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Tullbergia krausbaueri (BÖRNER) its interaction in agriculture: the biology, taxonomy and interaction with Beta vulgaris and Gamma-benzene hexachloride and the development of a pest-crop-pesticide model

by Ernest Obeng

A Doctoral thesis

Submitted in fulfilment of the requirements for the award of Doctor of Philosophy of the Loughborough University of Technology.

February 1992

ABSTRACT.

The association between a monoculture crop, an established pest and a means of chemical pest control is an important consideration in modern agriculture.

Collembola, in particular the Onychiuridae Tullbergia krausbaueri and Onychurus armatus, have been associated with the cultivation of sugar beet (Beta vulgaris) since 1958 (Jones and Dunning 1972). Since the 1960's, pests of sugar beet have been controlled with Gamma benzene hexachloride (BHC). Although the association between sugar beet, Collembola and BHC has been established for some time, the specific interactions have not been evaluated by laboratory methods.

The aims of this study were to clarify the plant, pest and pesticide interactions and to develop mathematical models to assist in control of the pest.

Laboratory techniques were developed for culturing populations of the phytophagous soil inhabiting insect, T. krausbaueri over a 120 day time period. Insects were removed from population cohorts to study their biology and taxonomy using scanning electron microscopy. The response of the whole population to different diets and concentrations of BHC was also examined. Both short term studies, using 24 hour toxicity tests and long term studies involving population cultures were carried out to determine BHC effects.

An examination was made of the effects of the pesticide BHC on the germination and growth of varieties of Sugar beet (monoire, julia, IBB83 and primhill) which were germinated and grown to the two true leaf stage. The phytophagy of T. krausbaueri on sugar beet in culture was also confirmed.
The interactions between sugar beet, Collembola and pesticide observed in the laboratory were incorporated into mathematical probability-matrix population growth models. The models, in the form of computer spreadsheets, predicted population changes under pesticide application using population simulation techniques.

The specific morphological features of *T. krausbaueri* (the pseudocelli, post antennal organ and antennal organ) were identified and differentiated from those of the morphologically similar species *O. armatus*. It was confirmed that *T. krausbaueri* reproduces by parthenogenetic means and juvenile reproductive and post-reproductive stages could be differentiated by size when cultured under similar environmental conditions. The reproductive stages of the insect were found to be the least susceptible to the pesticide BHC and the Spearman Karber LC50 test over 24 hours gave a value of 5.4x10^-4 mg a.i. ml^-1 for this group.

Long term evaluation of population development identified the Rm value, the intrinsic rate for natural increase. Rm values varied depending on different conditions of diet, the presence of pesticide and the culture temperature.

The pesticide BHC was found to have a significant effect on the germination and growth of all four sugar beet varieties. As pesticide concentrations increased significant reductions in root length and weight were observed.

Population growth matrix models produced by computer spreadsheet programs accurately predicted the interactions between populations of *T. krausbaueri*, sugar beet and the pesticide BHC and can potentially be used as the basis for pest-control strategies.
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Finally I thank my wife Sharon for her uncompromising support my son Adam for his unique scientific perspective. Lou, Joyce and David Cohen for their encouragement, my mother Letitia, Bob, Edward Susan and Letitia for keeping me motivated and Jah for guidance.
1. General Introduction.

Sugar is produced in temperate climates from the cultivation of sugar beet (B. vulgaris). This cultivation started in Europe in AD 1800 (Hough and Emsley 1986). As a farm crop, sugar beet is one of the most demanding to grow (Bray and Thompson 1985). It involves a delicate seed and seedling stage which require the application of correct crop production and protection strategies and precise harvesting and post-harvest techniques to obtain a good yield. Sugar beet can be cultivated on a wide variety of soil types using one of the sugar beet seed varieties produced by sugar beet seed growers. Varieties are recommended by seed testing bodies, such as the National Institute of Agricultural Biology, for their suitability to different soil and climatic conditions. Varieties are produced as a result of extensive breeding programmes. Information provided on recommended seed varieties also includes their germination percentage (which should exceed 90%), the percentage of seedling establishment in soils, resistance to sugar beet diseases and the quality and yield of the sugar produced.

In order to produce a good harvest, a series of cultivation practices have to be adopted.

In summary, the main cultivation steps include seed planting, seed germination, seedling emergence from the soil, seedling establishment in the soil, rapid assimilation of photosynthates by the crop and finally, harvesting.

When the crop has developed from seed to maturity and is ready for harvesting, the tap roots are extracted from the soil and it is from these that sugar in the form of sucrose, is obtained.
History of Sugar beet cultivation.

1.1 Seeds and germination.

The cultivation of sugar beet has undergone several changes throughout its history. Early growers planted the sugar beet fruit containing poly-germinating seeds (several seeds within the fruit capable of germination). Germinated seeds therefore had to be 'thinned out' at the early seedling stage and replanted so that individual seedlings, which developed from seeds of the same fruit, had a better chance of surviving because of a better spatial distribution. In addition, the population distribution of seedlings in the field was then sufficient to ensure good yields by the correct utilization of available sunlight and other resources.

Monogerm seeds.

The introduction of monogerm seeds (fruits with only one viable seed) significantly affected cultivation practices. Fruits containing only one viable seed could be planted individually in the field and the 'thinning out' step was no longer necessary. This drastically reduced the number of man hours for cultivation from 500 to 50 hours per hectare. To make the planting of these monogerm seeds even more efficient, fruits containing the monogerm seeds were pelleted, (coated with an inert material such as clay or wood flour) (Durrant and Loads 1984, Fletcher 1984), a process which started in the 1960's (Winder and Dewar 1988). The small size of the seeds (0.5-5.0 mg) made it more viable to coat the whole fruit rather than removing and coating individual seeds. Although some chemical inhibitors were identified within the fruit which could affect germination (Akenson et al 1981) their effect was not regarded as significant. Pelleted seeds could then be planted in rows using direct drilling farm machinery which selects individual pellets with uniform size and shape and plants them with precision.
The next historical development was to impregnate the pelleted seed coating with crop protection chemicals such as Benzene hexachloride (gamma benzene hexachloride, BHC) so that the seeds and seedlings also had some protection against pest attack.

By 1961, seeds were available to farmers which had been impregnated with the pesticides dieldrin, heptachlor or BHC as a crop protection treatment.

Because of this pesticide treatment, a long and direct association of the seed and seedling with crop protection chemicals developed. This occurred from the pelleting stage throughout early germination and continued as the pellet coating material was left in the soil as the seedlings grew.

It was apparent that the addition of crop protection chemicals to the soil would have some environmental consequences such as effects on non-injurious soil arthropods. But farmers perceived that the benefits of these protective chemicals outweighed any detrimental environmental effects.

More recently, it has been demonstrated that pesticides like BHC can also have an effect on the germination of sugar beet seeds (Winder and Dewar 1988) and that seed varieties which showed poor germination were the ones most affected by pelleting. Pelleting was also found to produce a decline in seed emergence by an average of 16% in wet and in dry conditions (Durrant and Loads 1984).

Seed bed treatments

During the 1960's, BHC and other pesticides were also introduced in the preplanting and planting stages of the sugar beet crop, either as an overall spray which could then be lightly incorporated into the soil, or as a granular soil application.

This type of application involving BHC was used in 2% of the UK Sugar beet crop in 1970, 7% in 1975, 19% in 1980 and in 1989 accounted for 16%.

This additional application of BHC was more for insurance against any potential damage than as a direct response to specific damage by arthropod pests. It is difficult to estimate pest densities, economic
damage thresholds or indeed the effects of the applied pesticide in the field and therefore, to make any decisions on specific pest control strategies. (Winder 1984, Brown pers comm, Brown 1984).

One major problem involved in such estimations is that soil arthropods exhibit vertical migration in soils in response to changes in humidity and temperature, thus making representative soil sampling and accurate assessment of population densities very difficult. In particular, Heijbroek (1971) noted migration of the Collembolan O. armatus to a depth of 700mm although the majority of soil pests normally inhabit the top 250mm of soil. Furthermore, it was not always possible to assign crop damage to a particular species. Species migration occurs in the soil and the presence of one particular species did not exclusively imply that it was grazing.

The changes in seed planting and pesticide application were also accompanied by other cultural practices involved in preparing the seedbed for planting. These changes involved the use of herbicides to limit the spread of weeds which could act competitively with vulnerable monogerm seeds as they germinated and grew in the field.

1.2 Seedling growth

The seedlings of sugar beet are very delicate (Jones and Dunning 1972) and particularly vulnerable to soil pests until the 2-4 true leaf stage is reached (Bray and Thompson 1985, Brown 1984). Although the reduction of weed cover in sugar beet fields improves seedling development, the reduction of the weed cover using crop protection chemicals also has several effects on the arthropod soil populations. Weeds which provide food reservoirs for the soil arthropods are no longer present and the more virulent soil arthropods which can survive this reduction in their dietary sources are then limited to sugar beet seedlings as their main food source, making sugar beet seedlings more vulnerable to pest attack.

There is therefore a reservoir of arthropods in the soils called the soil pest complex (Brown 1981b), comprising Symphilids, (Scutigerella immaculata), Wire worms (Agriotes lineatus, A. obscurus, A.
sputator), Springtails (Collembola, Onychiuridae) Millepedes, Blaniulus guttulatus, Brachydesmus superus, pygmy beetles (Atomaria lineatus), leather jackets, (Tipula paludosa) which feed on sugar beet plants. Seedlings attacked at vulnerable stages can be destroyed. Springtails and millepedes in particular, tend to aggregate around the sugar beet seedlings (Baker and Dunning 1975) intensifying the damage. Aggregation around the root zone of the seedlings is found to increase with the density of the individual species recorded (Baker and Dunning, 1975). A list of insects in the soil pest complex and Collembola found in agricultural soils is presented in Appendix 2.

1.3 Seedling emergence.

The depth at which seed pellets are planted (25-30mm) to ensure rapid emergence from the soil assists in the development of pest problems. It is at this depth that pests are found to inhabit the soil. A lack of adequate crop protection by pesticides means that soil pests are able to feed directly on sugar beet once germination has started. Depending largely on the soil microclimatic conditions, the period for emergence has been found to vary (Jaggard 1979). Higher temperatures tend to accelerate emergence and lower temperatures increase the time for contact of seedlings with pests.

1.4 Seedling establishment

Damage caused by the grazing soil pest complex affects seedlings either by killing them with over-grazing or by causing lesions which could lead to subsequent damage by secondary pathogens such as fungi (Brown 1984). Damage caused to seedlings at this early stage of their development influences the establishment of the crop. Establishment was defined by Brown (1981a) as growth after the 6 true leaf stage of the seedling. At this stage, non-random gappiness in the plant stand, could be attributed to pest damage. As a result of poor establishment in the
field, patchy growth prevents the crop from utilising the available sunlight to produce good yields (Bray and Thompson 1985).

1.5 Soil Pest complex.

The arthropod pests found in sugar beet fields are referred to as the soil pest complex. The complex is made up of arthropods which spend most of their life cycle in the soil. There is little detailed knowledge on the behaviour and biology of the Onychiuridae in particular within the complex, although their association with sugar beet seedlings has been recognised since 1958 (Jones and Dunning 1972). The species of O. armatus and T. krausbaueri, in particular, merit closer examination. These species are the most highly distributed of the soil pest complex, (Baker and Dunning 1975 Brown, 1982b, Heijbroek and van De Bund 1982, Curry and Purvis 1982), with T. krausbaueri being the more abundant of the two.

The two species T. krausbaueri and O. armatus are morphologically similar species. T. krausbaueri is smaller with adults up to 700μm in length. Adults of O. armatus are 2000μm long. Most attention by researchers has focussed on evaluating the biology and taxonomy of the larger species (Brown 1982) although T. krausbaueri can be more abundant in sugar beet fields (Curry and Purvis 1982).

Significant damage to sugar beet seedlings was found to occur when as few as 10 O. armatus were found per litre of soil (Heijbroek and van De Bund 1982).

Brown (1982) has studied the taxonomy and biology of the larger species O. armatus but there is little information on the smaller and more abundant species T. krausbaueri.

Soil populations of insects are difficult to observe, identify and monitor effectively especially if they are of the size of the two Onychiuridae mentioned above. One effective technique for extracting arthropods from the soil uses differential heating gradients (Brown 1981). However such sampling techniques involve removal of the insects from their natural environment.

An alternative approach was employed in the present research. Culture techniques were developed which allow estimation and identification of
insect numbers as well as providing a method for continuous assessment of insect development.

1.6 Benzene hexachloride (BHC)

At present two thirds of the 2,000,000 ha of sugar beet cultivated in the UK are treated with pesticide at the sowing stage as a means of controlling soil pests, nematodes and aphid vectors of virus yellows. BHC, an organochlorine pesticide, is the gamma isomer of benzene hexachloride (C₆H₄Cl₆). The physical properties of BHC are given in Appendix 3. It is used in sugar beet fields at the recommended application rates of 1.4 litres ha⁻¹ (80% liquid) or as granules in a mixture with other pesticides like aldicarb, where the BHC concentration used is 0.136 kg ha⁻¹ (Winder 1984). Decisions on whether to use BHC and at what concentrations ultimately rely on farmers' knowledge of the history of the soil, previous damage and the economic viability of pesticide application doses. Jones and Dunning (1972) reported that the loss of 5% of seedlings was not sufficient to warrant BHC pesticide application. It is however difficult to estimate the effects of the pesticide in soils. BHC acts as both systemically as a stomach poison and topically through contact with phytophagous insects. Recent work (Devonshire 1985) shows that the effect is strongly associated with insects' nervous systems, neuronal transmissions and their production at the gaba receptor sites. BHC also has some residual persistence in soil. Edwards (1966), provides a review of the persistence of this pesticide in soils and evidence of its ability to taint the flavour of crops like potatoes.

The extensive use of BHC in sugar beet cultivation outlined above and its potential for affecting the different varieties of sugar beet seeds, seedlings as well as insects, in the soil pest complex, forms an integral part in the understanding of sugar beet cultivation techniques.
Thesis Aims.

The cultivation of crop plants like sugar beet relies on inputs from a variety of sources and specialisations in order to understand the complex interactions taking place in the field. In the areas of crop growth to the established seedling stage, inputs can be expected from meteorologists, providing climatic information affecting the time for soil cultivation and seed planting, from botanists and plant breeders, recommending the best crop variety to use in the cultivation area and soil scientists giving expertise on soil types, the depth at which seeds should be planted and which variety of seed can be used. In addition, zoologists and taxonomists identify the fauna present in the field which might prove injurious or helpful to the crop, provide specialist knowledge on the preferred diets of the fauna and how the fauna population will develop. Chemists also have an input into the cultivation process by synthesising and formulating crop protection chemicals, pesticides, fungicides and herbicides which can be used safely on the crop.

Crop production and protection scientists also work closely with the farmer evaluating information on pests, weeds and crop diseases. Finally, the farmer applies his knowledge, expertise and experience in growing the crop.

A synthesis of this body of knowledge and its application eventually produces seedlings which can develop into high yielding crops.

Studying the complex interactions which take place in the field is one way of understanding the crop system. However, monitoring variability within the field interactions can prove difficult (Connell 1983). Another approach is to study individual components of the system and examine how they interact with other parts of the system. This can be achieved by a laboratory based study.

The aims of this thesis are therefore to simplify the complex field interactions by studying them in the laboratory for a specific crop B.
vulgaris, pest, *T. krausbaueri* and pesticide BHC. This will be achieved by studying the insects' taxonomy and biology and the effects of BHC on both crop and insect in laboratory culture. The thesis also aims to identify and evaluate critical stages in the above interactions, to examine the interactions of BHC, temperature, diets of sugar beet and alternative diets of yeast on the biology and behaviour of *T. krausbaueri*, and on the germination and growth of sugar beet.

Finally, the thesis aims to develop population growth models for *T. krausbaueri* both as a function of total insect numbers and of insect growth developmental stages. These models are presented for use by computer simulation to predict how populations of *T. krausbaueri* will develop under different BHC treatments and diets. This will provide further data on the environmental system involving *B. vulgaris* sugar beet, *T. krausbaueri* and BHC so decisions on pest control strategies can be made to achieve good crop yields.
2. The Taxonomy of *T. krausbaueri* (Börner)

Introduction.

Collembola are small primitive apterygote insects and are considered to be the world's commonest hexapods (Lawrence 1979). There are two sub orders: the Symphypleona which possess a globular body with the thorax and 1st 4 abdominal segments fused and the Arthropleona to which the insects studied in this thesis belong. The family Onychiuridae contains 4 genera, two of which *Onychurus* and *Tullbergia* are commonly found in agricultural soils. The length of *T. krausbaueri* 200-700μm and *O. armatus* 500-2000μm are so similar that adults of *T. krausbaueri* can possibly be mistaken for juveniles of *O. armatus*.

Several morphological features can be identified under the scanning electron microscope which are important in taxonomic studies of these insects. Such features can show clearly the differences between the otherwise similar agricultural pests *Onychurus armatus* and *Tullbergia krausbaueri*.

The morphological features used in identifying the two species are presented in Chapter 2.1.

2.1 Morphological features of interest in the Taxonomy of *T. krausbaueri* and *O. armatus*.

The methods for specimen preparation for electron microscopy are given in Chapter 2.2.1.

2.1.1 The Pseudocelluli.

The pseudocelluli identified in Fig 1 and 3 are important taxonomic features which have relevance to the pest status of the insects. Pseudocelluli are characteristic of Onychiuridae and are distributed all over the insect's body. The electron micrographs in this section show differences in the two types of pseudocelluli in the two species. These
Fig. 1
A. Stereoscan electron micrograph of *T. krausbaueri*

B. Stereoscan electron micrograph of *O.armatus*.

Legends

ab. abdomen
an. antenna
as. anal spine.
c1. claw
h. head.
pao. post antennal organ
psoc. pseudocelli.
s. setae
sen. sensilla
tl. Ist thoracic segment.
types correspond to the two basic forms described by Rusek and Weyda (1981). The first type is poorly separated from the surrounding integument with a poor lid. The integument and the pseudocelluli have similar pigmentation. This type can be seen in micrographs of T. krausbaueri Fig 3B. The second type of pseudocelluli found in O. armatus (Fig 3D,3F) has a different granulation from the integument and is set in a circular furrow with a distinct lid covering. This has an epicuticular ring with a characteristic ribbing on the lid, the space below the lid being filled by secretory cells (Rusek and Weyda 1981). It has been suggested by Koncek (1924) that pseudocelluli have a secretory function. In the present study both T. krausbaueri and O. armatus have been observed to excrete droplets of fluid. In addition Karg (1961a), Hurlbert (1965) and Brown (1982) have suggested that such secretions are noxious and are produced in response to stress by O. armatus. This has been confirmed by Usher and Balogan (1966, 1967) and Brown (pers comm) who found the excretion repelled other Collembola and the mesostigmatid mite Paragamasus lapponicus (Tragad). In this study, a similar secretion of fluid has been observed in T. krausbaueri under the stress of the pesticide Benzene Hexachloride (BHC) and in response to tactile stimuli. These secretions are suggested by Brown (pers comm) to originate on pseudocelluli located on abdominal segment 5. Fig 2A shows the location of the pseudocelluli in O. armatus.

The arrangement of the pseudocelluli on Onychiuridae is one of the characteristics used for identifying the insect to species level (Gisin 1952,1956). Unless the pseudocelluli are distinct in their granulation like those found in O.armatus, they are hard to locate under the magnifications of the light microscope. However the production of a pseudocelluli formula which records the dorsal arrangement of pseudocelluli has been used, (Gisin 1952,1956) as part of an identification key. However the precise distribution may be hard to determine because any differences in the pseudocelluli arrangements on the insects are thought to be intra-specific (Bodvarson, 1970, Christiansen 1964) and can not be used exclusively for identification. In addition, the distribution of pseudocelluli can
Fig 2.

A Stereoscan electron micrograph detail of abdomen of O. armatus.
B Stereoscan electron micrograph detail of antenna of O. armatus.
C Stereoscan electron micrograph detail of abdomen of T. krausbaueri.
D Stereoscan electron micrograph detail of antenna of T. krausbaueri.

Legends
ano. antennal organ
as. anal spine.
as. 6th abdominal segment.
pao. post antennal organ
s. setae
sen. sensillae

A 250μm.
B 150μm
C 60μm
D 20μm
be an ecotypic response in adapting to specific environmental conditions (Lawrence 1979).

2.1.2. The post antennal organ

The post antennal organ (poa) is situated below the antennal base. This organ in *T. krausbaueri* consists of a row of v - shaped bodies whilst the organ in *O. armatus* has a distinctive oblong arrangement of the sensoral bodies. (Fig 3E and Fig 3F).

2.1.3. The antennal organ

The antennal organ is situated dorso - laterally on the third antennal segment. It is a sense organ consisting of sensoral bodies protected by papillae and hairs. Fig 2B shows this organ in *O. armatus* with the papillae and protecting hairs. Fig 2D shows the antennal organ of *T. krausbaueri* which is less distinct in this species.

2.1.4. The hairs, setae, macro and microchaetae

The hairs, setae, macro and microchaetae are differentiated on the basis of the relative size on the insects. Setae are hairs which cover the whole organism and vary in size to form micro and macrochaetae. The larger sensillae (sen) are modified setae which have a sensory function. They are shown on the 4th abdominal segment of *T. krausbaueri*. (Fig 2C) The dorsal arrangement of the setae on the insects has, like the pseudocelli, been used in keys for identification of the insects to species level (Fjellberg 1980). Although these keys give details of the arrangement of micro and macrochaetae, examination using the the light microscope has shown the possibility of variation in morphology and location of these setae.

Other morphological features of interest in the electron micrographs are the anal spines (Fig 2) and the absence of any crests on the 6th abdominal segment.
Fig 2

A. Detail of head of *T. krausbaueri*.
B. Detail of Pseudocelli of *T. krausbaueri*.
C. Detail of post antenal organ of *O armatus*.
D. Pseudocelli of *O armatus*.
E. Detail of head of *O armatus*.
F. Pseudocelli in abdomen of *O armatus*.

Legends

an. antenna
h. head.
pao. post antenal organ
psoc. pseudocelli.

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Because of the degree of variability within the external morphology of these species, the number of insect specimens required to identify these species with statistical confidence is thought to be quite large (Lawrence 1979). The insects used in this thesis were populations cultured in the laboratory consisting of single species lines.

Discussion

The difficulties associated with identifying the species groups in O. armatus and T. krausbaueri have been referred to in the section above. Not only are these complex species but they are also species complexes (Rusek 1971, Petersen 1975, Lawrence 1979, Pitkin 1980, Brown, 1982). Although Hale (1968), stresses the need for using large numbers of insects to determine species, this is often not practical. Relying on a few specimens may therefore produce individuals which can not be easily assigned to a group because of individually abnormal morphological characteristics. The use and arrangement of the pseudocelli and the setae also present difficulties in taxonomic identification. Preparation techniques of specimens for light microscope identification can also produce anomalies in the identification of these structures (Wetton 1983 pers. comm.). The distinctive differences however in the pseudocelli, the post antennal organ and the antennal organ are clear under the electron microscope. The electron microscope technique shows the external morphological differences between T. krausbaueri and O. armatus.

2.2. Species identification using the scanning electron microscope.

Introduction.

As mentioned in section 2.1, T. krausbaueri and O. armatus have a complex taxonomy which at present is still unclear. It is therefore a difficult group to identify under the light microscope (Wetton 1985 pers. comm.). T. krausbaueri, in particular has been listed as synonymous with T. macdougallii (Bagnall 1939) by Gisin (1960), whilst
Fjellberg (1980) separates out the two similar species on the basis of size. Of the 13 species of Tullbergia identified by Fjellberg however, Brown (1982) lists 6 of them as belonging to the 'T. krausbaueri group'. Using the scanning electron microscope however it is possible to produce detailed photographs of the external morphology which identify unmistakable differences between the two.

2.2.1. Specimen Preparation for Electron Microscopy.

Insects were collected live from laboratory established cultures. They were then cleaned in acetone (O. armatus only) and then mounted on aluminium stubs with an araldite mixture. The specimens were then coated with a thin film of gold (10μm) using a polaron sputter coating unit. The specimens were then viewed with a scanning electron microscope ISI-SS40 using an accelerating voltage of 10kV. Information was then recorded photographically. Micrographs were used in conjunction with the following keys and examination under the light microscope to identify insect specimens.

