismore soils at Winchmore. Plates 13 and 14 show the construction of the 5.1 cm and 7.6 cm corers, the method of removing the core and the type of core produced.

Surface dwelling larvae were not sampled until they were of sufficient size to be easily seen. This meant sampling was carried out about five to six weeks after peak hatching. Initially the soil cores were assessed in the field using a mounted needle to gently lift and probe the surface of the core. Visual assessment was aided by removing the bulk of the plant material with a pair of scissors. No larvae were ever found on this material. Later on, operator comfort was improved by examining the samples in the laboratory.

A washing technique developed by Pottinger and Welsh (pers. comm.) was also used, both for a comparison and as a check on direct assessment. The washing technique was not developed for use by itself, but as a stage towards improving direct examination. The results of the comparisons are given in Tables 10 and 11.

The direct method of assessment appeared to be just as accurate overall as the washing, because in most cases the 95 per cent confidence limits overlapped. The means did, however, vary considerably. This statistically insignificant difference was attributed to larval size variations, to some extent sample size and the small sample number. Large larvae (greater than 5 mm long) were easily counted by the direct

method and surprisingly, so were the very small larvae (2 mm long), especially in the 2.5 cm and 5.1 cm diameter samples. On the other hand, although the washing method was slightly more accurate in some cases, surface tension difficulties coupled with excess debris, allowed small to medium sized larvae (2 mm - 3 mm) to be easily missed. It was considered that direct assessment by examining the dry sample, with a check by washing, was a method capable of giving the absolute number of larvae per sample.

The error inherent in either technique lay in the number of samples assessed and to some extent the timing of sampling, as the larger the larvae, the easier they were to see.

Other results presented in Tables 10 and 11 revealed that, generally there was little difference in sample accuracy between any of the cores tested. There were two exceptions. Firstly, when the comparisons were based on low population levels, and secondly the smallest sample size (2.5 cm) was always associated with high percentage standard error of the means.

Because overall there was little statistical difference between the different sized samples the final choice of sample size rested on the cost of sampling. Although the 2.5 cm diameter sample was the smallest and easiest to directly visually assess, the high standard errors and the large number of samples required to achieve an acceptable estimate of the population were considered impracticable for general life table work.

The largest of the remaining sample sizes tested (10.2 cm) was found to be costly in the time taken for assessment,

tedious to search through and too bulky to handle. It caused considerable operator fatigue. The 7.6 cm diameter sample also presented similar difficulties although the cost of sampling (time) was considerably reduced by approximately two-thirds. The 5.8 cm diameter sample was the most acceptable on all counts, i.e. accuracy, cost and ease of assessment. Sampling low populations less than $190/m^2$ with this sized sample could, however, result in high percentage standard errors of the means if the sample number taken was not increased. Initially, the results suggested that 200 to 400 5.8 cm diameter samples for each life table study area would give a reasonable percentage standard error of the mean (approximately 10 per cent) for populations as low as $190/m^2$. I_n the study, however, the percentage standard error of the means of some life table populations sampled were as high as 20 - 35 per cent. This error margin however, was considered acceptable for the following reasons.

1. Replication between and within life table study areas gave greater confidence in the conclusions arrived at from sampling results even though sample error margins were high.

2. Calculations showed that very high mortality occurred during the surface dwelling larval age interval. This meant error margins could be somewhat higher for this age interval without unduly influencing any conclusions. Measuring small changes in survival would obviously require greater sampling accuracy.

3. The cost of narrowing error margins was prohibitive considering the limited time and labour available.

It was finally estimated that it would require approximately 24 man hours to assess 240 5.8 cm diameter cores, taken from one life table study area (Table 13). This was a minimum of two samples per subplot. The estimate of cost did not include travelling time, nor delays caused by weather and transport difficulties. When these factors were considered 240 samples was the maximum number practicable. Although initially, double the number per subplot were taken it was found that the slight increase in accuracy was not worth the proportionally greater amount of effort involved.

Sampling the subterranean larval (autumn and mid-winter), prepupal and pupal stages

Once larvae formed tunnels, they were difficult to sample. Larvae began to form tunnels in early January in Canterbury and early February in Otago. All subterranean stages, including the prepupal and pupal were sampled by the removal of a cubical volume of soil with a surface area of 15 cm x 15 cm square taken to a depth of approximately 25 cm, or down to the subsoil. Larvae were never found in the subsoil.

As the soil was removed it was placed on a sack or tray, broken up by hand and carefully sorted through. Drought conditions caused problems, as dry lumpy soil made the sorting operation difficult and time consuming.

The time taken to dig, sort, count and return the soil to the hole was approximately 3 - 5 minutes depending upon the

soil structure.

From previous insecticide work a volume of soil cut out by a spade had been used as the sample unit, the surface area being either an 18 cm x 18 cm square or a 30 cm x 30 cm square. Preliminary work showed that both these sizes were too big for the following reasons.

1. The time taken to sort through the large amount of soil was excessive. Up to ten minutes could be spent on one sample.

2. It took too long to cut a hole greater than the spade width.

3. The chances of finding small larvae (less than 12 mm long) decreased as the volume of soil increased.

4. It was extremely difficult to remove large samples from stony soils.

After consideration of these problems, it was finally decided to use a 14 cm wide spade which was commercially available. This was used to take a 15 cm x 15 cm square sample (= $.023m^2$) to a depth of approximately 25 cm. This sample size was found suitable in all respects even on stony soils, provided they were not too dry.

In this study four samples per life table subplot were initially taken. This gave reasonable accuracy for bulked data approaching the 10 per cent standard error of the mean.

Bulking of the results was achieved by adding together the sample units from various plots. For example, at Hindon the results from three plots each having the same treatment

were added together to increase the sample number from a total of 40 (one plot) to 120. This had the effect of reducing the standard error of the mean. In comparison the percentage standard error of the means for single plots ranged from 11 per cent to 30 per cent depending upon population density. Later, sample number was decreased to two per subplot, mainly due to labour problems and harsh winter weather conditions, particularly at Hindon. This increased the sampling error margin, but it was considered still sufficiently low for this type of broad based ecological study. Even with the decreased number of samples the percentage standard error of the mean for the bulked figures still ranged between 12-15 per cent, although the percentage standard error of the means for single plots were sometimes as high as 35 per cent especially for low populations.

It is still inconclusive, however, whether the 10 per cent standard error of the mean originally aimed at, is necessary or practical when studying subterranean insects. Analysis of completed life tables later in this study suggested it was not.

Sampling the prepupal and pupal stages

Both the prepupal and pupal stages were sampled with the 14 cm wide spade. The timing of when to sample was based mainly on a calendar date, although initially pilot sampling was carried out. This showed when the majority of larvae were in either the prepupal or pupal stage.

Sampling the adult stage

It was extremely difficult to sample the adults once they

had eclosed. The method used in this study was to sample the initial moth number by counting exuviae and then estimate moth mortality. This was done by calculating the difference between expected and actual eggs (Pottinger, 1967).

Exuviae were relatively easy to count as they were usually found lying on the soil surface or protruding from the tunnel entrance (Plate 17). Although relatively robust they were easily swept away by winds. For protection from both wind and stock a number of .3 m x .3 m square wire mesh cages were constructed about 15 cm high (Plate 18). These very robust cages were placed on some Hindon life table plots only, about late October. As the cages were expensive to construct, 40 cages only were used. Two plots were chosen at random and 20 cages sited on each. They were left undisturbed till late January when they were lifted, the vegetation cut down to ground level, and the exuviae and hatched moths trapped under the cage, counted.

Alternative sampling techniques for subterranean larvae

To find less tedious sampling methods, other techniques were tested. A rapid method was also required for large scale population surveys and sequential sampling.

One very promising technique consisted of cutting and removing the turf to a depth of 1-2 cm. A 30 cm x 30 cm square sheet of 16 gauge galvanised flat iron was placed over the cleared area. The plates were lifted in two - three days, during which time most of the larvae had cleared their blocked tunnels. The entrances were clearly visible and easily counted (Plates 15 and 16).

A single trial carried out, showed that approximately

80 per cent of the larvae were accounted for. Those larvae which did not clear their tunnels were either in a moulting phase, diseased, or undergoing a rest period during their feeding cycle. A correction factor would bring the means obtained from such a method well within the 95 per cent confidence limits of the means obtained from more absolute sampling methods.

The advantages of such an easy and quick method are obvious. It would be very suitable for use with sequential sampling and assessing damage over large areas.

Final plan for the sampling of life tables

After a certain amount of preliminary work the sample plan given in Table 13 was used for life table work.

During the egg stage the funnels were examined at least twice. The eggs were visually counted using the method described on page 125.

Samples taken for suface dwelling larvae were visually assessed in the laboratory. A proportion of the samples were later washed to compare and check the accuracy of the direct visual assessment.

For determining the density of autumn and mid winter subterranean larval populations the samples were sorted in in the field as described earlier on page 135.

Sampling for the prepupal and pupal stages was timed so that the maximum number were in each relative stage. Unchanged larvae were recorded and included in these counts.

Exuviae counts were carried out in late January by removing the grass and closely examining the soil surface

Table 13 Summary of final sampling plan for life tables

Age interval	Type of sample	Size of sample	No. of samples to achieve a 10-20 percent standard error of the mean			Cost for sampling and extracting-per study area (man hours)
			Per sub-plot	Per plot	Per study area	
Egg	Wire meshed topped plastic funnel	11.4 cm diameter	2	40	240	32
Surface dwelling larvae	Soil core	5.8 cm diameter approx. 3 cm deep	2	40	240	24
Autumn subterranean larvae	Spade square	15.0 cm x 15.0 cm sq. x approx. 23-25 cm deep	2	40	240	30
Mid Winter subterranean larvae	Spade square	15.0 cm x 15.0 cm sq. x approx. 23-25 cm deep	2	40	240	24
Prepupal	Spade square	15.0 cm x 15.0 cm sq. x approx. 23-25 cm deep	2	40	240	24
Pupal	Spade square	15.0 cm x 15.0 cm sq. x approx. 23-25 cm deep	2	40	240	24
Initial moth number	Wire cage	30 cm square	1	20	40	16

previously covered by a cage.

Adult survival was deduced by calculating the difference between actual eggs sampled and the expected number which should have been laid.

Overall, the sampling plan, as shown in Table 13, meant visiting the life table study areas six times a year, but only about 1-2 per cent of the surface area of each 20 m x 20 m subplot was disturbed. It was assumed that this did not constitute a significant human induced mortality. When sampling, movement over the plots was kept to a minimum at all times to reduce possible human induced porina mortality.

DISTRIBUTION PATTERN OF THE SUBTERRANEAN LARVAL STAGES

Introduction

It was obvious from a preliminary analysis of field counts and observation of damaged areas that porina larval populations were overdispersed or aggregated (Bliss and Owen, 1958). Further investigation of this distribution pattern was considered necessary for the following reasons.

1. To ascertain the degree and type of aggregation and to determine whether transformation of life table data would be required for meaningful analysis and interpretation.

2. To determine the biological mechanisms involved in causing aggregation and whether or not such mechanisms could be used to complement life table mortality data and be of use for the prediction of porina infestations.

3. To assist in the development of simplified sampling systems, e.g. sequential.

4. To allow meaningful interpretation of economic injury thresholds.

Methods

For this particular study a paddock population was considered as the biological unit and sampled as such. The distribution of infested paddocks on a regional basis was not considered at this stage. This regional distribution pattern was thought to be more dependent on the interaction between farm management practices and geographical differences as well as biological effects.

As labour was limited and pasture damage usually only became significant in autumn, it was decided to restrict the study of larval distribution patterns to the autumn sub-terranean stage.

The following were considered before the sampling plan was finalised.

1. The number of samples required per population in relation to;

   (a) population density
   (b) the proposed sample pattern
   (c) size of paddock
   (d) available labour
   (e) time available

2. The number of populations required to obtain

sufficient results to meaningfully calculated a common k* factor. The symbol "k" stands for one parameter used to describe the negative binomial distribution model (Waters, 1959).

3. Size of sample unit.

The number of samples was initially estimated by extrapolating results obtained from life table work. Calculations showed that two 15 cm x 15 cm spade square samples on a 20 m x 20 m square taken over 2.43 ha (= 122 samples) gave a percentage standard error of the mean of approximately 15 per cent for a population density of 44-55/m^2.

The average size of Canterbury farm paddocks was assumed to be between 8 ha and 12 ha (Frengley, pers. comm.). To achieve a 10-15 per cent standard error of the mean would therefore require approximately 300 - 500 samples per paddock, depending upon the population density. In order to determine sample positions, a grid system which could be paced out was decided upon for a number of reasons.

1. A systematic grid system which could be paced out in lines was about a third faster and easier to manage than a random system.

2. A number of different sized paddocks were sampled each year. The grid system was readily adaptable to obtain the required sample number by merely altering the grid size.

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*Footnote: For convenience and because it resulted in a tidier script it was decided not to italicise formulae nor single mathematical symbols mentioned in the text.

3. The results from a grid system were easier to decipher from field notes and maps.

4. The use of a random system can sometimes cause artificial clumping of the population under study.

The sample size used successfully on the life table plots was an obvious choice, viz. 15 cm x 15 cm sample dug by a spade 14 cm wide.

The first paddock sampled served as a trial run. This was a badly infested paddock (55-66 larvae/m^2) at Templeton, which was selected after a certain amount of pilot sampling. Four hundred and seventeen samples were taken with the aid of a 14m grid. Provisional analysis to determine the percentage standard error of the mean and mapping the counts in the laboratory, indicated that the grid system gave an acceptable result. The same system of sampling was used on a number of paddocks for three years.

The results were compared and contrasted with those obtained from paddocks sampled earlier. This enabled minor sampling modifications to be made when required. It also assisted in understanding the formation of the distribution patterns and the environmental influences involved.

Methods of analysis and results

Visual method of analysis

Frequency distributions of the data were graphed (Figure 9) to determine whether the distributions were skewed or normal. They are obviously skewed.

Statistical method of analysis

The variance (s^2) and mean $\bar{x}$ were calculated for each population and the results graphed in Figure 10. From the general trend of the plotted points it was obvious that the distributions were not normal (s^2 independent of $\bar{x}$) nor Poisson ($s^2 = \bar{x}$) nor any distribution implying a lineal relationship ($s^2 = a\bar{x}$) where a is a constant. The curve plotted in Figure 10 ($s^2 = \bar{x} + \frac{\bar{x}2}{.808}$ where k = .808) represents the relationship to be expected between s^2 and $\bar{x}$ for a negative binomial model with a k value of .808. The curve was not fitted mathematically and the value of k was obtained only as an approximation, using a formula given by Katti and Gurland (1962).

$$k = \frac{\bar{x}^2}{s^2 - \bar{x}} \qquad \text{----------} \quad (1)$$

Nevertheless, the curve fitted the plotted points reasonably well, therefore it was concluded that the population counts were adequately represented by the negative binomial distribution model. The k value of .808 can also be thought of as an approximate k_c value for the data given in Figure 10.

Calculation of the negative binomial distribution parameter (k).

A computer programme was developed to determine the k parameter using Method II of Anscombe (1949) (Table 14).

The method consists of equating the observed proportion of zeros to the expected proportion given by,

$$Po = \left(1 + \frac{m}{k}\right)^{-k} \qquad \text{---------- (2)}$$

where m = the mean of a negative binomial distribution model.

The actual computation for k is to choose k by successive approximation to satisfy the formula.

$$No = \left(1 + \frac{\bar{r}}{k}\right)^{-k} \qquad \text{---------- (3)}$$

where $\bar{r}$ is the best estimate of m and N = the sample number.

Testing the fit of the negative binomial.

Further statistical confirmation of the suitability of the negative binomial was obtained by using the two methods given by Southwood (1966). This involved calculating the statistics U and T and comparing their respective standard errors (Table 15).

The statistic U, which is the difference between the actual variance and the expected variance is given by the following formula

$$U = s^2 - \left(\bar{x} + \frac{\bar{x}^2}{k}\right) \qquad \text{---------- (4)}$$

If U is significantly less than its standard error then the negative binomial may be taken as a satisfactory model.

The value of T involved the calculation of the difference between the skewness of the data and its value predicted from the mean and variance of the same sample.

$$T = \left(\frac{\sum f\bar{x}^3 - 3\bar{x}\sum f\bar{x}^2 + 2\bar{x}^2\sum fx}{N}\right) - s^2\left(\frac{2s^2}{\bar{x}} - 1\right) \text{--- (5)}$$

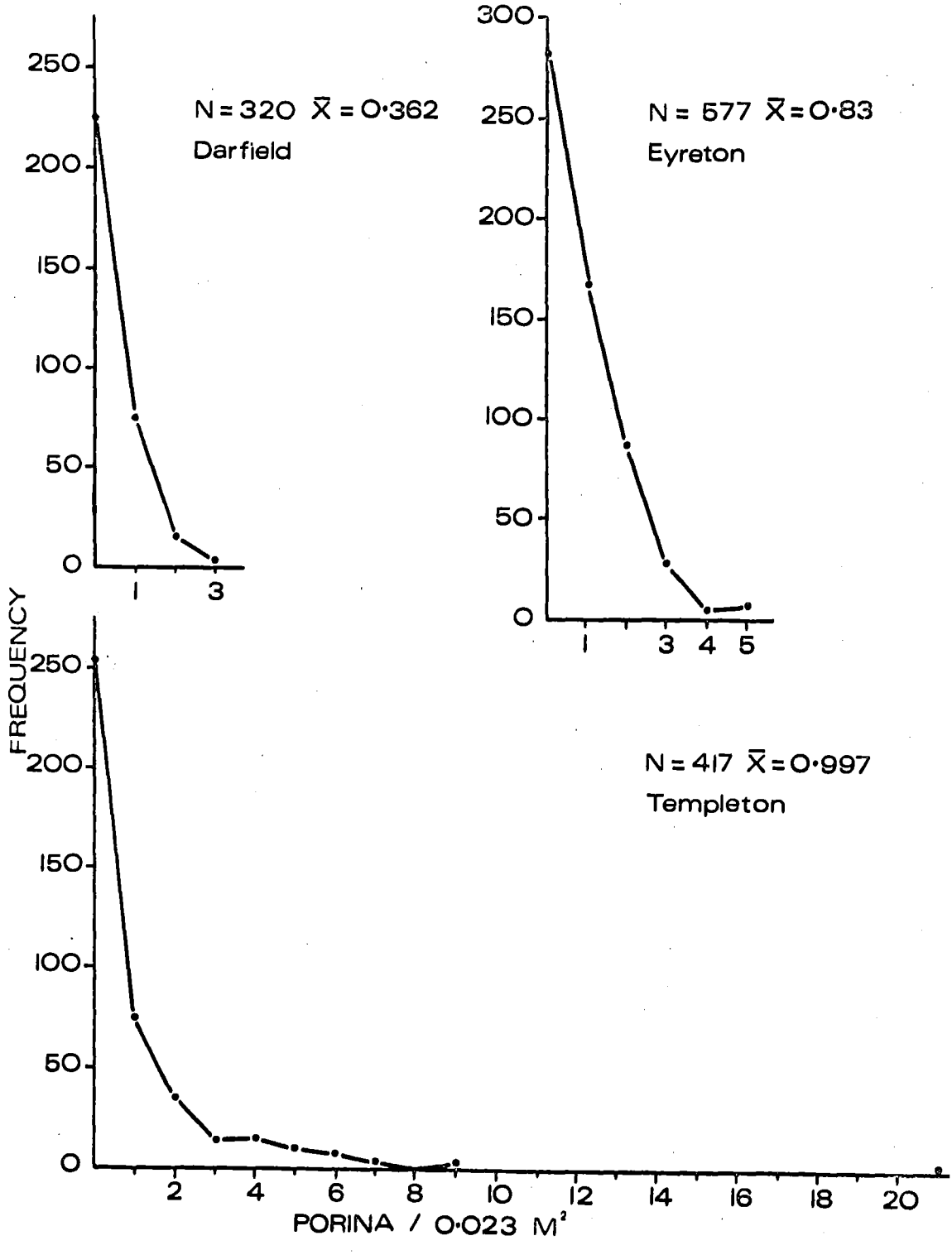


FIG 9

Graphs of frequency distribution data for subterranean larval populations sampled at various locations.

Contd.

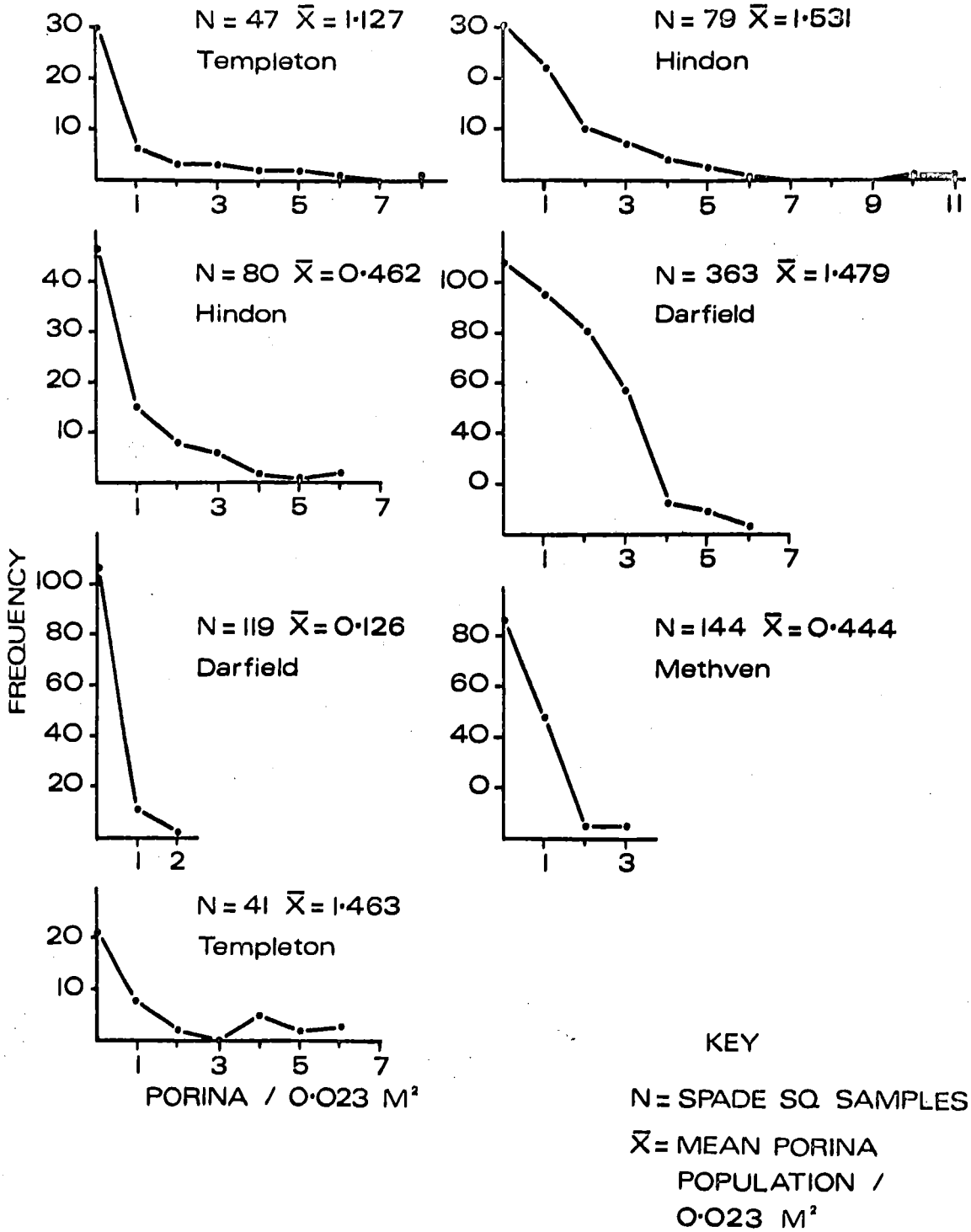


FIG 9 contd.

Graphs of frequency distribution data for subterranean larval populations sampled at various locations.