2.2.2. Identification key for T. krausbaueri. (Fjellberg, 1980)

**KEY TO FAMILY.**

1. Body elongated, segments well separated. ..2

2. Thorax 1 with at least a few dorsal setae(s)
   Skin often granulated or with distinct warts. ..3

3. 3rd antennal segment with 2 or 3 large sensoral bodies (ano),
   often partly hidden by finger like papillae. [Fig 2 D]
   Pseudoecelli (psoc) present, colour of species white or yellow.
   Eyes absent

   4 generas of ONYCHIURIDAE, Wankellia, Tullbergia,
   Karlstejnia and Onychiurus (Fjellberg 1980) 2 of which, Onychiurus
and Tullbergia are common in agricultural soils.

**KEY TO GENERA OF ONCHIURIDAE OF AGRICULTURAL IMPORTANCE.**

1 _The two sensoral clubs (partly hidden by papillae), (Fig 2D) in antennal organ 3, both directed dorsally.

Cylindrical species usually larger than 1000µm

............Onychiurus (Gervais).

2 _Number of sensoral clubs 1-3. If more than one club two of them directed towards each other, body usually less than 1000µm, of very narrow shape

2 _Post antennal organ(pao) with numerous sensillae(sen) Fig 3A the number of pseudocell11 differs.

............Tullbergia (Lubbock).

**KEY TO GENUS TULLBERGIA. Lubbock, 1876.**

Tullbergia are a large genus of soil inhabiting insects. The systematics of the group is far from settled and the likelihood is that a species complex exists. (Brown 1980, Fjellberg 1981, Petersen 1975.)

2 _Post antennal organ consists of two rows of elongated sensillae (Fig 2A) Antennal organ 3 with two or three sensoral clubs.

18
2 Abdominal 6 with two anal spines (Fig 2C).  
4 Abdominal 6 simple (Fig 2C)  
5 Small species (<700μm). Anal spine shorter than claw. (Fig 1A)  
8 Abdominal 5 with 3+3 microchaetae between the a4 (Fjellberg 1980 Fig 4)  
9 Thorax 3 with 1+1 pseudocelli. Abdominal 4 without seta x Thorax 3 with a2 (Fjellberg 1980 Fig 4)  
10 Pseudocelli on thorax closer to median line  
11 Posterior median macrochaetae of Abdominal 4 closer together than microchaetae.  
12 Abdominal 4 without m5 Anal lobe without 12 (Fjellberg 1980 Fig 4)  

TULLBERGIA KRAUSBAUERI. (Borner, 1901) Rusek 1971

Positive identification of the material used in this study was confirmed by Wetton M (1984) Department of Entomology, British Museum (Natural History) London.
Fig 4.

Taxonomic detail of Tullbergia species.

(a) _Tullbergia tenuisensilla_ abdomen 4-6

(b) _Tullbergia yossi_ Thorax 3

(c) _Tullbergia tenuisensilla_ thorax 2-3.

(d) _Tullbergia yossi_ Abdomen 4.
(c) *Tullbergia tenuisensillata* Thorax 2 - 3
(a) *Tullbergia* tenuisensillata  Abd. 4 - 6

(b) *Tullbergia* yossi  Thorax 3
(d) *Tullbergia yossi* Abd. 4
3. The biology of *T. krausbauer*i.

Introduction.

In agricultural fields cultivated for Sugar Beet, (*Beta vulgaris*) several insect species can be identified as soil pests of young seedlings, namely Springtails (*Collembola* sp.) pigmy beetles (*Atomaria linearis*) and wire worms (*Agriotes* sp.). Associated with these insects are other arthropods which can damage sugar beet seedlings including millipedes (*Blanius* sp.) and symphilids (*Scutigerella* sp.). This collection of arthropods associated with the seedlings has been called the soil pest complex (Brown, 1980). An analysis of the composition of the *Collembola* species in soils by Ulber (1978) identified 28 species of *Collembola* with the *Onychluridae*, *O. armatus*, *T. krausbauer*, and some Isotomidae being the dominant species. Appendix 2 lists the *collembola* and other arthropods identified in these fields.

The two *Onychluridae* collembolans *T. krausbauer* and *Onychiurus armatus*, which are similar in their external morphology and pigmentation, have been associated with damage caused to young seedlings, in the field by several authors, (Winner 1959, Schaelfelle, 1969, Heijbroek 1982, Dunning 1972, Baker and Dunning 1975, Ulber 1978, Feeny 1979, Curry and Purvis 1979, Brown 1981b). An analysis of the dissected guts of these insects shows that plant material is a large constituent of the diets of the insects in the field. In addition the presence of grazing marks on the root and shoot fractions of sugar beet seedlings confirm that sugar beet is a part of the diet of these insects.

The damage caused by direct grazing on sugar beet seedlings can be particularly harmful to the crop if it occurs during the early growth period before the plant has obtained two true leaves, (Brown, 1981b, 1984). At this early developmental stage the seedling is not sufficiently vigorous to recover fully from the grazing, as it is relying mainly on the food reserves of the cotyledon. Direct and
sustained attacks on the seedlings can cause seedling death. Although the seedling grows throughout the soil plane, the depth at which the seedlings are sown (2.5-3cm) corresponds to the soil fraction which contains these two species of Collembola. Glasgow (1939) records Tullbergia sp. to depths of 3 inches (7.5cm) while Lienaaas, (1978) in a more recent study found little migration for T. krausbaueri below 3cm depth in soils.

The slow sluggish movement of the two species in soil and the reduced furca, the organ responsible for the springing propulsion in Collembola in these two species, suggests that movement in soils will be quite restricted by the soil leaving little room for migration to and from food sources. There will therefore be a concentration of feeding activity at sites of infestation.

Many soil core samples in sugar beet fields have been shown to contain both T. krausbaueri and O. armatus. Such studies have shown consistently that the numbers of T. krausbaueri exceed those of O. armatus in May and June, 17 to 47 days after planting, (Curry and Purvis 1982 Dunning 1972), especially in weedy soils. Pesticide protection is recommended for sugar beet seedlings at the time of seed planting (Winder 1984). This can be applied as an overall spray of Gamma Benzene Hexachloride (BHC) in an 80% liquid formulation at a rate of 1.4 litres ha⁻¹ of an 80% solution or as a 1.7% mixture with aldicarb (8.3%) applied at a rate of 7.3kg ha⁻¹, in a granular formulation. Little understanding however has been obtained of the action of BHC treatment on the soil pest complex. Winder (1984), for example suggests that there is little evidence for a drastic reduction of pest populations following this treatment; effects of this pesticide being largely ascertained from indirect evidence obtained from the percentage of seeds established. In addition the risks to potentially beneficial insects have been overlooked.

An understanding of the Biology of the Onychluridae is therefore fundamental to understanding their pest status. Reproduction rate, development rate and feeding rate are relevant in establishing the pest status of these insects. Using the biology of the insect it will be possible to predict with some accuracy the following:
a) the potential of the populations for growth in different ecoclimates,
b) whether populations in the soil are large enough to damage the sugar beet seedlings and warrant control measures, and
c) at what age the insect is most vulnerable to pest control measures.

The studies presented in this chapter relate to individuals in the population and their growth rate. The results for the population growth of T. krausbaueri and the modelling of this population growth rate in lethal and sublethal pesticide treatments are presented in Chapter 5 and 7.

3.1 Studies of insect biology

Methods.

Insect populations of T. krausbaueri were cultured using the methods outlined in Chapter 4. Insects were then removed from the cultures and used for the basic biological studies of the insect.

The experimental method used in section 3.1.1 involved counting the number of eggs which hatched out from a population sample of 80 eggs removed from a population of T. krausbaueri cultured at the specified temperature of 20°C. To obtain the hatching times for the eggs at the specified temperatures, (15°C and 20°C) eggs were isolated in marked culture vessels and examined daily to determine whether hatching had taken place.

The methods for study for sections 3.1.2, 3.1.3, 3.1.4, 3.1.5 involved a daily examination of cultures under a binocular microscope. A graticule with a measuring scale was used to measure the insect lengths.

The observation technique was carried out for 100 days.
Results

3.1.1 Egg laying and egg development.

The eggs of *T. krausbaueri* are laid singly or in clusters. They are globular, smooth and unpigmented measuring 90-120µm in diameter. The eggs hatch by splitting the chorion across the width of the disc. In this study, 50% of the eggs laid in culture hatched (N=80). The development time to hatching estimated in this study was 10-20 days. The hatching times at 15°C and 20°C are shown in Fig 5a. Ten days were required for the first eggs to hatch out at 20°C, whereas the minimum time at 15°C was 14 days. The distribution of the numbers of eggs hatched covered a range of 10-17 days at 20°C and 14-20 days at 15°C. The time for the first hatching to occur was four days sooner at 20°C than for eggs in the cultures at 15°C. The large variation in development times indicates the non uniformity in this process even at a constant temperature and suggests a large amount of variability within the insect population. Table 1 shows the time for reproduction and for the appearance of the first juveniles of *T. krausbaueri* in culture. These results indicate that not only did temperature influence the time taken for the appearance of juveniles but also that diet played a significant role. These relationships are discussed further in Chapter 5 and 7.

3.1.2. Development of Juveniles.

The juveniles of *T. krausbaueri* are insects with a narrow body shape. After the eggs hatch out, development is ametabolous through a series of moults. The juveniles are opaque white and measure 200-250µm (N=100) on hatching. Moulting in the juveniles starts with a split in the old exuviae followed by a series of undulating and circling movements. These are used to detach the exuviae from the abdomen, leaving it attached to the substrate. Estimates of the time and number of moults occurring in these insects were not possible for two reasons: 1) the shed exuviae were hard to locate on the culture substrate and 2) *T.
Figure 5A: The time for egg hatching in two populations of
*T. krausbaueri* cultured at 15°C and 20°C on a diet
of *B. vulgaris* (sugar beet) var Monoire.

Legend.
15°C.

20°C.

Figure 5B: The size (total body length) of insects in two populations
of *T. krausbaueri* cultured at 20°C on diets of *B. vulgaris*
(sugar beet) var Monoire or *S. cerevisiae* (yeast).

Legend.
Sugar beet *Beta vulgaris* var monoire.

*Yeast Saccharomyces cerevisiae.*
Figure 5A:

TIME (DAYS.)

% HATCHED.
Table 1: The time for juvenile appearance in newly initiated cultures of *T. krausbaueri* cultured at 10°C, 15°C, 20°C and room temperature on diets of *B. vulgaris* (sugar beet) var Monolre or *S. cerevisiae* (yeast).
<table>
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<th>DIET for culture</th>
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<th>TIME (days) Replicate. no.</th>
<th>MEAN</th>
<th>Standard deviation</th>
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<tr>
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<td>64</td>
<td>3.5</td>
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<tr>
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<td>20</td>
<td>43 43 32 32</td>
<td>38</td>
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</tr>
<tr>
<td>Sugar beet</td>
<td>20</td>
<td>24 35 24 24</td>
<td>26</td>
<td>5.5</td>
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<tr>
<td>var mononiere</td>
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<td>room temp</td>
<td>49 57 49 49</td>
<td>51</td>
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</tr>
<tr>
<td>Sugar beet</td>
<td>room temp</td>
<td>24 28 24 24</td>
<td>25</td>
<td>2.0</td>
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<tr>
<td>var mononiere</td>
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</table>
Krausbaueri feed on the cast exuviae thereby consuming the evidence of moulting. These difficulties were also taken into account in determining which insect growth models to use to monitor growth changes.

3.1.3. Development of Adults.

Moulting continued in isolated insects even after egg laying had ceased in the post reproductive adults. No visible sexual dimorphism exists in this species. The largest insect size measured was a total maximum body length of 780µm (N=150) in laboratory culture. The population structure of the insects is shown in Fig 5b and records the sizes of insects reared on two different diets in established populations. The final maximum size of the adults was dependent on the diet on which the insects were cultured. Insects cultured on a diet of sugar beet (Beta vulgaris cv monoire) were smaller and achieved a smaller maximum size than those cultured on the yeast (Saccharomyces cerevisiae) diet when two insect populations were compared after 100 days (Fig 5b). The effects of diets on the population growth of the insects are examined in Chapter 5.

The ambient temperature also had an effect on the size of the adult insects in the population after identical time periods. Culturing insects at 10°C resulted in smaller adult insects than at 20°C. The mean length of 10 insects after 60 day period cultured at 10°C was 450µm. A size of 600µm was obtained for cultures at 20°C. These results are treated fully in Section 3.2. Adults were a darker shade of white compared with the juveniles. The only other visible difference apart from size, distinguishing the adults from the juveniles, was a distended abdomen in some adults. Estimating the age of the insects by their size without a prior knowledge of the environment (diet and temperature) will produce misleading and erroneous results since these factors affect the size of the insects at different ages.
3.1.4 Reproduction and fertility.

No spermatophores were identified in this study and reproduction was observed in 96% of individual isolated insects. (N=50) This strongly suggests a parthenogenetic process for reproduction with a low sex ratio of males to females. It was not possible to give a precise time or adult size for the onset of sexual reproduction in this study. The end point of reproduction, namely the eggs, were the first signs that reproduction had taken place. The length of the time lag in cultures before the appearance of juveniles is recorded in Table 1. The appearance of juveniles in the culture depended on the diet and the culture temperature. This process was longer in cultures at lower temperatures and for diets of yeast compared with other higher temperatures and diets of sugar beet. The fecundity of individual insects was also not recorded in this series of experiments although individual insects were found to reproduce parthenogenetically and lay eggs either singly or in clusters. Two distinct adult types were recorded in these cultures, these were reproductive adults which were actively involved in egg laying and older post reproductive which failed to produce eggs in isolated culture. The post reproductive stage was achieved by insects which when measured were found to be the largest size in the cultures.

3.2 Insect growth and growth rates .

Introduction.

Insect growth is normally expressed as a change in the biomass of the insects over time .
Several species of Collembola show a Dyers rule (Dyar 1890) relationship for growth. This relationship was recorded by by Argell (1948) in Hypogastura sahlbergi, (Nicolet) and Mertens et al (1982) found that measurements of the body length (total length - head length) of Orchsella cincta (Linne) also adhered to this rule.
Dyars rule can be expressed as
\[ y = k \times p^n \]  \hspace{1cm} (1)

where \( y \) is the length of any measured body part, \( n \) is the number of ecdysis (moults), \( p \) and \( k \) are constants with \( p \) being the progression factor which relates to the growth of the species.

Hale (1965a,b) used a log transformation of Dyars equation to give the equation
\[ \log y = \log k + n \log p \]  \hspace{1cm} (11)

Using this equation he found that when measurements were made of head capsule length, Dyars rule was adhered to in \( T. krausbaueri \) and other Onychiurid collembolans [\( Onychiurus procamptus \) (Gisin 1956), \( Onychiurus latus \), \( Onychiurus furcifer \) (Gisin 1956), \( Onychiurus tricamptus \), Gisin 1956].

Argell (1948) however stated that the progression factor \( p \) is not a constant but diminishes with increasing development. This finding was confirmed by Mertens et al (1982) studies on \( O. cincta \). In addition Hale (1965b) estimated that after four moults \( T. krausbaueri \) attained sexual maturity. In order to monitor insect growth therefore some other temporal measurement which produces a growth curve and does not rely on estimating the number of moults the insect has been through (this is hard to estimate in this species 3.1.2) would therefore be preferable for this study. Although growth is mainly confined to periods of ecdysis (Mertens et al 1982), monitoring growth as a function of length can produce a growth curve for these insects (Bengtsson 1983). In his study, Bengtsson 1982 was able to fit the growth of \( O. armatus \) to the growth curve
\[ L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \]
where \( L_t \) = length of individuals at time \( t \) \hspace{1cm} \( L_\infty \) = the asymptotic length \hspace{1cm} \( k \) = growth rate and \( t_0 \) = the hypothetical negative time estimated from hatching date for an individual of length 0.
Hale (1965b) makes the assumption that measures of the body length of the Collembola will also conform to Dyars rule, (Hale 1965b) and Bengtsson et al. (1983) used a similar modelling technique for Onychiurus armatus relying on the change in the length of the insect and not the number of instars found that a relationship could be found between the length of the insect and time. A relationship of this sort for T. krausbaueri will also be established by examining growth equations in Chapter 3.2.1.

Change in insect weight.

The relationship between the increase in the length of T. krausbaueri and the dry weight of field samples of T. krausbaueri have been recorded by Peterson (1975), and a regression equation computed to model the relationship. This takes the form of:

\[ \text{Log dry weight (g)} = \log 0.504 + 2.502 \log \text{body length (mm)} \]  

This indicates a linear relationship between the log of the body length and the log of the body dry weight for this species. This relationship between dry weight and length was confirmed by regression analysis. The relationship between dry weight of the insect and the insect length was found to hold true for all the developmental stages of the insects.

Growth of T. krausbaueri (increase in biomass) can therefore be modelled on the basis of changes in the weight or length of the insect which both conform to the Dyars relationships already established above. The change in the growth of the insect can be used to indicate its preference and adaptation to different environmental conditions.

3.2.1. Estimates of insect growth.

Methods

A workable modified model was constructed on the basis of the above relationships. The change in the biomass of the insects expressed by
changes in the dry weight can be represented by a change in the length of the insect. This model also has the advantage that it does not rely on a) the estimation of the insects' biomass which involves the destruction of the insects and b) the total number of moults that occurred, an estimate which is unreliable in this species as cast exuviae are difficult to identify and are also invariably consumed by the insects.

The measurement of live insects is more precise if any telescopic joints are excluded, and if locomotion is not excessive, (Hale 1965a). To create these conditions for the insects studied, it was necessary to exclude the telescopic head joint from the measurement. Bengtsson et al (1983) for O. armatus, also excluded the head in the length measurement measuring from the tip of the abdomen to the 1st thoracic segment. For this species, a measurement from the 1st thoracic segment to the abdominal tip was used for the body length measure. Because of the sluggish movement of the species this measurement could be recorded accurately and quickly.

In addition, Mertens et al (1980) compared measurements of the length of live O. cincta with measurements of length made after insects were collected, stored in fixative and measured with a magnification of 5:1. He concluded that the measurement of live insects gave a similar growth curve fitting the same function (taking into account the fixation constant). Measurement of live insects should therefore provide an adequate means of monitoring change in growth.

The length of the insect was used as the unit for measurement and was then used to fit several growth models to assess the change in length of insects with time. These measurements were carried out under high magnification under a binocular microscope (×6.4). Each insect was kept in isolated culture and measured at specified time intervals. Two temperatures 10°C and 20°C were used and 10 insects were used at each temperature in cultures fed on sugar beet.

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The following relationships were then examined to determine if they exhibited a relationship between the change in insect body length with time for *T. klausbaueri*.

1) The insect growth curve (change in length with time).
2) The natural log of the insect body length plotted against time.
3) The square of the insect body length plotted against time.

This series of experiments will form the basis for establishing a relationship between insect length and time and therefore insect's developmental stage, in order to produce a model of the growth and change in an insect population. Measurements of the structure of the population are needed and these can be obtained by measurements of the insect length. See Chapter 4.1.4.

**Results.**

1) The Insect growth curve.

The growth rate (increase in body length μm) of the insects cultured at 20°C and at 10°C are shown in Fig 6. The change in length was more pronounced at the higher temperature. After 40 days the mean insect length had increased at 20°C by 240μm whilst the comparable increase at 10°C was 126μm. The mean final body length of the insect at the asymptotic point of the growth curve was 618μm at at 20°C and 468μm at 10°C after 60 days of culture.

2) The natural log transformation.

The Specific growth rate used by Bengtsson et al (1983) for models of *O. arnatus*, defined the population growth by the rate of growth divided by length

\[
\ln L_2 - \ln L_1 / t_2 - t_1 \quad \ldots \ldots \ (iv)
\]

This can be estimated from the plot of ln body length against time where \( \ln = \) natural logarithm. \( L_1 \) and \( L_2 \) are insect length measurements at time \( t_1 \) and \( t_2 \).
Figure 6: The change in the body length (length from the 1st thoracic segment to the abdominal tip) for individuals from two populations of *T. krausbaueri* cultured at 10°C and 20°C on a mixed diet of *B. vulgaris* (sugar beet) var Monoire and *S. cerevisiae* (yeast).

Legend.

10°C.

■

20°C.

●
The ln transformation is shown in fig 7A. A straight line plot was obtained for this transformation at 10°C and 20°C.

The regression equations for the ln plot showed a good fit for the regression equations used in analysis. At 20°C the goodness of fit was 81% and the regression equation was

\[ \ln \text{body length} = 5.598 + 0.0156 \times \text{time} \quad \ldots \ldots (v) \]

At 10°C the regression gave a 93% goodness of fit

the regression equation was

\[ \ln \text{body length} = 5.468 + 0.0104 \times \text{time} \quad \ldots \ldots (vi) \]

These equations (v, vi) emphasise the difference in the growth of insects at the two temperatures.

The relative growth rates (change in insect length with time) can be calculated up to day 53 and they are $1.9 \times 10^{-2}$ at 20°C and $9.6 \times 10^{-3}$ at 10°C.

There is however a limit to the ability to predict from the regression line and the specific growth rates. This restriction is imposed by the final maximum insect length at the two temperatures.

3) The body length $^2$ transformation.

A plot of the change in the square of the length with time (Fig 7B) also gave a good fit to the regression equation. A goodness of fit of 88% was obtained for the 10°C and 94% for the 20°C treatment. The regression equations were

at 20°C \[ \text{body length}^2 = 69158 + 5336 \times \text{time} \]

at 10°C \[ \text{body length}^2 = 47330 + 2309 \times \text{time} \]
Figure 7A. The change in the ln body length (length from the 1st thoracic segment to the abdominal tip) for individuals from two populations of *T. krausbaueri* cultured at 10°C and 20°C on a mixed diet of *B. vulgaris* (sugar beet) var Monoire and *S. cerevisiae* (yeast).

Legend.

10°C.

20°C.
Figure 7B The change in body length = (length from the 1st thoracic segment to the abdominal tip) for individuals from two populations of *T. krausbaueri* cultured at 10°C and 20°C on a mixed diet of *B. vulgaris* (sugar beet) var Monoire and *S. cerevisiae* (yeast).

Legend.

10°C. ■

20°C. ○
Body length$^2$ [mm$^2$]

Time (Days)
3.3 Determination of the size class, developmental stage of *T. krausbaueri*.

Introduction.

Ametabolous insects like Collembola have been studied on the basis of the increase in length by several authors (Longstaff 1974, Bengtsson *et al* 1983). The point reached in the developmental stage of the insect measured by its length is often the only means by which the age of the insect can be estimated. The results above have confirmed that in a species like *T. krausbaueri* which observes Dyar's law and increases in length over a time period, the change in the insect length can be used to monitor developmental growth. These relationships were established for the asymptotic growth rates, the log and square transformations.

The assignment of arbitrary developmental stage insect size classes based on insect length to these populations can be made to assist in the process of modelling the growth in insect populations. The number of developmental stage insect size class units selected will determine the modelling precision. The use of one class, in effect a total insect number count, is the simplest modelling procedure possible. The selection of several size classes can therefore be more precise and can also give an idea of the developmental processes taking place in insects of different sizes.

Method

The populations were modelled by dividing the insects in the population into 4 arbitrary size classes on the basis of length. The size class for each insect was estimated from a measurement from the 1st thoracic segment to the tip of the 6th abdominal segment. This measurement was carried out in the same manner as the insect length measures used for the previous sections. Size class 1 was recorded for insects measuring less than 250 µm, size class 2 measuring
between 250µm and 350µm, size class 3 measuring between 350µm and 450µm and size class 4 for insects measuring more than 450µm.

Results.

The pie chart Fig 8 shows the numbers in each of the size classes used for a population cultured at 20°C on a diet of sugar beet. 50% of the insects were of size class 1, 26% of size classes 2, 15% of the insects were of size class 3 and 9% assigned to size class 4. Of these size classes, size class 1 included all the juveniles since juveniles hatched from eggs and measured less than 250µm, (Chapter 3.1.2) The other three size classes, 2, 3 and 4 contained the reproductive and the post reproductive developmental stages. Since it has been demonstrated that the insects increase in length with time the significance of these three size classes is clear in indicating the developmental stage of the insect at that size. However Chapters 5 and 7 will examine the size class further in the development of population growth and Matrix models.

3.4 The effect of diets of S. cerevisiae. and B. vulgaris var Monolire on T. krausbaueri.

Introduction.

There has been much debate in the literature concerning the function of collemboila in recycling nutrients in soils and their feeding mechanisms. This work has been summarised by Christiansen (1964). The debate has mainly been to estimate their potential status as pests in agricultural fields. It has been suggested that they feed on decayed and decaying organic material (Christiansen 1964), feed on living plant roots, (Winner 1959, Edwards 1962), disseminate bacteria (Törne 1951) and fungi (Poole 1959) or act as filters for decaying organic and mineral matter. This apparent diversity of feeding behaviour occurs because species such as T. krausbaueri with chewing mouth parts are able to graze on both living and decaying plant material. Lawrence, (1979) found no evidence of plant material in the
Figure 8: The distribution in insect size classes (developmental stages) in an established population (N = 586) of *T. krausbaueri* cultured at 20°C using diets of sugar beet *B. vulgaris* var Monoire.

(insect body length measured from 1st thoracic segment to abdominal tip)

Legend:

- Developmental stage 1 (insects less than 250μm)
- Developmental stage 2 (insects 250μm - 350μm)
- Developmental stage 3 (insects 350μm - 450μm)
- Developmental stage 4 (insects more than 450μm)
guts of Onychluridae whereas Mcmillan (1976) was able to show that
the gut contents of Onychluridae contained fungal, plant and mineral
fractions. These were in a ratio which could not be differentiated
from the ratios of the living and non living constituents obtained
from soil samples in the same environment. His findings suggest that
the Onychluridae are non selective feeders. The nutritional value of
the foods eaten is still not clear although development of cultures
fed on *B. vulgaris* var *Monoire* in this study was more rapid (measured by the onset of reproduction) than those fed on yeast. The
fact that the group consists of indiscriminate feeders was confirmed
by Brown (1981 b) and in this study there is also evidence that
members feed on their own exuviae, faecal pellets, and the plaster of
paris /charcoal culture substrate. Experiments were carried out to
examine the effects of the diet on the insect in the populations
studied.

Method.

Culture vessels were prepared for these two experiments as outlined in
Chapter 4.1.

The population structures of populations reared on *B vulgaris* var
monoire were compared with one reared on *S. cerevisiae*. The feeding
preference of a population of *T. krausbaueri* which had been reared
on a diet of *S. cerevisiae* and *B vulgaris* was compared at 20°C by
using the culture vessels as choice chambers.

Four segments of *B vulgaris* var *monoire* beet 5mm in diameter and four
*S. cerevisiae* pellets 5mm diameter were placed in an alternating
sequence in a circle in the choice chamber. One hundred *T
krausbaueri* were introduced into the middle of the food circle and
the numbers feeding on the different diets recorded after 12, 24 and
56 hours. A chi square test was then used to estimate the food
preference.
Results.

After a comparable time period insects reared on a diet of *S. cerevisaeae* were larger than those reared on a diet of *B. vulgaris* in the two populations studied at 20°C Fig 5. It was also found that the time lag for the onset of reproduction (measured by the presence of juveniles), also reflects the different diets. The time lag was longer for insects reared at the same temperature on a diet of yeast compared with one of Sugar beet. Table 1 has summarised these results and shows the mean time lag at 10°C was 90 days for yeast reared insects and 64 days for sugar beet reared insects. At 20°C, the time lag was found to have a mean of 38 days on yeast diets and 26 days on sugar beet diets. The effect of the different diets was to reduce the time lag for insects fed on Sugar beet diets when compared with yeast diets at the same temperatures. The variable room temperature treatments showed a halving of the time lag from 50 to 25 days for insects reared on sugar beet. An assessment of the effects of diets on the number of moults and shed exuviae was also attempted. However this had to be abandoned because of the difficulties involved in measuring the presence of exuviae in cultures referred to in Chapter 4.

There is laboratory evidence to confirm that both *O. armatus* and *T. krausbaueri* feed on sugar beet seedlings and can cause considerable damage to these seedlings whilst grazing. Fig 9 illustrates the nature of the damage possible in a culture of *T. krausbaueri*. Bite marks and the presence of cellular material in insect guts indicate that grazing on sugar beet seedlings is common. The preference for diets was found to be significant at the 0.1% level after 24 hours for yeast but after 56 hours this preference was not in evidence (Table 2).

General Discussion

Instar numbers.

Hale (1965a), records the presence of 13 instars in *T. krausbaueri*
Table 2: Statistical comparison between the numbers of
T. krausbaueri feeding on B. vulgaris var
Monole (sugar beet) and S. cerevisiae
(yeast) at 20°C after 24 hours and 56 hours using
the Chi Square test.
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Degrees of freedom = 4, chi square value 27.89 significant at .01 level.

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Degrees of freedom = 4, chi square value .95 not significant at .01 level.
Figure 9: *T. krausbaueri* in culture at 20°C feeding on cotyledon of *B. vulgaris* (sugar beet) var Monoire.

Scale

10mm
at 15°C with each instar lasting between 10 and 16 days and a decrease in the duration of the intervals between moulting in the instars with time. The number of instars to sexual maturity has been recorded as 4, (Hale 1968) whilst Milne (1960) puts this figure at 3 when observing *T. krausbaueri* at a different temperature.

**Temperature**

At 10°C, Milne (1960) recorded a time of 30-40 days for development of *T. krausbaueri* to maturity. In field populations, Hale (1965a) records the time to attain maximum size in *T. krausbaueri* as 50 days in June, but 209 days in the colder month of October suggesting an effect of temperature on development. The development times and time lag estimates obtained in this study confirm the significant effect of temperature on insect development. The time differences for juvenile production in cultures varied by as much as 62 days in comparisons of cultures at 10°C and 20°C for insects cultured on yeast.

The diets for culturing insects in this study also had an effect on the development times. Development to the reproductive stage, as measured by the appearance of juveniles in the culture, was more rapid in cultures which used sugar beet than in yeast. At 15°C this time was 65 days for yeast reared insects and 40 days sugar beet, values which compare with the estimates of Milne (1960) although the diets used in these studies are not identical.

The time for egg development was also variable and ranged from 10-17 days at 20°C to 14-20 days for 15°C (n= 50)

This study did not measure the numbers of instars each individual goes through but used as a basis for growth modelling the change in the size of the insect (insect body length) under different environmental stresses.

The population parameter, the time lag for the appearance of juveniles in culture was an important estimate in this study. This identified clearly significant differences caused by different temperatures and diets. Strict adherence to the change in the length of the insect should therefore be qualified by the insects diet and also the temperature.
Insect length.
The maximum size of *T. krausbaueri* has been recorded as 630μm (Milne 1960), 600μm (Fjellberg 1980) and 630μm in field populations (Lineaas 1978). In this study, laboratory cultures produced some insects with a total length of 680μm and maximum body length of 625μm. Field populations of *T. krausbaueri* in spruce forests in Norway were shown to have little change in the overall population size structure measured throughout the year (Lineaas, 1978). This suggests the establishment of a stable population structure in the field under specified conditions and is an important feature for population modelling (Chapter 5 and 7).

Milne (1960), records the egg diameter as 90-100μm; this was found to be similar to the diameters measured in this work (90-120μm). The sizes of insects measured in this study under laboratory conditions were larger than those mentioned by other authors.

Reproduction and Egg Development.
According to Mayer (1957), reproduction in the Onychiuridae is by single sperm drops which occur irrespective of the presence of other insects. Although the possibility of sexual reproduction can not be eliminated from multi-insect culture, Hale, (1965), and Milne (1960) assume that there is a sex ratio of 1:1 without providing any evidence to support this. However, 96% production of eggs in isolated individuals in this work suggest that there are parthenogenetic females and a low male ratio in the laboratory populations used in this study. The time for the development of eggs was recorded in this study as 10-17 days at 20°C. Milne (1960) gives a time of 10-20 days at 12°C and records that there is no development of eggs at 5°C or 24°C.

Dietary Effects.
The ecotypic response of the species to diets observed in this study, has not been previously recorded. However, this factor is very important when an attempt is made to age the insects on the basis of their size. For example, smaller insects were obtained in cultures on yeast compared with those on a sugar beet diet although populations
were of the same age.
Although the developmental time lag for the appearance of juveniles was longer for insects reared on yeast, larger insects developed on the yeast diets. Clearly an assessment of insect age based on size alone without consideration of environmental influences such as diet and temperature is open to criticism.

The food preference of Collembola was studied by Mcmillan in 1976. Using diets of yeasts and fungi he concluded that there was selectivity in the choice of foods by these insects. *Onychiurus armatus* in particular showed selectivity when he compared 18 species of yeast and 14 species of fungi. There was however, even in laboratory studies little migration to other food sources once preferred diets had been located. Ulber (1980) observed *Onychiurus fimitus* showed a decline in the ingestion of sugar beet seedlings when weed seedlings or soil fungi were present as alternate food sources.

Where populations of *T. krausbaueri* were given a choice of diet, behavioral studies have identified that after 24 hours, these insects showed a significant preference for yeast compared with sugar beet. After 56 hours however this initial preference was not maintained by feeding behaviour. Populations have already been shown to survive on either of the two diets. In the field where soil structure might prevent migration to other food sources, this lack of preference will therefore not inhibit population development.

*B vulgaris* damage.

Damage caused to growing sugar beet seedlings by Collembola was clearly identified in this study. This has been noted by other authors; *O. armatus* and *T. krausbaueri* damage was noted by Brown (1981b, 1984). Ulber (1978) noted damage caused by *Onychiurus fimitus* in laboratory studies on sugar beet, and although he suggests that the damage caused by grazing *T. krausbaueri* might be insignificant.
because of the insect size, he noted an increase in the damage caused by increased pest density and with reduced temperatures.

Insect growth models.
The growth models produced for the individual insects showed that the insect growth could be estimated using the models prepared which utilize relationships between body length and ln body length with time which yielded the regression lines that gave 88% or better R² values for the goodness of fit. These models can be reliably used to measure the growth of individual insects in the culture once the conditions have been specified. Insect growth also corresponds to the modified Dyar’s law.

Although there are several drawbacks in measuring the length of insects precisely using this method; for example the insect may actually be slightly curled, about to moult and therefore in a turgid state, or due to the presence of telescopic joints may not be fully extended when the measurement is made, the measurements of the insects in this study were used to produce models which predicted growth. Mertens and Blancquart (1980) also concluded that growth curves which fitted a function when measurements were made of insects in a fixative would fit the same function for measurements of live insects taking into account a fixative constant. Longstaff 1974 was also able to model populations of insects using measurements of live insects.

In addition since the population is to be finally modelled by dividing the insect into size classes, with a range of lengths within the class of 100µm, this would be of a much larger order of magnitude than any inaccuracies in the length measure. The insects were to be grouped into 4 size classes. Therefore only the insects grouped at the beginning and at the end of each size class will the precision of the length measurement be important. Inaccurate measurements could mean that they are assigned into the wrong size class. T. krausbaueri is therefore a population which can be divided into representative developmental size classes for further population modelling studies. The insects cultured in this study were divided into 4 size classes; 1= insects less than 250µm, 2= 250-350µm, 3= 350-450µm, 4= 450-680µm.
The temperature of 20°C was chosen for the construction of the population growth models used in this thesis. At this temperature, the insect egg development and insect growth is rapid enough to ensure that selected time intervals will be short enough to produce a realistic model.

Introduction

This chapter outlines the methodology for culturing populations of T. krausbaueri in the laboratory and the experimental design for all the experiments conducted in the thesis. A culture rationale had to be designed to produce a steady supply of insects in large enough numbers for use in experiments and cohorts of insects with the same environmental background.

In culturing arthropods in the laboratory a high relative humidity can be obtained by several methods. Ripple (1930) and Strebel (1932) cultured insects in containers with moist soil. Although this early attempt at laboratory culture was successful, the resultant difficulty in observing insects which burrowed into the soil led to inaccuracies in censusing and inaccurate observations of insect populations. The use of such a 3 dimensional substrate was found to be unacceptable for this study.

The use of a Plaster of Paris base as the substrate for arthropods was first recorded by Searls (1928). This provides a substrate which can retain a high volume of water and therefore humidity and also provides a firm 2 dimensional substrate on which insects can be observed.

Whatman (1946) and Edwards (1955) introduced decolourising charcoal to a plaster of paris block to improve the quality of the observation of light coloured insects. In addition there have since been claims of improved culture performance resulting from the absorption of culture impurities by the charcoal (Booth 1983), but this has not been fully substantiated.

At present the standard culture method for Collembola involving a Plaster of Paris substrate and charcoal pioneered by Gotto (1960,1961), Green (1964) is used by most researchers.
4.1 General methods for culturing T. krausbaueri.

The laboratory culture was established from insects extracted from soil core samples obtained from Weaverthorpe Farm West Driffield on May 30th 1984. The soil cores were taken back to the laboratory and using a simple floatation technique, (Hansen 1984) Collembola were picked off the water surface with a mounted needle and transferred to culture vessels. A binocular microscope (eyepiece magnification x3.2) was used to ensure all the Collembola were removed from the water surface.

4.1.1 Preparation of Culture Vessels.

The standard culture substrate preparation technique for Collembola (Gotto 1960) was used. Particular attention was paid to the pH of the culture substrate and the maintenance of a high relative humidity in the culture vessels. Pill boxes of diameter 3.5mm, 5mm and plastic cups of diameter 6.5mm with air tight lids were used as culture vessels. The stock cultures were kept in sandwich boxes at room temperature.

The culture substrate was prepared from a mixture of Plaster of Paris and powdered charcoal. Different mixtures of Plaster of Paris and charcoal have been shown to produce different pH values (Hutson 1978). The pH of the substrate can have an effect on the growth and fecundity of the Collembola, (MacIagen 1932, Ashraf 1969, Hutson 1978, Booth 1983). Therefore to ensure uniformity in the culture vessel the ratio of Plaster of Paris and charcoal used was standardised for all the cultures.

The substrate mixture for cultures of F. candida used by Usher (1977) was found to be the most suitable in this instance. This was made up of a ratio of 18:9:1 by volume of water : Plaster of Paris : charcoal.

The culture substrate was prepared by mixing the ingredients in the proportions listed above in a beaker and then, after thorough stirring, the contents of the beaker was decanted into the culture vessels. Once prepared, the mixture was left to stand for 7 days.
before use to avoid the possibility of unaccountable mortalities in
the cultures as was found by Usher (1977) when substrates were used
too soon after preparation.
The level of substrate in the culture vessels could be adjusted if
required by scraping off any excess substrate with a scalpel. The
sides of the culture vessels were cleaned of any excess substrate to
discourage any escape by insects.
The mixture above gave a pH value of 8. This mixture also produced
a dark grey substrate which was an ideal background for viewing the
white insects. The consistency of this mixture was also not affected
by repeated wetting and drying and provided an ideal surface for
culturing the insects.
The culture chambers were saturated with water maintaining a relative
humidity of approximately 100%.

4.1.2. Preparation of the diets for T. krausbaueri populations.

Introduction.

Field populations of T. krausbaueri have been shown in this thesis to
have gut contents which contained B vulgaris, S cerevisiae and culture
substrate (Chapter 3). S cerevisiae, bakers yeast, is a fungus commonly
used for culturing populations of Collembola, (Usher 1975).
Four varieties of B. vulgaris; Julia, Primahill, IBB83 and Monoire
were provided for use in this study from Brooms barn Experimental
Station and Sugar beet Seed growers. It was therefore decided to
study the effects of the above diets on T. krausbaueri as they
represent also diets the insects may encounter in the field.

Insects in the cultures were fed regularly on pellets of moistened
S. cerevisiae. (John Allinsons bakers yeast) or B. vulgaris (sugar
beet) seedlings. The variety of sugar beet used for cultures is given
in the text for each experiment. In the experiments which involved
contaminating the diets with the pesticide benzene hexachloride (BHC),
the diets were prepared prior to their introduction into the culture.
Two methods of treating the diets were used. In the first, S.
cerevisiae was mixed into a paste with concentrated pesticide solution. The second method involved germinating and growing the sugar beet in the pesticide solution. The concentrations of the BHC used for these mixtures varied. Different pesticide concentrations were used and they are recorded in the subsequent sections in this chapter.

4.1.3. Transferring insects in the culture.

Insects were transferred from the culture chambers using a fine mounted needle. T. krausbaueri have a reduced furca and are unable to spring away from tactile stimuli. The insects were scooped up with the needle or adhered to the needle by fluids present in their ventral groove. These operations were carried out under the binocular microscope because of the size of the insects (250-700μm) and to avoid mortalities. Eggs in the culture were also transferred using a flattened mounted needle.

4.1.4 Censusing the insects in culture.

The insects were counted by scanning the culture chamber under a binocular microscope. The substrate colour facilitated the identification of the insects under natural light. A photographic technique previously used by Usher and Stoneman (1977) and Longstaff (1974,1976,1977) for F. candida, O. armatus, H. denticulata was found to be unsuitable because of the relatively small size of T. krausbaueri, 200-700μm, as compared with 600-2500μm for the other species. Photographic resolution and identification of T. krausbaueri was difficult because of a) insect size was similar to substrate particle size and b) the presence of some cast exuviae which could not be distinguished from live insects in still photographs also contributed to the inaccuracy of the photographic technique. Since T. krausbaueri is not highly mobile, a precise live census was possible as long as the numbers in the culture did not exceed 400 individuals. The insects were counted twice at each census or until two consecutive censuses gave the same count. Where the developmental
stage of the insects was required for modelling purposes, the
censusing was carried out in a similar manner for each different
developmental stage.

4.1.5. Maintenance of contamination free cultures.

To reduce contamination of the culture vessels, care was taken to keep
the vessels air tight and to use fresh tap water to moisten the
substrate. There was however some contamination in some culture
vessels, which were invaded by mites and nematodes. The mites were
found feeding on T. krausbaueri as well as the yeast S. cervisea
diet. It is thought that the source of the contamination might have
been from the yeast.
Nematode contamination occurred in two of the culture vessels which
contained a diet of sugar beet seedlings. It is thought that the
sugar beet seeds might have been the source of the contamination.
Where contamination occurred, cultures were either destroyed or used
for experiments which did not require population censuses. The majority
of the cultures were however single species agglomerative cultures of
T. krausbaueri.

4.2 The effects of temperature and diet on T. krausbaueri.

Introduction.

The soil temperature and diet are two of the most important factors
likely to influence the growth and development of T. krausbaueri and
therefore its pest status. The temperatures encountered in sugar beet
fields cover a wide range 4°C-22°C at the seedling stage (Gummarson
and Jaggard 1985). Information obtained on the growth of insect
populations in this temperature range can provide an insight into the
pest status of insects.
Insect behaviour will also be affected by different temperatures and
diets (Southwood 1978.) The temperature and diet effects can be
changed to monitor effects on insect populations.
The controlled environmental temperatures available for this study
were 10°C 15°C and 20°C. These temperatures were selected for the experiments on culturing *T. krausbaueri* in this thesis. However since populations of Collembola experience a temperature range in the field, a variable room temperature (4°C-24°C) was also used in some of the studies.

*T. krausbaueri* in the field has available a large number of possible food sources. These include sugar beet from the planting to the harvesting stage, indigenous fungi, soil, and decaying organisms. However the restricted spatial movement of the insect will dictate to some extent, the food source available. How well the populations of insects survive on restricted and mixed diets is of relevance not only at that instant in time but also for the future pest status of the insect. Successful insect feeding on sugar beet at the present time may therefore produce significant damage to the crop and elevate its pest status. Insects which are therefore not in contact with sugar beet but also increasing in numbers through feeding on other diets, might present future problems for young seedlings.

The appropriate population modelling techniques were used to measure the population growth of the insects under the conditions of continuous breeding. The specific relationships examined were the changes in the insect numbers with time. Plots of the numbers of insects (*Nₜ*) at time (*t*) examine this relationship. Graphical and mathematical representations were also made.

The population growth equations (*Begon and Mortimer 1986*) were used to assess population characteristics.

These were:

\[ N_{t+1} = N_t R \]

and

\[ N_t = N_0 R^t \]

and the transformation to

\[ \log N_t = \log N_0 + t \log R. \]
where
\[ N_t = \text{population size at time } t. \]
\[ N_0 = \text{population size at time } 0 \]
\[ R = \text{growth rate of population.} \]
\[ \log_2 R = 'R_n' = \text{intrinsic rate of natural increase.} \]

Method and experimental design..

The culture vessels were prepared by the methods outlined in 4.1. Experiments were then constructed to measure the effects of temperature and diets on *T. krausbaueri*. 10°C 15°C 20°C and the variable room temperature (range 4°C-24°C) were used for these experiments. The cultures were initiated with nine insects of developmental stage 2 (250μm -350μm). Four replicates were used for each temperature and four for each of the diets of yeast, Sugar beet and mixed (sugar beet and yeast) diets. The insects were censused on a regular basis once the population had started growing. The insects were censused using total insect counts.

4.3. The response of *T. krausbaueri* to Benzene hexachloride.

Introduction.

The response of insects to toxicants can be measured as a continuous variate or as a quantal (all or nothing) response. Measurements of a continuous variate usually occur at the biochemical or physiological level where chemical quantities, the extent of the activity generated or the change in other cellular components such as neurone activities can be accurately measured. For example, the degree of inhibition of acetyl choline esterase (AChE), an enzyme responsible for the transmission of nervous impulses depends on the type of toxicant and the duration of the contact it has with the insect (Devonshire 1985).
Obtaining the measurements outlined above requires the use of freshly killed insects or the dissection of insect parts *in vitro*, the dissectionants being suspended in solution to measure activities. Large insects like the cockroach *Periplanata americana* and the locust *Schistocerca gregaria* lend themselves to these techniques because their nervous systems can be easily identified and nerve activities measured with electrodes. Davenport et al. (1985) showed a clear response to the neuromuscular transmission caused by the pesticide Chlordemform and desmethyl Chlordemform in the exposed tibiae of the two species mentioned above.

The results obtained from measuring such a continuous variate provide information as to how the insect responds to the toxicant *in vitro*. This information can be related to the behaviour of the live insect only if the effects of the *in vitro* activity correlate directly with *in vivo* activity. Predicting these correlations is not however possible in most situations (Burt 1979) and it is therefore necessary to measure *in vivo* activity changes caused by pesticides as a quantal response.

4.3.1. Measurement of *in vivo* sublethal responses to Benzene Hexachloride.

In the field of pesticide science the *in vivo* behavioural responses of insects to toxicants are also important. These responses provide an insight into the insects behaviour in the field when pesticides are applied. These behavioural effects together with the knockdown quantal effects will eventually influence the effect of the pesticide on the pest population.

Von Keyseling (1985) stresses the importance of behavioural studies because they:

a) characterise the toxicants activity by measuring the symptoms.

b) help in determining the nature of the behavioural modification.

c) can provide information on how the target species might behave on its host. These responses are mostly measured in a quantal manner, the insect either having its behaviour modified or not.
The level of the toxicant in contact with the insect will affect the insect's normal behaviour when applied in a lethal or a sublethal concentration. At sublethal concentrations the insect's normal behaviour is affected over an extended time period. Feeding, moulting, reproduction and growth are some of the parameters affected by sublethal doses. These changes can reflect on the pest status of the insect and also have an effect on the overall population structure of the species.

It is possible to estimate the effects of these doses on behavioural processes. The dose in contact with insects which causes an effect on 50% of the population studied is measured as the $ED_{50}$. The $EC_{50}$ value however estimates the concentration of the pesticide in the insects environment. Similarly the $LD_{50}$ and $LC_{50}$ values relate to the concentration in direct contact with the insect and the concentration in the immediate environment of the insect which prove lethal to the median number of insects.

Method

In order to produce a substrate which could support populations of the insect and allow the toxicant effect to be measured, it was decided that $in situ$ measurements of the toxicant effects would be carried out instead of using techniques which isolated the test insect from its environment. This approach also meant that sublethal long term studies could also be evaluated.

The culture substrate was prepared by the method outlined in section 4.1. Plastic cups (6.5cm diameter) were used for this series of experiments. The substrate in each container contained substrate measured a depth of 1cm. Each culture chamber was saturated with pesticide solution of the required concentration and then subsequently moistened with water as the experiment continued in order to maintain the relative humidity.