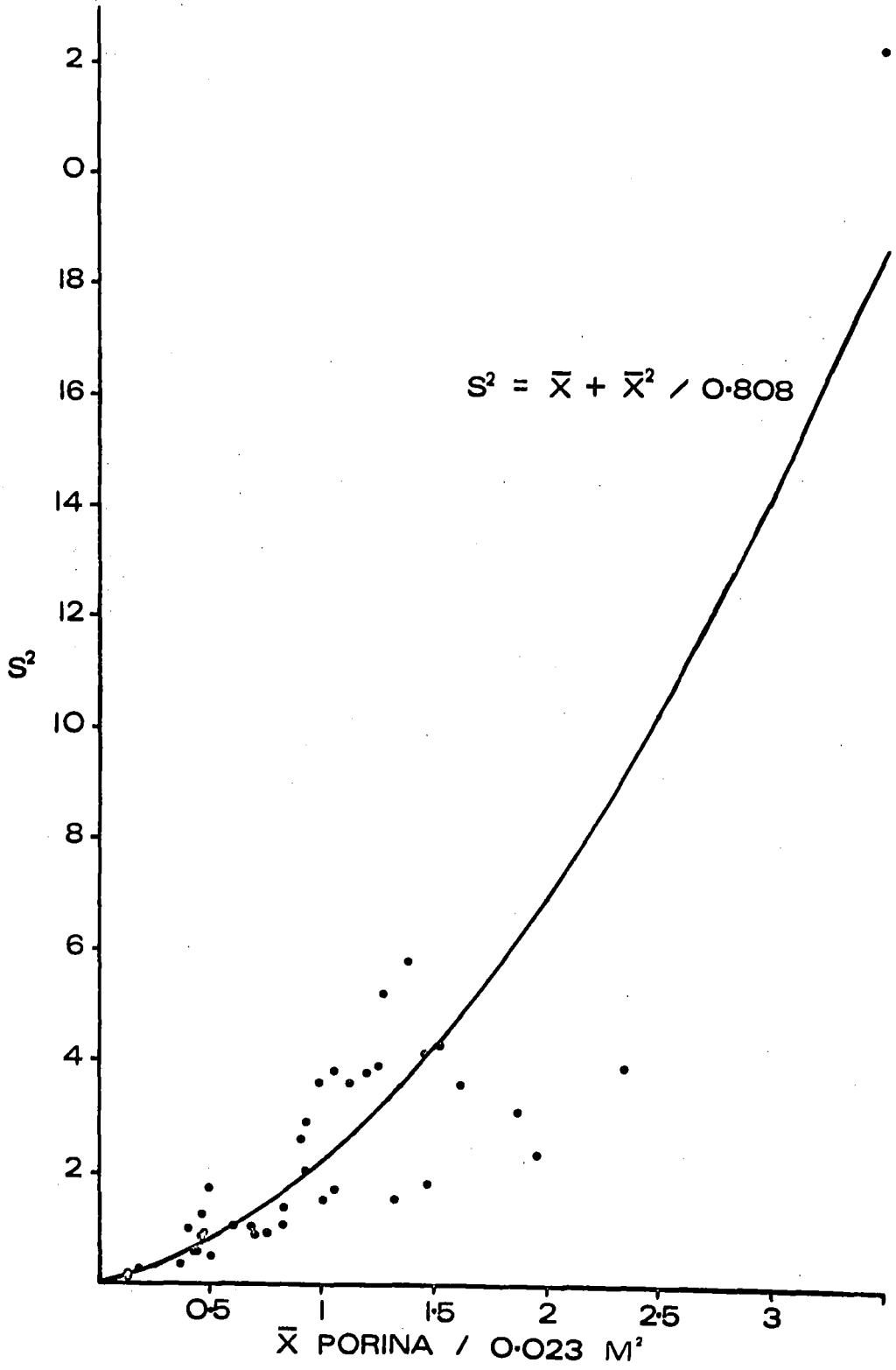


FIG. 10

Relationship between the variance (S^2) and the mean ($\bar{x}$). The curve represents the relationship to be expected between S^2 and $\bar{x}$ for a negative binomial distribution with a k value of .808.

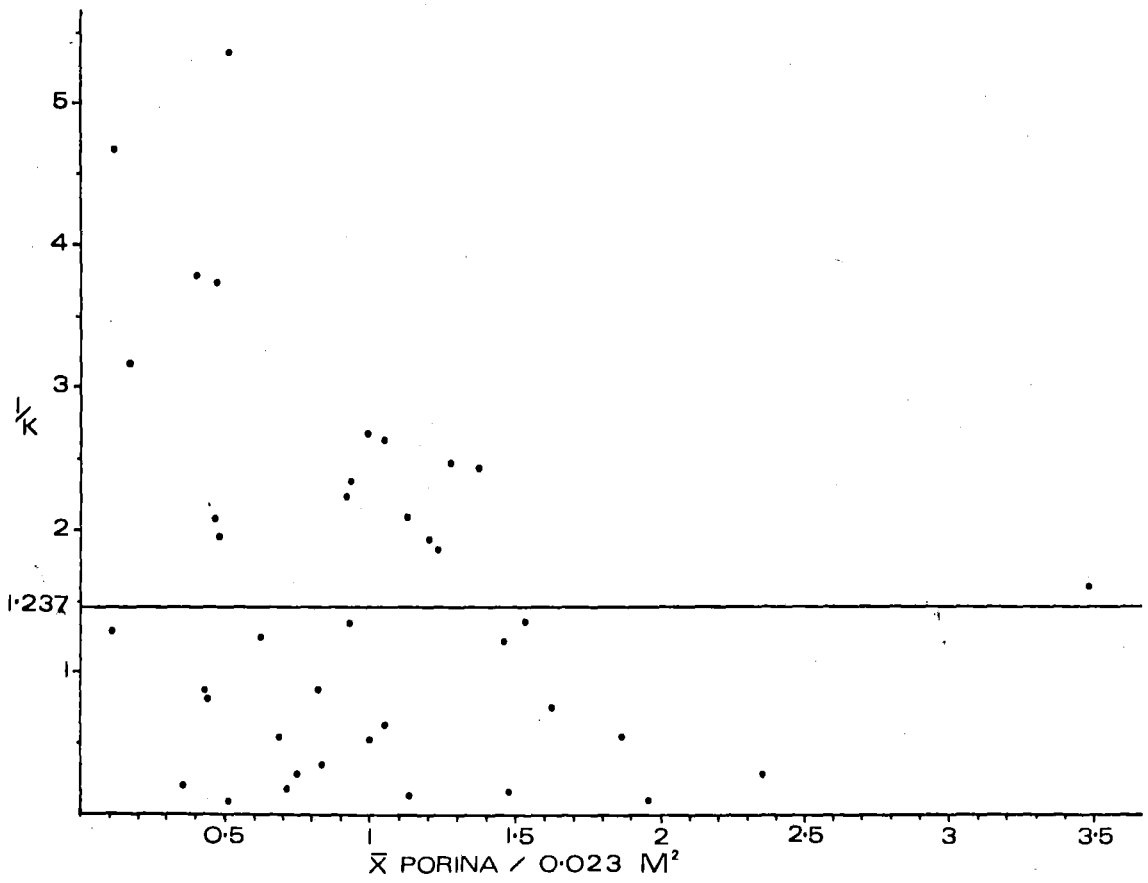


FIG. 11

Relationship between $\frac{1}{k}$ and the mean ($\bar{x}$) for subterranean larval populations (see text p 153).

Table 14 Calculated k values for subterranean larval populations sampled in Autumn

	Place	Year	$\bar{x}$ per .023m^2 spade square sample	k	$\frac{\bar{x}}{k}$
1	Templeton	1969	.997	.403622	2.470
2	Lincoln	1968	1.625	1.24154	1.308
3	Russley	1968	2.366	3.66611	.645
4	Eyreton	1968	.830	2.68381	.309
5	Hindon	1970	1.531	1.00321	1.526
6	"	"	.935	.44396	2.106
7	"	"	1.379	.369748	3.729
8	"	"	.462	.746426	.618
9	"	"	.687	2.02348	.339
10	"	"	1.052	1.03310	1.018
11	"	"	1.000	1.99372	.501
12	"	"	.925	.625281	1.479
13	"	"	.468	.242017	1.933
14	Methven	1969	.444	1.90920	.232
15	Methven	1969	.747	4.12982	.180
16	Southbridge	1968	.610	.723348	.843
17	Darfield	1969	.362	4.90305	.073
18	Methven	1969	.506	13.8445	.036
19	Methven	1969	.715	4.86153	.147
20	Darfield	1969	1.333	11.3333	.117
21	Darfield	1969	1.965	10.6642	.184
22	Hororata	1968	.126	.739132	.170
23	Lincoln	1970	.171	.25398	.673
24	Hindon	1969	.125	.300549	.415
25	"	"	.475	.658894	.720
26	"	"	.428	1.01921	.419
27	Templeton	1968	1.069	.433249	2.467
28	"	"	1.243	.504557	2.463
29	"	"	1.463	.516931	2.830
30	"	"	3.488	.646467	5.395
31	"	"	1.872	1.59311	1.175
32	"	"	1.204	.48378	2.488
33	"	"	.510	.24227	2.105
34	"	"	1.127	.346905	3.249
35	"	"	.911	.572471	1.591
36	"	"	.826	1.12732	.732
37	"	"	.400	.289608	1.381
38	"	"	1.277	.430945	2.963
Total			39.133		
$\bar{x}$			1.003		

Table 15 Calculated T, S.E.T., U and S.E.U. values (see Southwood 1966) for testing the goodness of fit of the negative binomial model (see text p. 146)

T	S.E.T.		U	S.E.U.
5.37677	3.8585		188	.366
.914911	4.76992		.433	.675
.0330	.117379		.005023	.0058
1.81696	3.171		.2846	.4472
-14.9633	20.021		-1.4513	1.5617
-.0258	.0414		-.0074	.005
-7.384	22.595		-1.1577	1.458
-0.0146	.017		-.00348	.0009
-.6804	.355		-.05166	.1205
-.11174	.13945		-.0114	.0499

Table 16 Calculation and tests for a k_c value for subterranean larval populations sampled in autumn. See text, pages 155 to 157.

Unweighted estimates of k_c

k_{c1}

From equation one given in text. k_{c1} = .808

k_{c2}

From " nine " " " k_{c2} = 1.168

k_{c3}

From " ten " " " k_{c3} = .64

Weighted estimates of k_c

k_{c4}

From equation 11 given in text. k_{c4} = .694

Tests for agreement with a single k_c

1 χ^2 test using equations 13, 14, 15 given in text

χ^2 = 246.4 with 37 d.f.

2 ANOVA test using equations 16, 17, 18, 19, 20 given in text

	d.f.	$\bar{x}$ sq.	F	
Slope $\frac{1}{k_{c4}}$	1	454.53	66.67	xx
Computed intercept against 0	1	.988	.144	N.S.
Error	36	6.817		

Confidence limits

From equation 21 given in text V = .0288 S.D. = .5367

95% c.l. = .184

$\therefore$ k_{c4} = .694 $\pm$ .184

The value of T was then compared with its standard error given by the following formula.

$$\text{S.E. } (T) = \sqrt{\frac{2\bar{x}(k+1)\,\frac{\bar{x}^2}{k^2}\left(1+\frac{\bar{x}}{k}\right)^2\left[2\left(3+5\,\frac{\bar{x}}{k}\right)+3k\left(1-\frac{\bar{x}}{k}\right)\right]}{N}} \quad \text{--- (6)}$$

If the negative binomial is a satisfactory model, T will be significantly smaller than its standard error.

As both U and T were less than their respective standard errors (Table 15) it was concluded that the negative binomial was a satisfactory model which could describe the population distribution pattern of this particular age interval.

Justification of calculating a common k.

The calculation of a common k (= k_c) is needed for data transformation in any analysis of variance involving skewed data and for developing sequential sampling systems. To determine whether a common k is justified, a test of sample homogeneity is required. This was carried out graphically as shown by Southwood (1966), by plotting $\frac{1}{k}$ against the mean (x) of each population sampled (see Figure 11). The value of $\frac{1}{k}$ also equals $\frac{X'}{Y'}$.

The values of X' and Y' were calculated using the following formula.

$$X' = \frac{\bar{x}^2 - s^2}{N} \quad \text{---------- (7)}$$

$$Y' = s^2 - \bar{x} \quad \text{---------- (8)}$$

As no significant clumping or trend could be seen, it was concluded that the fitting of a common k was justified. The line drawn in Figure 11 was fitted using the first estimate of k_c (= .808) calculated from equation 1 and calculating $\frac{1}{k_c}$ to

equal 1.237.

Calculation of k_c.

A provisional estimate of k_c was given as .808 (k_{c1}) (Figure 10). For a more precise estimate the following equations detailed in Bliss and Owen (1958) were used.

$$\frac{1}{k'} = \frac{\sum Y'}{\sum X'} \qquad \text{---------- (9)}$$

where k' = a provisional value of k_c

$$k' = \frac{g}{\sum \frac{Y'}{X'}} \qquad \text{---------- (10)}$$

where g = the number of ratios $\frac{Y'}{X'}$

This gave estimates of k_c as 1.168 (k_{c2}) (equation 9) and .64 (k_{c3}) (equation 10) (Table 16).

It is stressed that these values are provisional. They would, however, be adequate for most analyses of variance and sequential sampling systems. For critical cases (not used in this study) a weighted estimate of k_c would be required. This was calculated to be .694 (k_{c4}) using the following equation (Bliss and Owen, 1958).

$$k_c = \frac{\sum (wx'^2)}{\sum (wx'y')} \qquad \text{---------- (11)}$$

$$\text{where } wx' = \frac{A}{(\bar{u} + k')^2} \qquad \text{---------- (12)}$$

A = a constant.

This value is very close to k_{c3} and reasonably close to the other estimates of k_c. An earlier estimation of k_c based on limited data was calculated as 1.19 (French, 1969). Again this is in close agreement with later calculations.

Tests for agreement with a common k.

The weighted value of .694 was used for two tests, both of which have been outlined by Bliss and Owen (1958). The first test is an approximate chi-square which follows from the weighting of each contribution inversely as its variance. A value of wy' is calculated.

$$wy' = (wx') \frac{y'}{x'} \qquad \text{---------- (13)}$$

The product of multiplying y' by wy' is summed over g distributions of the series to obtain $\sum(wy'^2)$. Part of this total, with one degree of freedom can be attributed to the slope of a line fitted with a zero intercept.

$$B^2_o = \sum^2 (wx'y') / \sum(wx'^2) \qquad \text{---------- (14)}$$

The remainder is an approximate χ^2 where,

$$\chi^2 = \sum(wy'^2) - B^2_o \qquad \text{---------- (15)}$$

nominally, with g - 2d.f.

In this test, the χ^2 value was 246.4 (Table 16), which at 37 d.f. indicates agreement with a single k_c.

The second test was also confirmatory and involved an intercept component with 1 d.f. which is split off from the

approximate χ^2 and which measures the difference between two straight lines. One line was fitted with, and the other without, the constraint of a zero intercept. After calculating the additional term $\sum W = \frac{wx'}{x'}$, the weighted sum of squares and products for the g series are then reduced to deviations about their means.

$$wx'^2 = \sum(wx'^2) - \sum^2(wx')/\sum W \quad \text{---------- (16)}$$

$$wx'y' = \sum(wx'y') - \sum(wx')\sum/wy'/\sum W \quad \text{---------- (17)}$$

$$wy'^2 = \sum(wy'^2) - c \quad \text{---------- (18)}$$

$$\text{where } c = \sum^2(wy')/\sum W \quad \text{---------- (19)}$$

The variation attributable to the slope of the line passing through the origin (B^2_o) is given in equation 14. The variation accounted for, without this constraint, is as follows.

$$B^2 = \frac{(wx'y')^2}{wx'^2} \quad \text{---------- (20)}$$

The required test can be arranged as an analysis of variance.

Effect of	d.f.	S.S.	M.S.	F
Slope $\frac{1}{kc}$	1	B^2	B^2_o	B^2_o / s^2
Computed intercept against 0	1	$C+B^2 - B^2o$	Io	Io / s^2
Error	g -3	$(wy'^2)- B^2$	S^2	-

This analysis is set out in Table 16. A single k_c was justified because the F value in the first row of the table is clearly significant and that in the second row not significant.

Calculation of confidence limits.

The chi-square value at 37 d.f. exceeded the expected value at P = .1. Therefore to determine confidence limits, the following equation was used from which the approximate variance was computed (Bliss and Owen, 1958).

$$V\left(\frac{1}{kc}\right) \doteq \frac{\chi^2}{(n \sum(wx'^2)} \qquad \text{---------- (21)}$$

This gave limits of $\pm$ .184 calculated from the approximate variance.

Discussion on the subterranean larval distribution pattern

The above analysis shows that the subterranean larval stages are moderately aggregated, as indicated by the k_c value of .694. The smaller the value of k_c the greater the degree of aggregation. A large value of eight or more indicates that the individuals in a population are almost randomly distributed. The usual k values for a "normal" insect population are about two (Southwood, 1966).

There are a number of factors which could all contribute to aggregation of porina populations.

1. Uneven oviposition pattern
2. Uneven egg and surface dwelling larval mortality
3. An interaction between one and two
4. Sampling technique

The first three factors imply a behavioural and/or environmental influence. Unfortunately, the value of k is

also often influenced by the size of the sampling unit (Cole (1946) and Morris (1954). For this particular study, care was taken to compare similar sized sample units and the same age interval. It was concluded that the aggregation seen is real and not a sampling or statistical manifestation. This does not mean, however, that the negative binomial model is the best mathematical description of the distribution pattern. This can be confirmed only by acquisition of more data and comparison of other mathematical models.

Assuming the distribution to be aggregated the likely biological reasons are as follows.

1. The behavioural response of surface dwelling larvae and to a limited extent oviposition behaviour.

2. Microclimatic changes.

Earlier it was shown that eggs were generally laid in a random manner with a slight tendency for the moths to oviposit on areas well covered with pasture. Occasionally eggs were laid in clumps (Plate 9) but this was considered not common. After the eggs hatch, larvae require well sheltered sites in order to survive on the soil surface. They actively seek these out and can cover some considerable distance in doing so (Figure 8). As observations have shown that sheltered sites are unevenly distributed within paddocks, likewise so the surface dwelling larvae. For example in a typical Canterbury pasture only certain areas within a paddock made relatively safe survival sites. Broadleaved, clumped grasses such as cocksfoot (Dactylis glomerata), Phalaris tuberosa and clover plants (Trifolium spp.) offered good shelter, particularly if they

were growing in areas of higher soil moisture.

Soil moisture which is also important for larval survival can also vary independently of plant cover. It is a reflection of other factors such as variable soil type, rainfall and soil temperature.

Superimposed on behavioural aggregation is mortality caused directly by environmental changes which cannot be compensated for by larval movement. This includes gross climatic changes, such as continual drought. For example, areas within paddocks having light soils dry out more rapidly than parts with heavier soils. This would cause variation in both surface soil moisture levels and plant growth, both of which affect surface dwelling larval survival. Larval mortality would increase as areas of the paddock became progressively drier (and hotter) with decreasing plant cover, and the commencement of summer. Those larvae not incapacitated would tend to move towards the dwindling area of relatively favourable shelter. This combination of site seeking and mortality would cause larval clumping or an aggregated distribution pattern. This process would continuously take place from hatching till the more protected subterranean stage is reached. Thereafter, the aggregation pattern becomes more stable as mortality becomes less and gross larval movement ceases. Therefore, the k values for the autumn subterranean larval stages shown in Table 14 and the resultant k_c have really been predetermined by the effect of the environment on the egg and surface dwelling larvae. If this is so, it may be possible to use k_c values both as an index of environment variability and population mortality.

Further evidence for the hypothesis on larval aggregation discussed above was obtained in 1968. A paddock at Templeton was shut for grass seed in spring 1967 and was cut on 6th January 1968. Precut sampling showed the existence of a surface dwelling larval population of approximately 600/m^2. On 10th January thirty 8.9 cm diameter core samples were taken under the cut swath and another 30 taken from an adjacent position between swaths (Table 17). It was obvious from the results that a certain amount of larval movement and/or mortality had occurred in the four day period after cutting. Sampling of the subterranean larvae on 29th January 1968 indicated a further population decrease. The highest larval numbers were found in the area previously under the swath and this resulted in a clumped distribution pattern. It was also observed that larvae protected by the swath prior to its removal dug their tunnels much later than those exposed between swaths.

A final indirect piece of evidence which supports the behavioural/environmental induced larval aggregation pattern, is provided by the application of the following formula developed by Arbous and Kerrichs (1951).

$$\lambda = \frac{\bar{x}}{2k} v$$

where $\bar{x}$ = the mean,

v = a function with χ^2 distribution with 2k degrees of freedom, and

λ = the number of individuals in the aggregation for the probability level allocated to v.

If λ is found to be less than two, then the aggregation would seem to be due to some environmental effect and not

an active process. Aggregations of two or more insects could be caused by either factor.

The figures used in the above formula were obtained from the data in Table 14 from which the overall mean was calculated and the kc value of .694 was used. A figure of 1.083 was calculated for 2. This implies that the porina aggregations are probably caused by environmental interactions.

CONCLUSIONS

The subterranean larval age intervals were aggregated sufficiently to warrant transformation of life table counts. For the reasons discussed by Morris (1955) which were mainly centred around difficulties interpreting transformed data, and because of the limited aims of this study, the analysis of life table results in this thesis is based on untransformed arithmetic means.

A k_c of .694 with a range of $\pm$ .184 was calculated. The reasonably high aggregation indicated by this low k_c was postulated as being caused by a behavioural and environmental interaction influenced by

(a) oviposition pattern,
(b) site seeking by surface dwelling larvae, and
(c) pasture variation brought about by an interaction between soil type differences, farm management and climatic variation during the period larvae are on the surface.

It was concluded that k_c values for all stages of the porina life cycle could be used as an index of aggregation for various populations and should appreciably assist in the

Table 17 Summary of a number of samples taken at different times from a larval population at Templeton 1968-69

Sample 1 21/12/67 9 cm dia. core

n = 20 $\bar{x}$ = 3.92 95% c.l. = ± 1.345 Number per m^2 = 625 ± 212

Sample 2 10/1/68 9 cm dia. core (a) under cover (b) no cover

(a) n = 32 $\bar{x}$ = 2.75 95% c.l. = ± .815 Number per m^2 = 435 ± 127

(b) n = 32 $\bar{x}$ = .500 95% c.l. = ± .375 Number per m^2 = 85 ± 64

Sample 3 29/1/68 .023m^2 spade square (a) under cover (b) no cover

(a) n = 207 $\bar{x}$ 2.077 95% c.l. = ± .026 Number per m^2 = 85 ± 2

(b) n = 285 $\bar{x}$ .701 95% c.l. = ± .011 Number per m^2 = 32 ± 1.5

Summary (numbers given per m^2)

Sample 1

Sampled just before cutting grass-seed crop 625 ± 212

Sample 2

Sampled four days after cutting
Half the samples taken from under the cut swath (a)
The other half taken in the gap between swaths (b)

(a) = 435 ± 127

(b) = 85 ± 64

Sample 3

Sampled after the larvae had formed tunnels. Some samples were taken from where the swath had been. The swath was not removed until about 17/1/68. Other samples were taken between swaths.

(a) = 85 ± 2.0

(b) = 32 ± 1.5

interpretation of mortality data.

The calculations of a k_c value should enable a useful sequential sampling system to be developed. Such a system has been developed by French (1969). This should assist rapid sampling of large areas at much reduced cost.

As porina larval populations have been shown to have an aggregated distribution pattern, this phenomenon must be considered when assessing damage.

CHAPTER 5

THE DEVELOPMENT OF LIFE TABLES

Introduction

The primary aim for developing life tables for porina was to devise some means of forecasting porina populations in sufficient time for effective control measures to be applied.

A second aim of this study was to try and reveal age intervals within which key mortalities operate. Subsequent research could then be designed to study these in greater detail.