The cultures were established with four insects of developmental stage 2. Four replicates were used for each culture treatment. The
concentrations of pesticide used for the tests ranged from $5.34 \times 10^{-7}$ mg to $8.75 \times 10^{-3}$ mg ml$^{-1}$. Each set of treatments included replicates with no pesticide. The pesticide was either administered to the insects' diet (sugar beet or yeast) or to the insects' culture substrate by the methods outlined in 4.1.2. The population of insects was censused by the method outlined in section 4.1. The cultures were maintained at 20°C.

4.3.2. Measuring in vivo toxic responses to Benzene Hexachloride.

Insect behaviour becomes affected in a more drastic manner when a lethal concentration of a pesticide is applied. After the initial detection of the toxicant, the insect responds in a series of mutually exclusive steps which are in essence semiquantal. These steps result in the death of the insect. The series of steps has been called a dose-time-course (Devonshire, 1979, Von Keyseleng 1985) and is characteristic of the toxicant and the insect affected by it. The steps usually involve an initial knockdown of the insect, periods of heightened muscular activity, paralysis, a moribund state and then mortality. The dose-time-course for T. krausbaueri is presented later in this chapter and the irreversible steps involved are highlighted. Once knockdown has occurred the speed of the processes leading to death depends to a large extent on the pesticide concentration. Estimates of the lethal concentration required in the environment for 50% mortality in the population (LC$_{50}$) can then be estimated. The final outcome of the dose-time-course, mortality, is however a quantal response which can also be used to measure insect behaviour. At a lethal dose the pest status of the insect disappears. However not all the insects in any population will however be killed by the same concentration. There will be variations due to the age of the insects and also within the insects' developmental stages. This biological spectrum of quantal responses is used in the bioassay techniques.
The use of bioassay techniques however depends on several assumptions which have been shown to hold true for most species (Wolf 1968, Sokal and Rohlf 1973 Hamilton et al 1977). These assumptions are:

1) The relationship between response and dose or log dose is a linear one over the response range;
2) The variation in response measured by the standard deviations is constant at all dose levels;
3) The variation in responses exists amongst all individuals in the population;
4) In each individual there is a level above or below which no response is obtained.

The experiments carried out in this section examine these relationships to determine whether the above assumptions hold true for populations of *T. krausbaueri* using Benzene Hexachloride (BHC) on the populations.

Bioassay Methods.

1. Examining the Bioassay assumptions.

Two hundred insects of developmental stage 3 were used and 40 insects were tested at each of five concentrations of BHC. In each test the insects were observed after 24hrs treatment and the numbers of moribund (insects not mobile but with some tactile responses) and the total number of insects moribund and completely inactive were recorded. The main plots of dose versus mortality, log dose versus mortality and probit log dose versus probit were recorded.

A plot of dose versus the number of insects affected produces a normal distribution where these responses over the effective concentration range (the highest concentration producing 0% mortality and the lowest concentration producing 100% mortality) plotted in the form of a cumulative frequency distribution. A log transformation of the dose plotted against the percentage mortality, produces a symmetrical (about the mean value) sigmoid curve. A further
Fig 10: The percentage mortality of *T. krausbaueri* (*N=200*) treated with BHC concentrations after 24 hours.

Legend

True mortality (dead and moribund insects)

•

Mortality (dead insects)

■
transformation of the curve expressing the response at different doses in standard deviation units (by adding 5 to all the values to eliminate the negative sign) produces the probit straight line graph usually used for interpreting toxicological data. The results presented here in Fig 10 for *T. krausbaueri* confirm that the population is one on which bioassay can be carried out and therefore assumption 1 appears to hold true. The LC₅₀, LD₅₀, can be estimated from the graphs in Fig 10 and is the antilog of the 50% intercept. The use of this method, however is more reliable for experiments involving large numbers of insects because it is insensitive to some of the practical considerations of experimentation, discussed in the next section.

Fig 10 shows the graphical interpretation of the dose versus mortality for *T. krausbaueri* populations. A clear distinction can be seen between dead and moribund insects which represent true mortality, and the exclusion of moribund insects from toxicity estimates. The true mortality was therefore selected for use in counts in further BHC tests.

4.3.3 The use of the 24 hr Trimmed Spearman Karber toxicity tests

Introduction.

The Trimmed Spearman Karber toxicity test (Hamilton 1977) was used to estimate the LC₅₀ values for each of the 4 developmental stages of *T. krausbaueri* which had been cultured on diets of *B. vulgaris*, *S. cerevisiae* or mixed diets. The probit model used above to test the bioassay assumptions for *T krausbaueri* populations estimated the mean values for toxicity. With the more sensitive Trimmed Spearman Karber method an estimate is made of the median value from tests on a range of pesticide concentrations. This median value in a population which is normally distributed is the mean value and the LC₅₀. In such a distribution the mean and median points are coincident.

Use of the Trimmed Spearman Karber method to estimate the the median LC₅₀ value permits smaller numbers of insects to be used for each individual toxicity test. Reproducible and reliable results can be
obtained with this test and any anomalies or experimental errors can be corrected as part of the test procedure. The final results can also be trimmed to measure the toxicity over a specific concentration range, working within the range which on the bioassay tests produced 0% and 100% mortality for T. kraiubaueri.

The theory behind the Trimmed Spearman Karber test and examples of its use can be found from Hamilton, (1977). An example of the test scoring sheet is presented in Appendix 3.

Method.

Treatment vessels (3.5cm diameter pill boxes) were used for the toxicity tests. The vessels were prepared by the method outlined in 4.1 and each pill box was filled to 1cm depth with the substrate. Between 10 and 25 insects were subsequently used in each individual LC50 test. Insects were selected for testing based on their developmental stage and the diet on which the insect was cultured. All the tests were carried out at 20°C and were carried out for 24 hours. Three replicates were made for each test treatment. The pesticide range of (5.34x10^-7 mg ai ml^-1, 1.37 x10^-6mg ai ml^-1, 2.05x10^-5mg ai ml^-1, 4.10x10^-5mg ai ml^-1, 5.46x10^-5mg ai ml^-1, 8.2x10^-5mg ai ml^-1, 1.09x10^-4mg ai ml^-1, 2.18x10^-3mg ai ml^-1, 8.75x10^-3mg ai ml^-1) was used.

BHC pesticide at the specified concentrations was used to saturate the substrate of the culture testing vessel. Insects were then removed from culture vessels and placed on the substrate. The treatment vessels were kept covered for each test. After 24 hours the insects were examined for signs of activity. Moribund insects were recorded as well as dead insects for this series of toxicity tests.

The practical use of this test involves the following steps:
1. recording the number of insects (n) used in each test at each concentration;
2. recording the mortality (r) in each of the units above;
3. estimating the percentage mortality (p) from 1 and 2;
4.4.4 recording the percentage mortality (p₄) as a fraction of 1
(p₄*). * indicates an adjusted mortality percentage.

4.4 The Germination and growth of Sugar beet seeds.

Introduction

Sugar beet germination can be studied either in field trials or by using laboratory germination tests. The unreliability of tests in the field due to variable soil microclimates, large testing areas and unexplained nonuniformity of the planted crops (Brown 1981a) makes the use of laboratory testing a preferable method. Laboratory tests carried out by the National Institute of Agricultural Botany provide standard testing techniques involving the use of filter paper or sand substrates. The use of filter paper for studying the germination of sugar beet seedlings was studied by Hibbert and Woodward (1969), and compared with results using sand. The authors found paper was a more reliable medium, less labour intensive and allowed more accuracy. These workers found that flat paper at 20°C was the best technique for monogerm sugar beet seeds. Other researchers, Akenson and Winder (1980) and Akenson et al (1981), still prefer the sand methods whilst Durrant and Payne (1974), Durrant and Payne (1983a, 1983b) modified the on top of paper technique using fluted filter paper in air tight plastic boxes at 15°C. An osmotic potential of -5 bar and a temperature of 8°C has been suggested by Durrant and Payne (1983a, 1983b) as being the closest approximation to the germination conditions in the field. Soil temperatures for germination are however shown to range from 0°C to 14°C (Gummerson and Jaggard 1985) in the first month of sowing.

It was decided not to control the osmotic potential of the medium in this study by adding sodium chloride solution because a) there might be interference with pesticide in further experiments and b) preliminary experiments showed that germination was significantly different in sodium chloride and distilled water treatments.
The ideal temperature used for germination would have been 10°C, however the time for germination at 10°C was found to be slow and therefore these experiments were carried out at 20°C a temperature where rates of germination were higher. This temperature was also selected for the production of the population growth models for *T. krausbaueri*.

The rate and pattern of germination will determine the ability for the production of a uniform stand of crop. If the rate is increased and all the seeds are equally affected and there is little effect on the spread of germination, the germination pattern is said to have been advanced (Genkel 1946, Genkel et al 1964, Austin et al 1969 Longden 1971). If the rate of germination is increased and all seeds are brought to the same physiological stage so that there is synchronous germination the seeds are said to have been primed by the environmental conditions. (Heydecker 1974). Any changes in these patterns can be due to temperature or pesticide which is discussed in 4.5.

Method

Four varieties of Sugar beet were used for these experiments. These were Monolre, IBB83, Julia, Primahill.

Fluted filter paper was placed in petri dishes (7.5cm diameter) for this series of experiments. The filter paper was moistened with 5ml water.

Twenty seeds of each variety were placed in each dish, this was replicated 4 times for each pesticide concentration. The petri dishes were then covered and each dish was sealed with cellotape.

The petri dishes were placed in a growth cabinet in the dark at 20°C. The dishes were removed and examined daily for signs of germination. Germination was judged to have occurred when the root tip was visible.

The growth of the seedlings was measured after 21 days using a pair of dividers to measure the length changes. The seedlings were measured for the root length, shoot length and total seedling length. The dry weight of the seedlings was measured after the seedlings had been
dried in a desiccator for 10 days. Individual estimates of the root and shoot dry weights were made for each seedling. The seedlings were coded so that the root shoot ratios could be determined for each individual seedling.

4.5 The effects of BHC on the germination and growth of Sugar beet.

Introduction

Pesticides may influence both the germination and growth of sugar beet. The percentage and the pattern of germination can be altered by pesticide use. Thus the parameters outlined in the Introduction in 4.4, the advancement or the priming of seeds may be changed. Sensitive plant species have been used to bioassay the effects of biocides. Eshel and Warren (1967) used cucumber (Cucumis sativus L var Wisconsin SMR 15) and grain sorghum (Sorghum vulgare pers var. R.S.610) to assay the differences in root length caused by concentrations of herbicide. The lithium salt of 2,4-dichlorophenoxyacetic acid (2,4-D), ammonium salt of 3-amino-2,5-dichlorobenzoic acid (amiben), isopropyl N-(3-chlorophenyl)carbamate (CIPC), and m-trifluoro-2,6-dinitro-N,N-dipropyl-p-toluidine (trifluralin) were the pesticides used. Although the experiments above only examined the effects of pesticides on the roots, the procedures used were modified to permit examinations of the change in length of both roots and shoots of sugar beet, and also the effects on total plant length. The dry weight of the root and shoot fractions was also measured in this study to provide a more detailed overview of the effect of BHC on sugar beet seedling growth.
Methods.

Four *B. vulgaris* varieties, Primahill, Monoire, IBB83, Julia were used for these experiments. The fluted filter paper and petri dish set up used in the experimental set up described in 4.4 was used for this study. Twenty seedlings were used for each treatment and each treatment was replicated 4 times. A concentration range (0 mg al ml$^{-1}$, 5.34x10$^{-7}$ mg al ml$^{-1}$, 2.18x10$^{-5}$ mg al ml$^{-1}$, 3.50x10$^{-2}$ mg al ml$^{-1}$) was used. The experiment was stopped after 21 days. Measurements of the length of the root and shoot fractions of the individual seedlings were made after the seedlings were divided up into the root and shoot fractions. Seedling fractions were individually placed in foil paper and dried in a desiccator for 10 days or until a constant weight was obtained. The temperature selected for these experiment was 20°C. The changes in the pattern of germination caused by BHC were recorded after 4 days and then on a daily basis for 13 days for the varieties Primahill, Monoire, IBB83, Julia. The concentrations of the pesticide used above were also used for these experiments which were carried out at 20°C.

4.6 The development of population growth models for *T. krausbaueri*.

Introduction.

Population growth models have been use to describe changes in insect populations Southwood (1978), Begon and Mortimer (1986). Several other population growth models rely on the changes in the numbers of individual insects within each developmental stage (Bernadelli 1941, Lewis 1942 Leslie 1945, 1948, Longstaff 1976). The advantages of creating a growth model for insects in a population include the ability to predict with some accuracy how the stresses of ambient temperature, diet and pesticide may affect the growth of the populations. A matrix model after Leslie (1945 1948) can be modified and used for the growth of ametabolous Collembola such as *T. krausbaueri* which
does not have discrete developmental stages. By dividing the insects into developmental stage classes and monitoring how numbers in each developmental stage change as the population develops, it is possible to produce a matrix model based on the probabilities of insects moving from one developmental stage to another.

The modified Leslie matrix model relates to the population growth models in 4.2

where \( N_{t+1} = N_t R \)

By substituting the matrix \( M \) for the growth rate \( R \). Hence

\[ M_{nt} = N_{t+1} \]

where

\( N_t \) = population size at time \( t \).
\( N_{t+1} \) = population size at time \( t+1 \).
\( R \) = growth rate of population.

Further details of the development of the matrix model are presented in the introduction to Chapter 7.

Method.

The experiments cultures were established as in section 4.2. The experimental modelling temperature of 20°C was selected. The cultures were initiated with nine insects of developmental stage 2. The production of population growth models was made by censusing insects of each developmental stage at 10 day time intervals.

The experimental design consisted of the following BHC treatments. Three replicates were used for each of two sugar beet varieties (Monoire and Primahill.) Four concentrations of BHC were used and applied to the diet. These were 0 mg ai ml\(^{-1}\), 5.34x10\(^{-7}\) mg ml\(^{-1}\), 2.18x10\(^{-5}\) mg ai ml\(^{-1}\), 3.5x10\(^{-2}\) mg ai ml\(^{-1}\). applied in the sugar beet diet.
Four concentrations of BHC added to the yeast diet, 0 \text{mg ai ml}^{-1}, 5.33 \times 10^{-7} \text{ mg ai ml}^{-1}, 5.46 \times 10^{-4} \text{ mg ai ml}^{-1}, 8.75 \times 10^{-3} \text{ mg ai ml}^{-1}. There were 3 replicates at each concentration.

In addition three concentrations of BHC applied to the substrate, 0 \text{mg ai ml}^{-1}, 3.37 \times 10^{-5} \text{ mg ai ml}^{-1}, 3.41 \times 10^{-5} \text{ mg ai ml}^{-1} were used. Each concentration was replicated 3 times.

Matrix models were then prepared and used to evaluate the following relationships:

1) The effects of BHC applied in \textit{B. vulgaris} diet on population growth of \textit{T. krausbaueri};

2) The effects of BHC applied in \textit{S. cerevisiae} diet on population growth;

3) The effects of BHC in the environment on population growth of \textit{T. krausbaueri}.
5. The Innate capacity for increase ($R_m$) in populations of *T. krausbaueri* and the development of population growth models

**Introduction**

The biology of *T. krausbaueri* has been examined in chapter 2. The method of reproduction and growth of developmental stages in response to temperature and dietary changes were examined. Those growth models measured changes in the length of individual insects. The ability of the insects to survive on a diet of sugar beet was also noted. Although the growth of individual insects is important and this growth can be monitored in the laboratory, the behaviour of insect cohorts or populations gives a clearer indication of population trends and behaviour which determine the overall population development and can affect the overall status of the insect as a pest species.

The results for the growth and nature of changes in the size of populations of *Tulibergia krausbaueri* studied under different diets, temperature, and pesticide treatments are presented in this chapter. The changes in the insect numbers in each population were measured and the innate capacity for increase ($R_m$) was estimated in each population studied. The $R_m$ value was then used to compare the changes in the population due to different culture treatments.

The $R_m$ value was used in preference to the total number counts to compare the individual cultures, and to estimate the potential individual populations have for increase. Total number counts are also presented in this section but their use is limited as they give only an instantaneous value which is characteristic for individual cultures and as such cannot be meaningfully compared with replicate treatments. Total population counts also do not take into account the number of insects in the population in prior or subsequent time periods.
The \textit{in vivo} effects of Gamma benzene hexachloride (BHC) on the insect populations are also presented in this chapter as 1) lethal effects estimated by LC50 values, and 2) sublethal long term effects caused by contact with or feeding on diets contaminated with BHC. The lethal effects of BHC were estimated using the Spearman Karber LC50 test (Hamilton 1977) which was modified for these insect populations and involves an estimation of the LC50 value for each developmental stage of the insects cultured at 20°C to identify the more susceptible developmental stages of the insect.

5.1. The innate capacity for increase ($R_m$) of \textit{T. krausbaueri}.

The innate capacity for increase in numbers ($R_m$) is a population statistic which can be estimated for every population as it develops. Individual organisms within a population have their own capacity for development, growth, longevity and fecundity (Lotka 1925). The summation of these effects within a population can be estimated and described as an $R_m$ which is an estimate of the potential within the population for increasing in numbers. This value is dependent to a large degree on the environment and factors such as, diet and temperature and can only be described in situations where other species are excluded and there is therefore no interspecific competition or predation. A laboratory culture can be used to provide these conditions. The use of cultures that are not limited by space gives the cultured population the potential to develop to its maximum efficiency and produces conditions in which the $R_m$ value can be estimated. The conditions in a laboratory can also be controlled so that populations can be compared on the basis of changes in diets (sugar beet, yeast) environment (pesticide concentration) and other environmental factors like diet and temperature.

The importance of estimating $R_m$ values should not be understated. Field surveys will give an instantaneous estimate of the numbers of insects in an environment. Typically sugar beet soils contain \textit{T. krausbaueri}, but whether or not the numbers present are a problem to the cultivation of sugar beet will be determined by both the numbers present and the rate at which these numbers increase. The herbivorous
effect will, by implication, be a product of these two things. It is only with an estimate of the $R_m$ value, the innate capacity for increase in numbers in optimum or defined conditions, that this potential can be estimated and from this the need for establishing some form of control predicted. The $R_m$ value, unlike population counts, is not a static statistic but records the dynamism within the population for increase.

Estimation of $R_m$ values.

Populations increase in numbers through a schedule of births (B) and deaths (D), (emigration and immigration are excluded from the laboratory cultures). The birth and death rates depend on the survivorship of the insects in each of the developmental stages which they pass through in their life cycle. *T. krausbaueri* has different developmental stages with different probabilities of survival under different conditions. However in estimating the $R_m$ value the population need not be classified into these stages. (In Chapter 7 a model is produced which uses the developmental stages). The populations studied therefore consisted of insects of all developmental stages. The increase in the numbers of insects in the population will therefore be continuous and not by discrete jumps relating to 'generations'.

Theory.

For a population like *T. krausbaueri* with a fixed age schedule in unlimiting space.

\[ B - D = R \text{ (Growth rate in the population.)} \]

\[ \frac{dN}{dt} = bN - dN \]

\[ \frac{dN}{dt} = (b - d)N \]

where $b$ and $d$ = instantaneous birth (B) and death (D) rates.

and $N$ = total number of insects in the population
Lotka (1922) has shown that a population with a constant schedule of births and deaths will gradually approach a fixed or stable age distribution and

\[ \frac{dN}{dt} = R_m N \]

where \( R_m \) = innate capacity for increase.

Equation 3 in integral form is.

\[ N_t = N_o e^{(R_m t)} \]

where \( N_o \) = population numbers at time 0, \( N_t \) = numbers at time \( t \), \( e \) = base of natural logarithm

and in log form

\[ \log e N_t = \log e N_o + R_m t \]

Equation 4 describes the differential form of a curve of geometric increase in an infinitely expanding population

By regressing \( \log e N_t \) against \( t \), the \( R_m \) value, (the slope of the line) can be estimated.

Methods

The methods of culture and census for these populations are given in Chapter 4. The same number of insects of the same developmental stage were used to initiate the cultures and all cultures compared were censused at the same time periods.

Results.

Plots of the geometric curve, \( (N \text{ versus } t) \) for \( T. \) krausbauieri populations are shown in Figs 11-18. These plots are the means of replicate treatments cultured at 10°C on a diet of \( S. \) cerevisiae, (Fig 11), 10°C on a diet of \( B. \) vulgaris, var Monoire, (Fig 12), 15°C on a diet \( S. \) cerevisiae, (Fig 13), 15°C on a diet of \( B. \) vulgaris, var
Fig 11: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 10°C using diets of yeast *S. cerevisiae*.

\[ t = \text{time in days} \]

Replicate means and Standard errors of means are plotted.
Fig 12: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 10°C using diets of sugar beet *B. vulgaris* var Monoire.

\[ t = \text{time in days} \]

Replicate means and Standard errors of means are plotted
Fig 13: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 15°C using diets of yeast *S. cerevisiae*.

$t = $ time in days

Replicate means and Standard errors of means are plotted.
Monoire, (Fig 14), room temperature on a diet of S. cerevisiae, (Fig
15), Room temperature on a diet of B. vulgaris, var Monoire, (Fig
16), 20°C on a diet of S. cerevisiae, (Fig 17), 20°C on a diet of
B. vulgaris, var Monoire, (Fig 18).

Table 3 compares the numbers of insects in cultures after an identical
culture time of 175 days. In the table four replicates of cultures at
four temperatures are given to establish the effects of the diets and
temperatures on the population growth using total insect number
counts.

At 10°C the number of insects produced in culture was low and
population numbers increased at a slow rate (Fig 11, 12). The highest
population number achieved over the time period studied was 40 for
insects cultured on sugar beet at this temperature. The growth curve
at 10°C (N vs t) did not demonstrate clear exponential growth
although the pattern was better when a diet of B. vulgaris was used
(Fig 12).

At 15°C populations developed faster over the time period studied
compared with previous cultures at 10°C. As many as 250 insects were
produced for a culture replicate on a diet of yeast. The population
growth curves did not also follow a smooth curve in all the replicates
but showed some oscillations. The mean population plots however showed
a gradual increase in the population numbers with time. Fig 13 and
14.

The population growth curves observed when insects were cultured at
the variable room temperature (Fig 15,16) showed growth which
resembled exponential growth. In addition insect numbers were high
with some replicates producing numbers in excess of 100 in the time
period studied.

At 20°C geometric growth curves were produced for all replicates (Fig
17, Fig 18) and also for the mean population number plots. The growth
curves for B. vulgaris var Monoire diets (Fig 18) produced a maximum
insect number of 240 in only one culture. whilst numbers of insects in

$75_n$
Fig 14: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 15°C using diets of sugar beet *B. vulgaris* var Monoir.

$t = \text{time in days}$

Replicate means and Standard errors of means are plotted.
Fig 15: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at room temperature using diets of yeast *S. cerevisiae*

\[ t = \text{time in days} \]

Replicate means and Standard errors of means are plotted
YEAST Room temperature

![Graph showing the number of T. krasuevi versus time (days). The x-axis represents time (days) ranging from 0 to 80, and the y-axis represents the number of T. krasuevi ranging from 0 to 140. The data points are scattered with error bars indicating variability.]
Fig 16: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at room temperature using diets of sugar beet *B. vulgaris* var Monoire.

\[ t = \text{time in days} \]

Replicate means and Standard errors of means are plotted.
SUGAR BEET var Monoire room temperature

Time (days)

Number of T. krausbauri
Fig 17: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 20°C using diets of yeast *S. cerevisiae*.

$t = \text{time in days}$

Replicate means and Standard errors of means are plotted
Fig 18: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 20°C using diets of sugar beet *B. vulgaris* var Monoire.

\[ t = \text{time in days} \]

Replicate means and Standard errors of means are plotted.
cultures in yeast at comparable time interval were in excess of this number in three replicates.