A third, more academic aim, was to gain insight into the fascinating, but complex, problem of insect population regulation.

It was decided that to fulfil the first two aims a full understanding of all the biological mechanisms which effect porina populations was not required. A type of project which involved a long term approach was beyond the scope of this study. Furthermore, because of the broad approach taken, it was not considered important to categorically differentiate between biologically meaningful or statistically induced causal relationships, as discussed by Varley and Gradwell (1970). The following study was primarily designed to

establish a useful practical relationship, proven in the field and which could reasonably and reliably forecast porina abundance. This does not imply that the analysis of true biological causal relationships and the development of predictive mathematical models should not lose priority.

Definition of life table populations

Unless otherwise stated the definition of population previously given on page 108, applies throughout this chapter. For example, a porina population at the Hindon study area was confined to a .8 ha plot. Within the study area moth migration occurred between plots, but once the eggs were deposited, the population "per se" remained within the plot.

Location and description of life table study areas

The following were chosen as life table study areas.

1. Templeton Farm, 15 km south of Christchurch situated on a Waimakariri silt loam (Ives, pers. comm.)

2. Winchmore Irrigation Centre, 9 km north west of Ashburton, situated on a Lismore stony silt loam (Ives, pers. comm.)

3. Hindon Lands and Survey Block, 400 km south of Christchurch and 73 km south west of Dunedin, situated on a Wehunga silt loam (Ives, pers. comm.).

These areas were chosen because of geographical and farm management differences which could be compared if necessary.

Templeton life table study area

The Templeton study area shown in Figure 12 was situated on flat land surrounded by cultivated paddocks. There was very little permanent pasture in the immediate vicinity, other than road verges on two sides of the study area.

The pasture was sown in autumn 1966 with an Italian ryegrass and white clover mixture (Lolium multiflorum and Trifolium repens). It was saved for grass seed in spring 1966 and harvested in summer 1966-1967.

Evidence of porina damage was seen in the following winter but was not serious enough to cause much damage or require control. No insecticide had been applied on the area for at least 20 years.

The total study area involved was 4.8 ha divided in the late spring of 1967 into six .8 ha plots. Three plots were ungrazed from October onwards each year until cut for hay in mid January. The other three plots were grazed throughout the year with an average of 9-10 ewe equivalents/ha. The stocking rate was increased when lambing occurred to 25-30 ewe equivalents/ha during spring and early summer. The hayed plots (termed ungrazed) were stocked in a similar manner other than during the haying period. This arrangement ensured plenty of cover for the egg and surface dwelling larval stages on three plots, where the pasture grew to a height of about .5 m. The pasture on the other three plots was only about 5 cm high over the same period.

Each basic treatment was replicated three times. This was done to enable more meaningful statistical analysis of any gross differences likely to occur in population numbers.

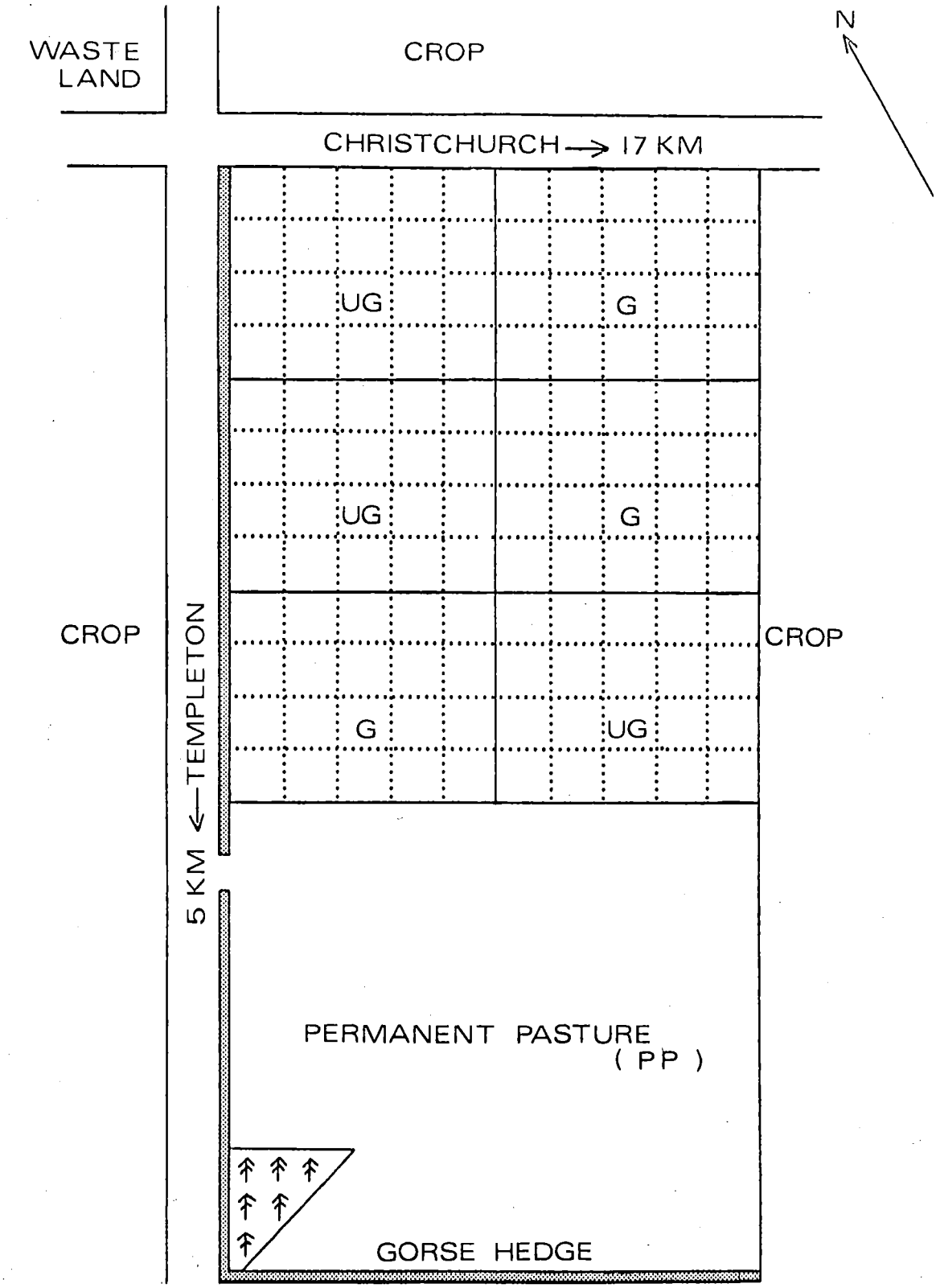


FIG. 12

Plan of the Templeton life table study area.

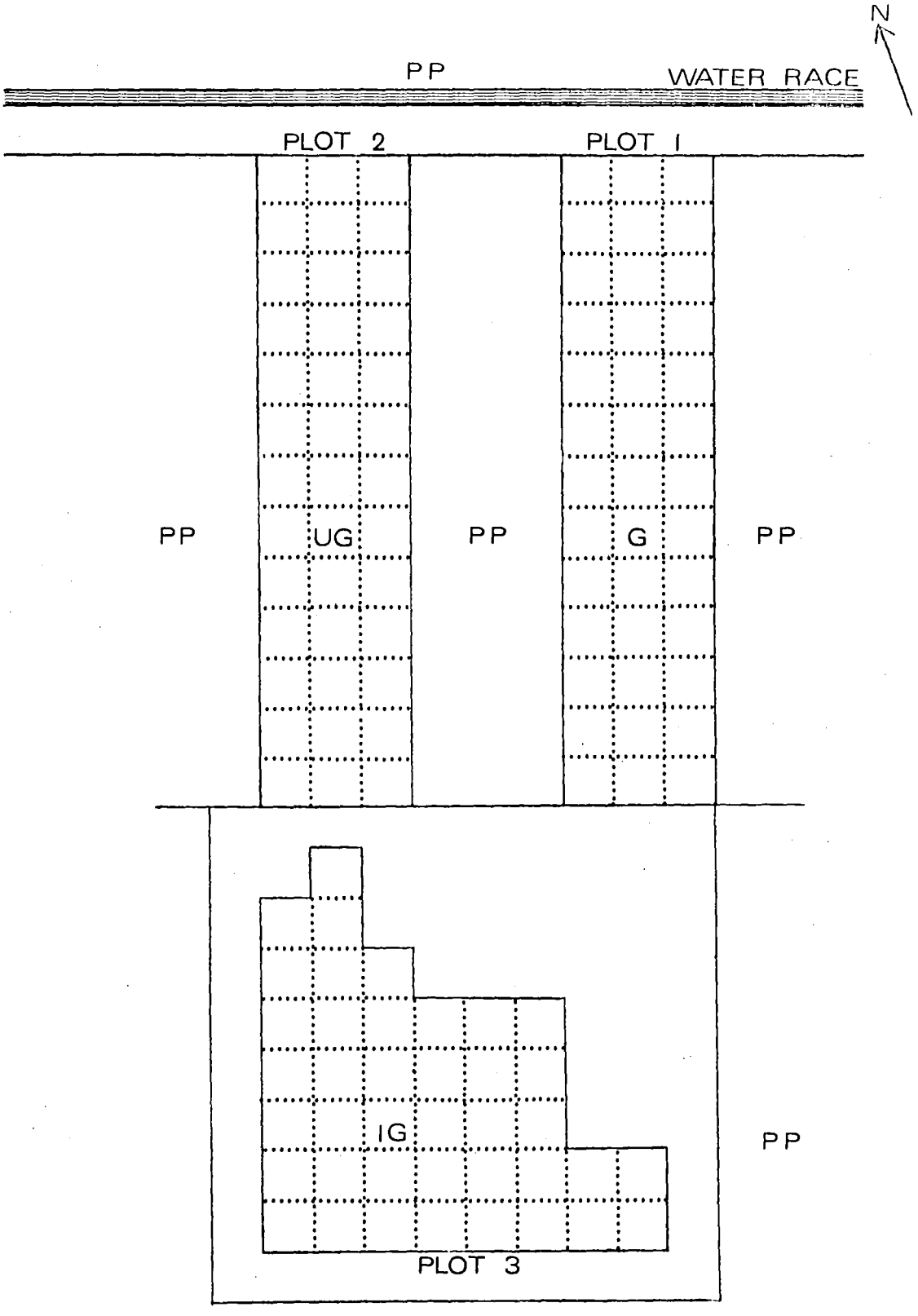


FIG. 13

Plan of the Winchmore life table study area.

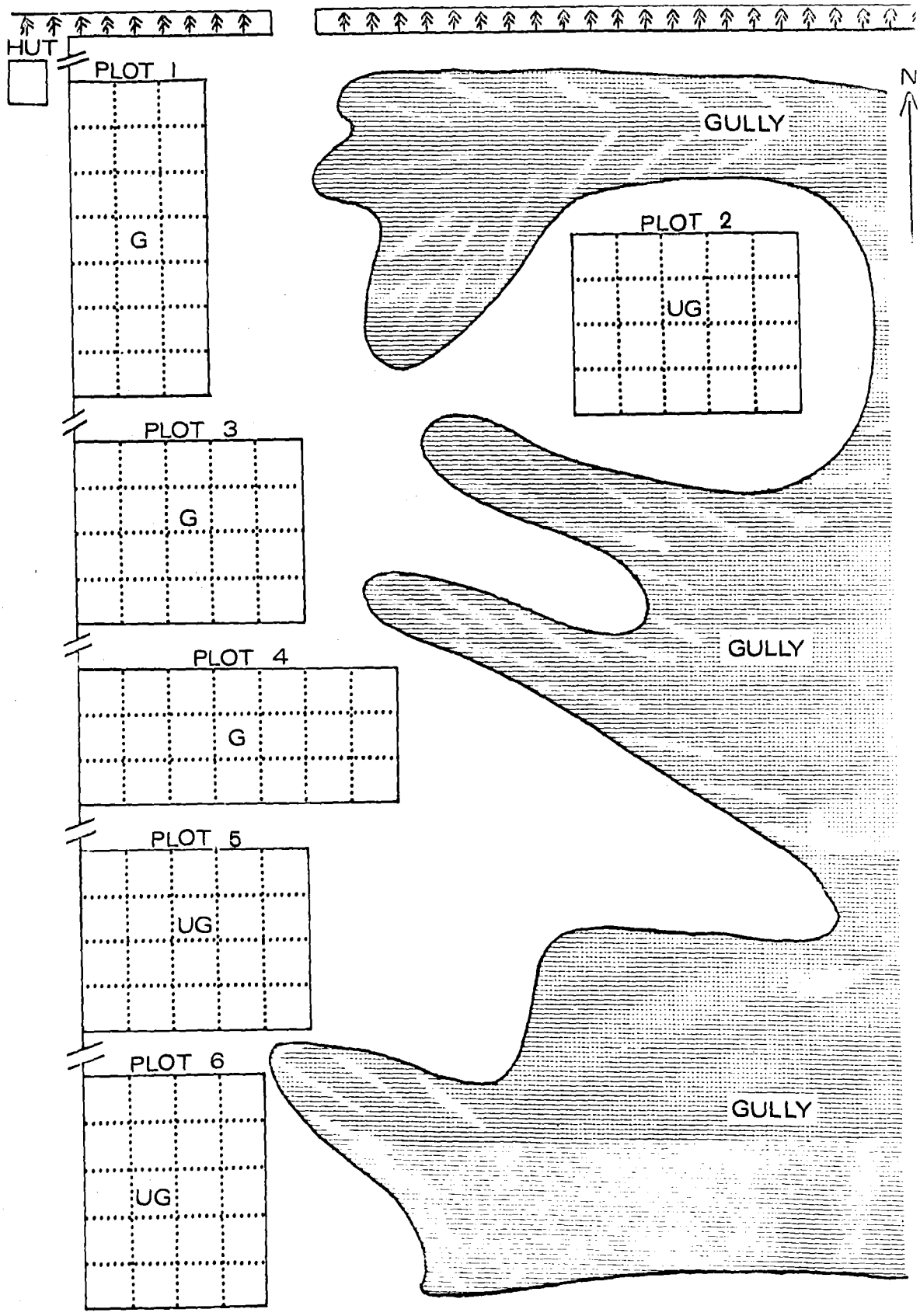


FIG. 14

Plan of the Hindon life table study area.

For example, the effect of the different grazing patterns on larvel numbers would be useful practical knowledge.

The .8 ha plot was considered the minimum size for the development of life tables. The size was accepted because only 1 per cent of the area would be disturbed when sampling during the study period. This ensured an insignificant insect mortality brought about by sampling.

Each plot was divided into twenty, 20 m x 20 m square subplots which were marked out with pegs sunk to ground level A herbage dessicant, ("Paraquat") was sprayed around each peg in spring. This removed the vegetation and helped when locating the pegs in long pasture. The pegs were used as points of reference when sampling positions were determined by the random method outlined on page 113. Sampling commenced at Templeton in December 1967 with an egg count. This was followed by the formal sampling plan as detailed on page 140 (Table 13).

Winchmore life table study area

A similar layout as above, with similar stocking management and densities, was used on the Winchmore study area shown in Figure 13. It was situated on flat land. Three unreplicated treatments were involved, namely non-irrigated grazed and ungrazed plots, and an irrigated grazed plot. Each plot had an area of 1.6 ha and was divided up into forty 20 m x 20 m square subplots. All three plots were bounded on all sides by permanent pasture, mostly irrigated, and subject to periodic porina infestations. The non-irrigated plots had

suffered a porina attack during the winter prior to when sampling commenced. Each plot had been sown some five years ago with an Italian ryegrass/white clover mixture. There had been no history of insecticide treatment.

The study area was first sampled in March 1968. Thereafter the area was formally sampled only when pilot sampling showed a measurable population was present.

Hindon life table study area

The Hindon study area consisted of six .8 ha plots (Figure 14). Each plot was separated from the others by deep tussock covered gullies, characteristic of this region. The gullies dissected undulating plateau land most of which was at an altitude of 460-500 m a.s.l. Most of the accessible plateau land was sown in permanent pasture and was used almost entirely for sheep grazing. The pasture consisted mostly of perennial ryegrass (Lolium perenne), white and red clover (Trifolium repens and T. pratense), and cocksfoot (Dactylis glomerata). The gullies were covered with native tussocks, mainly Poa pratensis and rushes (Juncus spp.) This area was renowned for severe porina infestations. The Farm Manager of the Lands and Survey block considered porina to be "the sole reason preventing an increase in ewe numbers."

For comparison with the Templeton and Winchmore study areas grazed and ungrazed plots were incorporated, with each treatment replicated three times. The ungrazed plots were shut for hay in late October and cut in late January. During this period the pasture height reached a maximum of about .8 m.

The grazed plots were stocked with 12-15 ewe equivalents/ha for most of the year. This was increased to 22-25 ewe equivalents/ha (ewe and lambs) during the spring and early summer, i.e. over the egg and surface dwelling larval periods. This ensured that the pasture was kept to a height of about 5 cm.

Sampling commenced in December 1967 with a limited egg sample. Intensive sampling began in January 1968 with an assessment of the surface dwelling larval population.

Basic meteorological data was recorded on or adjacent to each study area. The following variables were recorded: rainfall and daily maximum and minimum temperatures measured .9 m above the soil surface in a Stevenson screen. Whenever possible and practicable, surface soil temperatures and moistures were recorded.

Plan for sampling life table plots

A summary of the formal sampling plan used on each study area was outlined in Table 13 given on page 140 . The times of sampling, the size, number and types of samples, the methods of extraction and assessment are all detailed in Chapter 4.

Presentation of life table results

Because only the surviving populations were sampled from each age interval, survivorship curves were constructed as a summary of life table results. The figures obtained from sampling each age interval were used to calculate apparent

percentage mortalities. Interpretation of the life table results was facilitated by a statistical technique and a graphical assessment presented in the form of k values.

Description of methods used for analysis of life table results

Two methods were chosen, a statistical approach developed by Watt (1963) based on regression analysis, and a method of graphical assessment developed by Varley and Gradwell (1970). Both analysis were used to compare and contrast their ease of use and the degree to which they could assist in the interpretation of mortality data.

Method 1

The following formula was used to express the index of population trend, hereafter referred to as (I).

$$I = S_E \; S_{L1} \; S_{L2} \; S_{L3} \; S_{pp} \; S_p \; P \quad F \; S_A$$

where,

S_E = egg survival ratio

S_{L1} = surface dwelling larvae, survival ratio

S_{L2} = autumn subterranean larvae, survival ratio

S_{L3} = winter subterranean larvae, survival ratio

S_{pp} = prepupal stage, survival ratio

S_p = pupae stage, survival ratio

P = sex ratio

F = mean fecundity

S_A = adult survival ratio.

The above formula was modified from the one used by

Morris (1959) and Watt (1963).

A correlation coefficient (r) was calculated using I as the dependent variable and S_E to S_A as the independent variables. Levels of statistical significance were determined using, in most cases, only two degrees of freedom. This low number of degrees of freedom lessened confidence when using statistical methods to assist interpretation of results. The short time spent on this study, however, limited the number of life tables from which the number of degrees of freedom were calculated.

The second method consisted of calculating k values for each age interval and graphing these, together with values of total generation mortality (K). This method has been outlined in detail by Varley and Gradwell (1970).

Results from life table studies

The number of individuals alive at the beginning of each age interval (N_x) are shown graphically in Figures 15 to 19 as survival curves. The N_x values for each age interval for each plot are given, with 95 per cent confidence limits, in Tables 19 to 21.

Occasionally, sample means indicated a gain in insect numbers compared with the previous age interval. This was most common after sampling the autumn and mid-winter subterranean larval stages, particularly at Hindon. In all cases this was due either to a sampling or statistical anomaly. In such cases, when survival was high, it was assumed that no significant mortality had occurred. Therefore, in order to

carry out statistical analysis these means were adjusted so that a continuous, but at times, minimal mortality, was shown. In this study life tables were used to determine only key age intervals. Therefore, because concise life tables were thus not required, adjusted means were considered adequate. Both the real and adjusted means are given in Tables 19 to 21.

The survivorship values ($S\underline{x}$) which are really ratios are given in Tables 22 and 23. They were calculated from $N\underline{x}$ values by dividing the $N\underline{x}$ value from one age interval by the previous one.

Fecundity and sex ratio values are also given in Tables 22 and 23 and in this study both have been assumed constant. Because the moth flight period was short and coincided with a heavy work load, it was too difficult to obtain fecundity and sex ratio figures each year, from the widely scattered life table study areas.

The trend indices (I) are also given in Tables 22 and 23. They were calculated with the aid of a formula developed by Watt (1963) and given on page 173 of this thesis. The correlation coefficients which are given as r (not r^2) were calculated from the data given in Tables 22 and 23 using the formula given by Pottinger (1967). These values are given in Table 24. Those correlations showing statistical significance at $P < .05$ are denoted by an asterisk.

The percentage mortalities for each age interval are given in Tables 25 and 26 for all age intervals except adults. The mean mortality for each age interval was also calculated

Table 18 Key to abbreviations of age intervals and other titles used for the presentation of life table results in Tables 19 to 27.

Age Interval	Abbreviation
Eggs	E
Surface dwelling larvae	S.D.L.
Autumn subterranean larvae	A.S.L.
Winter " "	W.S.L.
Prepupae	P.P.
Pupae	P
Adult (Moth)	M

Other abbreviations used:		
Ungrazed plots	=	U.G.
Grazed plots	=	G
Irrigated and grazed plots	=	I.G.
95% confidence limits	=	±
Moth fecundity	=	M.F.
Sex ratio	=	S.R.
Population trend index	=	I
Constant mortality rate	=	C.M.R.
Generation mortality		G.M.

Table 19 Numbers of survivors (Nx) per 4 square metres in the Hindon life table study area

Plot 1 G.					
Age Interval	1968	1969	1970	1971	1972
E.	2844	577 ± 603	777 ± 95	1818±715	458
S.D.L.	948 ± 308	282 ± 215	469 ± 366	375±230	188±220
A.S.L.	78 ± 27	51 (29 ± 22)	99 (57 ± 36)	119 (110±50)	
W.S.L.	77 (95 ± 35)	50 (57 ± 25)	98 (53 ± 29)	118±52	
P.P.	51 ± 18	19	97 (148 ± 57)	57±29	
P.	6 ± 6	35 ± 19	82 ± 49	45±30	
M.	5	1	34	16 10	

Plot 2 U.G.					
Age Interval	1968	1969	1970	1971	1972
E.	2844	2056±2003	1509±426	347±128	119
S.D.L.	475±180	641±593	1233±682	121±234	49
A.S.L.	71±27	190±63	268±96	17±16	
W.S.L.	54±22	124±53	193 (91±40)	16	
P.P.	26±13	123	130 (155±77)	1	
P.	2±4	81±34	30±20	1	
M.	2	13±12	13	.5	

contd.

Table 19 contd.

Plot 3 G.					
Age Interval	1968	1969	1970	1971	1972
E.	2844	3131±2668	434±208	707±309	319
S.D.L.	522±232	105 (99±134)	295±258	246±246	99±135
A.S.L.	39 (21±18)	104±51	100 (169±69)	78±56	
W.S.L.	38 (44±22)	86±41	79 (47±32)	77	
P.P.	37±15	85	78 (155±81)	46±24	
P.	1	29±19	60 ± 29	38±22	
M.	1	1	26 ± 15	22±15	

Plot 4 G.					
Age Interval	1968	1969	1970	1071	1972
E.	2844	202±335	846±268	759±305	180
S.D.L.	425±187	187±219	516±370	376±327	99±135
A.S.L.	85±36	103±15	115±54	98±50	
W.S.L.	71±26	65±28	83 (58±43)	97	
P.P.	70±25	64	82±59	36±21	
P.	4±5	63	74±43	29±19	
M.	4	2	32	19	

contd.

Table 19 contd.