The comparison of numbers at an identical time in insect culture after 175 days after culture initiation is shown in Table 3. This showed that mean values for cultures at 20°C gave the highest values. Although the cultures at room temperature had one replicate with beet diet and one with yeast which produced a high number the standard deviations of the replicate sets was high (115.8 with sugar beet 93.7 with beet). It is expected that because of this variability in temperature population growth would be erratic when comparisons were made of replicates. Standard deviation values for the replicates at 20°C were lower (65) for sugar beet cultures. A larger value for yeast diet at 20°C was however obtained (120) but this was due mainly to low figures (99) obtained in one culture replicate.

At 15°C standard deviation values were large for yeast cultures and low for beet cultures which in addition produced fewer mean insect numbers, 56 compared with 80. Cultures at 10°C were poor for yeast replicates with lower numbers (5) for yeast compared with a mean value of 17 for sugar beet.

Summary.

a) Geometric increase curves.

These plots showed that with the continued increase in time (t), the population numbers (N) continued to increase throughout the experimental time period for most cultures for population which developed under these culture conditions. Since the numbers within the population continued to increase it is therefore evident that there were no culture factors (eg space, substrate type) present limiting to population development in this manner in the culture. The carrying capacity for the population had therefore not been reached after 175 days. These populations can therefore be used for estimating the R∞ values.
Regression equations for individual replicates are shown in Table 4.

The $R_m$ values for the different population cultures are shown in Table 4. These values were obtained from the regression of the population growth equation and were used to compare population replicates as was obtained from equation 5.

$$\log_e N_t = \log_e N_0 + R_m \cdot t$$

5.2. The effects of temperature and diets of *E. vulgaris* and *S. cerevisiae* on the $R_m$ value and population growth of *T. krausbaueri*.

A comparison of the population growth in cultures at 10°C, 15°C, 20°C, and room temperature was shown in Fig 11-18. The numbers of insects $N$ in populations after identical time intervals of culture were shown in Table 3. An examination of the $R_m$ values (Table 4) which relate more directly to the population development showed these to be much less variable than total number counts and with a good $R^2$ value for the regression equations a more useful parameter. In addition because each population has its own characteristic $R_m$ value although a comparison of numbers of insects is useful it does not provide information which is by itself applicable to population modelling. The $R_m$ values presented in Table 4 also increased with an increase in the culture temperature.

For cultures on yeast, the mean values were 0.0064 at 10°C, 0.0277 at 15°C, 0.0418 at 20°C, and 0.0411 at room temperature. The $R^2$ values for the growth equations which measures the goodness of fit of the equation used to produce the $R_m$ were characteristically high (60%-97%).

The $R_m$ values for populations cultured on sugar beet var. Monoiré also increased as the culture temperature increased. The mean values were 0.0126 at 10°C, 0.0111 at 15°C, 0.0362 at 20°C, and 0.0414 at room temperature. The $R^2$ values were also high (80%-98%) except for one replicate at 10°C for these cultures.
Table 3: A comparison of the mean number *T. krausbaueri* cultured at 10°C, 15°C, 20°C and room temperature on diets of *S. cerevisiae* (yeast) and *B. vulgaris* (sugar beet) var Monoire after 175 days.
<table>
<thead>
<tr>
<th>Temp/°C</th>
<th>Diet</th>
<th>Insect numbers</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>culture replicate</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>10</td>
<td>Sugar beet var monoire.</td>
<td></td>
<td>20</td>
<td>10</td>
<td>12</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>yeast</td>
<td></td>
<td>4</td>
<td>2</td>
<td>8</td>
<td>-</td>
</tr>
<tr>
<td>15</td>
<td>Sugar beet var monoire.</td>
<td></td>
<td>63</td>
<td>45</td>
<td>68</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td>yeast</td>
<td></td>
<td>149</td>
<td>31</td>
<td>81</td>
<td>61</td>
</tr>
<tr>
<td>20</td>
<td>Sugar beet var monoire.</td>
<td></td>
<td>233</td>
<td>149</td>
<td>114</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>yeast</td>
<td></td>
<td>245</td>
<td>99</td>
<td>269</td>
<td>394</td>
</tr>
<tr>
<td>room temp.</td>
<td>Sugar beet var monoire.</td>
<td></td>
<td>330</td>
<td>76</td>
<td>141</td>
<td>97</td>
</tr>
<tr>
<td></td>
<td>yeast</td>
<td></td>
<td>235</td>
<td>43</td>
<td>119</td>
<td>33</td>
</tr>
</tbody>
</table>
Table 4: Values for the innate capacity for increase $R_m (\log R)$ in populations of T. krausbaueri cultured at four temperatures (10°C, 15°C, 20°C and room temperature) on diets of S. cerevisiae (yeast) and B. vulgaris (sugar beet) var Monoir.

Legend:

Population equation.

$$\log N_t = \log N_0 + t \log R$$

$R^2$ = fit of the regression line for the population equation.

SD = standard deviation.

$R_m$ = intrinsic growth rate.

$R$ = finite population growth rate.

$N$ = Total population number.

$t$ = time
<table>
<thead>
<tr>
<th>Diet Temperature °C</th>
<th>( \log \log N )</th>
<th>( \log \log R )</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yeast 10</td>
<td>0.612</td>
<td>0.059</td>
<td>57%</td>
</tr>
<tr>
<td></td>
<td>0.757</td>
<td>0.022</td>
<td>02%</td>
</tr>
<tr>
<td></td>
<td>1.207</td>
<td>0.011</td>
<td>41%</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td>0.054</td>
<td>0.045</td>
</tr>
<tr>
<td>Sugar beet var Monoire 10</td>
<td>1.546</td>
<td>0.166</td>
<td>73%</td>
</tr>
<tr>
<td></td>
<td>1.680</td>
<td>0.100</td>
<td>60%</td>
</tr>
<tr>
<td></td>
<td>1.759</td>
<td>0.046</td>
<td>33%</td>
</tr>
<tr>
<td></td>
<td>1.722</td>
<td>0.019</td>
<td>18%</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td>0.126</td>
<td>0.066</td>
</tr>
<tr>
<td>Yeast 15</td>
<td>2.032</td>
<td>0.039</td>
<td>34%</td>
</tr>
<tr>
<td></td>
<td>1.833</td>
<td>0.045</td>
<td>77%</td>
</tr>
<tr>
<td></td>
<td>1.783</td>
<td>0.019</td>
<td>67%</td>
</tr>
<tr>
<td></td>
<td>1.341</td>
<td>0.037</td>
<td>82%</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td>0.027</td>
<td>0.123</td>
</tr>
<tr>
<td>Sugar beet var Monoire 15</td>
<td>3.059</td>
<td>0.140</td>
<td>84%</td>
</tr>
<tr>
<td></td>
<td>3.037</td>
<td>0.122</td>
<td>76%</td>
</tr>
<tr>
<td></td>
<td>2.538</td>
<td>0.015</td>
<td>81%</td>
</tr>
<tr>
<td></td>
<td>3.360</td>
<td>0.025</td>
<td>61%</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td>0.011</td>
<td>0.053</td>
</tr>
<tr>
<td>Yeast 20</td>
<td>2.515</td>
<td>0.047</td>
<td>95%</td>
</tr>
<tr>
<td></td>
<td>3.083</td>
<td>0.171</td>
<td>50%</td>
</tr>
<tr>
<td></td>
<td>2.565</td>
<td>0.050</td>
<td>34%</td>
</tr>
<tr>
<td></td>
<td>3.032</td>
<td>0.053</td>
<td>95%</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td>0.048</td>
<td>0.017</td>
</tr>
<tr>
<td>Sugar beet var Monoire 20</td>
<td>1.746</td>
<td>0.043</td>
<td>83%</td>
</tr>
<tr>
<td></td>
<td>2.646</td>
<td>0.041</td>
<td>97%</td>
</tr>
<tr>
<td></td>
<td>2.643</td>
<td>0.019</td>
<td>86%</td>
</tr>
<tr>
<td></td>
<td>1.706</td>
<td>0.020</td>
<td>87%</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td>0.036</td>
<td>0.014</td>
</tr>
<tr>
<td>Yeast room temp</td>
<td>2.434</td>
<td>0.040</td>
<td>96%</td>
</tr>
<tr>
<td></td>
<td>1.612</td>
<td>0.046</td>
<td>81%</td>
</tr>
<tr>
<td></td>
<td>1.920</td>
<td>0.042</td>
<td>90%</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td>0.041</td>
<td>0.012</td>
</tr>
<tr>
<td>Sugar beet var Monoire room temp</td>
<td>2.980</td>
<td>0.043</td>
<td>97%</td>
</tr>
<tr>
<td></td>
<td>2.008</td>
<td>0.042</td>
<td>95%</td>
</tr>
<tr>
<td></td>
<td>2.694</td>
<td>0.035</td>
<td>88%</td>
</tr>
<tr>
<td></td>
<td>1.832</td>
<td>0.044</td>
<td>96%</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td>0.041</td>
<td>0.041</td>
</tr>
</tbody>
</table>
5.3. The effect of Gamma benzene hexachloride (BHC) on the population development of *T. krausbauseri*.

Introduction.

Under field conditions any soils treated with BHC will retain a wide spectrum of the applied dose depending to a large extent on the pesticide formulation, soil type, climate, degree of incorporation and run off in soils. The potential efficiency of pesticides applied to soils reaching the target organism is usually patchy (Mathews 1979). It is not unusual to apply 3,000 times the dose needed to kill the pest to soils (Brown 1951), in order to ensure that pests are killed. There is therefore some uptake of pesticide by soils, plants, fungi and other organisms. The pesticide can reach the target organism by a direct route (contact) or indirectly through feeding. Populations of *Tullbergia krausbauseri* were cultured on substrates treated with BHC, or on diets which contained BHC. The contact effect from the substrate in the 2 dimensional Plaster of Paris/charcoal set up and the feeding effect show how the population growth is affected by the pesticide. By applying doses of BHC which do not kill the insects but modify the behaviour of the population, an understanding of the response of the population to sublethal doses can be obtained.

Methods

The standard culture techniques (Chapter 4) were used. Populations were censused at 10 day intervals. Population growth of *T. krausbauseri* was studied at 20°C. The pesticide was applied either to the substrate to obtain an effect with the insects being in contact with the pesticide, or in the diet (*B. vulgaris* var Monioire and *S cerivisae*) to produce a systemic feeding effect. It was not possible to separate any effects which could be achieved by insects feeding on the substrate in this series of
experiments as in vivo and not effects on isolated insects were to be measured.

Results

5.3.1. The in vivo sublethal responses of T. krausbaueri in contact with BHC and its effect on the $R_m$ values.

Three pesticide concentrations were used for this data set and are presented as population growth curves $N$ versus $t$ and Log $N$ versus $t$ at 0mg al ml$^{-1}$, (Fig 19), 3.37x10$^{-6}$ mg al ml$^{-1}$, (Fig 20), 3.44x10$^{-5}$mg al ml$^{-1}$. (Fig 21).

At the highest pesticide concentrations used 3.44x10$^{-5}$mg al ml$^{-1}$, three of the four replicate populations did not survive for more than 60 days in culture. In the time interval recorded there was a rapid decline in the population numbers. Only one of the four replicates showed population growth (Fig 21), but this was also slow. A sublethal effect on population development was obtained however at 3.37x10$^{-6}$ mg al ml$^{-1}$. This intermediate pesticide concentration produced a sublethal effect on population development although initially populations developed erratically and did not show any clear trend towards increase. There was however a drop in population numbers, the highest value being 120.

The population growth curves give a further indication of how the pesticides can affect the development within the population. There was an extended time interval characterised by a period of instability during the early stages of population growth before population growth reached the geometric stages presented above. This stage was reached in the lower pesticide concentrations. At the the higher concentration 3.44x10$^{-5}$ mg al ml$^{-1}$ the populations failed to survive after extended time intervals.

Regression lines for the population development and estimates of the $R_m$ value were poor for these treatments. (Table 5). Replicates gave $R^2$ values of less than 40%, values of 35% and 31% being the highest found in two replicates. The values for the $R_m$ were also low with the highest 0.00573 found in one replicate, being ten times less than in
Fig 19: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 20°C using diets of sugar beet *B. vulgaris* var Monoire.

\[ t = \text{time in days} \]

Replicate means and Standard errors of means are plotted.
0 mg ai ml$^{-1}$

Number of T. krausbaueri

Time (days)
Fig 20: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 20°C using diets of sugar beet *B. vulgaris* var Monoire treated with BHC $3.37 \times 10^{-6}$ mg ai ml$^{-1}$ in substrate.

$t = \text{time in days}$

Replicate means and Standard errors of means are plotted
3.37 \times 10^{-8} \text{ mg ai ml}^{-1}

Number of T. krausiieral

Time (days)
Fig 21: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 20°C using diets of sugar beet *B. vulgaris* var Monoire treated with BHC 3.44 x10^{-5} mg ai ml^{-1} in substrate.

\[ t = \text{time in days} \]

Replicate means and Standard errors of means are plotted
3.44 \times 10^{-5} \text{ mg ai ml}^{-1}

Number of T. krasbauri

Time (days)
Table 5: Values for the innate capacity for increase $R_m \ (\log_\equiv R)$ in populations of *T. krausbaueri* cultured at 20°C on *B. vulgaris* var Monoire (sugar beet) with the pesticide BHC applied to the culture substrate.

Legend.

Population equation.

$$\log_\equiv N_t = \log_\equiv N_0 + t \ log_\equiv R$$

- $R_m$ = fit of the regression line for the population equation.
- $R_m$ = intrinsic growth rate.
- $R$ = finite population growth rate.
- $N$ = Total population number.
- $t$ = time
Diet Sugar beet var monoire

<table>
<thead>
<tr>
<th>BHC concentration (mg g⁻¹)</th>
<th>log₁₀ N₀</th>
<th>log₁₀ R</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.37 x 10⁻¹,</td>
<td>3.358</td>
<td>.00573</td>
<td>35%</td>
</tr>
<tr>
<td></td>
<td>3.172</td>
<td>.00524</td>
<td>31%</td>
</tr>
<tr>
<td></td>
<td>3.655</td>
<td>.00225</td>
<td>28%</td>
</tr>
<tr>
<td></td>
<td>3.314</td>
<td>.00452</td>
<td>14%</td>
</tr>
</tbody>
</table>
populations cultured without pesticide. (discussed in previous section). A mean value based on the the four populations gave a value of 0.00443 over 150 days.

5.3.2. The in vivo sublethal responses of T. krausbauri. to BHC in diets and its effects on the R_m. values.

The systemic effects of the pesticide were assessed with insect populations feeding on either the yeast diet or on sugar beet var Monoire and Primahill treated with BHC.

S. cerevisiae

The mean population growth curves for the treatments using yeast are shown in Figs 22-25 for treatments with 0 mg ai ml^{-1}, 5.34x10^{-7} mg ai ml^{-1}, 5.46x10^{-4} mg ai ml^{-1}, 8.75x10^{-3} mg ai ml^{-1}.

The development of the populations exhibited growth at all concentrations even though the numbers of insects were reduced at higher pesticide concentrations. The numbers of insects in culture at the highest concentration showed a maximum of 20 compared with 200 at treatments which did not use pesticide.

The R_m. values for these populations are shown in Table 6. These were reduced from a high of 0.0619 without pesticide to 0.0134 at the highest concentration of 8.75x10^{-3}mg ai ml^{-1} for populations cultured on yeast. This indicated a significant pesticide effect on insects feeding on treated yeast diets. The R^2. values were 90% or more in these cultures. This goodness of fit of the regression equation was however reduced at the pesticide concentration of 8.75x10^{-3}mg ai ml^{-1}. As the concentration of BHC increased there was a decrease in the mean R_m. values. At 5.34x10^{-7} mg ai ml^{-1} the mean value was 0.0448, at 5.46x10^{-4} mg ai ml^{-1}, 0.0361 and 0.0146 at 8.75x10^{-3} mg ai ml^{-1}.

The mean R_m. value was highest in cultures without pesticide at 0.0454.

The R^2 values for the goodness of fit gave values in excess of 90% in all replicates except at the highest concentration of 8.75x10^{-3} mg ai ml^{-1}, which gave values of 46% and 74%.
Fig 22: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 20°C using diets of yeast *S. cerevisiae*.

t = time in days

Replicate means and Standard errors of means are plotted
Fig 23: Plot for the increase in population numbers ($N$) for populations of *Tulbergia krausbaueri* cultured at 20°C using diets of yeast *Saccharomyces cerviseae* treated with $5.34 \times 10^{-7}$ mg ai ml$^{-1}$.

$t = \text{time in days}$.

Replicate Means and Standard errors of means are plotted.
$5.34 \times 10^{-7}$ mg ai ml$^{-1}$

Number of T. kruschkei

Time (days)
Fig 24: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 20°C using diets of yeast *S. cerevisiae* treated with \((5.4 \times 10^{-4} \text{ mol m}^{-1})\).

\(t = \text{time in days.}\)

Replicate Means and Standard errors of means are plotted.
Fig 25: Plots for the increase in population numbers \( N \) and \( \log e N \) for populations of \( T. krausbaueri \) cultured at 20°C using diets of yeast \( S. cerevisiae \) treated with \( (8.75 \times 10^{-3} \text{ mg ai ml}^{-1}) \).

\[ t = \text{time in days}. \]

Replicate Means and Standard errors of means are plotted.
$8.75 \times 10^{-3}$ mg ai ml$^{-1}$
Table 6: Values for the innate capacity for increase
\( R_m (\log_R R) \) in populations of *T. krausbaueri*
cultured at 20°C on *S. cerevisiae*
(yeast) treated with the pesticide BHC.

**Legend.**

**Population equation.**

\[
\log N = \log N_0 + t \log R
\]

- \( R^2 \) = fit of the regression line for the population equation.
- \( R_m \) = intrinsic growth rate.
- \( R \) = finite population growth rate.
- \( N \) = Total population number.
- \( t \) = time
Yeast,
BHC concentration
mg ai ml⁻¹.

<table>
<thead>
<tr>
<th>log ( \cdot N_0 )</th>
<th>log ( \cdot R )</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.781</td>
<td>0.0619</td>
<td>98%</td>
</tr>
<tr>
<td>1.937</td>
<td>0.0522</td>
<td>94%</td>
</tr>
<tr>
<td>3.477</td>
<td>0.0241</td>
<td>90%</td>
</tr>
<tr>
<td></td>
<td>0.0464</td>
<td></td>
</tr>
<tr>
<td>5.34x10⁻⁷</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.759</td>
<td>0.0354</td>
<td>96%</td>
</tr>
<tr>
<td>2.635</td>
<td>0.0440</td>
<td>97%</td>
</tr>
<tr>
<td>1.235</td>
<td>0.0551</td>
<td>95%</td>
</tr>
<tr>
<td>mean</td>
<td>0.0448</td>
<td></td>
</tr>
<tr>
<td>5.46x10⁻⁶</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.239</td>
<td>0.0347</td>
<td>94%</td>
</tr>
<tr>
<td>2.273</td>
<td>0.0470</td>
<td>95%</td>
</tr>
<tr>
<td>2.584</td>
<td>0.0266</td>
<td>98%</td>
</tr>
<tr>
<td>mean</td>
<td>0.0361</td>
<td></td>
</tr>
<tr>
<td>8.75x10⁻⁵</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.143</td>
<td>0.0134</td>
<td>46%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.025</td>
<td>0.0159</td>
<td>75%</td>
</tr>
<tr>
<td>mean</td>
<td>0.0146</td>
<td></td>
</tr>
</tbody>
</table>
B. vulgaris.

Mean population plots using diets of sugar beet var Primahill are shown in Fig 26 (0mg ai ml⁻¹, 5.34x10⁻⁷mg ai ml⁻¹), Fig 27 (2.18x10⁻³mg ai ml⁻¹, 3.52 x 10⁻²mg ai ml⁻¹.), and for variety Monoire in Fig 28 (0mg ai ml⁻¹, 5.34x10⁻⁷mg ai ml⁻¹), Fig 29 (2.18x10⁻3mg ai ml⁻¹, 3.52 x 10⁻²mg ai ml⁻¹.). These plots showed geometric increase and gave straight lines for the log e plots. Population development was possible at both concentrations with insects developing on the diets. When the concentration of pesticide was increased to 2.18x10⁻³mg ai ml⁻¹ and 3.52 x 10⁻²mg ai ml⁻¹, geometric population increase was still obtained in the replicates presented here (Fig 27). The variety Monoire also gave plots which exhibited geometric increase at the four replicates for concentrations shown here. At the highest concentration 3.52 x 10⁻²mg ai ml⁻¹. In Fig 29 however the replicate presented here showed non uniform growth even though population numbers were high. The Rₘ values for the two varieties of Primahill and Monoire, are shown in Table 7 for populations reared on a diet treated with BHC. These values for the four replicates at the four treatments gave good R² values of the regression equations and were shown to be high (54%-96%). The mean Rₘ values suggests that at the lowest concentration 5.34x10⁻⁷ mg ai ml⁻¹, values obtained were similar to those of populations cultured without BHC for the monoire variety (0.301 and 0.302). Primahill however showed a mean reduction in the Rₘ value from 0.316-0.246. There was however an increase in the Rₘ value at the higher concentrations. This apparent anomaly should not be misunderstood. The population numbers were reduced at the higher concentrations and the Rₘ value therefore relates to the survival and reproduction of the least susceptible insects in the populations. The Rₘ values did not appear to be dissimilar for the two varieties although they were lower than those obtained for yeast cultures.

Discussion.
Fig 25: Plots for the increase in population numbers (N) and log e N for populations of *T. krausbaueri* cultured at 20°C on a diet of sugar beet (*B. vulgaris var Primahill*) treated with Benzene hexachloride (BHC).

\[ t = \text{time in days.} \]
Number of *T. krausbaueri*

Time (days)
Number of T. krausbaueri

Time (days)
Fig 27

Plots for the increase in population numbers (N) and log e N for populations of *T. krausbaueri* cultured at 20°C on a diet of sugar beet (*B. vulgaris* var Primahill) treated with Benzene hexachloride (BHC).
Number of T. krausbaueri

-2.3 \times 10^{-2} \text{ mg ai ml}^{-1}

Time (days)
Fig 28: Plots for the increase in population numbers (N) and \( \log N \) for populations of *T. krausbaueri* cultured at 20°C on a diet of sugar beet (*B. vulgaris* var. Monoire) treated with Benzene hexachloride (BHC).

\[ t = \text{time in days} \]
$5.34 \times 10^{-2} \text{ mg ai ml}^{-1}$

Number of T. krausbaueri

Time (days)
Fig 29: Plots for the increase in population numbers (N) for populations of *T. krausbaueri* cultured at 20°C on a diet of sugar beet (*B. vulgaris* var Monoire) treated with Benzene hexachloride (BHC).
$2.45 \times 10^{-3}$ mg ai ml$^{-1}$

Number of T. krausbaueri

Time (days)
Number of T. krausbaueri

3.52x 10^{-2} \text{ mg ai ml}^{-1}

Time (days)
Table 7: Values for the innate capacity for increase $R_m (\log R)$ in populations of *T. krausbaueri* cultured at 20°C on *B. vulgaris* var Monoire and var Primahill (sugar beet) treated with the pesticide BHC.

Legend.

Population equation.

$$\log N_t = \log N_0 + t \cdot \log R$$

- $R^2$: fit of the regression line for the population equation.
- $R_m$: intrinsic growth rate.
- $R$: finite population growth rate.
- $N$: Total population number.
- $t$: time.
<table>
<thead>
<tr>
<th></th>
<th>log × N0</th>
<th>log × R</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>0</strong></td>
<td>2.202</td>
<td>0.0293</td>
<td>93%</td>
</tr>
<tr>
<td></td>
<td>2.087</td>
<td>0.0342</td>
<td>93%</td>
</tr>
<tr>
<td></td>
<td>2.036</td>
<td>0.0313</td>
<td>92%</td>
</tr>
<tr>
<td><strong>mean</strong></td>
<td></td>
<td>0.0316</td>
<td></td>
</tr>
<tr>
<td>5.34 × 10⁻⁷</td>
<td>0.982</td>
<td>0.0134</td>
<td>60%</td>
</tr>
<tr>
<td></td>
<td>1.701</td>
<td>0.0236</td>
<td>89%</td>
</tr>
<tr>
<td><strong>mean</strong></td>
<td></td>
<td>0.0246</td>
<td></td>
</tr>
<tr>
<td>2.18 × 10⁻⁸</td>
<td>1.733</td>
<td>0.0360</td>
<td>88%</td>
</tr>
<tr>
<td></td>
<td>0.781</td>
<td>0.0421</td>
<td>76%</td>
</tr>
<tr>
<td></td>
<td>1.172</td>
<td>0.0355</td>
<td>94%</td>
</tr>
<tr>
<td><strong>mean</strong></td>
<td></td>
<td>0.0379</td>
<td></td>
</tr>
<tr>
<td>3.5 × 10⁻⁹</td>
<td>1.774</td>
<td>0.0282</td>
<td>92%</td>
</tr>
<tr>
<td></td>
<td>1.298</td>
<td>0.0457</td>
<td>95%</td>
</tr>
<tr>
<td></td>
<td>1.648</td>
<td>0.0337</td>
<td>96%</td>
</tr>
<tr>
<td><strong>mean</strong></td>
<td></td>
<td>0.0359</td>
<td></td>
</tr>
</tbody>
</table>

**Sugar Beet var Primahill**

BHC concentration
mg ai ml⁻¹

<table>
<thead>
<tr>
<th></th>
<th>log × N0</th>
<th>log × R</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1.195</td>
<td>0.0425</td>
<td>98%</td>
</tr>
<tr>
<td></td>
<td>1.847</td>
<td>0.0258</td>
<td>77%</td>
</tr>
<tr>
<td><strong>mean</strong></td>
<td></td>
<td>0.0356</td>
<td></td>
</tr>
<tr>
<td>5.34 × 10⁻⁷</td>
<td>1.717</td>
<td>0.0249</td>
<td>77%</td>
</tr>
<tr>
<td></td>
<td>0.927</td>
<td>0.0435</td>
<td>76%</td>
</tr>
<tr>
<td></td>
<td>0.371</td>
<td>0.0219</td>
<td>91%</td>
</tr>
<tr>
<td><strong>mean</strong></td>
<td></td>
<td>0.0301</td>
<td></td>
</tr>
<tr>
<td>2.18 × 10⁻⁸</td>
<td>1.642</td>
<td>0.0369</td>
<td>96%</td>
</tr>
<tr>
<td></td>
<td>1.687</td>
<td>0.0358</td>
<td>71%</td>
</tr>
<tr>
<td></td>
<td>1.154</td>
<td>0.0253</td>
<td>62%</td>
</tr>
<tr>
<td><strong>mean</strong></td>
<td></td>
<td>0.0253</td>
<td></td>
</tr>
<tr>
<td>3.5 × 10⁻⁹</td>
<td>1.599</td>
<td>0.0374</td>
<td>87%</td>
</tr>
<tr>
<td></td>
<td>1.721</td>
<td>0.0248</td>
<td>84%</td>
</tr>
<tr>
<td></td>
<td>2.086</td>
<td>0.0184</td>
<td>54%</td>
</tr>
<tr>
<td><strong>mean</strong></td>
<td></td>
<td>0.0268</td>
<td></td>
</tr>
</tbody>
</table>
The growth curve for population development was one of geometric increase and the mean $R_m$ values reflected changes in the culture conditions. In cultures fed on yeast for example, a threefold reduction in the $R_m$ value at the highest BHC concentration of $8.75 \times 10^{-3}$ mg ai ml$^{-1}$, suggests that the population will take longer to reach the numbers obtained in the cultures where pesticide was not present.

The systemic effect through feeding on sugar beet or yeast exposed to one of 3 concentrations of BHC, showed that where the pesticide was introduced the sublethal effect could be monitored as a change in the $R_m$ values. Because of the different manner in which yeast and beet were exposed direct comparisons can not be made between treatments but, a within treatment (concentration effect) and a sugar beet varietal comparison can be made. These statistical results are summarised in Table 8. They show that there was no significant difference due to varieties, or in the pesticide treatment range used.

The unexpectedly high tolerance to BHC at high concentration levels may be because of avoidance of the contaminated diet by the insects. There might also be some detoxification mechanism in the insects. There is evidence for avoidance in feeding from work in this thesis and the possibility that the insects feed less (reduction in individual insect size and lengthening in time to pass through developmental stages) on pesticide treated seedlings.

With the two Sugar beet varieties used (Monoire and Primahill), the patterns obtained were by no means clear. There appeared to be little effect on the insect if it fed on Sugar beet which had been germinated and grown for 8 days in BHC solution although the effect of the pesticide on the Sugar beet was visually evident, at these concentrations (chapter 6). In addition the $R_m$ values obtained for the treatments were not greatly reduced. It is possible that like other plants, (Audus 1979) there might be a detoxification process occurring in the Sugar beet which presents a less toxic diet to T. krausbaueri.
Table 8: A summary of analyses of variance for $R_m$ values
Effects of temperature on $R_v$ values for *T. krausbaueri* fed on a diet of yeast.

$F=173$ (df 3, 2) ANOVA calculations terminated following homogeneity of variance test.

Effects of temperature on $R_v$ values for *T. krausbaueri* fed on a diet of sugar beet.

$F=13.04$ (df 3, 3) ANOVA calculations terminated following homogeneity of variance test.

Effects of diet on $R_v$ values for *T. krausbaueri* cultured at 10°C

$F=1.907$ (df 1, 5) Not significant at 0.05 level

Effects of diet on $R_v$ values for *T. krausbaueri* cultured at 15°C

$F=5.504$ (df 1, 6) Not significant at 0.05 level

Effects of diet on $R_v$ values for *T. krausbaueri* cultured at 20°C

$F=0.199$ (df 1, 6) Not significant at 0.05 level

Effects of diet on $R_v$ values for *T. krausbaueri* cultured at room temperature

$F=10.437$ (df 3, 3) ANOVA calculations terminated following homogeneity of variance test.

Effects of pesticide on $R_v$ values for *T. krausbaueri* fed on a diet of sugar beet variety Primahill.

$F=2.259$ (df 3, 7) Not significant at 0.05 level

Effects of pesticide on $R_v$ values for *T. krausbaueri* fed on a diet of sugar beet variety Monoire.

$F=0.385$ (df 3, 7) Not significant at 0.05 level
A comparison of the $R_m$ values for populations on the two diets used at identical temperatures showed that except for the populations cultured at 10°C and room temperature, the $R_m$ values on the diets of yeast were higher.

The population growth of insects cultured at 20°C gave higher $R_m$ values 0.0418 for yeast and 0.0362 for sugar beet which indicates a rapid rate of increase in numbers. Regression equations measuring the goodness of fit of the growth curves also gave high values (85% or higher) in most replicates. The temperature of 20°C was therefore chosen as the temperature for population modelling.
5.3.3 The *in vivo* toxic responses to BHC using the Spearman Karber 24 hour toxicity tests on populations of *T. krausbaueri*.

Method.

The Spearman Karber LC$_{50}$ toxicity test was used to estimate the LC$_{50}$ values (BHC concentration producing 50% mortality in populations) for *T. krausbaueri*. The experiments were carried out as described in chapter 4.3.3. and Appendix 4. Insects used for these tests were cultured on diets of *S. cerevisiae*, *B. vulgaris* var Monoire or on a mixed diet to determine if there was a dietary effect. The four different developmental stages introduced in chapter 3 were used for these tests. The values obtained were an estimate of the concentration of BHC which when applied to the substrate would produce 50% toxicity to the developmental stages used.

Results.

Tables 9 and 10 give the results for the LC$_{50}$ values. The grand mean values show that size class 1 (juveniles of size 250µm) had an LC$_{50}$ value of $4.2 \times 10^{-4}$ mg ai ml$^{-1}$. size class 2 (reproductives 250-350µm) a mean value of $5.4 \times 10^{-4}$ mg ai ml$^{-1}$ and size class 3 (reproductives 350-450µm), $3.6 \times 10^{-4}$ mg ai ml$^{-1}$, with the size class 4 (post reproductives greater than 450µm) insects producing the lowest mean value of $2.9 \times 10^{-4}$ mg ai ml$^{-1}$. Table 10 summarises the effects of diet on the LC$_{50}$ values. When insect LC$_{50}$ values were recorded on the basis of the diet consumed, The population means gave a value of $4.8 \times 10^{-4}$ mg ai ml$^{-1}$ for populations cultured with a yeast diet, $5.3 \times 10^{-4}$ mg ai ml$^{-1}$ for mixed diet and $3.2 \times 10^{-4}$ mg ai ml$^{-1}$, for insects cultured on Sugar beet var Monoire.

Discussion.

Insect Size Classes and Developmental Stage..
Table 9: The mean Spearman Karber LC₅₀ values for size classes (developmental stages) of T. krausbaueri cultured on B. vulgaris var Monoir (sugar beet), S. cerevisiae (yeast) and a mixed diet.
<table>
<thead>
<tr>
<th>Developmental stage</th>
<th>population replicate number</th>
<th>diet</th>
<th>Sperran Karber LC50 x10^-6 g a.i ml^-1</th>
<th>stage mean</th>
<th>stage mean/size um</th>
<th>diet mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 juvenile</td>
<td>1</td>
<td>yeast</td>
<td>6.302</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>yeast</td>
<td>6.793</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>yeast</td>
<td>3.993</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>best</td>
<td>2.295</td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>best</td>
<td>2.9127</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>best</td>
<td>2.1785</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>mixed</td>
<td>2.9785</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>mixed</td>
<td>4.1509</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>mixed</td>
<td>7.8875</td>
<td>4.2</td>
<td>0.0168</td>
<td></td>
</tr>
<tr>
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<td>1</td>
<td>yeast</td>
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<tr>
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<td></td>
</tr>
<tr>
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<td>yeast</td>
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</tr>
<tr>
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<td>best</td>
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</tr>
<tr>
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<td>5</td>
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<td>6.6122</td>
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</tr>
<tr>
<td></td>
<td>6</td>
<td>mixed</td>
<td>6.6381</td>
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Table 10: The mean Spearman Karber LC50 values for populations of *T. krausbaueri* cultured on *B. vulgaris* var Monoire (sugar beet), *S. cerevisiae* (yeast) and a mixed diet.
<table>
<thead>
<tr>
<th>developmental stage</th>
<th>diet</th>
<th>mean LC50 x10^-4 mg ai ml^-1.</th>
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</table>
The insects in the population have previously been divided into 4 size classes Chapter 3.3. on the basis of length. All the juveniles were included in size class 1 and the adults and the reproductives and post reproductives in size classes 2, 3 and 4. (Size class 1 was recorded for insects measuring less than 250μm, size class 2 measuring between 250μm and 350μm, size class 3 measuring between 350μm and 450μm and size class 4 for insects measuring more than 450μm).

The size class 4 which contained the post reproductive developmental stage showed the highest sensitivity with the lowest toxicity LC₅₀ value whilst the juveniles in size class 1 and the first adult stage (size class 2) were able to tolerate a higher concentration of BHC pesticide than the other stages. The variability between the values obtained was quite large in some replicates of cultures on yeast and in mixed diets. The mean values presented here did not however take into account the previous diets the insects were cultured on. Differential development of insects cultured in different diets however, could produce insects of different sizes after identical time periods. In fact development to size class 4 did not normally occur in populations cultured on sugar beet var Monoir (Chapter 3). A clearer picture of the toxicity to BHC is obtained when the LC₅₀ takes account of the mean size of the insects in each developmental stage. This records the effect of insect class size on the LC₅₀ values obtained and is shown in Table 9. Size class 1 therefore had a value of 0.0186 x10⁻⁴ mg a.i. ml⁻¹ μm⁻¹. size class 2, 0.01356 x 10⁻⁴ mg a.i. ml⁻¹ μm⁻¹. size class 3, 0.008 x10⁻⁴ mg a.i. ml⁻¹ μm⁻¹. and size class 4, 0.006 x10⁻⁴ mg a.i. ml⁻¹ μm⁻¹. This suggests that as the insect size increases so the LC₅₀ toxicity caused by BHC decreases. Toxicity can therefore be related to insect size and therefore developmental stage and age in T. krausbaueri. There appears to be an inverse relationship between size and the 24 hour LC₅₀ toxicity to BHC as recorded by the Spearman Karber Tests.
Diet effects

Table 10 shows the mean values for the stage LC$_{50}$ values for the pesticides related to the insects diets. Diets of yeast, beet and a mixed diet are shown. The mean values for the population diets, show that the insects reared on a diet of beet had the lowest resistance to the pesticide. Insects reared on a yeast diet produced a larger LC$_{50}$ value whilst the mixed diet of beet and yeast gave a value which was larger than the other two. The mean LC$_{50}$ values for the juvenile developmental stages was lowest in all the diet treatments. The mean value for the juveniles was lowest on the sugar beet diet $2.46 \times 10^{-4}$ mg ai ml$^{-1}$, and highest in yeast cultures $5.558 \times 10^{-4}$ mg ai ml$^{-1}$. The size classes 2 and 3 gave the highest mean LC$_{50}$ values for all the diet treatments.

General Discussion.

The determination of the innate capacity for increase $R_m$, as defined from the Lotka equation (1925), was carried out under conditions of different temperatures (10°C, 15°C, 20°C and room temperature). The effect of the pesticide BHC was also studied and $R_m$, values assessed when pesticide was present in the culture diet of sugar beet or yeast or when pesticide was administered to the substrate.

The estimation of the $R_m$ value using the regression of the numbers of insects in culture censuses was a useful population statistic. Murray (1979) has suggested the $R_m$ value as the measure for individual fitness in populations. Nur (1984) however suggested that this parameter should be used only for populations or to gain insight into measures of individual fitness in clones and other non-interbreeding populations. Both authors agree with Krebs (1978), that the $R_m$ value is a useful population statistic for the measurement of population fitness. The measure of population fitness using the $R_m$, values in this chapter relate to the development of individual population cultures. Although there may be a relation to individual insect fitness this has not been examined.
Fecundity of the individual insects is presented in Chapter 3 and measurements of individual age-specific parameters and development of second order growth models which relate to individual fitness are discussed in more detail in Chapter 7.

The estimation of the \( R_m \) value in this chapter proved useful in comparing the population growth rates and has highlighted the effects of diet quality, temperature and BHC on \( T. krausbaueri \) populations. The range in individual \( R_m \) values for different cultures reflected the effects of varying culture conditions. At 10°C on a diet of yeast, the lowest \( R_m \) value of 0.006 was obtained. In contrast a culture replicate on yeast at 20°C produced the highest \( R_m \) value 0.0619, ten times as large.

Gregoire Wibo and Snider (1983) estimated the \( R_m \) values for \( F. candida \) and \( Protophorura armata \) (Tullberg), and Bengtsson et al (1983) the \( R_m \) values for \( O. armatus \). The \( R_m \) values were found to increase from a value of 0.09 at 15.5°C to 0.14 at 26.6°C for \( F. candida \) and 0.03 to 0.07 for \( P. armata \). \( O. armatus \) however had higher \( R_m \) values of 0.186. The manipulations of environmental conditions in this study produced changes which relate specifically to the \( R_m \) values. The highest \( R_m \) value obtained in this culture for \( T. krausbaueri \) was 0.0619.

The highest \( R_m \) values of 0.0619 therefore gives a population which increase by 1.06 per day, the lowest \( R_m \) value 0.006 gives an increase of 1.006. \( (R = e^{R_m}) \) The doubling time for the populations are therefore after 11 days, and after 116 days at these two extremes. This doubling time for populations on diets of yeast at 10°C (116) days was however obtained from an \( R_m \) value which had a poor \( R^2 \) value (57%). This low value and poor regression would suggest that it is more likely that the population will fail to develop substantially under these conditions.

Population growth curves for single species cultures of Collembola, (\( Onychiurus, Hypogastura \)), have been presented by Longstaff (1974, 1976, 1977). These studies showed that populations characteristically increase to a maximum size and then decline as
the cultures became saturated. The decline was attributed to the accumulation of waste products or the density of population in the culture vessels. Longstaff (1976) also notes a time lag in comparisons of Collembola populations at different temperatures. Population growth examined in this study showed geometric growth rates, incidentally not discussed by Longstaff. The time period used for the population in this study was not long enough to produce declines in the population numbers due to population density. Decline would certainly have occurred over longer time periods. The time lags for populations to develop were longer at lower temperatures of 10°C, 15°C (90 and 65 days respectively for yeast, and 65 and 40 days respectively for sugar beet) compared with 38 and 26 for yeast and beet at 20°C. Not only was the time lag extended at 10°C but the population development was also slow, and the fit of regression equations was poor. Cultures at this temperature would therefore be very difficult to monitor.

In general however, the regression equations produced for population growth rates showed high goodness of fit, (90% or more), and demonstrated a good fit to the model. Table 8 summarises the results of statistical tests on \( R_m \) values measured in this study. None of the tests reached statistical significance.

The effects of sugar beet diets compared with those of yeast on the populations' development were shown to be not significant. Measures of the \( R_m \) values showed that the populations had similar potential for increase. However at the lower temperatures of 10°C the populations had a higher mean \( R_m \) value when feeding on sugar beet var monolore (0.0126) compared with yeast (0.0064), the \( R_m \) values measuring the instantaneous potential for increase on the populations.

Although the \( R_m \) value gives the instantaneous growth rate it can be converted to a finite growth rate by \( \frac{1}{1-e^{Rm}} = V \). This finite growth rate will tend towards 1 (Murray 1985) and the \( R_m \) value towards 0. It can be used to estimate the growth rate for each individual. The
finite growth rate allows the use of comparative statistics within the population. Nevertheless it is evident that the size class /developmental stage specific probabilities of survival in the population are difficult to measure for an individual because, either the individual insect dies or survives and reproduces leaving little to measure. It is therefore more significant to develop a Stochastic (probability) growth model which takes into account the probabilities for birth death and reproduction of the different developmental stages. The sum of these probabilities for all insects within the population will enable the prediction of population development to be more accurate and will help in identifying parameters specific to the different developmental stage.

The relationships examined above for the growth of the population of T. krausbaueri conform to the models for the population development.

\[ N_t = N_0 e^{(R_m \cdot t)} \] ........ 4

and

\[ \log_e N_t = \log_e N_0 + R_m \cdot t \] ........ 5

The development of a population growth models which use size class relationships is presented in Chapter 7.
Toxicity.

The toxicity of pesticides to Collembola populations has been assessed by several authors. The approach of Tomlin 1975 was to use F. candida, O. justi posteri and Hypogastura armata (Nicolet) as test insects to measure the spectrum of toxicity after 24 hours exposure to a range of pesticides. The approach taken in the present study was to focus on a particular pesticide BHC (Gamma Benzene Hexachloride) and estimate changes caused to insect populations. This method of using one organism with one pesticide allows the successful manipulation of environmental conditions in a systems analysis process (Hollingsworth 1988) because once the relationships between insect and pesticide are established, changes to these relationships caused by the environment can be estimated. Although Tomlin's (1975) work resulted in estimates of concentrations of pesticides which could cause mortalities to Collembola, little emphasis was placed on estimating the LC₅₀ values or the sublethal effects of the pesticides and no attempts were made to analyse the effects of the pesticides on different developmental stages within the insect population. These factors are very important to the assessment of the pest potential of the insect.

The results presented here however show that there is a difference in the toxicity produced on different developmental stages and this will have a bearing on the way in which a population receiving a sublethal dose subsequently develops.

The summary of the LC₅₀ values show that of all the developmental stage groups, the reproductive stages are the least susceptible ones.

Therefore, in a new population which has a large number of the other growth stages especially the juveniles, (Chapter 3), a total population mortality estimate will bear little relation to the populations' potential for reproduction. Although mortalities are high due to the abundance of juveniles, the potential for reproduction
will be affected to a lesser degree since juveniles at this stage will not be contributing to reproduction.

The post reproductive stages are also susceptible to pesticide application. Being larger insects they are easy to identify but mortalities caused to them will not be relevant to population development, as their function is a limited one, once reproduction ceases.

Where sublethal pesticide doses were applied the pesticide had an effect on population growth although effects were only observed at higher BHC concentrations.

Although the mean LC50 values are 1.0 x 10^-4 mg ai ml^-1 to 10.4 x 10^-4 mg ai ml^-1. for T. krausbaueri, the pesticide concentrations of 3.4 x 10^-8 mg ai ml^-1 applied to the substrate in the same manner was found to be toxic to the population development in the long term. The importance of the 24 hour tests should be carefully examined. Knockdown is an important component in assessing LC50 values, but there is a possibility of some recovery and also the numbers which do survive, the more robust insects, can be important in future population development.

The cuticular barrier presented by the insect to pesticide is an important feature in the pesticide - insect interaction. The LC50 is measures of contact effects; the long term effects of contact have also been estimated in the population studies. The processes of penetration, distribution, binding - (concentration of pesticide) and detoxication and elimination - (loss of pesticide) will occur simultaneously as the poisoning symptoms develop. The sum of these processes in the individual insect will determine toxicity. The use of the LC50 (contact effect) instead of the LD50 (dosage effect involving the administration of a specified dose to the insect) provides a temporal continuous exposure to pesticide which more closely represents field conditions. The difference between a contact effect measured by the LC50 in these experiments and the LD50 where it is ensured that a specified dose is applied to the insect studied,
allows field conditions to be simulated in the laboratory. Although
the concentration of pesticide in contact with the insect can not be
accurately estimated, the concentration of pesticide in the insects' 
environment is known and its application to the insect and the
insects' development of toxic symptoms more closely represent field
conditions where pesticides are found in the soil the insect comes
into contact with. In the field the preferred route of entry of the
pesticide will be taken and this will also occur in the LC₅₀ studies
where the pesticide is applied to the substrate.
The pesticide may however have a more effective route into toxic sites
via the diet. The diets of yeast and beet contaminated with pesticide
showed a clear difference in their activity spectrum. Although the
pesticide effects were significant ones reducing the Rₘ values to 0.016 at the lowest concentration 5.34x10⁻⁷ mg ai ml⁻¹ to 0.05 at
the highest concentration of 8.7x10⁻³ mg ai ml⁻¹, the regression values (R²) at the lower concentrations were poor. The intermediate Rₘ value
with concentrations of 5.46x10⁻⁶ mg ai ml⁻¹ gave a 96% R² value. A
decline in population numbers and developmental stage structure showed
clearly the long term susceptibility to the pesticide BHC by this
route of entry. Sibagia and Snider (1981) noted the sublethal effects
of the pesticides (herbicides) atrazine and paraquat in yeast diets on
T. granulata and F. candida and demonstrated that juveniles could
survive on diets with 5,000 ppm of pesticide for up to 2 years
although there was some repellent action away from the sources of
diet. Additional effects that were observed were the increase in the
instar times and corresponding reductions in the Rₘ values at the
higher concentrations. Bengtsson et al (1985) found changes in the
Rₘ values for populations of O. armatus cultured on the fungus
Verticillium bulbillosum. The reduction in values due to the presence
of metal pollutants were found to be varied, with both increased
and decreased values over the metal pollutant concentration range
examined. The Rₘ values of the cultures without any biocide were
however large for this species (0.186) compared with 0.06 in this
study. It would be expected that O. armatus which is one of the
insects comprising the soil pest complex for Sugar beet, (Brown 1980)
would increase in numbers faster than _T. krausbauer_/ on the fungus diet used by Bengtsson (1985).

The 24 hour contact LC₆₀ values obtained for insects fed on _B. vulgaris_ var Monoi re were in the range of 2.4-4.5 x 10⁻⁴ mg ai ml⁻¹. The BHC concentrations used for examining the dietary effects on _T. krausbauer_/ were 5.34 x 10⁻⁷ mg ai ml⁻¹, 2.1 x 10⁻⁵ mg ai ml⁻¹, 3.52 x 10⁻² mg ai ml⁻¹. These concentrations were however able to support population growth. The toxicity by contact therefore appears to be the more important effect when equivalent concentrations are applied by the two methods described, even though contact tests were for 24 hours only. When the contact effect was maintained for long term sublethal studies however, 3.37 x 10⁻⁶ mg ai ml⁻¹ did not destroy populations whilst concentrations above 3.44 x 10⁻⁵ mg ai ml⁻¹ stopped population development after 60 days.

There was also no significant difference between the two varieties of Monoi re and Primahill on the Rₚₚ statistic when pesticide was applied in the diet even though the growth of the two varieties was significantly different under pesticide conditions (Chapter 6). The mode of action of the pesticide BHC provides some information on the visible toxic effect produced. The normal route of entry of this pesticide is through the Sodium channels in the insect cuticle. Action sites of BHC are at the point of synaptic transmission between axons, at the release sites to target cells and also on the Glial cells responsible for the nutrition of the Axons.