Plot 5 U.G.					
Age Interval	1968	1969	1970	1971	1972
E.	2844	92 (81±102)	1303±430	535±387	67
S.D.L.	1238±403	91	986±497	394±286	49
A.S.L.	132 (119 ± 37)	90±43	376±77	9±11	
W.S.L.	131±32	33±21	308±81	8	
P.P.	56±26	32	190±84	7±11	
P.	4±6	31±19	91±45	1	
M.	4	6	35 19	1	

Plot 6 U.G.					
Age Interval	1968	1969	1970	1971	1972
E.	2844	666±842	1232±115	222 (145±77)	70
S.D.L.	1141±316	295±138	1183±660	221 (345±388)	49
A.S.L.	185±47	95±45	169±52	26±22	
W.S.L.	123±40	74 (52±26)	160±69	1	
P.P.	41±17	73	138±75	1	
P.	9±8	72±27	60±31	1	
M.	8	12	24	1	

contd.

Table 19 contd.

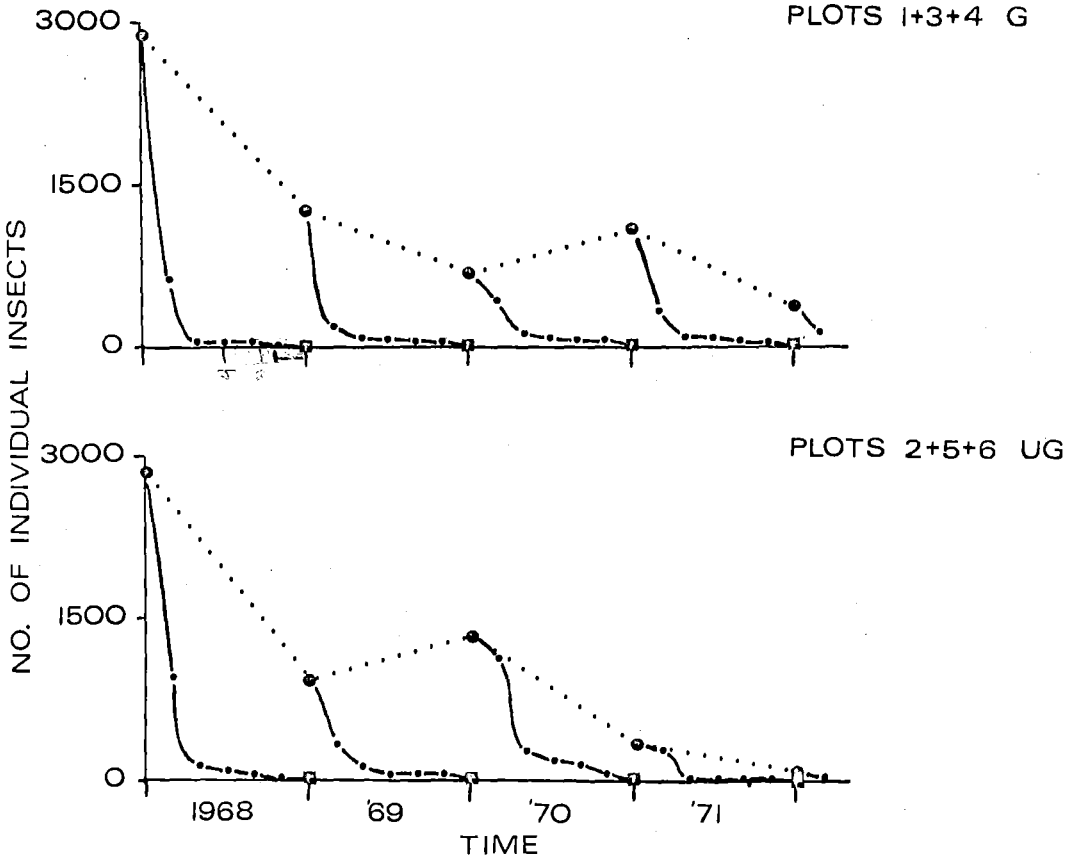
Plots 2+5+6 U.G.					
Age Interval	1968	1969	1970	1971	1972
E.	2844	931±733	1347±315	343±139	83
S.D.L.	948±181	315±224	1125±325	296±167	49
A.S.L.	124±23	124±44	270±47	17±10	
W.S.L.	102±18	69±22	185±41	16	
P.P.	42±11	68	160±45	3±5	
P.	3±3	60±16	61±20	1	
M.	3	10	24	1	

Plots 1+3+4 G.					
Age Interval	1968	1969	1970	1971	1972
E.	2844	1272±795	689±104	1101±294	396
S.D.L.	632±150	197±112	414±195	335±163	127±79
A.S.L.	59±16	78±25	112±32	97±30	
W.S.L.	58 (69±28)	69±18	74 (54±20)	96	
P.P.	54±12	68	73 (128±38)	47±14	
P.	4±3	40±12	71±24	37±14	
M.	4	2	30	19±9	

Key

( ) = calculated mean from sample results.

see pages in text 174 to 175.



KEY to FIGS. 15 - 19

G	GRAZED
UG	UNGRAZED
IG	IRRIGATED & GRAZED
....	POPULATION TREND
●	EGG
■	MOTH

FIG. 15

Survivorship curves using mean Nx values from Table 19 - bulked results from the ungrazed and grazed life table plots at the Hindon study area.

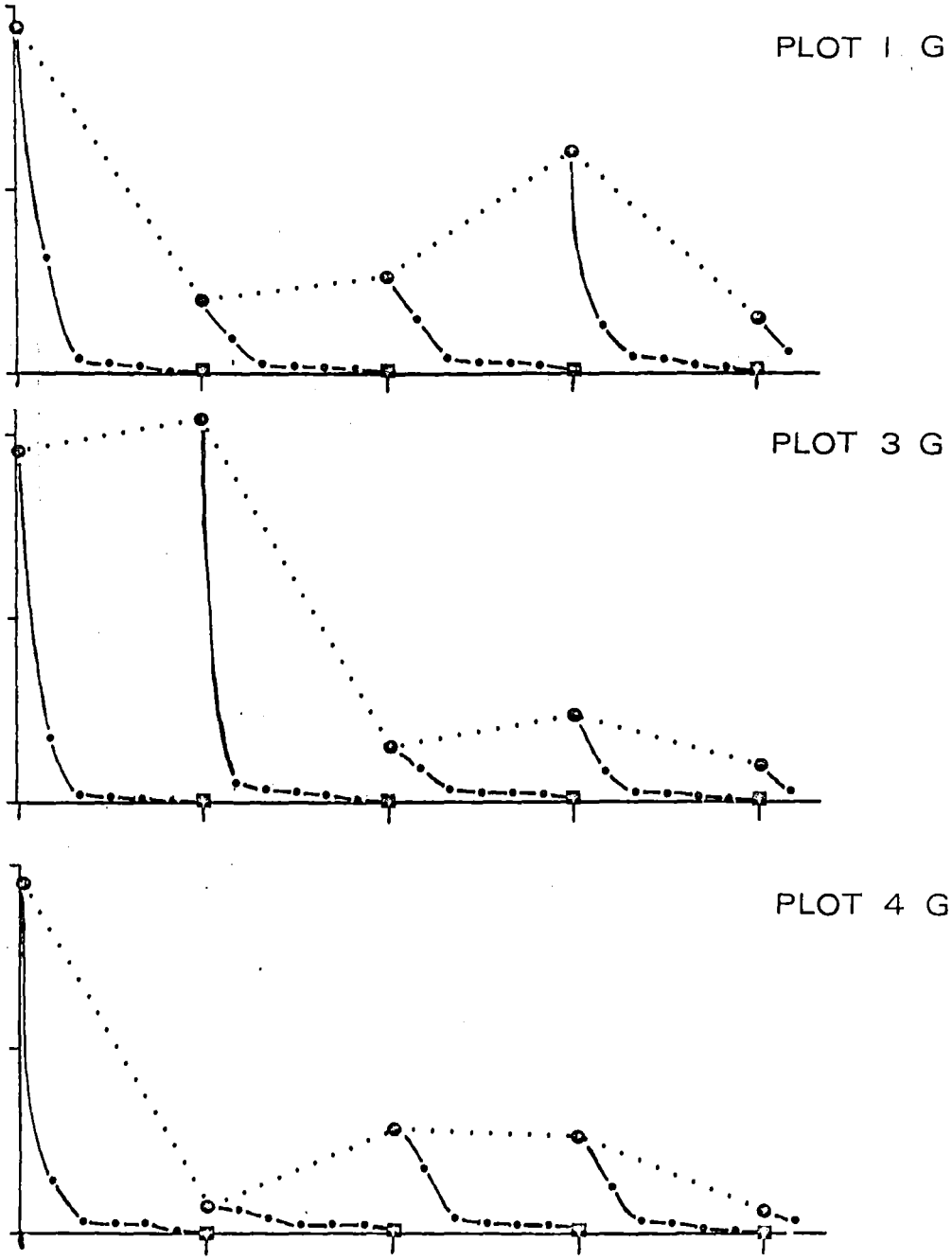


FIG. 16

Survivorship curves using mean Nx values from Table 19 - results from the grazed life table plots at the Hindon study area. Key as for Fig. 15.

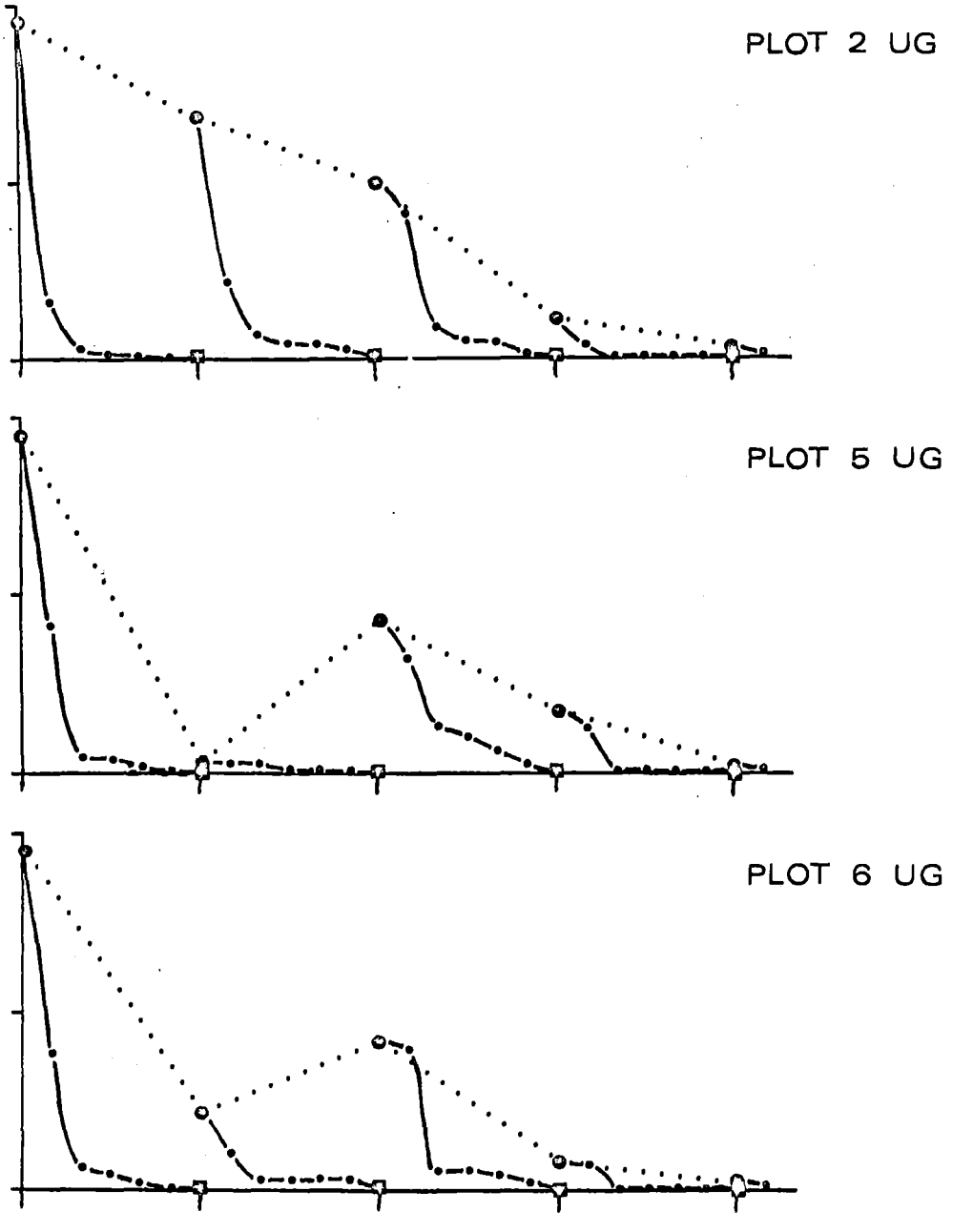


FIG. 17

Survivorship curves using mean Nx values from Table 19 - results from the ungrazed life table plots at the Hindon study area. Key as for Fig. 15.

Table 20 Numbers of survivors (Nx) per 4 square metres in the life table plots Winchmore study area

Plot 1 G				
	1968	1969	1970	1971
E	2160	133596±51123	564±196	282±89
S.D.L.	37	90	1	
A.S.L.	36 ± 17	90	1	
W.S.L.	36	89	1	
P.P.	36	88	1	
P	36	30 ± 23	1	
M	36	6	1	

Plot 2 U.G.				
	1968	1969	1970	1971
E	120	16714±13746	398±128	1789±2304
S.D.L.	3	2	1	
A.S.L.	2±3	2	1	
W.S.L.	2	2	1	
P.P.	2	2	1	
P	2	1	1	
M	2	1	1	

Plot 3 I.G.				
	1968	1969	1970	1971
E	360	8038±17103	210±102	192±91
S.D.L.	7	6	1	
A.S.L.	6±5	6	1	
W.S.L.	6	6	1	
P.P.	6	6	1	
P	6	5	1	
M	6	5	1	

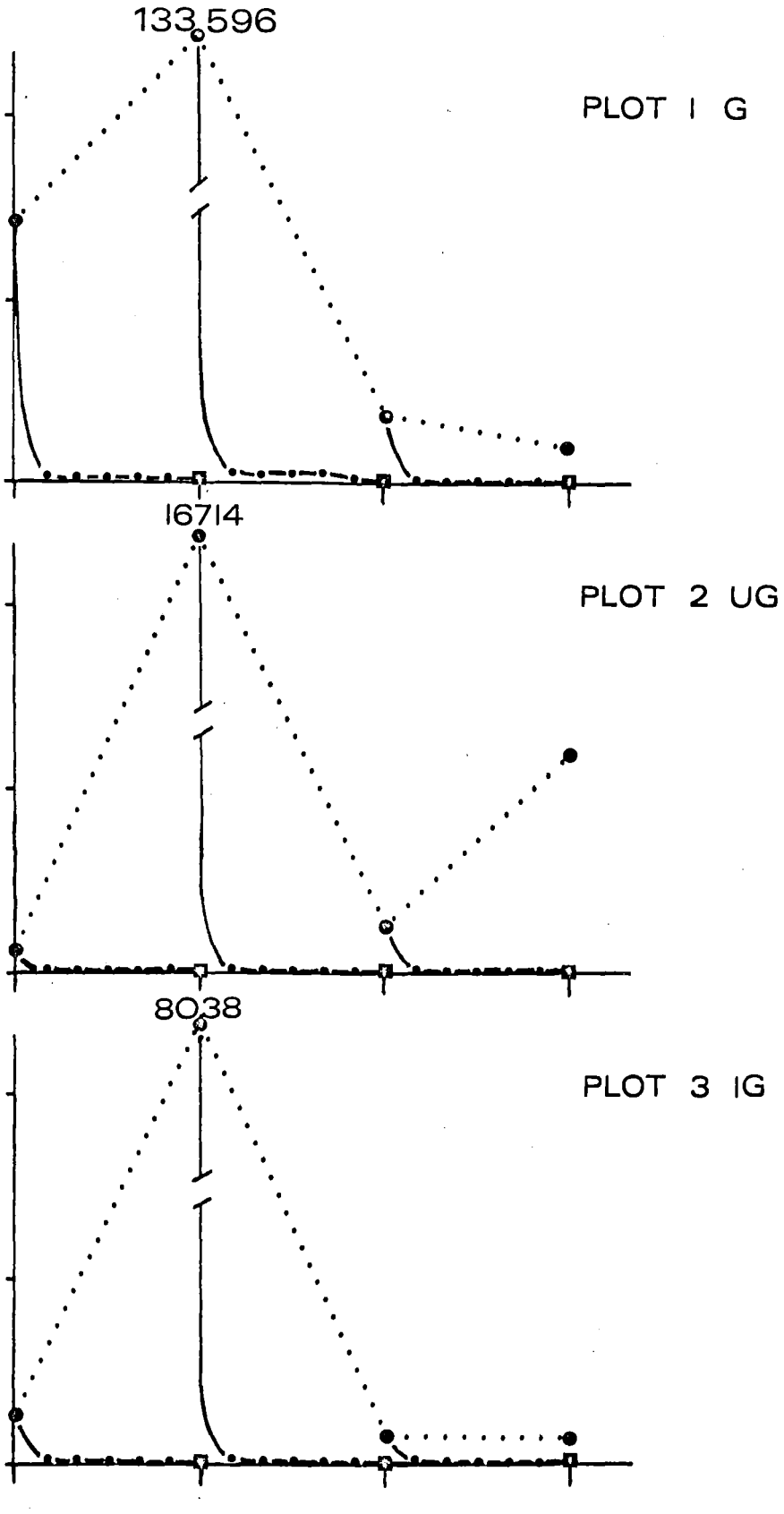


FIG. 18

Survivorship curves using mean Nx values from Table 20 - results from the grazed, ungrazed and irrigated plus grazed life table plots at the Winchmore study area.

Table 21 Numbers of survivors (Nx) per 4 square metres in the life table plots Templeton study area

Plots 1 + 2 + 3 U.G.				
	1968	1969	1970	1971
E	338±173	148±145	303±63	39±21
S.D.L.	12	15	1	
A.S.L.	1	14	1	
W.S.L.	1	14 (10±4)	1	
P.P.	1	14	1	
P	1	14 (22±8)	1	
M	1	12	1	

Plots 4 + 5 + 6 G				
	1968	1969	1970	1971
E	338±173	648±213	63±21	10±8
S.D.L.	1	82±36	1	
A.S.L.	1	4	1	
W.S.L.	1	3±2	1	
P.P.	1	2	1	
P	1	1	1	
M	1	1	1	

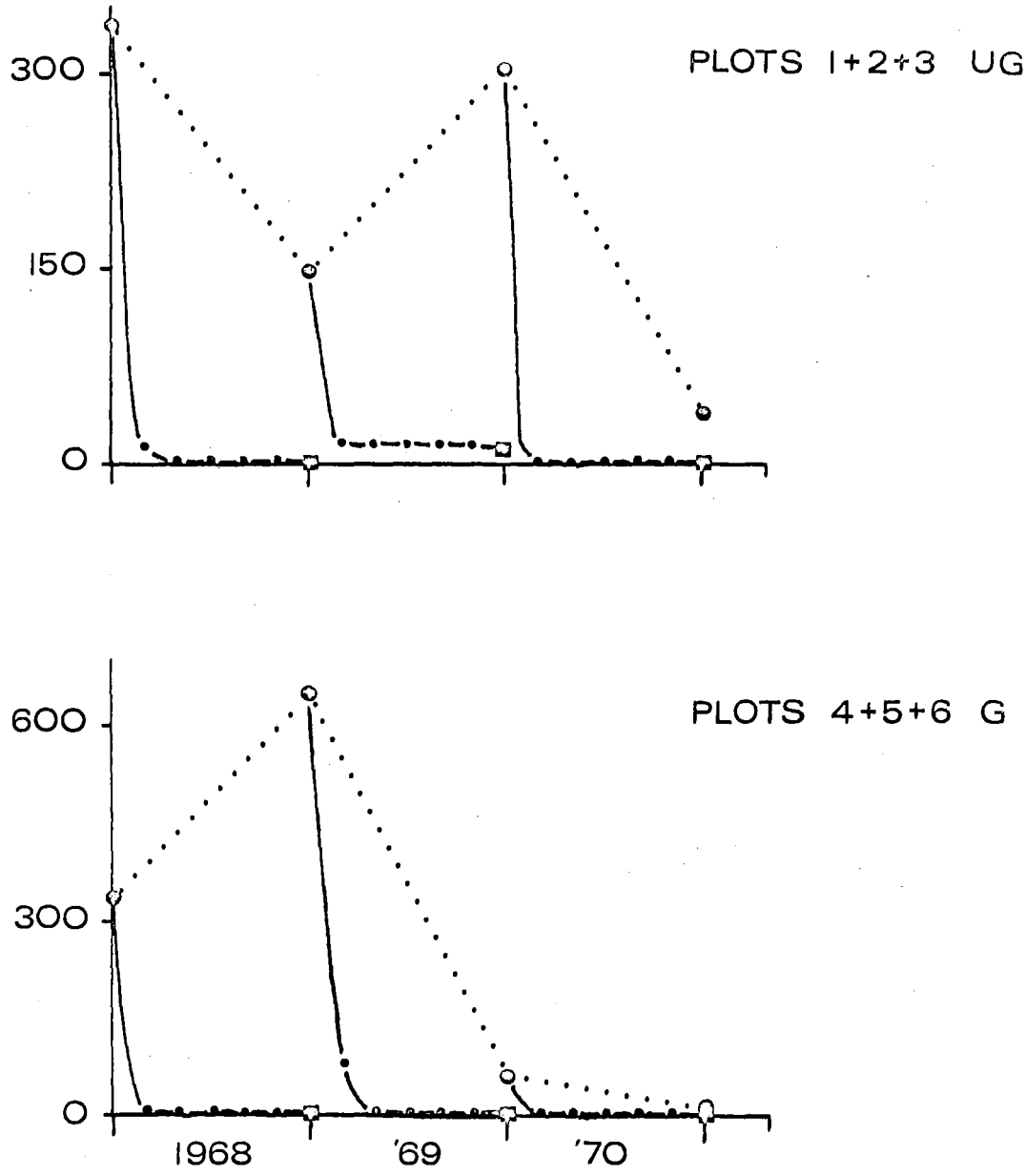


FIG. 19

Survivorship curves using mean N_x values from Table 21 - results from the grazed and ungrazed life table plots at the Templeton study area.

Table 22 Survivorship ratios (Sx) for each stage sampled at the Hindon life table study area

Plot 1 G.				
	1968	1969	1970	1971
E.	.333	.489	.604	.206
S.D.L.	.082	.181	.211	.317
A.S.L.	.987	.980	.989	.991
W.S.L.	.662	.980	.989	.483
P.P.	.118	.714	.845	.789
P.	.833	.029	.414	.355
M.F.	1123	1123	1123	1123
S.R.	.500	.500	.500	.500
M.	.205	1.385	.095	.051
I.	.202	1.370	2.324	.251

Plot 4 G.				
	1968	1969	1970	1971
E.	.149	.925	.610	.495
S.D.L.	.200	.550	.223	.261
A.S.L.	.835	.631	.721	.989
W.S.L.	.985	.984	.987	.371
P.P.	.057	.984	.902	.805
P.	1.000	.032	.432	.655
M.F.	1123	1123	1123	1123
S.R.	.500	.500	.500	.500
M.	.089	.753	.042	.017
I.	.070	4.206	.889	.238

Plots 2 + 5 + 6 U.G.				
	1968	1969	1970	1971
E.	.333	.338	.834	.863
S.D.L.	.131	.394	.240	.057
A.S.L.	.822	.556	.685	.941
W.S.L.	.412	.985	.865	.187
P.P.	.071	.882	.381	.333
P.	1.000	.167	.393	1.000
M.F.	1123	1123	1123	1123
S.R.	.500	.500	.500	.500
M.	.553	. 40	.025	.148
I.	.326	1.447	.250	.239

contd.

Table 22 contd.