The symptoms of poisoning observed in this study included secretions from pseudoeccelii, a symptom noted by Osborne (1985) following BHC poisoning, heightened muscular activity and an enhanced curling response. These suggest an interference with neuromuscular transmission as the mode of pesticide action. The contention by Bryce (1985) that insects are difficult to poison efficiently will appear to hold true. The populations were able to survive at high concentrations and to increase in numbers.

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There is therefore a complex relationship between BHC and *Tullbergia krausbaueri*. Toxicity can occur both in the short term and through a long term effect on population development for insects in contact with BHC or feeding on Sugar beet diets treated with BHC. The different developmental stages exhibit selective toxicity to this pesticide. Population development and growth of *T. krausbaueri* was found to be geometric and the Rm. statistic was a useful estimate of this development. In Chapter 7 the relationships established here will be further developed to take into account the developmental stages within the population, the effects of diets on these development stages and the toxic effects of BHC on *T. krausbaueri*. 
6. The germination and growth of \textit{B. vulgaris} seedlings and the effects of Benzene hexachloride BHC.

Introduction.

The previous chapter has examined the effects of grazing \textit{T. krausbaueri} on diets which included \textit{B. vulgaris} containing a range of concentrations of BHC. The effects of these diets on the population's development were fully discussed. In this chapter, the germination and growth pattern for \textit{B. vulgaris} are examined. In addition, the effects of BHC on the germination and growth of \textit{B. vulgaris} are evaluated using the same concentrations of pesticide as were applied to \textit{T. krausbaueri} in Chapter 5.

The growth of \textit{B. vulgaris} seedlings can be described in terms of cell division, cell enlargement and cell differentiation. The efficiency of these processes determine the nature of the emergence of the seedling from the soil. Although these are the underlying physiological processes involved in seedling growth, they can be measured by changes in the size and morphology of the seedling.

The percentage emergence of \textit{B. vulgaris} seedlings from the soil after planting is a useful criterion for judging the future percentage establishment and the potential yield from the crop. Since the emergence of seeds from the soil will depend on the percentage germination of the seeds, the best tests to determine how seeds will perform in the field are laboratory germination trials, (Fletcher and Prince, 1987). Although laboratory germination trials in general produce a greater percentage of successful germination than those expected in the field, laboratory germination will still indicate the maximum potential for seed germination under ideal conditions and show what percentage of the seeds are capable of germination. The National Institute of Agricultural Botany (NIAB) carries out annual \textit{B. vulgaris} germination trials and will only recommend seeds that produce 90\% or better germination. In addition, it is important to determine whether the seedling germination pattern is uniform or varies with time as this will influence the future emergence and establishment of
the crop. *B. vulgaris* seedlings are also said to form a sigmoid pattern for percentage germination when seed germinations are plotted against time. This process is affected by different environments and also depends on the variety of seed used. Therefore the percentage germination and the pattern of germination will be examined in this chapter.

The successful emergence of *B. vulgaris* plants also depends on the nature of the seedlings' growth following germination and this can vary depending on which variety of *B. vulgaris* is used. Several varieties of *B. vulgaris* are recommended yearly to farmers by the NIAB. Four of these varieties of *B. vulgaris* (Primahill, Monoir, IBB83, Julia) were used in the experiments presented here.

The growth of individual seedlings, like their germination, is critically affected by the environment around the seedling. The presence of pesticides in the environment of the developing seedling can cause an environmental stress. Although the effects of pesticides on crops have been little studied, *B. vulgaris* seedlings are likely to be most susceptible to these stresses in their early growth stages as it is at this stage that they are most vulnerable. Any reduction in the growth rates at this time caused by pesticides, will affect the rate of seedling emergence and thus successful establishment.

The pattern of the emergence of seedlings is also an important parameter. If there is uniform emergence, the seedlings are uniformly able to utilize the available sunlight and nutrients. Some field estimates have shown that seeds can take up to 3 months to emerge from the soil and produce only 30% emergence in adverse conditions in the field, (Durrant, Draycott and Payne, 1974). If a pesticide such as BHC affects germination and growth of seedlings, the uniformity of germination may be affected and therefore the utilization of available resources for *B. vulgaris* growth.

Methods.

The methods for the preparation of the seeds for germination and growth of seedlings trials are outlined in Chapter 4. The varieties
studied were Primahill, Monoirre, IBB83 and Julia. A two way ANOVA test was carried out to estimate if there was any effect attributable to the different varieties or pesticide concentrations used on germination and seedling growth.

6.1 The germination of seeds of *B. vulgaris* varieties

Introduction.

The germination patterns of *B. vulgaris* seeds give an estimate of the development of *B. vulgaris* in the field. Durrant and Payne (1983 b) have shown that germination patterns in sugar beet seeds are of a sigmoid nature when plotted against time. This is not dissimilar to patterns observed for other plant species. Temperature and pesticide concentrations can affect this germination pattern reducing both the numbers germinating and the rates at which germination occurs.

Results

6.1.1 The effects of temperature on *B. vulgaris* germination.

Figure 30 shows the effect of two temperatures on the pattern of germination in *B. vulgaris* var Monoirre. Although the sigmoid distribution for the germination was found at both 10°C and 20°C, the number of seeds which reached final germination and the rate of this germination was much higher (60%) at the higher temperature compared with 40% at 10°C over a 30 day time interval. The germination patterns for the other varieties Julia, Primahill and IBB83 were also examined at 20°C. The results of this series of experiments are shown in Fig 31. The temperature of 20°C has previously been suggested as suitable for modelling the variables in this thesis. This temperature was found suitable in this series of experiments.

The maximum percentage germination of seeds achieved by the varieties was Primahill 95%, IBB83 80%, Julia 55% and Monoirre 60% after 14 days.
Figure 30  The percentage germination of *B. vulgaris* (sugar beet) var. Monoire at 10°C and 20°C.

Legend.
10°C  ●
20°C  ■
Figure 31 The percentage germination of *B. vulgaris* (sugar beet) var Primahill, Monoiire, IBB83 and Julia at 20°C.

Legend:
- Primahill: ○
- Monoiire: △
- IBB83: ▽
- Julia: □
6.1.2 The effects of BHC on *B. vulgaris* germination.

The four varieties of *B. vulgaris* responded differently to pesticide treatment Fig 32-35. Primahill, (Fig 32) the variety which showed the highest percentage germination in untreated seeds, showed a reduced germination in the presence of all the BHC concentrations. However the percentage germinations achieved were still high (79%) at the highest pesticide concentration \(3.5 \times 10^{-2}\) mg ai ml\(^{-1}\). Initial germination figures were however much lower in the presence of all pesticide concentrations. For example after 4 days, at 0 mg ai ml\(^{-1}\) BHC 50% of seeds germinated whilst treated seeds only exhibited 47%, 39% and 32% when BHC was present.

In contrast, varieties Monoiré (Fig 33) and IBB83 (Fig 34) which exhibited poor germination percentages when untreated, did not show reduced germination in response to BHC concentrations. Both the initial and the final germination values in these varieties were similar to the untreated values. Monoiré had initial germination values of 22% in untreated seeds this value was reduced to 14% at the highest concentration of \(3.5 \times 10^{-2}\) mg ai ml\(^{-1}\). The final germination values in the trials with BHC were within 10 percentage points of the final germination without pesticide applications for both of these varieties.

The variety Julia however responded in a different manner to pesticide treatment (Fig 35). This variety in the absence of pesticide, showed poor germination with the final percentage being the lowest of the untreated varieties. The application of all concentrations of pesticide to seeds of variety Julia resulted in not only an increased rate of germination initially but also an increased maximum germination percentage. The final germination percentage for treatments with \(5.34 \times 10^{-7}\) mg ai ml\(^{-1}\) was 72% whilst untreated seeds achieved a germination value of 58%.

These results shown in the percentage germination plots, suggest that in all the varieties studied, germination patterns were affected by
Figure 32  The germination pattern of *B. vulgaris* (sugar beet) var Primahill seeds at 20°C in four BHC pesticide concentrations.
(The means percentage germination of 4x100 seeds are plotted).

Legend.
0 mg ai ml⁻¹. ○
5.34x10⁻⁷ mg ai ml⁻¹. □
2.18x10⁻⁸ mg ai ml⁻¹. ●
3.50x10⁻² mg ai ml⁻¹. ■
variety Primahill

Germination (% of seeds sown)

Days after sowing
Figure 33 The germination pattern of \textit{B. vulgaris} (sugar beet) var Monoire seeds at 20°C in four BHC pesticide concentrations. (The means percentage germination of 4x100 seeds are plotted).

Legend.

- 0 mg ai ml$^{-1}$. ○
- 5.34x10$^{-7}$ mg ai ml$^{-1}$. □
- 2.18x10$^{-6}$ mg ai ml$^{-1}$. ●
- 3.50x10$^{-5}$ mg ai ml$^{-1}$. ■
variety Monoire

Germination (% of seeds sown) vs Days after sowing
Figure 3

The germination pattern of B. vulgaris (sugar beet) var 18833 seeds at 20°C in four BHC pesticide concentrations. (The means percentage germination of 4x100 seeds are plotted).

Legend.

0 mg ai ml\(^{-1}\). ○

5.34x10\(^{-7}\) mg ai ml\(^{-1}\). □

2.18x10\(^{-8}\) mg ai ml\(^{-1}\). ●

3.50x10\(^{-8}\) mg ai ml\(^{-1}\). ■
variety IBB83

Germination (% of seeds sown)

Days after sowing
Figure 35 The germination pattern of *B. vulgaris* (sugar beet) var Julia seeds at 20°C in four BHC pesticide concentrations. (The means percentage germination of 4x100 seeds are plotted).

Legend.
0 mg ai ml\(^{-1}\).  
5.34x10\(^{-7}\) mg ai ml\(^{-1}\).  
2.18x10\(^{-8}\) mg ai ml\(^{-1}\).  
3.50x10\(^{-8}\) mg ai ml\(^{-1}\).
Variety Julia

Germination (% of seeds sown)

Days after sowing

4 5 6 7 8 9 10 11 12 13
the presence of BHC even at the low concentration value of \(5.34 \times 10^{-7}\) mg ai ml\(^{-1}\).

A two way analysis of variance of these responses was carried out and is shown in (Table 11). There was no significant difference in germination between the varieties. There was however a significant pesticide effect at the 0.01 level on the percentage germination of sugar beet seeds after 21 days, in the four varieties used. As a percentage of the untreated seeds, the percentage reduction in germination due to the pesticide was greatest in treatments with \(3.5 \times 10^{-2}\) mg ai ml\(^{-1}\). in the Primahill variety (84%). The percentage reduction in germination for the other varieties due to BHC, were in general lower than this throughout the concentration range used (Table 12).

6.2. The effects of BHC on \textit{B. vulgaris} seedling growth.

Method

The effects of BHC on the growth of seedlings of the four varieties (IBB83, PM45, Julia, Monoire,) were studied. The measurements carried out on seedlings dried to a constant weight were total seedling weight (mg), total seedling length (mm), root weight (mg), shoot weight (mg), root length (mm) shoot length (mm) and the root shoot ratios for measurements of length and weight. Four pesticide concentrations were used; these were, 0 mg ai ml\(^{-1}\), \(5.34 \times 10^{-7}\) mg ai ml\(^{-1}\), \(2.18 \times 10^{-5}\) mg ai ml\(^{-1}\), \(3.5 \times 10^{-2}\) mg ai ml\(^{-1}\). The plants were divided into the root and shoot fractions at the point of root extension.

Results.

The morphological changes produced by BHC on the sugar beet varieties Primahill, Julia and Monoire and IBB83, are shown in Fig 36 and 37. The visual effects are a reduction in the size of the seedlings with
Table 11: The two way analysis of variance of the effects of four pesticide concentrations on the germination in four varieties of *B. vulgaris* (sugar beet) after 13 days.

Varieties used: Primahill, Monoir, IBB83, Julia.

Concentrations used:
- 0 mg ai ml\(^{-1}\)
- 5.34 \times 10^{-7} mg ai ml\(^{-1}\)
- 2.18 \times 10^{-6} mg ai ml\(^{-1}\)
- 3.50 \times 10^{-5} mg ai ml\(^{-1}\).
Analysis of variance for the 4 varieties 4 replicates at 4 pesticide concentrations

<table>
<thead>
<tr>
<th>Source</th>
<th>SOS</th>
<th>DF</th>
<th>Variance</th>
<th>F Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>variety</td>
<td>6318.75</td>
<td>3</td>
<td>2106.25</td>
<td></td>
</tr>
<tr>
<td>Pesticide</td>
<td>378.125</td>
<td>3</td>
<td>126.04</td>
<td></td>
</tr>
<tr>
<td>variety x pesticide</td>
<td>953.125</td>
<td>9</td>
<td>105.90</td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>5050.0</td>
<td>48</td>
<td>105.20</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>12700</td>
<td>53</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Pesticide effect 2106.25 /105.20
Variety effect 126.04 /105.20

There is no significant effect due to varieties at .01 level.
There is a significant effect due to the pesticide at .01 level.
Table 12: The effect of BHC on germination of *B. vulgaris* (sugar beet) varieties. (Measurements expressed as a percentage of germination in the absence of BHC after 15 days.)
<table>
<thead>
<tr>
<th>BHC concentration against al⁻¹</th>
<th>0</th>
<th>5.34x10⁻⁷</th>
<th>2.18x10⁻⁶</th>
<th>3.5x10⁻⁵</th>
</tr>
</thead>
<tbody>
<tr>
<td>percentage germination</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>var monoire</td>
<td>70</td>
<td>55</td>
<td>50</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>55</td>
<td>65</td>
<td>75</td>
<td>55</td>
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<tr>
<td></td>
<td>50</td>
<td>55</td>
<td>55</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>60</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>percentage of untreated replicate (0)</td>
<td>100</td>
<td>95</td>
<td>85</td>
<td>88</td>
</tr>
<tr>
<td>var primahill</td>
<td>90</td>
<td>95</td>
<td>85</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>90</td>
<td>80</td>
<td>85</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>80</td>
<td>70</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>95</td>
<td>70</td>
<td>70</td>
<td>65</td>
</tr>
<tr>
<td>percentage of untreated replicate (0)</td>
<td>100</td>
<td>87</td>
<td>85</td>
<td>84</td>
</tr>
<tr>
<td>var julia</td>
<td>45</td>
<td>75</td>
<td>65</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>75</td>
<td>70</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>80</td>
<td>50</td>
<td>70</td>
</tr>
<tr>
<td></td>
<td>55</td>
<td>60</td>
<td>75</td>
<td>75</td>
</tr>
<tr>
<td>percentage of untreated replicate (0)</td>
<td>100</td>
<td>125</td>
<td>113</td>
<td>110</td>
</tr>
<tr>
<td>var 18889</td>
<td>70</td>
<td>55</td>
<td>80</td>
<td>70</td>
</tr>
<tr>
<td></td>
<td>90</td>
<td>80</td>
<td>75</td>
<td>80</td>
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<td>85</td>
<td>65</td>
<td>75</td>
<td>75</td>
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<tr>
<td></td>
<td>75</td>
<td>85</td>
<td>60</td>
<td>65</td>
</tr>
<tr>
<td>percentage of untreated replicate (0)</td>
<td>100</td>
<td>90</td>
<td>90</td>
<td>90</td>
</tr>
</tbody>
</table>
Increased pesticide concentration and the production of more pigmentation of the root and shoot fractions in all the varieties.

6.2.1 The effects of BHC on individual components of \( B. vulgaris \) seedlings

Total seedling dry weight.

Table 13 shows the effects of BHC on seedling dry weight. The mean total seedling dry weight after 15 days increased from 1.685mg to 1.813mg for plants of variety IBB83 as the pesticide concentration increased, although this was not significant at the .01 level. The other three varieties showed no clear trend and the mean seedling weight values fluctuated in the intermediate concentrations although appearing to decrease with increased pesticide concentration. The amount by which these values decreased however was not significant enough to produce an effect for any of the varieties at the .01 level of significance when the analysis of variance for the pesticide effect on the seedlings was carried out.

Total Seedling length.

Although no significant changes in total plant dry weight were observed following the application of the pesticide, the total plant length (Table 14) showed a clear and consistent pesticide effect significant at the 0.01 level (Table 14). The seedling length was adversely affected by the pesticide. Primahill and Monoire showed the most marked effects with seedlings reduced in length by 4-5 times at the highest concentrations, the lengths being reduced from 112.5mm to 30.52mm for Primahill and from 132.43 to 25.93mm for Monoire. IBB83 however produced smaller seedlings than the other varieties throughout the pesticide range which varied only slightly in the presence of the highest pesticide concentration of 3.5x10^{-2} mg at \( \text{ml}^{-1} \). Lengths were reduced from 57.87 mm in the absence of BHC to 28.22mm. The visual effects of the pesticide concentration range on the growth of the \( B. vulgaris \) seedlings after 14 days are shown in Fig.
Table 13: Mean measurements of the growth (increase in dry weight mg·') of seedlings of four sugar beet varieties after 15 days in a range of BHC concentrations at 20°C (The standard errors are given in brackets).
<table>
<thead>
<tr>
<th></th>
<th>BHC concentration</th>
<th>0.0</th>
<th>5.34x10^-7</th>
<th>2.18x10^-3</th>
<th>3.50x10^-3</th>
<th>AoV.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>at.01</td>
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<td></td>
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<tr>
<td>a) (root + shoot) weight (mg)</td>
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</tr>
<tr>
<td></td>
<td>variety.</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Priahill</td>
<td>1.928 (.37)</td>
<td>1.803 (.06)</td>
<td>1.886 (.05)</td>
<td>1.915 (.06)</td>
<td>nosig</td>
</tr>
<tr>
<td></td>
<td>Julia</td>
<td>2.010 (.06)</td>
<td>1.955 (.06)</td>
<td>2.001 (.05)</td>
<td>1.924 (.08)</td>
<td>nosig</td>
</tr>
<tr>
<td></td>
<td>Monoire</td>
<td>2.086 (.09)</td>
<td>2.020 (.09)</td>
<td>2.065 (.06)</td>
<td>1.967 (.09)</td>
<td>nosig</td>
</tr>
<tr>
<td></td>
<td>IBB83</td>
<td>1.665 (.17)</td>
<td>1.846 (.06)</td>
<td>1.807 (.06)</td>
<td>1.813 (.05)</td>
<td>nosig</td>
</tr>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) root weight (mg)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Priahill</td>
<td>0.706 (.02)</td>
<td>0.385 (.02)</td>
<td>0.365 (.01)</td>
<td>0.356 (.01)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>Julia</td>
<td>0.688 (.02)</td>
<td>0.405 (.01)</td>
<td>0.343 (.01)</td>
<td>0.325 (.01)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>Monoire</td>
<td>0.724 (.03)</td>
<td>0.405 (.02)</td>
<td>0.372 (.02)</td>
<td>0.289 (.01)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>IBB83</td>
<td>0.483 (.06)</td>
<td>0.341 (.01)</td>
<td>0.320 (.01)</td>
<td>0.312 (.02)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>c) shoot weight (mg)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Priahill</td>
<td>1.221 (.05)</td>
<td>1.414 (.05)</td>
<td>1.521 (.04)</td>
<td>1.558 (.06)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>Julia</td>
<td>1.342 (.05)</td>
<td>1.549 (.05)</td>
<td>1.637 (.05)</td>
<td>1.598 (.06)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>Monoire</td>
<td>1.361 (.07)</td>
<td>1.621 (.07)</td>
<td>1.693 (.05)</td>
<td>1.677 (.07)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>IBB83</td>
<td>1.182 (.06)</td>
<td>1.304 (.036)</td>
<td>1.487 (.01)</td>
<td>1.497 (.02)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>d) root/shoot ratio (weight)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Priahill</td>
<td>0.605 (.03)</td>
<td>0.275 (.01)</td>
<td>0.242 (.01)</td>
<td>0.275 (.04)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>Julia</td>
<td>0.531 (.04)</td>
<td>0.264 (.01)</td>
<td>0.209 (.007)</td>
<td>0.213 (.01)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>Monoire</td>
<td>0.543 (.02)</td>
<td>0.249 (.001)</td>
<td>0.229 (.01)</td>
<td>0.174 (.006)</td>
<td>sig</td>
</tr>
<tr>
<td></td>
<td>IBB83</td>
<td>0.408 (.05)</td>
<td>0.263 (.01)</td>
<td>0.215 (.008)</td>
<td>0.212 (.01)</td>
<td>sig</td>
</tr>
</tbody>
</table>
Table 14: Mean measurements of growth (increase in length mm⁻¹) of seedlings of four sugar beet varieties after 15 days in a range of BHC concentrations at 20°C. (The standard errors are given in brackets).
<table>
<thead>
<tr>
<th>BMC concentration (mg ai ml⁻¹)</th>
<th>0.0</th>
<th>5.34x10⁻⁷</th>
<th>2.18x10⁻⁸</th>
<th>3.50x10⁻¹</th>
<th>ANOVA at 0.01</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) (root + shoot) length (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>variety</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PrimaHill</td>
<td>112.52 (4.3)</td>
<td>50.43 (1.2)</td>
<td>34.36 (1.2)</td>
<td>30.55 (0.9)</td>
<td>sig</td>
</tr>
<tr>
<td>Julia</td>
<td>95.63 (5.7)</td>
<td>49.22 (1.5)</td>
<td>35.22 (1.4)</td>
<td>29.54 (1.0)</td>
<td>sig</td>
</tr>
<tr>
<td>Monioire</td>
<td>132.43 (6.6)</td>
<td>48.70 (1.8)</td>
<td>32.00 (1.1)</td>
<td>25.93 (0.9)</td>
<td>sig</td>
</tr>
<tr>
<td>IPP83</td>
<td>57.87 (7.7)</td>
<td>40.82 (1.0)</td>
<td>32.48 (1.0)</td>
<td>28.29 (0.8)</td>
<td>sig</td>
</tr>
<tr>
<td>b) root length (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PrimaHill</td>
<td>66.39 (4.6)</td>
<td>12.14 (0.7)</td>
<td>7.38 (0.2)</td>
<td>8.45 (0.4)</td>
<td>sig</td>
</tr>
<tr>
<td>Julia</td>
<td>50.11 (5.1)</td>
<td>10.91 (0.9)</td>
<td>8.30 (0.4)</td>
<td>7.85 (0.3)</td>
<td>sig</td>
</tr>
<tr>
<td>Monioire</td>
<td>85.71 (6.6)</td>
<td>9.07 (0.5)</td>
<td>7.11 (0.2)</td>
<td>6.13 (0.3)</td>
<td>sig</td>
</tr>
<tr>
<td>IPP83</td>
<td>20.00 (3.3)</td>
<td>8.25 (0.4)</td>
<td>7.80 (0.3)</td>
<td>6.68 (0.2)</td>
<td>sig</td>
</tr>
<tr>
<td>c) shoot length (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PrimaHill</td>
<td>45.12 (2.3)</td>
<td>38.28 (1.1)</td>
<td>26.97 (1.1)</td>
<td>22.09 (0.6)</td>
<td>sig</td>
</tr>
<tr>
<td>Julia</td>
<td>45.51 (2.4)</td>
<td>38.34 (1.1)</td>
<td>26.71 (1.1)</td>
<td>21.69 (0.8)</td>
<td>sig</td>
</tr>
<tr>
<td>Monioire</td>
<td>45.71 (2.8)</td>
<td>39.60 (1.5)</td>
<td>24.88 (1.0)</td>
<td>19.80 (0.6)</td>
<td>sig</td>
</tr>
<tr>
<td>IPP83</td>
<td>37.37 (0.8)</td>
<td>32.58 (0.8)</td>
<td>24.68 (0.8)</td>
<td>21.60 (0.6)</td>
<td>sig</td>
</tr>
<tr>
<td>c) root/shoot ratio (length)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PrimaHill</td>
<td>1.765 (0.2)</td>
<td>0.329 (.02)</td>
<td>0.288 (.01)</td>
<td>0.387 (.01)</td>
<td>sig</td>
</tr>
<tr>
<td>Julia</td>
<td>1.766 (0.1)</td>
<td>0.291 (.02)</td>
<td>0.282 (.02)</td>
<td>0.230 (.01)</td>
<td>sig</td>
</tr>
<tr>
<td>Monioire</td>
<td>1.943 (0.1)</td>
<td>0.233 (.01)</td>
<td>0.299 (.01)</td>
<td>0.308 (.01)</td>
<td>sig</td>
</tr>
<tr>
<td>IPP83</td>
<td>0.535 (.06)</td>
<td>0.255 (.01)</td>
<td>0.319 (.01)</td>
<td>0.315 (.01)</td>
<td>sig</td>
</tr>
</tbody>
</table>
36-37. All varieties with no pesticide applied exhibited normal growth. The seedling roots were longer and tapered, an adaptation which would enable seedlings to exploit the uptake of nutrients in the soil. In IBB83 however, the seedlings were longer than in the pesticide treated replicates but the root lengths were much smaller. There was however a reduction in the lengths, stunted growth and the absence of a tapering of the roots even at the lowest concentration of $5.34 \times 10^{-7}$ mg ai ml$^{-1}$.