Plot 2 U.G.				
	1968	1969	1970	1971
E.	.167	.312	.817	.349
S.D.L.	.149	.297	.217	.140
A.S.L.	.761	.653	.489	.941
W.S.L.	.482	.992	.992	.962
P.P.	.077	.658	.230	1.000
P.	1.000	.161	.433	.500
M.F.	1123	1123	1123	1123
S.R.	.500	.500	.500	.500
M.	1.831	.206	.047	.425
I.	.719	.735	.226	.340

Plot 5 U.G.				
	1968	1969	1970	1971
E.	.435	.989	.757	.736
S.D.L.	.107	.989	.381	.023
A.S.L.	.992	.366	.819	.888
W.S.L.	.427	.969	.616	.875
P.P.	.071	.968	.479	.143
P.	1.000	.193	.384	1.000
M.F.	1123	1123	1123	1123
S.R.	.500	.500	.500	.500
M.	.036	.387	.027	.119
I.	.028	14.083	.405	.125

	Plots 1 + 3 + 4 G.			
E.	.222	.155	.601	.304
S.D.L.	.093	.396	.270	.289
A.S.L.	.983	.885	.661	.989
W.S.L.	.931	.985	.986	.489
P.P.	.074	.588	.972	.789
P.	1.000	.050	.422	.513
M.F.	1123	1123	1123	1123
S.R.	.500	.500	.500	.500
M.	.566	.613	.065	.037
I.	.445	.540	1.583	.356

contd.

Table 22 contd.

Plot 3 G.				
	1968	1969	1970	1971
E.	.184	.033	.679	.348
S.D.L.	.075	.990	.338	.317
A.S.L.	.974	.827	.790	.987
W.S.L.	.973	.988	.987	.597
P.P.	.027	.341	.769	.826
P.	1.000	.034	.433	.579
M.F.	1123	1123	1123	1123
S.R.	.500	.500	.500	.500
M.	5.581	.774	.048	.026
I.	1.097	.135	1.606	.453

Plot 6 U.G.				
	1968	1969	1970	1971
E.	.401	.443	.960	.995
S.D.L.	.162	.322	.143	.117
A.S.L.	.665	.779	.947	.038
W.S.L.	.333	.986	.862	1.000
P.P.	.219	.986	.434	1.000
P.	.889	.166	.400	1.000
M.F.	1123	1123	1123	1123
S.R.	.500	.500	.500	.500
M.	.148	.182	.011	.125
I.	.233	1.833	.120	.311

Table 23 Survivorship ratios (Sx) for each stage sampled at the Winchmore and Templeton life table study areas

Winchmore

Plot 1			
	1968	1969	1970
E.	.017	.0007	.0018
S.D.L.	.973	1.000	1.000
A.S.L.	1.000	.989	1.000
W.S.L.	1.000	.988	1.000
P.P.	1.000	.341	1.000
P.	1.000	.200	1.000
M.F.	1123	1123	1123
S.R.	.500	.500	.500
M.	6.609	.167	.503
I	61.379	.0043	.508

Plot 2 U.G.			
	1968	1969	1970
E.	.025	.0001	.0025
S.D.L.	.666	1.000	1.000
A.S.L.	1.000	1.000	1.000
W.S.L.	1.000	1.000	1.000
P.P.	1.000	.500	1.000
P.	1.000	1.000	1.000
M.F.	1123	1123	1123
S.R.	.500	.500	.500
M.	14.883	.709	3.188
I	139.142	.020	4.475

Plot 3 I.G.			
	1968	1969	1970
E.	.019	.0007	.005
S.D.L.	.857	1.000	1.000
A.S.L.	1.000	1.000	1.000
W.S.L.	1.000	1.000	1.000
P.P.	1.000	.833	1.000
P.	1.000	1.000	1.000
M.F.	1123	1123	1123
S.R.	.500	.500	.500
M.	2.386	.075	.342
I	21.810	.024	.960

contd.

Table 23 contd.

Templeton

Plots 1 + 2 + 3 U.G.			
	1968	1969	1970
E.	.035	.101	.003
S.D.L.	.083	.933	1.000
A.S.L.	1.000	1.000	1.000
W.S.L.	1.000	1.000	1.000
P.P.	1.000	1.000	1.000
P.	1.000	1.000	1.000
M.F.	1123	1123	1123
S.R.	.500	.500	.500
M.	.264	.045	.069
I.	.431	2.041	.117

Plots 2 + 5 + 6 G.			
	1968	1969	1970
E.	.003	.126	.016
S.D.L.	1.000	.049	1.000
A.S.L.	1.000	.750	1.000
W.S.L.	1.000	.667	1.000
P.P.	1.000	.500	1.000
P.	1.000	1.000	1.000
M.F.	1123	1123	1123
S.R.	.500	.500	.500
M.	1.155	.112	.018
I.	1.945	.097	.163

Table 24 Correlation coefficient values for each age interval with the index of population trend for each plot from each life table study area located at Templeton, Winchmore and Hindon

Hindon								
Age Interval	Plots						1+3+4 Grazed plots (bulked)	2+5+6 Ungrazed plots (bulked)
	1 G.	2 U.G.	3 G.	4 G.	5 U.G.	6 U.G.		
E.	.941 N.S.	.803 N.S.	.418 N.S.	.869 N.S.	.772 N.S.	.583 N.S.	.898 N.S.	.641 N.S.
S.D.L.	.046 N.S.	.056 N.S.	.605 N.S.	.971 *	.943 N.S	.959 *	.276 N.S.	.885 N.S.
A.S.L.	.311 N.S.	.141 N.S.	.239 N.S.	.781 N.S.	.971 *	.199 N.S.	.982 *	.805 N.S.
W.S.L.	.880 N.S.	.125 N.S.	.365 N.S.	.381 N.S.	.669 N.S.	.410 N.S.	.490 N.S.	.676 N.S.
P.P.	.592 N.S.	.189 N.S.	.092 N.S.	.575 N.S.	.909 N.S.	.599 N.S.	.598 N.S.	.913 N.S.
P.	.429 N.S.	.139 N.S.	.494 N.S.	.898 N.S.	.734 N.S.	.687 N.S.	.192 N.S.	.742 N.S.
M.	.192 N.S.	.558 N.S.	.194 N.S.	.973 *	.967 *	.665 N.S.	.444 N.S.	.926 N.S.

	Winchmore			Templeton	
Age Interval	Plots			4+5+6 Grazed plots (bulked)	1+2+3 Ungrazed plots (bulked)
	1 G.	2 U.G.	3 I.G.		
E.	.986 N.S.	.969 N.S.	.984 N.S.	.616 N.S.	.985 N.S.
S.D.L.	.022 N.S.	.988 N.S.	.985 N.S.	.528 N.S.	.300 N.S.
A.S.L.	.004 N.S.	- -	- -	.525 N.S.	- -
W.S.L.	.005 N.S.	- -	- -	.522 N.S.	- -
P.P.	.505 N.S.	.530 N.S	.526 N.S.	.616 N.S.	- -
P.	.505 N.S.	- -	- -	- -	- -
M.	.788 N.S.	.991 N.S.	.997 *	.994 N.S.	.449 N.S.

Key * significance at P < .05 for n-2 d.f.

Table 25 Percentage apparent mortality for each age interval, percentage constant mortality rate and percentage generation mortality for each life table in the Hindon study area

Plot 1 G.						
Age Interval	1968	1969	1970	1971	$\bar{x}$	S.D.
E.	66.6	51.1	39.6	79.4	59.2	17.4
S.D.L.	91.7	81.9	78.9	68.3	80.2	9.6
A.S.L.	1.3	1.9	1.0	.8	1.25	.48
W.S.L.	33.7	2.0	1.0	51.7	22.1	24.9
P.P.	88.2	28.5	15.4	21.1	38.3	33.7
P.	16.6	97.1	58.5	64.4	59.1	33.1
G.M.	99.789	99.826	95.626	99.119		
C.M.R.	98.219	98.219	98.219	98.219		

Plot 2 U.G.						
Age Interval	1968	1969	1970	1971	$\bar{x}$	S.D.
E.	83.3	68.8	18.3	65.1	58.9	28.2
S.D.L.	85.1	70.3	78.3	85.9	79.9	7.2
A.S.L.	23.9	34.7	51.1	5.9	28.9	18.9
W.S.L.	51.8	.8	.8	93.7	36.8	44.9
P.P.	92.3	34.1	76.9	0	50.8	41.8
P.	0	83.9	56.6	50	47.6	34.9
G.M.	99.929	99.367	99.138	99.856		
C.M.R.	98.219	98.219	98.219	98.219		

Plot 3 G.						
Age Interval	1968	1969	1970	1971	$\bar{x}$	S.D.
E.	81.6	96.6	32.0	65.2	68.8	27.7
S.D.L.	92.5	.9	66.1	68.3	56.9	39.2
A.S.L.	2.5	17.3	21.0	1.3	10.5	10.1
W.S.L.	2.6	1.2	1.3	40.2	11.3	19.2
P.P.	97.3	65.9	23.1	17.4	50.9	37.7
P.	0	96.6	56.7	42.1	48.8	39.9
G.M.	99.965	99.936	94.009	96.888		
C.M.R.	98.219	98.219	98.219	98.219		

contd.

Table 25 contd.

Plot 4 G.						
Age Interval	1968	1969	1970	1971	$\bar{x}$	S.D.
E.	85.0	7.4	39.0	50.5	45.5	32.0
S.D.L.	80.0	44.9	77.7	73.9	69.1	16.3
A.S.L.	16.5	36.9	27.8	1.0	20.5	15.4
W.S.L.	1.4	1.5	1.2	62.9	16.7	30.7
P.P.	94.3	1.5	9.7	19.4	31.2	42.7
P.	0	96.8	56.7	34.4	46.9	40.5
G.M.	99.859	99.009	96.217	97.496		
C.M.R.	98.219	98.219	98.219	98.219		

Plot 5 U.G.						
Age Interval	1968	1969	1970	1971	$\bar{x}$	S.D.
E.	56.5	1.1	24.3	26.3	27.0	22.7
S.D.L.	89.3	1.1	61.8	97.7	62.5	43.7
A.S.L.	.7	63.3	18.1	11.1	23.3	27.6
W.S.L.	57.2	3.0	38.3	12.5	27.7	24.6
P.P.	92.8	3.1	52.1	85.7	58.4	40.9
P.	0	80.6	61.5	0	35.5	41.7
G.M.	99.859	93.478	97.314	99.813		
C.M.R.	98.219	98.219	98.219	98.219		

Plot 6 U.G.						
Age Interval	1968	1969	1970	1971	$\bar{x}$	S.D.
E.	59.9	55.7	3.9	.4	29.9	32.2
S.D.L.	83.8	67.8	85.7	88.2	81.4	9.2
A.S.L.	33.5	22.1	5.3	96.1	39.2	39.6
W.S.L.	66.6	1.3	13.7	0	20.4	31.4
P.P.	78.0	1.4	56.5	0	33.9	39.4
P.	11.1	83.3	60.0	0	38.6	39.5
G.M.	99.683	98.198	98.052	99.549		
C.M.R.	98.219	98.219	98.219	98.219		

contd.

Table 25 contd.

Plots 2+5+6 U.G.						
Age Interval	1968	1969	1970	1971	$\bar{x}$	S.D.
E.	66.6	66.1	16.5	13.7	40.7	29.6
S.D.L.	86.9	60.6	76.0	94.2	79.4	14.6
A.S.L.	17.7	44.3	31.5	5.9	24.8	16.6
W.S.L.	58.8	1.4	13.5	81.2	38.7	37.5
P.P.	92.8	11.6	61.9	33.3	49.9	35.2
P.	0	83.3	60.6	0	35.9	42.5
G.M.	99.894	98.926	98.218	99.417		
C.M.R.	98.219	98.219	98.219	98.219		

Plots 1+3+4 G.						
Age Interval	1968	1969	1970	1971	$\bar{x}$	S.D.
E.	77.7	84.5	39.9	69.6	67.9	19.6
S.D.L.	90.6	60.4	72.9	71.0	73.7	12.5
A.S.L.	1.7	11.5	33.9	1.0	12.0	15.3
W.S.L.	6.9	1.4	1.3	51.0	15.1	24.0
P.P.	92.6	41.2	2.7	21.3	39.4	38.7
P.	0	95.0	57.7	48.6	50.3	39.1
G.M.	99.859	99.842	95.646	98.274		
C.M.R.	98.219	98.219	98.219	98.219		

Table 26 Percentage apparent mortality for each age interval, percentage constant mortality rate and percentage generation mortality for each life table in the Winchmore and Templeton study areas

Winchmore

Plot 1 G.

	1968	1969	1970	$\bar{x}$	S.D.
E.	98.3	99.9	99.8	99.3	.89
S.D.L.	2.7	0	0	.9	1.56
A.S.L.	0	1.1	0	.4	.63
W.S.L.	0	1.1	0	.4	.63
P.P.	0	65.9	0	21.9	38.0
P.	0	80.0	0	26.7	46.1
G.M.	98.333	99.995	99.823		
C.M.R.	98.219	98.219	98.219		

Plot 2 U.G.

	1968	1969	1970	$\bar{x}$	S.D.
E.	97.5	99.9	99.7	99.0	1.3
S.D.L.	66.6	0	0	22.2	38.4
A.S.L.	0	0	0	-	-
W.S.L.	0	0	0	-	-
P.P.	0	50.0	0	16.6	28.8
P.	0	0	0	-	-
G.M.	98.333	99.994	99.748		
C.M.R.	98.219	98.219	98.219		

Plot 3 I.G.

E.	98.0	99.9	99.52	99.1	1.00
S.D.L.	14.3	0	0	4.7	8.2
A.S.L.	0	0	0	-	-
W.S.L.	0	0	0	-	-
P.P.	0	16.6	0	5.5	9.6
P.	0	0	0	-	-
G.M.	98.333	99.937	99.524		
C.M.R.	98.219	98.219	98.219		

contd.

Templeton

Plots 1 + 2 + 3 U.G.					
	1968	1969	1970	$\bar{x}$	S.D.
E.	96.4	89.8	99.6	95.2	4.99
S.D.L.	91.7	6.7	0	32.8	51.1
A.S.L.	0	0	0	-	-
W.S.L.	0	0	0	-	-
P.P.	0	0	0	-	-
P.	0	14.3	0	4.7	8.2
G.M.	99.704	91.892	99.670		
C.M.R.	98.219	98.219	98.219		

Plots 4 + 5 + 6 G.					
E.	99.7	87.3	98.4	95.1	6.8
S.D.L.	0	95.1	0	31.7	54.9
A.S.L.	0	25.0	0	8.3	14.4
W.S.L.	0	33.0	0	11.0	19.0
P.P.	0	50.0	0	16.6	28.8
P.	0	0	0	-	-
G.M.	99.704	99.845	98.413		
C.M.R.	98.219	98.219	98.219		

Table 27 Expected and actual percentage population trend index for each life table in the Templeton, Winchmore and Hindon study areas

Hindon					
		1968	1969	1970	1971
PLOT 1 G.	Expected	98.6	97.2	2457	494
	Actual	20.2	134.6	233	25.2
PLOT 2 U.G.	Expected	39.4	355	483	80.7
	Actual	72.2	73.3	22.9	34.1
PLOT 3 G.	Expected	19.7	17.9	3363	1747
	Actual	110	13.8	162.9	45.1
PLOT 4 G.	Expected	78.9	556	2123	1405
	Actual	7.1	418	89.7	23.7
PLOT 5 U.G.	Expected	78.9	3662	1508	104
	Actual	2.8	1416	41.1	12.5
PLOT 6 U.G.	Expected	158	1011	1093	252
	Actual	23.4	185	11.7	31.5
PLOTS 2+5+6 U.G.	Expected	59.2	603.1	1000	163.5
	Actual	32.7	144.7	25.5	24.1
PLOTS 1+3+4 G.	Expected	78.9	88.3	2444	961
	Actual	44.7	54.1	159.7	35.9

Winchmore					
		1968	1969	1970	
PLOT 1 G.	Expected	935	2.52	99.4	
	Actual	6185	.422	30	
PLOT 2 U.G.	Expected	936	3.4	141	
	Actual	13928	2.4	449	
PLOT 3 I.G.	Expected	936	35	267	
	Actual	22.33	2.6	91.4	

Contd.

Table 27 contd.

Templeton					
		1968	1969	1970	
PLOTS 1+2+3 U.G.	Expected	166	4553	185	
	Actual	43.7	204.7	12.8	
PLOTS 4+5+6 G.	Expected	166	86.5	890	
	Actual	792	9.7	15.8	

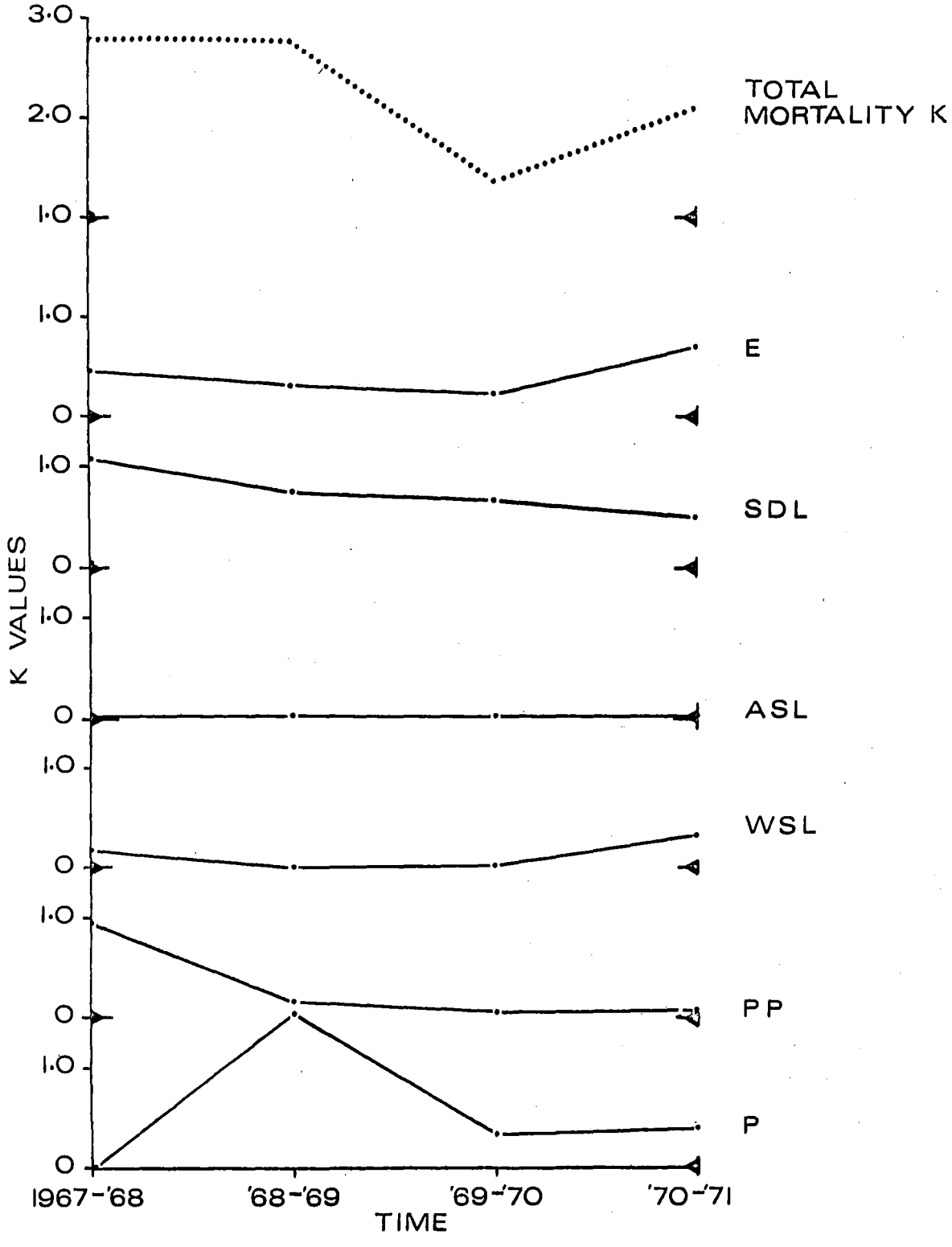


FIG. 20

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot one (grazed) at the Hindon life table study area. Key for age interval abbreviations given in Table 18 p 176.

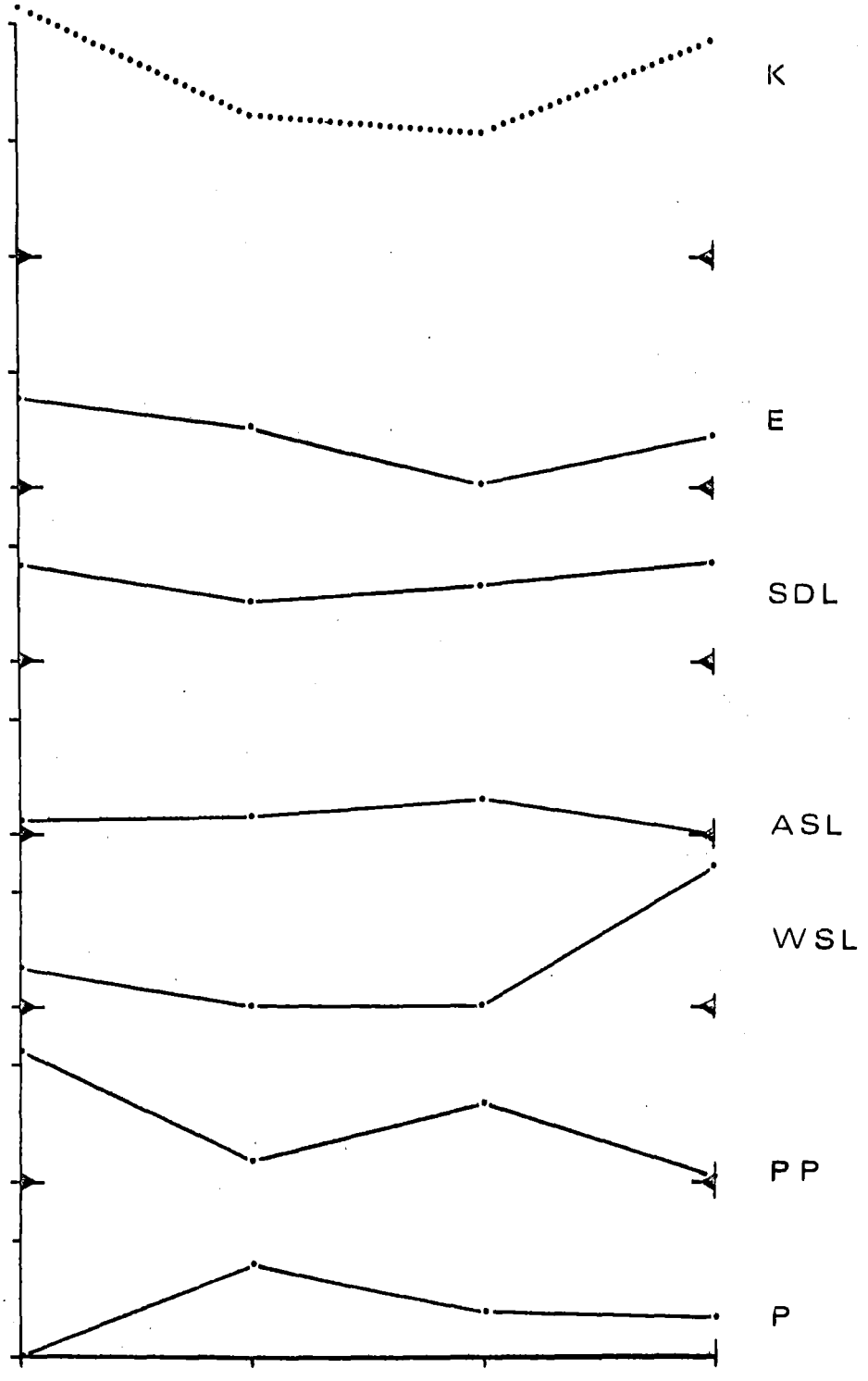


FIG. 21

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot two (ungrazed) at the Hindon life table study area. Key for age interval abbreviations given in Table 18

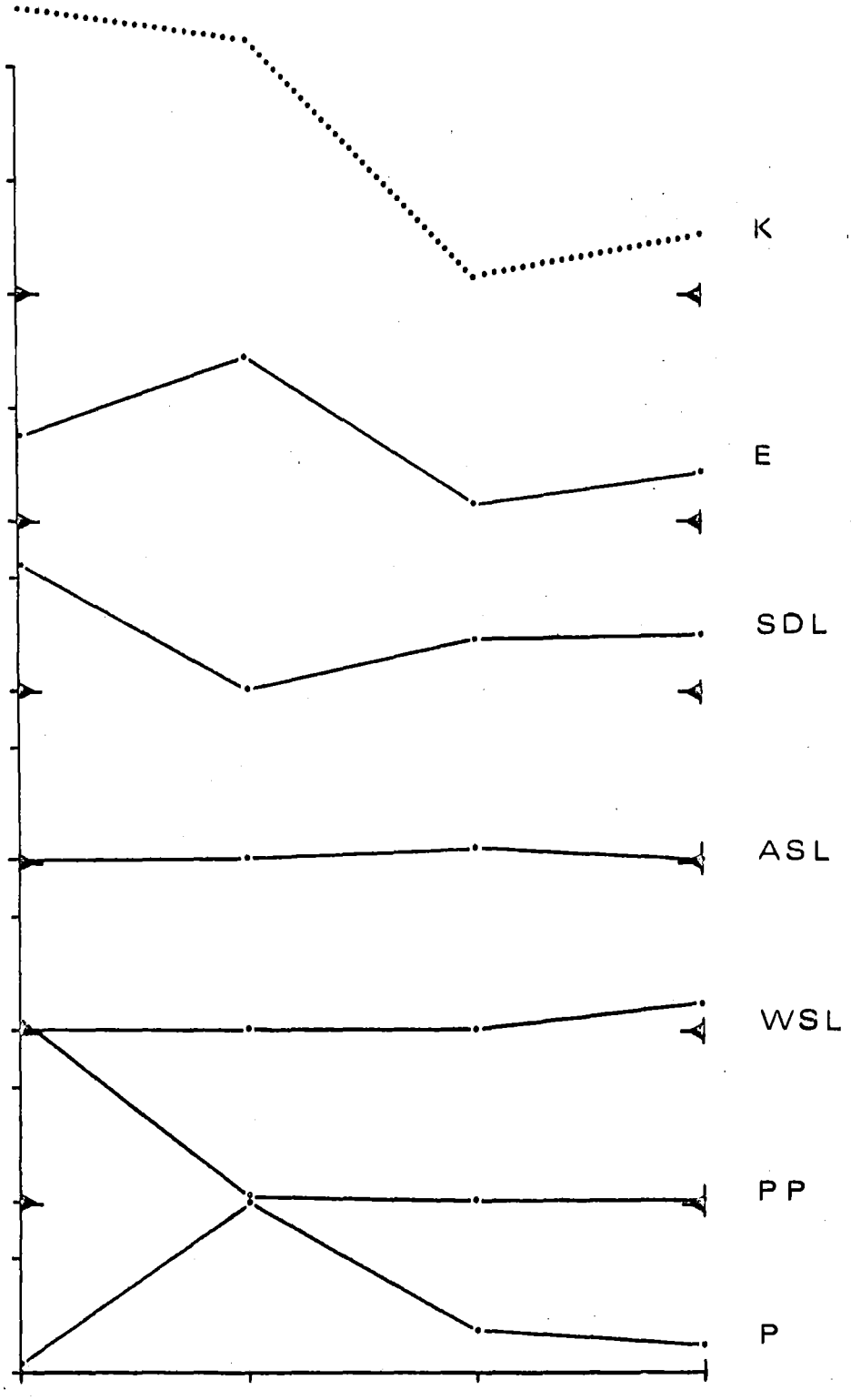


FIG. 22

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot three (grazed) at the Hindon life table study area. Key for age interval abbreviations given in Table 18

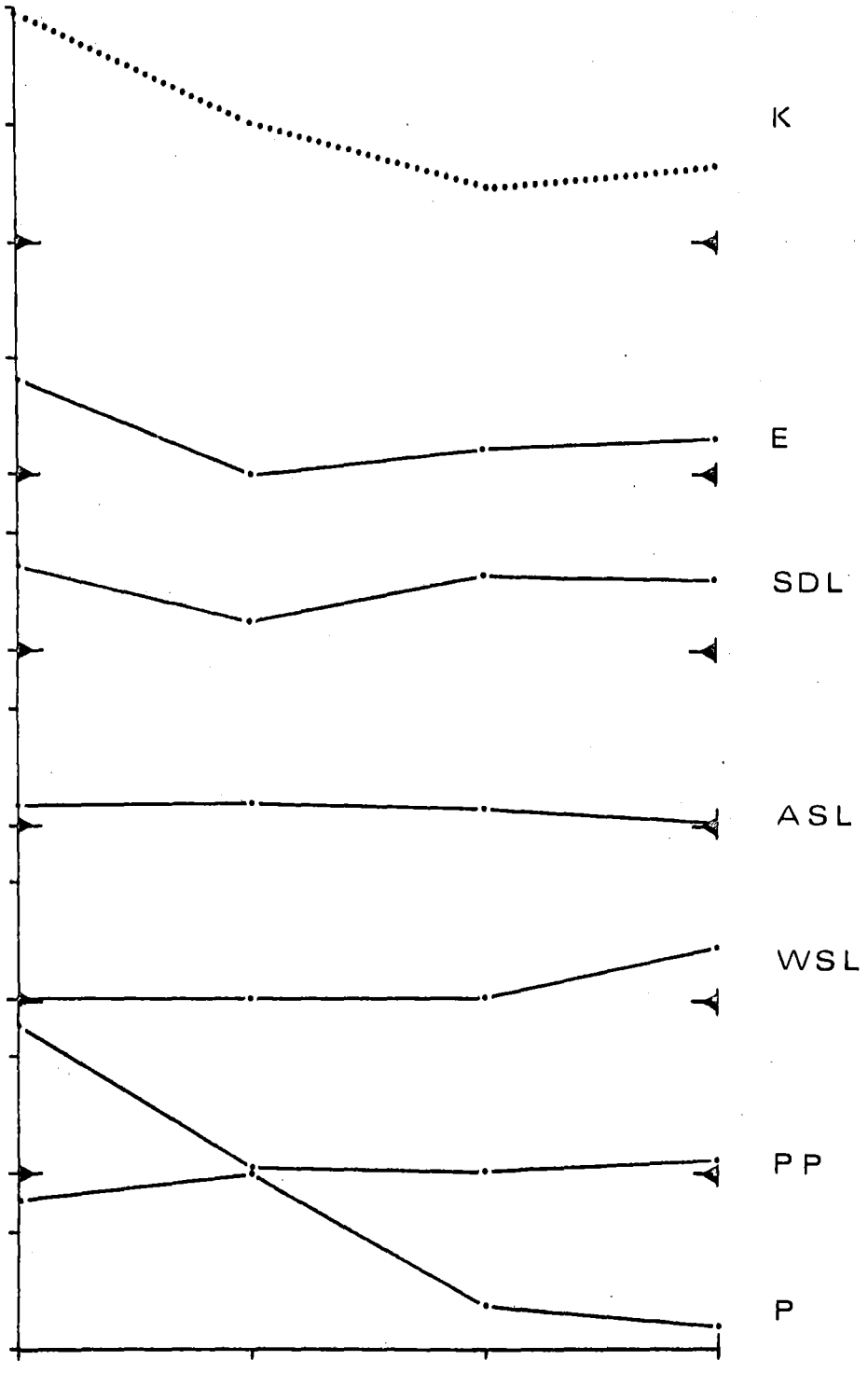


FIG. 23

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot four (grazed) at the Hindon life table study area. Key for age interval abbreviations given in Table 18

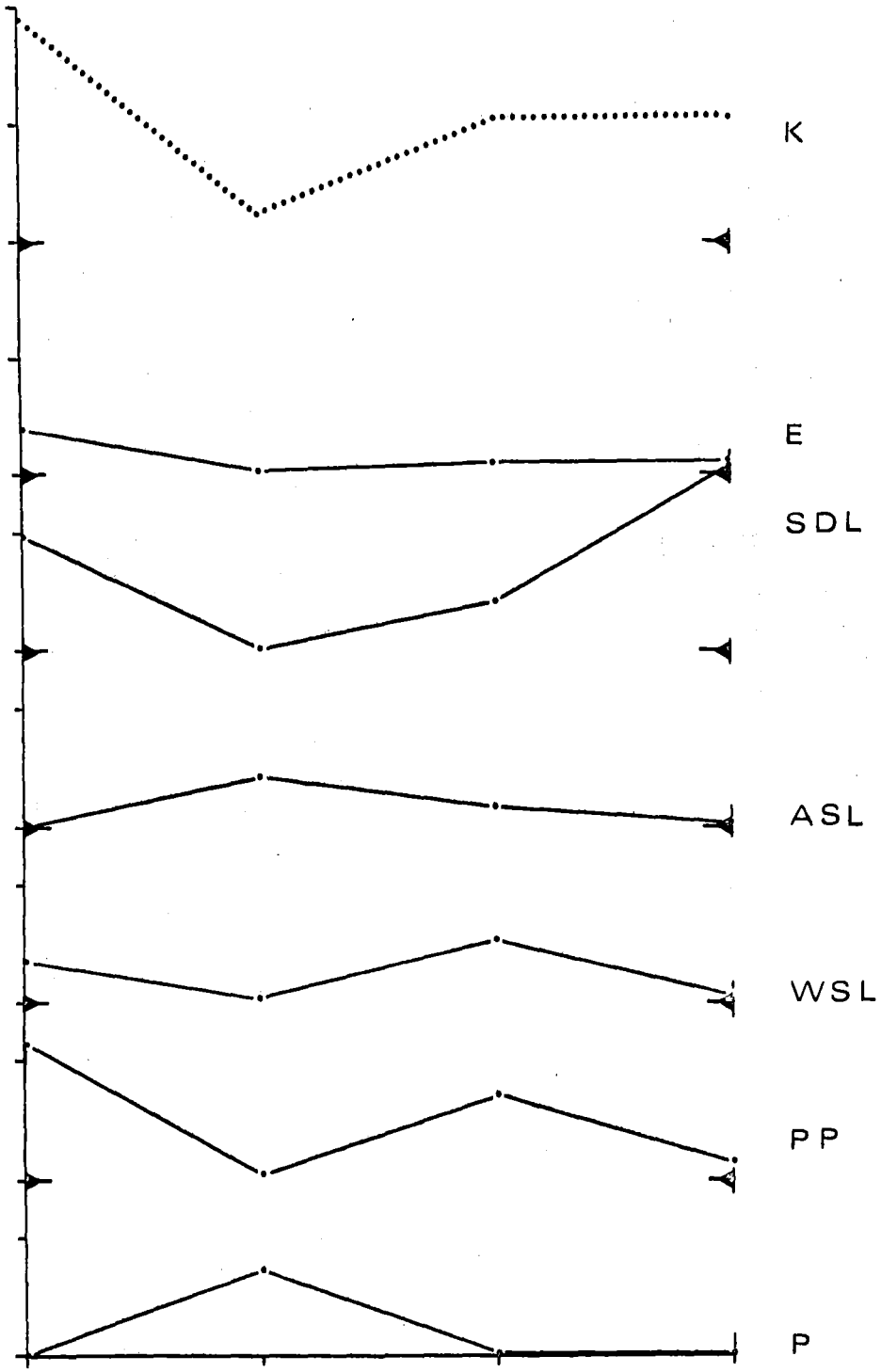


FIG. 24

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot five (ungrazed) at the Hindon life table study area. Key for age interval abbreviations given in Table 18

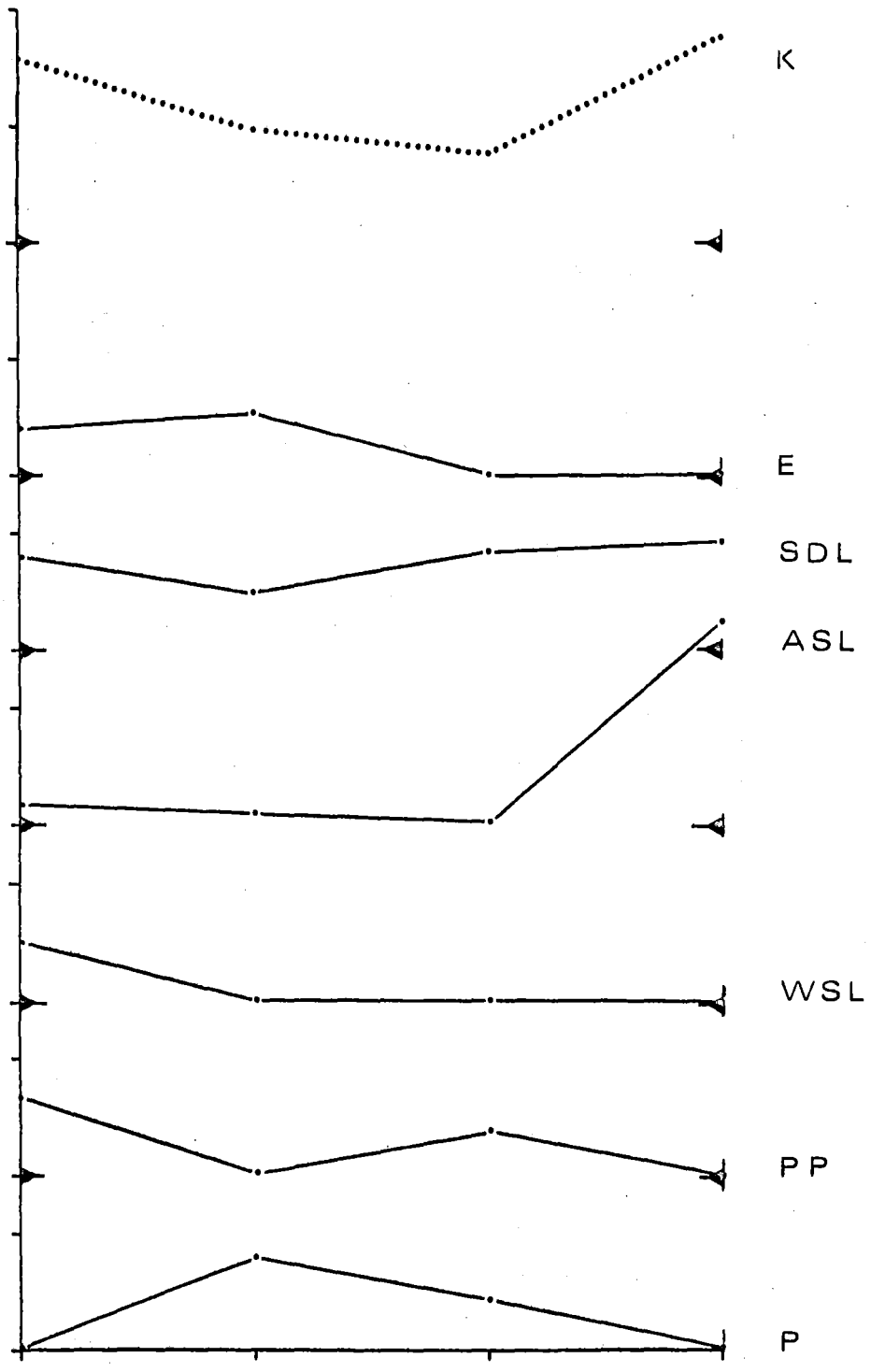


FIG. 25

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot six (ungrazed) at the Hindon life table study area. Key for age interval abbreviations given in Table 18

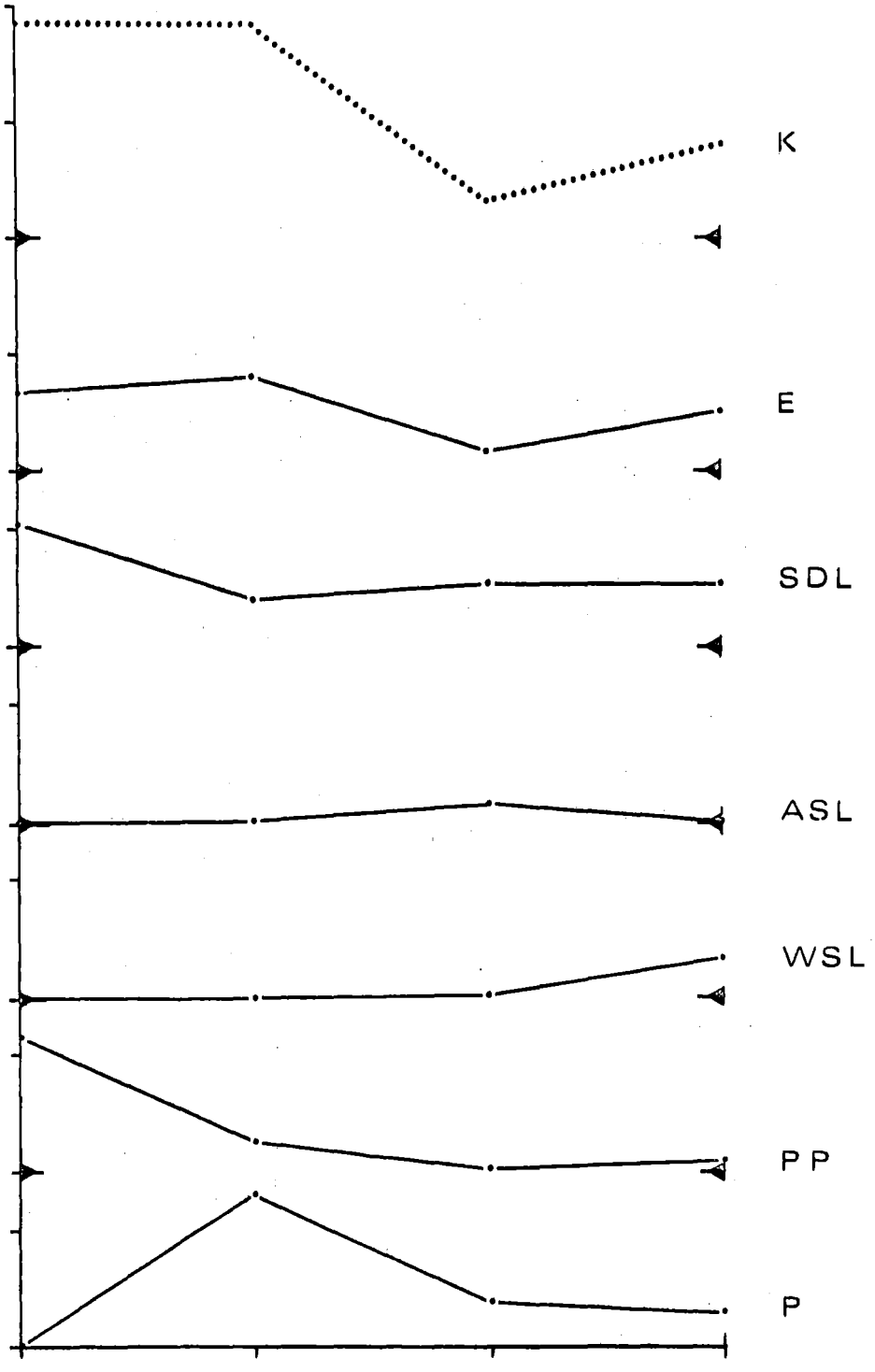


FIG. 26

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plots 1+3+4 (grazed) at the Hindon life table study area. Key for age interval abbreviations given in Table 18

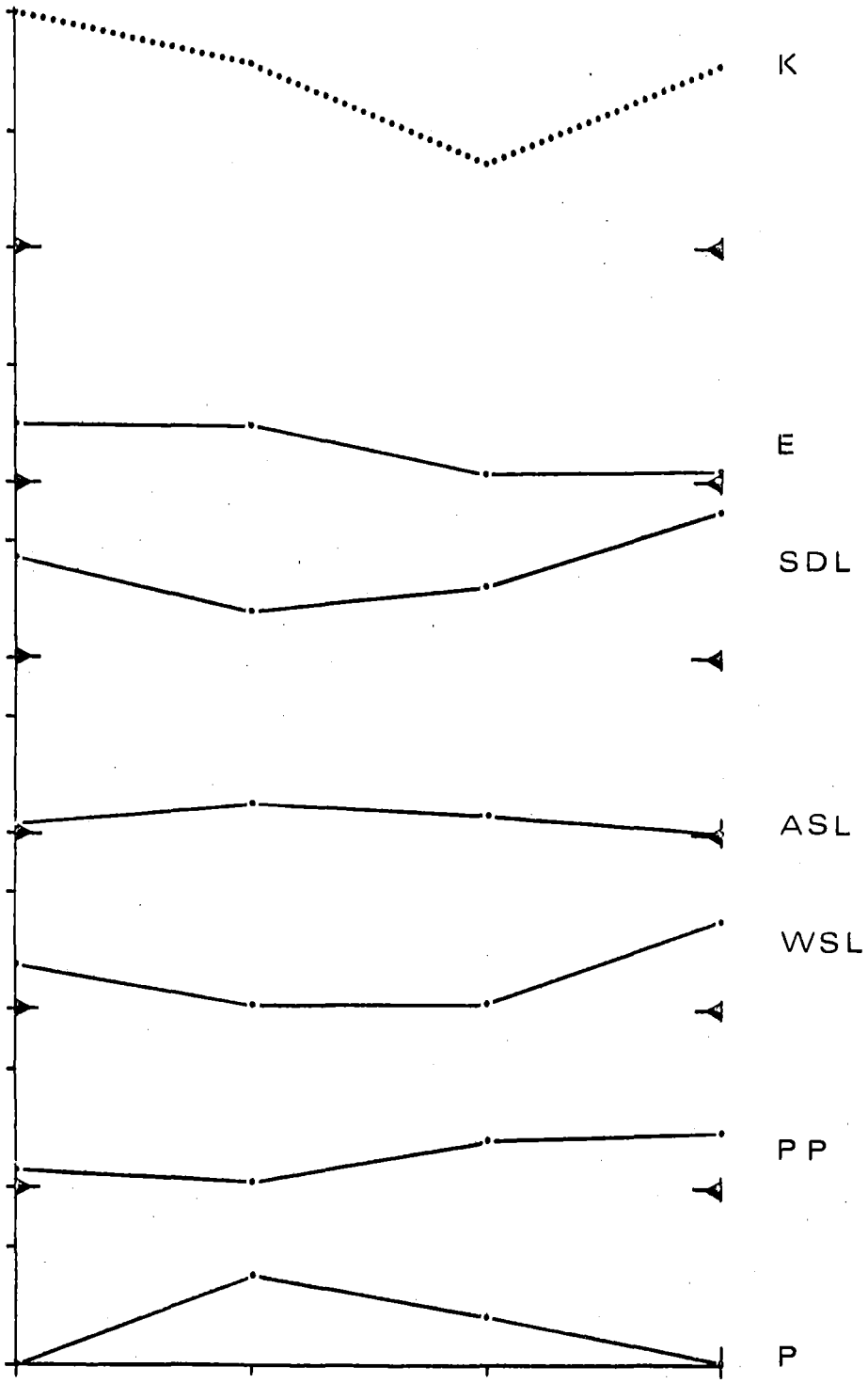


FIG. 27

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plots 2+5+6 (ungrazed) at the Hindon life table study area. Key for age interval abbreviations given in Table 18

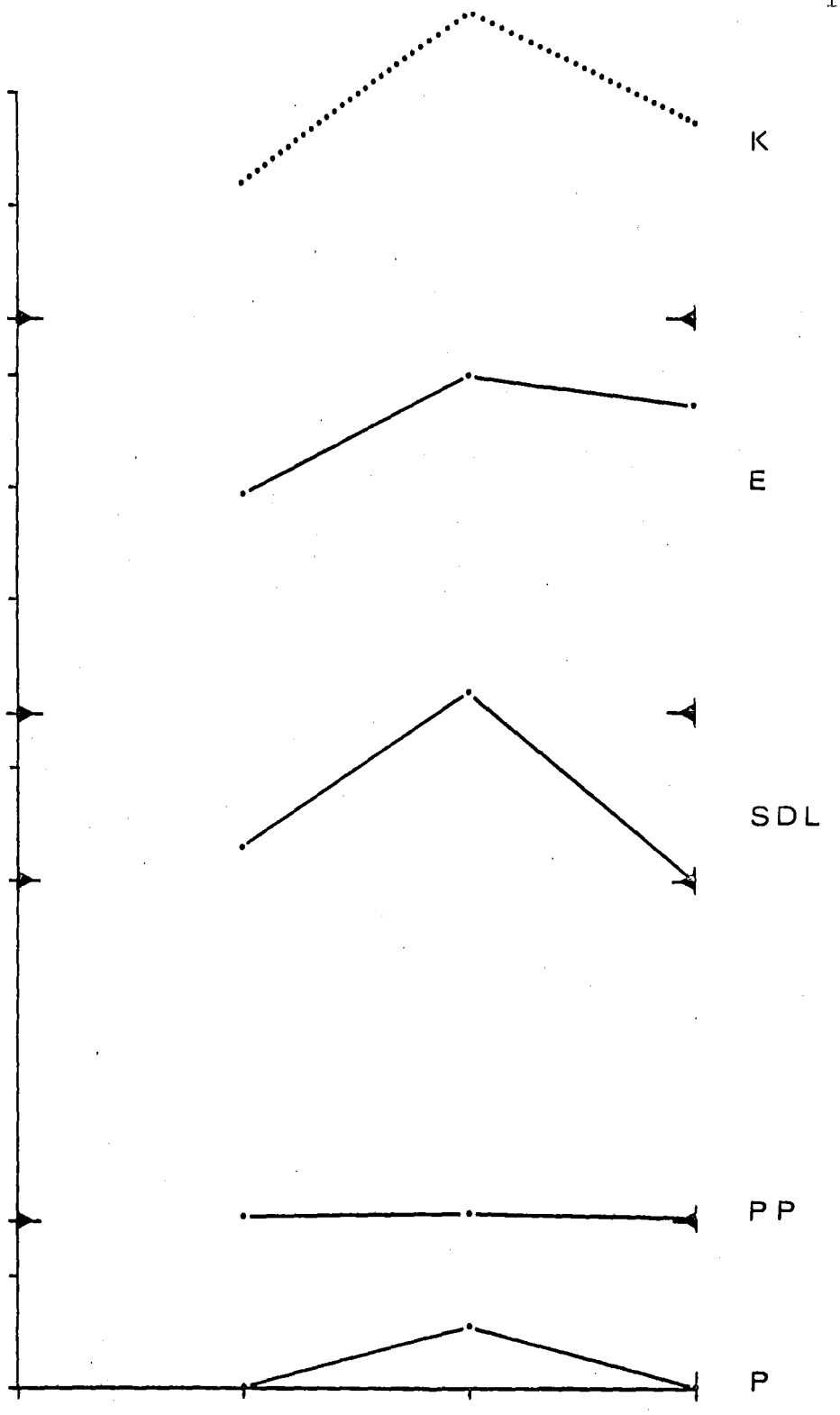


FIG. 28

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot one (grazed) at the Winchmore life table study area. Key for age interval abbreviations given in Table 18

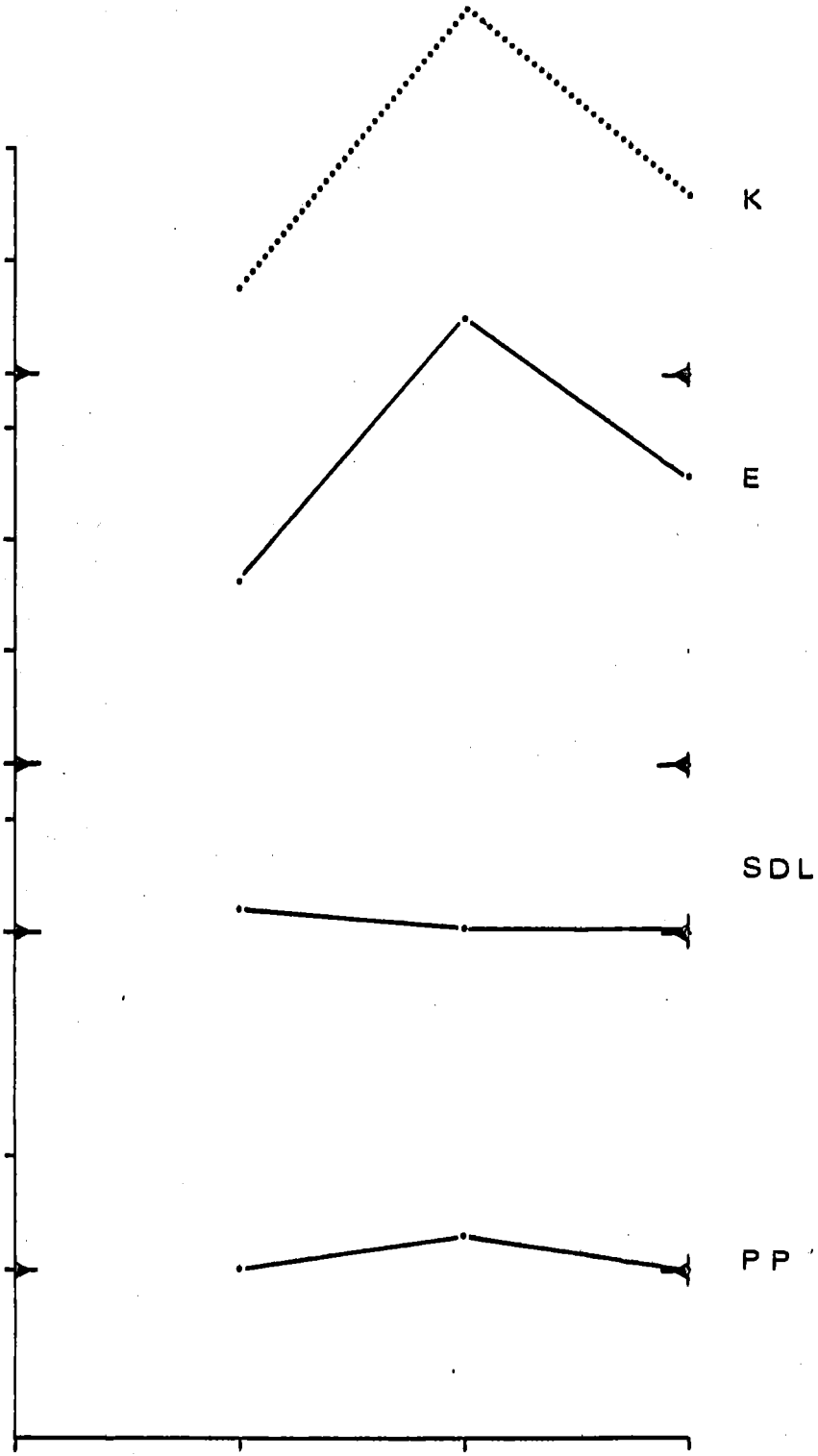


FIG. 29

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot two (ungrazed) at the Winchmore life table study area. Key for age interval abbreviations given in Table 18

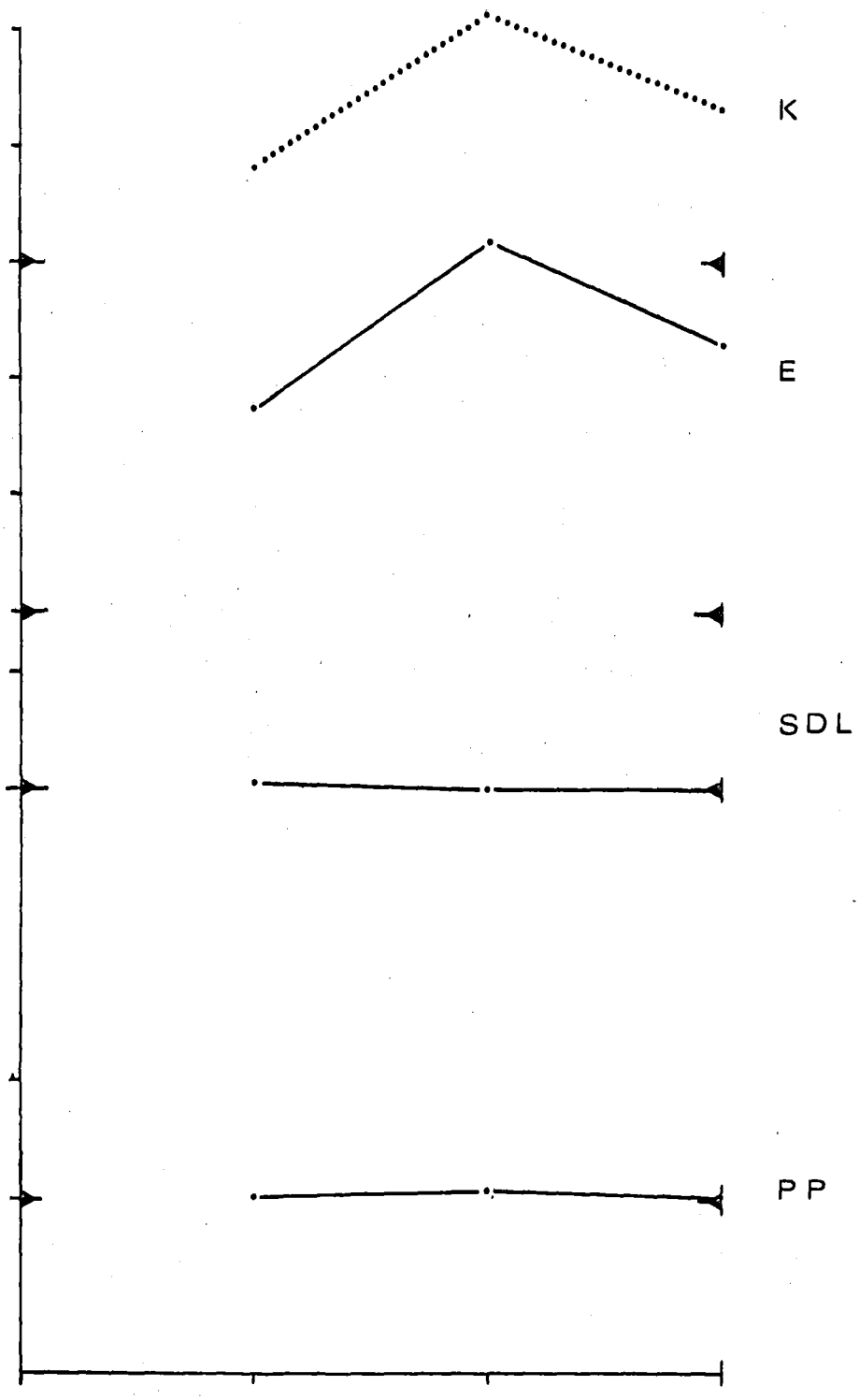


FIG. 30

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plot three (irrigated plus grazed) at the Winchmore life table study area. Key for age interval abbreviations given in Table 18

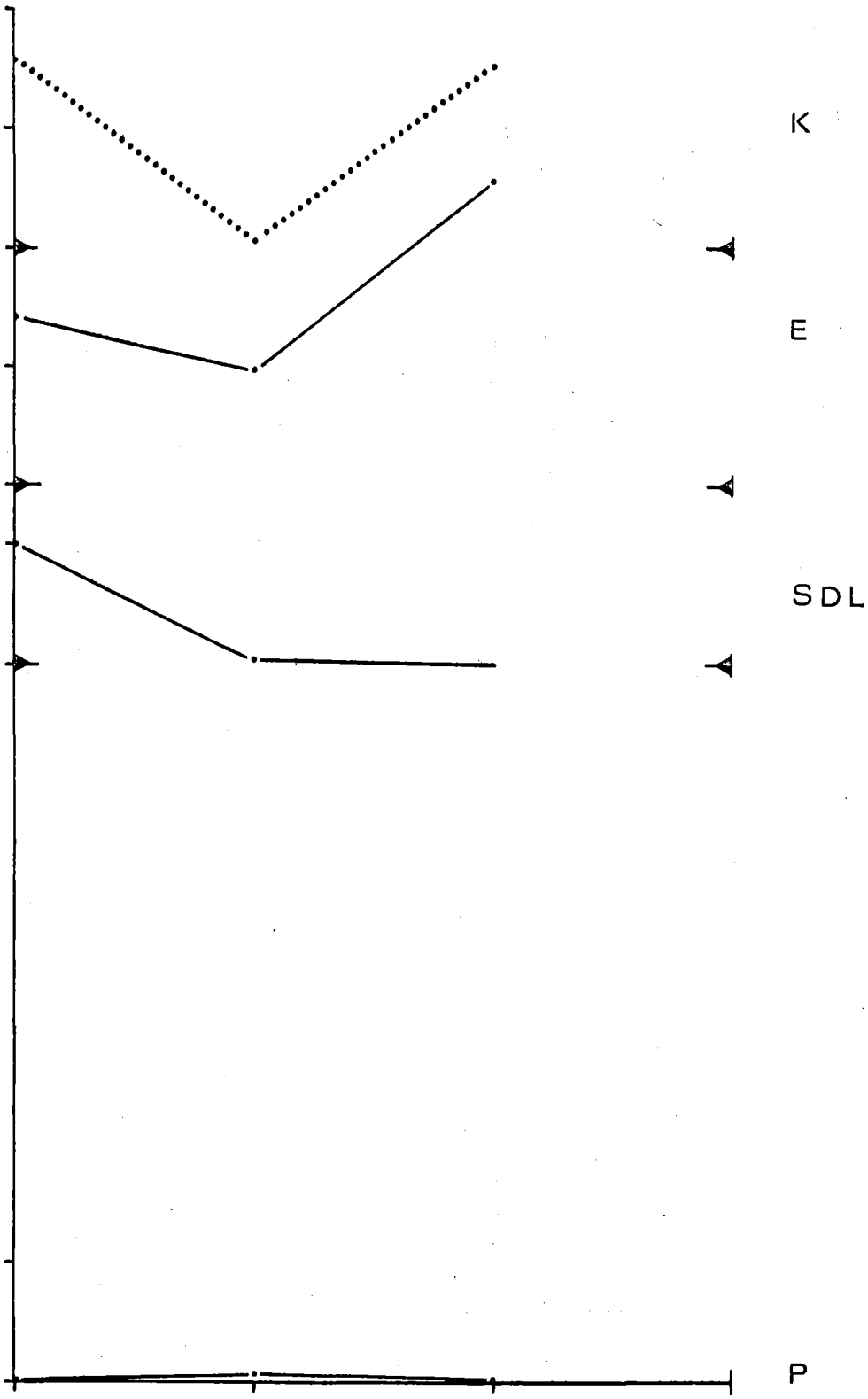


FIG. 31

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plots 1+2+3 (ungrazed) at the Templeton life table study area. Key for age interval abbreviations given in Table 18

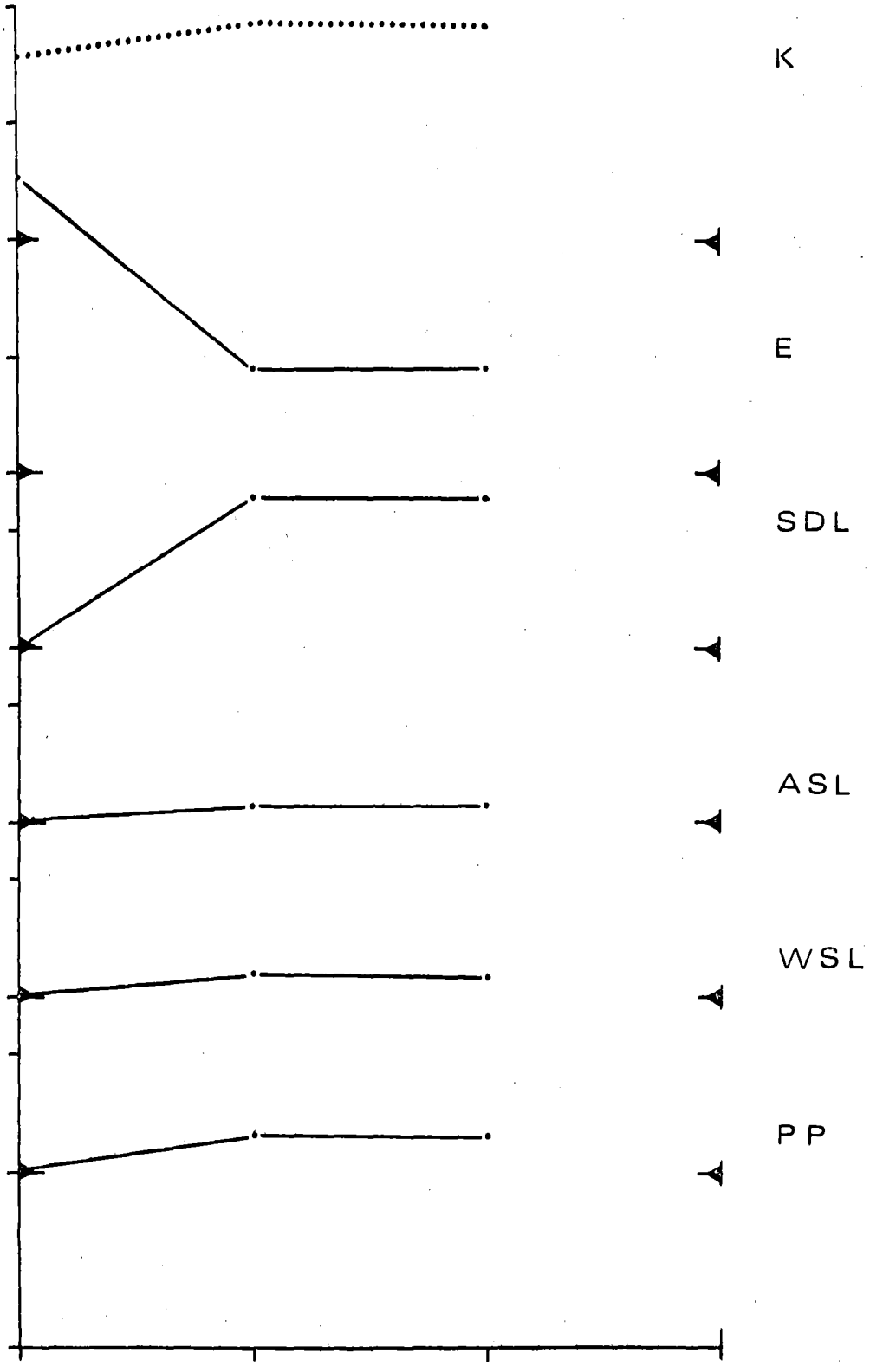


FIG. 32

Graphical correlation between age interval k values (Varley and Gradwell, 1970) and generation mortality (K) for plots 4+5+6 (grazed) at the Templeton life table study area. Key for age interval abbreviations given in Table 18

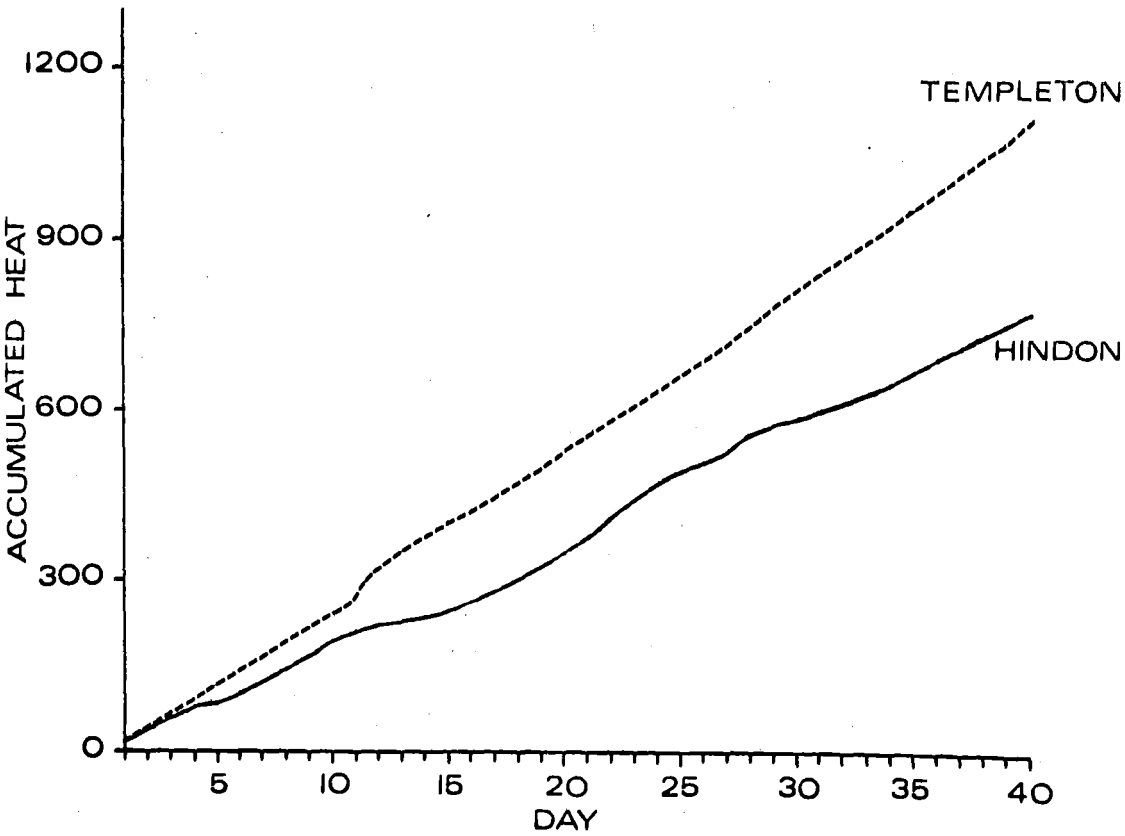


FIG. 33

A graph of accumulated heat energy in "degree days" showing the climatic difference between the Templeton and Hindon life table study areas for the period November 1st to December 9th 1970.

Table 28 Rainfall, spot temperatures and soil surface moisture records from life table study areas

Temperature °C

Date	Time	Position	n	$\bar{x}$	S.D.	95% c.l.
Hindon						
10/12/69	midday	B	60	25.4	1.63	± .4
"	"	C	60	22.7	2.04	± .5
13/12/69	"	B	40	24.8	2.81	± .9
"	"	C	40	23.1	2.28	± .8
22/12/69	"	B	60	27.5	2.83	± .7
"	"	C	60	24.2	2.28	± .5
9/ 1/70	"	B	11	20.8	2.27	±1.5
"	"	C	11	20.3	1.90	±1.3
13/ 1/70	"	B	60	27.4	1.79	± .4
"	"	C	60	24.1	1.93	± .5
30/ 1/70	"	B	60	26.8	1.64	± .4
"	"	C	60	22.5	1.46	± .3
5/ 2/70	"	B	60	26.5	1.57	± .3
"	"	C	60	22.1	1.37	± .3
17/ 2/70	"	B	-	-	-	-
"	"	C	60	20.8	1.62	± .4
Templeton						
3/11/69	1 pm	B	6	26.7		
"	"	C	6	25.6		

% Soil Moistures (0-6 mm depth)

Hindon	Plots					
20/12/69	1-3-4	B	15	33.6	4.9	± 2.7
"	"	C	15	55.2	13.2	± 7.2
"	2-5-6	B	15	33.4	10.6	± 5.8
"	"	C	15	47.3	10.9	± 6.0
9/1/70	1-3-4	B	15	47.9	9.5	± 5.2
"	"	C	15	63.9	10.6	± 5.8
"	2-5-6	B	15	49.9	5.6	± 3.1
"	"	C	15	56.9	9.7	± 5.3
19/1/70	1-3-6	B	15	48.9	13.1	± 7.2
"	"	C	15	61.9	12.6	± 6.9
"	2-5-6	B	15	43.6	6.1	± 3.4
	"	C	15	51.8	8.6	± 6.7

Key

Position B = Measurement taken from bare exposed soil surface

Position C = Measurement taken from under plant leaves or debris

Note: soil temperatures taken with copper/constantine thermocouple and potentiometer

Table 28 contd. Monthly rainfall in mm

Hindon

	Nov.	Dec.	Jan.
1967-68	58.7	31.3	43.5
R.F.	9	14	11
1968-69	47.2	31.3	72.5
R.F.	12	11	15
1969-70	24.7	105.4	117.4
R.F.	9	14	19
1970-71	25.9	67.3	38.4
R.F.	7	6	9
1971-72	97.4	56.5	76.8
R.F.	7	6	9

Winchmore

	Oct.	Nov.	Dec.
1967	86.9	163.2	27.2
R.F.	7	11	9
1968	33.5	61.3	87.6
R.F.	11	8	8
1969	36.1	13.5	120.7
R.F.	9	7	8
1970	33.3	42.6	47.0
R.F.	6	4	9
1971	47.7	31.0	31.0
R.F.	14	7	7

Templeton

	Oct.	Nov.	Dec.
1967	-	-	-
R.F.	-	-	-
1968	18.8	44.7	56.7
R.F.	H	8	8
1969	45.7	10.2	26.7
R.F.	6	5	8
1970	29.7	19.6	5.4
R.F.	7	6	4
1971	28.7	41.1	14.0
R.F.	12	7	7

Key

R.F. = total rainfall days for the month

Note: The rainfall records are given for those months in each study area during which juvenile mortality is influenced by rainfall

Table 29 A list of predators, parasites and pathogens found in the life table study areas at Templeton, Winchmore and Hindon

Predators

Coccinella undecimpunctata L.

Micromus tasmaniae Walk.

Staphylinidae

Carabidae

Chilopoda (order Heterostigmata)

Opiliones

Lycosidae

Aves *Sturnus vulgaris* L.

Alauda arvensis L.

Gymnorhina hypoleuca Hutt.

Larus dominicanus Licht.

Larus novaehollandiae Steph.

Larus bulleri Hutt.

Parasites

Hexamera alcis Walk.

Hexamera signata Walk.

Pathogens

Diplocystis oxycani n.sp. Bhatia

Metarrhizium anisopliae Metchn.

Nucleopolyhedral virus

and the variation around each mean is given as a standard deviation (S.D.). Total generation mortality is shown in Tables 25 and 26 as well as the constant mortality rate (C.M.R.) which is based on a moth fecundity of 1123 eggs per female and a 1:1 sex ratio.

The expected and actual population trend indices, expressed as percentages, are given in Table 27. These indicate variability in adult mortality caused by such factors as moth migration, mating success and fecundity.

Graphical presentation of the mortalities occurring within each age interval (k) with overall generation mortality (K) are given in Figures 20-32. These graphs were formed by calculating and plotting k values for each age interval and total generation mortality (K) (Varley and Gradwell, 1970).

To illustrate the climatic differences between life table sites Figure 33 gives the accumulated heat in 'degree days' for the Templeton and Hindon study areas. Details of rainfall and some microclimate data are given in Table 28. Predators, parasites and pathogens found on all sites over the study period are listed in Table 29.

Discussion of the results from the life table studies

It became obvious early in the sampling programme that detailed life tables of the kind constructed by Morris (1963), Pottinger & Le Roux (1971) and Varley and Gradwell (1970) were not possible in this study. This was because of two difficulties.

1. It was not possible to measure variation in

adult fecundity and sex ratio, because of the short moth flight period, the distance between the three widely scattered study areas and other sampling commitments.

2. Arduous weather and labour problems caused sampling difficulties. Occasionally bad weather prevented sampling at the most appropriate time. If this occurred at the distant Hindon site, delays of up to two weeks could be expected.

Under these conditions it was not possible to accurately sample such things as predator and parasite populations. Despite these problems, however, the results obtained provided an insight into why porina populations fluctuate.

The interpretation of the results was greatly assisted by two factors.

1. The onset of a spring-summer drought period in Canterbury which occurred each season over the study period.

2. The adoption of two different treatments of pasture management (grazed and ungrazed) incorporated in the life table design at the beginning of the study. This led to the development of control measures which were later found to be practicable.

Although this study did not require the development of detailed life tables, future studies on porina population dynamics should be more detailed to fully understand the undoubtedly complex relationships which are briefly discussed below.

The discussion falls naturally into two sections.

1. Examination of the life tables to reveal any key age intervals.

2. The dynamics of porina populations.

Determination of key age intervals

The results obtained clearly revealed that catastrophic mortalities can occur in the early age intervals in the Templeton and Winchmore areas (Table 26). Occasionally, over 99 per cent mortality occurred within the egg and surface dwelling larval stages. Such a catastrophic mortality often resulted in an unmeasurable population by March, although egg numbers were initially high (see Table 20). A similar pattern was revealed in the Hindon study area over the same stages, but there was not the annihilating effect on the population.

This inverse J shaped mortality curve exemplified in Figures 15 to 17 appears to be a characteristic of porina population dynamics.

The correlation coefficients given in Table 24 showed that the surface dwelling larval stage was a key age interval in plots four and six at Hindon. Close study of the correlation coefficients for the same age intervals in other plots and in other study areas indicated that they also could be key intervals provided more replication in time and space was available. For example, the r values for Winchmore (Table 24) given as .988 and .985 are high, but with only one degree of freedom they were not statistically significant.

Microclimatic variations explained why the early age intervals sometimes suffer catastrophic mortalities. This is discussed more fully in Chapter 6. It was enlightening, however, to study the meteorological data, particularly rainfall which is given in Table 28. This information indicated how the geographical differences between the study areas were reflected in a different rate of early instar mortality. For example, Hindon did not experience periods of dessicating drought, common in the Canterbury region. This was exemplified in the normally abundant rainfall at Hindon over the November to January period, together with generally lower temperatures (Figure 33).

The soil profile was also markedly different at Hindon (Plate 19). The layer of semi-decayed organic matter (O.M.) obviously provided ideal survival sites for surface dwelling larvae, compared with the typically barer soil surfaces of the Canterbury Plains (Plate 20).

It was concluded, from the above evidence, that the surface dwelling larvae and the eggs were very susceptible to dry and/or hot conditions on the soil surface.

Furthermore, an even higher mortality could be induced by grazing sheep when the eggs and larvae are on the soil surface. A comparison of the replicated grazed and ungrazed treatments at Hindon showed that the numbers of autumn sub-terranean larvae differed by about 50 per cent in 1968 to 1970 (Table 19, ungrazed plots 2+5+6 and grazed plots 1+3+4). The smaller number occurred in the grazed plots. It was hypothesized that the greater the number of sheep grazed

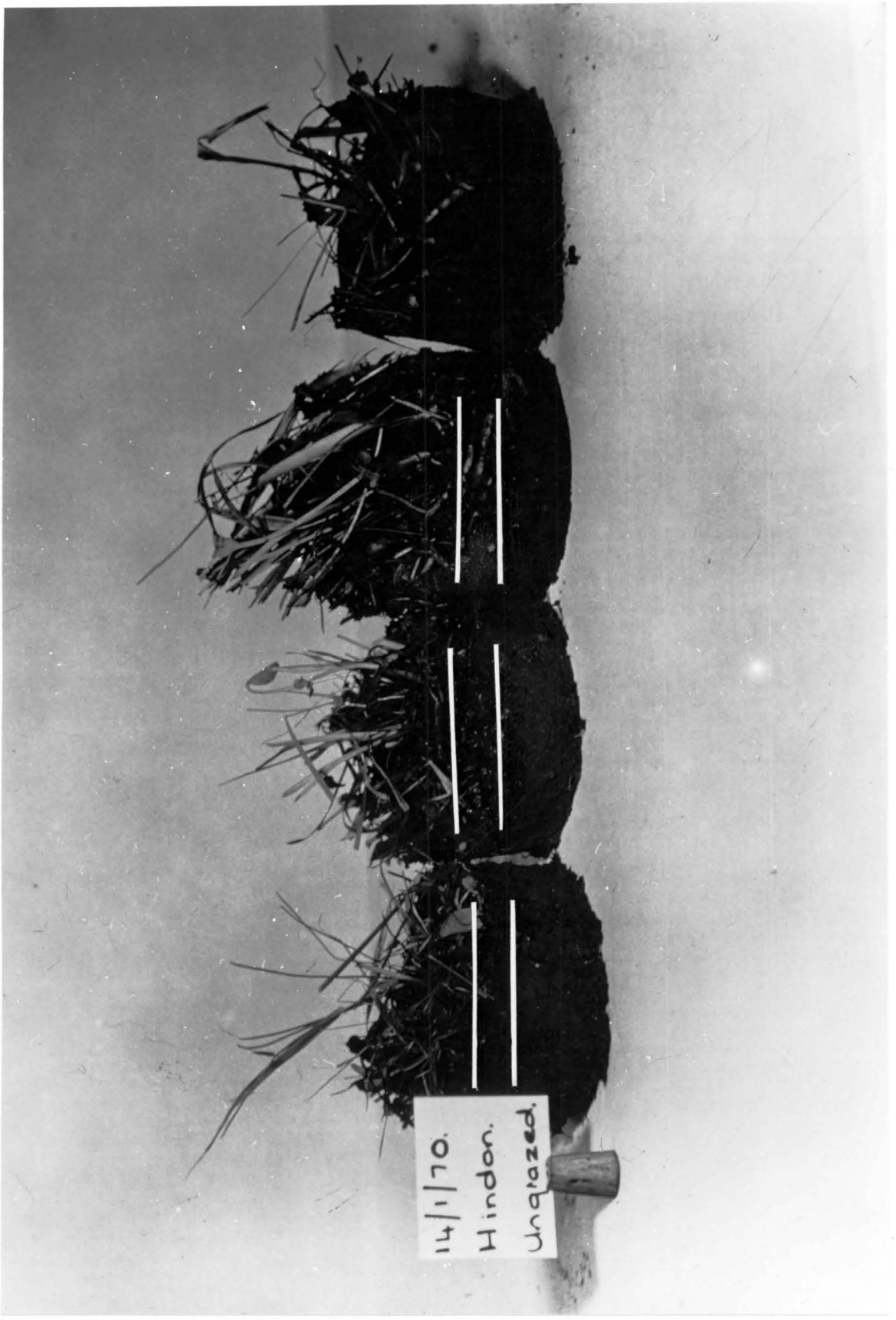


Plate 19 Soil cores from the Hindon study area showing semi-decayed organic matter layer in which surface dwelling larvae obtain shelter.
Note: The organic matter layer is that contained within the white lines.

Plate 20 Soil cores from the Templeton life table study area showing no sign of an organic matter layer.

during the juvenile stages (less plant cover = drier and warmer conditions on the soil surface), the greater the egg and surface dwelling larval mortality.

This preliminary study suggested that high mortality during the surface dwelling stages can depress the population trend in the following generation. This was indicated by the inverse J shaped survivorship curves (Figures 15 to 19). In some of the populations studied, the lower asymptote was reached before the next generation of pupae was formed (Figures 18 and 19).

An important adjunct is that if the density of these early stages is known the density of the subsequent age intervals, and possibly the trend of the following generation, could be forecast. This would be possible if the micro-climatic factors responsible for the early stage mortality were quantified. The detailed study of these factors and surface dwelling larval mortality is the subject for Chapter 6.

An explanation of the dynamics of porina population regulation

It was regrettable that the information obtained was not detailed enough to more than partially comprehend why porina populations change in the way they do. In an attempt to understand the phenomenon, limited information was supplemented by a combination of intuition and observation. The following interpretations are offered with the knowledge that other explanations of the results obtained may be just as meaningful.

In the following discussion it is stressed that age interval mortalities are interpreted more in relation to their overall effect on population trend. In the previous section emphasis was placed on the reduction, to sub-economic levels, of the density of certain age intervals within a particular generation. In the following section mortality is discussed in relation to regulation from generation to generation, as Morris (1957) has stated "that variations in individual mortalities should be interpreted according to their effects on population trend rather than on generation mortality alone". Furthermore he says, "the relationship between population trend and generation mortality is hyperbolic rather than directly proportional. He concluded "that variation is the important attribute of mortality and that low but variable mortalities may have more influence on population trend than high, but relatively constant mortalities."

The results presented in this thesis mainly confirm the above suggestions, but there were anomalies. It has already been shown that the surface dwelling larval period is a stage within which a highly variable key mortality operates. Closer study of Table 25, however, showed that although the surface dwelling larval mortality was at times high, it had low variability. In plot one (Table 25) the mean for the surface dwelling larval mortality over four years was 80.2 per cent but with a standard deviation of only 9.6. On the other hand, the mean mortality of the prepupal and pupal stages was 38.3 per cent and 59.1 per cent, respectively, with standard deviations of 33.7 and 33.1. This indicated

a relatively low mortality with high variation between generations. A similar pattern held for the other blocks to a greater or lesser extent. If, as Morris (1957) suggests, highly variable mortality is more important in determining population changes, then because of the inter-generation variability the pupal and prepupal stages should have contributed to a greater extent to trend index variation. Surprisingly, the analysis using Watt's (1963) technique (Table 24) did not show this. In no case were the prepupal and pupal stages significantly statistically correlated with the trend index. Furthermore, most of the r values were rather low for the two stages (Table 24) which suggested that they were not likely to become significant even with increased temporal replication.

When using the graphical technique of Varley and Gradwell (1970), however, it was puzzling that a number of the pupal stage k values, followed K variations (Figures 20-32) more closely than the other age interval k values.

On one hand graphical analysis suggested that pupal mortality contributed most to generation trend. On the other hand correlation coefficient analysis suggested they were not important. Intuitively, this author feels that the pupal and prepupal stages should be studied in more detail in any future work, as it was felt that these stages <u>do</u> have an important effect on population trend in some areas, as there are a number of mortality factors which can operate on the prepupal and pupal stages.

1. Density dependent factors such as, a Tachinid

fly (Hexamera alcis), a green muscardine fungus, (Metarrhizium anisopliae) and a nucleopolyhedral virus.

2. Density independent factors such as snow and frost.

Pottinger and Welsh (pers. comm.) have observed the following two factors which affected survival of pupae.

1. Earthworm activity blocking the tunnel thereby entrapping the pupa.

2. Failure to eclose because of very dry conditions.

Density dependent mortality factors were considered very important in some situations and years. When the muscardine fungus level was high, larval population levels were also initially high. Although not measured, it was assumed that the effects of the high level of fungus infestation was carried through into the pupal stage where high mortality occurred and this resulted in low pupal population densities. For example, there was a noticeable drop in the ungrazed plots (two, five and six) at Hindon in 1971 (Table 19) following a previously dense larval population which was observed to be extensively infested with muscardine fungus.

There was also one mortality factor whose effects could be triggered either by density dependent or independent means. This was the nucleopolyhedral virus which commonly infects the early larval instars (Moore,, 1972) and normally contributes insignificantly to total generation mortality.

It could act in a highly lethal and significant manner, however, if a stress was placed on the late larval stages. Such a stress could be induced by a shortage of food, or weather factors, such as abnormally heavy rain or snow which can flood burrows and also assist in the transfer of virus particles. All of these virus epidemic "triggering mechanisms" could act in a contemporaneous manner. These are only interesting suppositions, however, and confirmation would require more detailed life tables accumulated over a long period of time.

An interesting and completely unanticipated result was the occurrence of a key mortality in the autumn subterranean larval age interval (Table 24). After analysis, however, correlation was found to be negative, i.e. the age interval mortality varied inversely with the trend index. This unlikely relationship meant that an increase in autumn subterranean larval survival was significantly correlated with a decrease in population trend. If this relationship had not been statistically revealed on two occasions (Table 24) it could have been a chance statistical relationship of no real significance. A more likely explanation was that it had biological significance in the form of an inverse, density-dependent mortality acting in a delayed manner. Such a mortality factor could act in the following way —
If survival in the autumn subterranean larval stage is unusually high it is followed by a greater than usual mortality in the following age intervals which would be sufficient to cause a decrease in trend index. The extra

mortality would be spread evenly over the subsequent four age intervals, and therefore, by not being confined to one particular interval, would prevent any statistically significant trend index correlation with any of the four. Alternatively, a low autumn subterranean larval survival would not bring about significant mortality in the remaining stages, but could increase the trend index. Overall, this looks like the action of a delayed density dependent mortality factor whose action on the late age intervals depends upon the density of the autumn subterranean larval population.

It was tentatively concluded that the negative correlation was the effect of a combination of an inverse and delayed density dependent mortality (Varley and Gradwell, 1970). Moreover, it is likely that the mortality factors mentioned earlier (Tachinid fly, green muscardine fungus and nucleo-polyhedral virus) are responsible for this phenomenon.

To clarify the above hypothesis, further analysis using Varley and Gradwell's technique was warranted, but was beyond the scope of this study.

The mechanism described above could be responsible, however, for the significant decrease in population trend in the ungrazed plots at Hindon between 1970 and 1972. In these plots (two, five and six) the autumn subterranean larval numbers were relatively high in 1970 (Table 19) but a high percentage mortality occurred during the prepupal stage in that year. In direct previous contrast the population trend decreased thereafter. In fact, the density of porina in the ungrazed plots became much lower than in the grazed plots.

This was a complete reversal of the previous situation which occurred in 1968-1969 (Table 19).

It was interesting to note that the adult stage was a key age interval in plots four and five at Hindon and plot three at Winchmore (Table 24). The fact that the r values for this age interval were high, (Table 24) indicated that with more life table replication, adult mortality would correlate significantly with the trend index in other plots as well.

It was assumed that migration accounted for most of the variation in moth mortality although differences in sex ratio, fertility and fecundity could also be important.

The factor which greatly influences migration is density independent, namely wind, although as Martyn (1965) points out, density dependent factors such as overcrowding, could also indirectly influence the extent of migration. The more overcrowded the larval population the lighter the moth and the lower the fecundity. The lighter moths would be more capable of emigrating from the crowded area.

The implications which arise from this discussion point to the difficulties involved if attempts are made to forecast porina densities more than one generation ahead. Because of the random nature of the density independent mortality factors long range population forecasts would be impossible. Moreover, other density independent mortality factors operating on the surface dwelling larval stage would cause more complications. The way these mortality factors act suggest that porina population fluctuations between epidemic and endemic levels occur only by chance, if the

hypothesis is accepted that weather variables operate randomly. For this reason it would appear unwise to try and calculate an equilibrium or mean population level for porina, and forecast fluctuations about this mean, by developing a predictive mathematical model.

Large, and apparently random, changes in trend index can be seen in Table 27, particularly at the Winchmore site. In more equitable environments such as Hindon the range was generally much less and consequently the population densities were less variable between generations.

There is, however, no great necessity to forecast levels of porina populations two or more generations ahead, as it serves no practical purpose. All that is required is a timely reliable estimate of the subterranean larval population densities, so that control measures can be applied if required.

An interesting feature of porina population dynamics revealed in Table 27 was the amplitude of the trend index fluctuations. The trend index ranged from .421 per cent to 13,928 per cent. This appeared to be a direct effect of high fecundity supplemented by immigration. Porina fecundity is very high compared with most other Lepidoptera. For example, the mean egg number/female for Lithocolletis blancardella was estimated to be only 21.6 (Pottinger and Le Roux, 1971) and the mean egg number for Choristoneura fumiferana was 200 (Morris, 1963). Assuming porina fecundity for an average population was about 1,200 eggs per moth, the mean maximum possible increase in a generation could be as high as 600 per cent, even if no mortality or immigration took place.

It was therefore very easy to see why violent fluctuations in trend index occurred.

Thus, if any mortality factor relaxes in the mortality sequence and other factors do not compensate, a large increase will occur in the subsequent generation. For example, because porina population survival can be described by a J shaped curve, any reduction of early age interval mortality followed by normal mortality thereafter, will have a considerable effect on the density of the following age intervals. This does not happen very often, although cases are known in pastures shut for grass seed or hay. Under these very favourable microclimatic conditions very high numbers of surface dwelling larvae can result from a previous population too low to measure.

Criticism of analyses used in the life table studies

This study clearly demonstrated that the two methods used to analyse the dynamics of porina populations should be used together, as the deficiencies of one were covered by the other. For example, Varley and Gradwell's (1970) technique did not show moth mortality "per se", as it was lumped in with the pupal mortality. Consequently, the significance of pupal k value variations was misinterpreted. Watt's (1963) technique overcame this deficiency because a survivorship figure for moth mortality was calculated. This figure, which was based on actual and expected egg numbers, was included in the correlation analysis.

Although the method of Varley and Gradwell was much

simpler to use and less time consuming than Watt's technique, the present author found difficulty in visually determining the significance of the contribution made by each age interval. This was mainly due to the small number of generations sampled (four) compared with the ten used by Varley and Gradwell (1960). Interpretation was further confused with the occurrence of both negative and positive correlations. Nevertheless, the amplitude of the age interval k value variations, were some indication of their relative importance to the trend index. In fact, the age intervals within which significant mortality occurred, were revealed by Varley and Gradwell's method prior to the application of Watt's technique on the Templeton and Winchmore life tables. This was because of the strong correlations.

The Hindon life tables were more complex and Watt's method of analysis allowed greater understanding of the dynamics of the porina populations at Hindon than was possible with Varley and Gradwell's method alone.

Overall, there was little to choose between the two techniques, particularly for a provisional type of project such as this study. For long term studies, however, the Varley and Gradwell (1970) technique appears preferable. This is because its philosophy is centred around the development of meaningful sub-models for each age interval. In comparison, Watt's technique was basically concerned with developing predictive statistical models rather than biological causal relationships.

Furthermore, a recent critique by Luck (1971) of the two

methods, showed that although Watt's technique could detect variation in mortality between generations, it could not satisfactorily distinguish the density relationships of that mortality. In contrast Varley and Gradwell's method can express such relationships.

CONCLUSIONS FROM THE RESULTS OF THE LIFE TABLE STUDIES

The above interpretation was in agreement with the suggestions of Morris (1957) although the mortality factor acting on one key age interval, i.e. surface dwelling larval instar, did not cause either particularly variable or low percentage mortality. The factor occurring in the other key age interval (moths), however, acted in close agreement with Morris's suggestions, and caused highly variable and low percentage mortality. The key mortality factors operating on these two age intervals were both considered to be density independent. Drought significantly affected the density of surface dwelling larval populations and wind influenced the migration of moths. Although not revealed in this study there was a suggestion that density dependent mortality factors played a role in influencing population trends. This was because a relationship was observed, but not proven, between this type of mortality factor and porina population density. For example, a high larval density preceded an attack of green muscardine fungus. Furthermore, because of the variability in numbers in some of the nonsignificant age intervals it was concluded that some density dependent mortality factors, operated in a compensatory manner. For example, in the absence of a major key mortality factor such as drought, compensatory mortality

would later occur, caused by secondary mortality factors such as a fungus, parasite or virus.

It was also concluded that geographical differences radically altered the importance of these mortality factors. Under favourable climatic conditions, such as usually exist at Hindon, higher population levels occurred, with relatively less violent fluctuations in numbers, compared with Canterbury which had an extremely variable climate.

At Hindon the density dependent factors acting on the later age intervals, no doubt often act in regulating populations. On the other hand, in Canterbury, such mortality factors would act less often, because the environment is more severe on the juvenile stages and this results in low population densities which prevents the effective operation of density dependent mortality factors.

Because porina inhabits an environment created by man, it is at a distinct disadvantage with regard to survival. In some areas the climate and farming practices combine to allow populations to survive from year to year, e.g. Otago. In some other areas such as Canterbury, porina only survives in favourable years. It is in the low rainfall areas that changes in pastures brought about by farming activities accentuate mortality most significantly. It is for this reason that porina occurs only sporadically in Canterbury. Man is therefore indirectly a major variable key mortality factor, supplementing natural mortality by his management of sheep and cattle and the consequent removal of plant cover during the susceptible egg and early instar stages.

This strongly suggests that the way to control porina

infestations without the use of insecticide, is to supplement man's influence on naturally occurring mortality.