6.2.2. The effects of BHC on *B. vulgaris* seedling roots.

Dry weight.

The mean dry weight of the roots of the *B. vulgaris* seedlings was reduced with increasing pesticide concentration. The effects are shown in Table 13. These results indicate that the decrease in weight is related to the pesticide concentration used. All four varieties showed significant reductions in the dry weight. The largest reductions in dry weight were exhibited by plants of the variety Monoirle which at 0 BHC concentration had a mean weight of 0.724mg. This was reduced to 0.289mg at the highest concentration ($3.5 \times 10^{-2}$mg ai ml$^{-1}$). IBB83 had a smaller mean root weight at 0 BHC than the other varieties. A value of 0.483mg was recorded which was only slightly reduced even by the highest pesticide concentration to 0.312mg. The analysis of variance of the results shown in Table 13 shows a significant pesticide effect at the .01 level for all the varieties and a sensitivity to the pesticide even at the lowest concentration of $5.34 \times 10^{-7}$ mg ai ml$^{-1}$.

Length

In all varieties there was a marked reduction in the length of the root fractions measured at the pesticide concentrations used (Table 14). In addition as Fig 36 and 37 show, the roots of treated seedlings became compressed and bulbous in appearance. There also appeared to be a concentration of pigmentation with the roots.
Figure 36: The effects of Benzene hexachloride on growth of *B. vulgaris* (sugar beet) var Julia and var Primahill after 21 days.

Legend

\[ a = 3.50 \times 10^{-2} \text{ mg ai ml}^{-1} \]
\[ b = 2.18 \times 10^{-5} \text{ mg ai ml}^{-1} \]
\[ c = 5.34 \times 10^{-7} \text{ mg ai ml}^{-1} \]
\[ d = 0 \text{ mg ai ml}^{-1} \]
Figure 37: The effects of Benzene hexachloride on growth of *B. vulgaris* (sugar beet) var Monoire and var IBB83 after 21 days.

Legend

a = $3.50 \times 10^{-2}$ mg ai ml$^{-1}$

b = $2.18 \times 10^{-5}$ mg ai ml$^{-1}$

c = $5.34 \times 10^{-7}$ mg ai ml$^{-1}$

d = 0 mg ai ml$^{-1}$
var Monoire

\begin{tabular}{cccc}
a & b & c & d \\
\end{tabular}

var IBB83

\begin{tabular}{cccc}
a & b & c & d \\
\end{tabular}
becoming dark red in colour.

Monoïre showed the largest pesticide induced change in length with the mean root length reduced from a value of 85.71mm without pesticide to 6.13mm at the highest concentration. The effect was also marked in Primahill and Julia. IBB83 showed the same trend but to a smaller extent with the reduction being from an initially low value of 20mm to 6.68mm at 3.5x10⁻²mg ai ml⁻¹. All the concentration effects were found to be significant at the 0.01 level of the analysis of variance. This highlights the sensitivity of the roots to the range of pesticide concentrations used.

6.2.3. The effects of BHC on B. vulgaris seedling shoots.

Dry weight.

The mean shoot dry weights, unlike those for the roots increased with increased pesticide concentration for all four varieties. IBB83 increased from a mean of 1.182mg to 1.497mg at the highest pesticide concentration (Table 13). Julia, Primahill and Monoïre also showed an average increase of 0.3mg at the highest concentration. The results for the pesticide effect on the shoot dry weight were found to be significant for all the varieties of sugar beet used. Visually the shoots appeared to increase in width and pigmentation with pesticide treatment.

Length.

Even though increases in shoot dry weight were observed, at the pesticide concentrations of 5.34x10⁻² mg ai ml⁻¹, 2.18x10⁻² mg ai ml⁻¹ and 3.5x10⁻² mg ai ml⁻¹, the length of the shoot fraction decreased with increased pesticide concentrations (Table 14). This reduction in length was apparent for all the varieties but was more visible in the Monoïre variety where lengths were reduced from a mean of 46.712mm to 19.80mm at the highest concentration. Effects were observed also at the lowest pesticide concentrations of
5.34x10^{-7} mg al ml^{-1}. All the shoot length differences due to the pesticide were significant at the 0.01 level.

6.2.4 The effects of BHC on *B. vulgaris* root/shoot ratios.

The root/shoot ratios in a growing plant can be used to indicate the efficiency with which a plant is utilising the available resources in its development.

The pesticide effect on the root/shoot ratios calculated using the root and shoot measurements for individual seedlings lengths was found to be significant at the 0.01 level when the analysis of variance was carried out for all the varieties studied (Table 14). The values for this ratio however decreased with increased pesticide concentration. The value for this ratio changed under different pesticide concentrations. This unexpected decline in the ratio indicates that the effect of the pesticide on the root was less than that for the shoot (the divisor for calculating the ratio).

The contribution of the root fraction to the root/shoot ratio is therefore the overriding criterion for determining this ratio value. The root/shoot ratios for dry weight also decreased with increased pesticide concentration. These decreases were shown to be significant at the 0.01 level.

The dry weight of the shoots however showed increases whilst the dry weight of the roots decreased with increasing pesticide concentration (Table 13). The rate of decrease in the root weight was not sufficient to offset the increase in the shoot dry weight to maintain the ratio and there was therefore a decline in the ratios. The ratio for the Monoire variety decreased from .543 to .174, Julla from .53 to .213, Primahill from .605 to .275, and IB883 from .408 to .212. (0 to 3.5x10^{-2}mg al ml^{-1}). The decrease in the ratios for measurements of length were also significant, Monoire decreased by the largest value from 1.943 to .308 and IB883 had the smallest decrease .535 to .315. There was a large difference in the ratios when varieties without pesticide added were compared. This difference would suggest a limitation to the use of this parameter on an intervarietal basis.
General Discussion.

The National Institute of Agricultural Botany recommends varieties of *B. vulgaris* seeds every year to farmers for planting. Several trials are carried out on the seeds and seedlings to approved minimum standards of germination and seedling growth. The germination standard for the seeds has increased from 73%, 20 years ago to 90% in 1987. Kimber and McCullan (1987). 16 varieties were recommended in 1987 which showed superior % establishment, relative yield, (roots, sugar, growers income) quality (sugar content, % impurities), bolters (normal late sowing), size of plant tops and resistance to downy mildew and powdery mildew.

Of the varieties used in this thesis, Monoire is the oldest and was first approved for planting in 1979. Julia was introduced in 1984 and Primahill in 1984. IBB83 was a new variety provided by Brooms Barn Experimental Station.

Germination.

The results for the final percentage germination in this study both at 10°C and 20°C for var Monoire (45% and 50%) and 20°C for the varieties Monoire 60%, Primahill 95%, IBB83, 80% Julia 55% showed good germination under the test conditions. Gummerson and Jaggard, (1985) found the weekly mean soil temperatures at 5cm soil depths could range from 5°C to 20°C for 1982 (March to May). Temperatures were reduced however in 1983 and 1984 having a maximum value of 15°C. The fluctuation of the soil temperature at the sowing depth was found to be similar to the air temperature fluctuations which occur. Comparisons of the percentage germination plots at 20°C, 15°C, 10°C and 5°C, by these authors produced a sigmoid germination pattern which were similar to the results obtained here. There was also more rapid and greater germination at the higher temperature studied. The percentage germination at 20°C of seeds in the absence of BHC fell within the range of 53-93%. This is greater than the 88-92 percentage
accepted by the seed testing association (Kimber and McCullugh 1987). However Kimber and McCullugh's 1987 results refer to tests which used hundreds of seeds whereas this study used replicates of 4x100 seeds. In addition this range covered the germination in 4 different varieties. When each variety was examined individually, the variety Primahill exhibited germination in the range of 60-95% which is closer to the acceptable values. All the other varieties exhibited lower germination with the variety Julia showing the least successful germination despite being one of the varieties recommended by the NIAE for the 1983 season. This varietal difference was significant at the 0.01 level following analysis of variance.

Environmental influences on germination.

The conditions under which germination of B. vulgaris is carried out can influence the percentage of seeds which germinate and the pattern of this germination. Temperature has an effect as is illustrated in Fig 30. There is also an effect created by the osmotic potential of the solution in which the trials are carried out. Durrant and Payne (1983 a b), using solutions with sodium chloride found that a 12 bar osmotic potential was the preferred solution for germination corresponding closely to field conditions. The use of a sodium chloride solution to assess germination was not used in this study because of the adverse effects this could have on the addition of pesticides and the inability therefore to measure the true pesticide effect. The 4 way analysis of variance of seed germination showed however that there was no significant difference in the germination of the varieties of Primahill, Monoirre, Julia and 18883 at the 0.01 level.

The percentage establishment of seedlings of Monoirre and Julia from field studies were listed as 70% and 74% for the 1988 season. The high germination values obtained by Monoirre 93% would predict this but the poor germination of Julia 55% would suggest that the establishment of this variety might be less than 74%. The difference in the osmotic potential at germination in these laboratory trials could account for this low value. Several other conditions such as available sunlight,
pests, (Brown 1980), Gummerrson and Jaggard (1985) and, as this study demonstrates, low pesticide concentrations, all may affect the germination and establishment of sugar beet seedlings.

Effects of BHC on germination.

There was a significant (P< 0.01) effect attributed to the presence of BHC in germination test solutions. This indicated clearly that BHC applied as a pesticide may affect the crop of sugar beet also. The effect of BHC was to reduce the percentage of seeds germinating in the pesticide solutions, except in the Julia variety where these effects were reversed. The implications of these significant pesticide effects suggest that in the field germination in the presence of BHC residues may affect the nature of germination by increasing the time for it to occur and the percentage achieved. The pattern of sigmoid germination however stayed the same under pesticide concentrations of 5.34x10^-6 mg ai ml^-1, 2.18x10^-5 mg ai ml^-1, and 3.5x10^-2 mg ai ml^-1. This spread has implications for planting out seeds in the field. A reduction in the numbers of seeds which germinate can be produced if the environment has residues of BHC.

Seedling growth.

It is also important to consider whether the pesticide treatments also have an effect on the germinated seed and seedling growth. This is important because it is at this stage that the crop of B. vulgaris can be susceptible to attack by the soil pest complex as the seedling grows through the soil layers before emergence. There is little in the literature on the effects of a pesticide on the growth of seedlings. Much of the work has centred on the effects of herbicides on non target species and on weeds. The volume by Audus (1979) gives a synopsis of the effects that occur with the application of biocides on plants. However this study has shown that a pesticide like BHC can affect the germination and the growth of sugar beet seedlings when present in low doses, 5.34x10^-6 mg ai ml^-1, 2.18x10^-5 mg ai ml^-1 and 3.5x10^-2 mg ai ml^-1.
The results presented here show that at the concentrations used there is a significant effect on the growth of the seedlings. The application of pesticide of the concentrations used above in the field will affect the development of pest populations and crop in a complex manner. Chapter 3 and 5 have shown that the pest has LC50 values of 2.5 - 5.4 x 10^{-4} mg al ml^{-1} at 20°C. In addition recorded sublethal effects on T. krausbaueri populations at concentrations of 3.37 x 10^{-6} mg ml^{-1} at 20°C were also obtained. These pesticide concentrations also affect seeds and seedlings in the early stages of germination and growth.

Of the parameters measured in this study the root and shoot length reductions showed consistently the pesticide effect. The overall weight of the plant was not affected by the pesticide significantly but the root weight increased whilst the shoot weight decreased. This suggests that there is a more marked effect on the root and a corresponding stimulation of the growth processes in the shoot fraction as a response to this. The reduction in the root /shoot ratios with an increased pesticide concentration would tend to support this contention. Pesticide effects on seedling growth are therefore characterised by a significant reduction in the root weight, a significant increase in the shoot weight, a significant decrease in the total seedling length, a significant decrease in root length and a significant decrease in shoot length. These changes caused by the pesticide BHC could therefore significantly affect sugar beet establishment.
7. Developmental stage population models for *T. krausbaueri*.

Introduction.

The growth of isolated, single species cultured populations of *T. krausbaueri* has been recorded in Chapter 5 in the form of population growth models which relied entirely on total insect number counts. The population growth conformed to the Lotka (1925) equation for geometric growth of insect populations. Estimates of the innate capacity for increase of the populations studied (R<sub>m</sub>), and the doubling time of different population cultures were also made. Differences were observed in the R<sub>m</sub> values due to culture temperature, culture diet and the pesticide BHC. The toxicity of BHC to *T. krausbaueri* examined in the same chapter showed that there was a significant sublethal pesticide effect on population development. In addition, examinations of values for 24 hour LC<sub>50</sub> toxicity tests suggest that there was selective toxicity to insects. This selective toxicity depended on the developmental stage the insect was in measured by the size class when the pesticide was applied. Size class 2 which included the reproductive developmental stage, was shown to be the most resistant.

The type of first order model presented in Chapter 5, although essential for population growth estimates, does not adequately emphasise the importance of the different developmental stages in the overall population growth. Total insect number counts and not counts of the number of insects in each developmental stage were used. A knowledge of which developmental stages are present is important when considering sugar beet, pest, and BHC interactions. It has been shown that the effects of grazing of *T. krausbaueri* on sugar beet can be severe enough to kill seedlings. (Chapter 3), and that insect pest damage to seedlings can be reduced by pesticide application. However the selective toxicity of the pesticide in both the short and long term can vary, depending on the population structure at the time of pesticide application. The short term effects vary because of the selective toxicity levels, whereas the long term effects vary because
the reproductive stages are more resistant to pesticide doses than the other insect stages and reproduction can occur. Unless knockdown and field toxicity tests take into account the selective toxicity and its temporal nature on the developmental stages of population development, a prediction of the efficacy of the pesticide can be difficult.

In this chapter mathematical models of populations of *T. krausbaueri* are presented. These models are constructed from results obtained from population cultures of *T. krausbaueri*. They are a further development of the models presented in chapter 5 and they also take into account the developmental stage structure of the populations as measured by the 4 size classes chosen.

7.1. Mathematical models of environmental systems.

Mathematical models of varying complexities can be used to measure insect population growth. The complexity of the model will usually reflect on its applicability but if the model is too complex it can be far removed from reality and nature. A useful model however is one which is able to simulate and predict population growth. Such a model applied to a pest allows some decisions to be made as to whether further pesticide applications are necessary to control the growth of the pest.

Several authors have produced population models for insects which are either empirical or theoretical. Reviews by O'Niell and Styron (1970), Mann (1971), Chaterjee (1973), Wiegert (1975), Ruesink (1976) and Mills (1981), present several models with specific uses. Although there are many models available, Ruesink (1976) states that the form of the model should be determined by the purpose for which it is needed.

Wiegert (1975) in his review on model taxonomy distinguishes theoretical models which provide some insight into how the biological system works, from empirical models which reproduce the behaviour of the system. The biology of the *T. krausbaueri* is now well understood (chapter 3), the empirical models developed here can also
be used for simulation and prediction. Models were therefore produced in this chapter to provide an insight into insect size class (developmental stage) relationships within populations, and to predict and simulate changes within populations caused by biotic and abiotic changes.

7.1.1 Modelling Theory.

The first population models which incorporated a developmental stage term were those by Bernadelli (1941) and Leslie (1942). These utilised developmental stage specific survival rates and fecundities to produce the model. Further development of these models by Leslie (1945, 1948) used a probabilistic element to form a Matrix model of population growth based on the relationship $N_{t+1} = M N_t$.

where $N$ = number of insects in time $t$ and $t+1$, and $M$ is a matrix used to represent the changes within the developmental stages with time.

In a further refinement of this procedure, Longstaff (1974, 1976, 1977) monitored competition within Collembola populations, in laboratory culture. These matrix models allowed Longstaff (1974, 1976, 1977) to predict population development based on a change in the size of the insect.

Producing a Leslie Matrix developmental stage population growth model which has a predictive ability involves a number of steps;

1 Production of a deterministic model which represents and simulates how the population develops in culture.

2 Production of a stochastic model based on the deterministic model which uses the probabilities of the specific relationships between the developmental stages of insects in culture to determine developmental stage population growth.

3 Combination of the stochastic terms in the stochastic models to produce a treatment model based on mean probabilities obtained for replicate treatment cultures.
4 Using data from cultures, insect size class (developmental stage) insect numbers, fecundity, $R^m$ and $R$ values, LC$_{50}$ values, to produce a model which incorporates predictability.

5 Testing and simulating the models in 1, 2, 3, and 4 using a spreadsheet to produce models which are specific. The use of a computer program which allows the production of a spreadsheet can be used so that the change in the number of insects in each size class (developmental stage can be observed).

7.2 Development of a deterministic Leslie Matrix model for $T. krausbauerI$.

The four size classes (1-4) for $T. krausbauerI$ were used. These developmental stages are based on the length of the insect (Chapter 3) conform to Dyars rule and can be used to monitor insect growth. The use of insect size classes to model populations in ametabolous insects is the only way insect growth in populations of such species may be readily observed and studied.

Insects which do not show clear morphological differences in the growth stages of - larvae - pupae - adult, are difficult to monitor since morphological changes which would distinguish cohorts of insects of different developmental stages are not as pronounced. However changes in the insects' length can be used to monitor growth and observe these changes. In addition changes in insect length also reflect changes in insect biomass.

Developmental growth of ametabolous insects can therefore be represented by an infinite number of length measurements throughout the life of each insect. However this approach is not a practical one. Instead insects can be grouped into developmental stage classes which are correlated with the length of the insect. This will allow conclusions about population development to be drawn from the population structure as well as the population numbers.
7.2.1. Selection of a census time interval.

The relative frequencies of the numbers of insects in each developmental stage (1-4) were recorded in selected time intervals. These time intervals were such that the only transitions possible were for an insect in each stage to either move up to the next stage or remain in the same stage. Also the time interval was such that insects did not remain in stage 1 during the time interval. Longstaff (1977) used such a method for O. armatus and H. denticulata where the time intervals selected were small in comparison to the life cycle of individual insects. An interval of 10 days was used and this has been shown to be adequate for T. krausbaueri at 20°C in Chapter 3. The probability of an insect either remaining in one of the 4 developmental stages or moving up into the next developmental stage can therefore be estimated for each time interval and this forms the basis of the model.

7.2.2. Modeling insect population developmental stages.

Juveniles. (size class 1 insects less than 250μm)

A schedule of hatching will relate to the production of juveniles in the population and these numbers can be estimated from censusing. In culture there is no emigration or immigration and therefore the juveniles will either move up to the next developmental stage or die. The probabilities of insects moving up in each stage will form the basis for the development of the models. This stage specific survivorship can be estimated from probabilities of numbers of insects in culture. (Begon and Mortimer 1986)
Therefore where \( t \) = time interval and \( t+1 \) = next time interval, and \( n \) = number of insects and the subscript for \( n \) refers to the developmental stage and \( F \) = population fecundity

\[ n_{t+1} = F_t. \]

Reproductive insects (size class 2 [250-350µm] & 3 [350-450µm])

The numbers of insects in these stages and their development in subsequent time intervals are based on the following:

1. The probability that insects will enter a developmental stage from the previous developmental stage during the time interval used.

2. The probability that insects will remain in the same developmental stage during the time interval.

3. The probability that the insects will die.

The sum of these probabilities will give the overall probability for the insects in each developmental stage.

Therefore where \( a \) = probabilities, and the subscript refers to the developmental stage, \( t \) = time and \( n \) = insect numbers.

\[ n_{2, t+1} = n_{1, a_{1,2}} + n_{2, a_{2,2}}. \]

\[ n_{3, t+1} = n_{2, a_{2,3}} + n_{3, a_{3,3}}. \]

These two size classes (2 and 3) are responsible for the fecundity term referred to above in the discussion of the juvenile stage and are discussed in greater detail in Chapter 7.3.3.

Post reproductive insects. (Size class 4 insects greater than 450µm)
The contribution of insects to this developmental stage will be based on the probabilities of movement from size class 3 and the number of insects remaining in size class 4 in prior time interval.

\[ n_{4, t+1} = n_{3, t+3, 4} + n_{4, t+4, 4} \]

7.2.3 Modelling Population Fecundity.

A fecundity term is needed in the model to predict the numbers of juvenile insects which will enter the population at each time interval.

Fecundity can be recorded in several ways.

\[ f_1 = \text{total number of young produced} / \text{number of adults initiating cultures} \]

\[ f_2 = \text{total number of young produced} / \text{number of days to produce young} \]

\[ f_3 = \text{total number of young produced} / \text{number of adult days. (Usher and Stoneman 1977)} \]

\[ F = \text{total number of young produced in time period} / \text{number of reproductive adults in culture in previous time period (Longstaff 1977)} \]

Reliable estimates of the fecundity of an insect can only be made with knowledge of the prior history of the insect. Laboratory cultures which clearly identify the insects' history are able to do this. In agglomerative cultures where juvenile insects are not removed and generations are not distinct, measuring fecundity must be specific. Alternative measurements of fecundity (Usher and Hilder 1975), have involved cultures where insects were removed from the culture. However by not removing eggs or juveniles from cultures a closer approximation
to reality is achieved and these estimates are then able to measure the culminative effect of the insects breeding through successive time intervals.

The effects of diet and temperature on fecundity have been outlined in Chapter 3 and 5.

By estimating the numbers of juveniles which hatch from the eggs laid and not the number of eggs produced, the true fecundity and not just the reproductive potential of the insects can be obtained.

The measure of fecundity, $F$ was therefore selected for use in the model. This represents the number of juveniles produced divided by the number of insects in the reproductive developmental stages, size class 2 and 3 responsible for their production.

This can be represented by the following equation.

$$F = \frac{n_{1,t+1}}{(n_{3,t} + n_{2,t})}$$

7.2.4 Deterministic Modelling steps.

A series of algebraic difference equations can therefore be constructed for the insects in each developmental stage to show how insect numbers change in different culture conditions. These equations are linear recurrence equations and are estimated from the relationships already established in equation 0, 0, 0 and 0.

The equations describe all the transitions possible for each insect within the time interval used and can be summarised in general for any number of size classes (developmental stages) by the following equation. (Longstaff 1974).

$$n_{i,t+1} = n_{i,t} a_{i,i} + n_{i-1,i} a_{i-1,i} + \ldots + n_{i-m,i} a_{i-m,i}$$

This describes the population growth where $n_{i,t}$ is the number in size class $i$ at time $t$.

$a_{i,j}$ is the probability of the transitions of an individual from size class $i$ to class $j$. 

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For the *T. k Krausbauerr* populations which were divided into 4 developmental stages the appropriate equations are therefore:

\[ n_{1,t+1} = a_{1,1} n_{1,t} + a_{1,1} n_{1,t} \]
\[ n_{2,t+1} = a_{2,2} n_{2,t} + a_{1,2} n_{1,t} \]
\[ n_{3,t+1} = a_{3,3} n_{3,t} + a_{2,3} n_{2,t} \]
\[ n_{4,t+1} = a_{4,4} n_{4,t} + a_{3,4} n_{3,t} \]

and from 0 and 5

\[ n_{1,t+1} = F x (n_{3,t} + n_{2,t}) \]

The population growth estimated from the population growth models in chapter 3 conformed to the equation

\[ N_{t+1} = M N_t \]

where \( N \) is the total number of insects in the population and \( t \) and \( t+1 \) are time periods.

In this form \( M \) is a Leslie transition matrix which is used to represent the equations 0, 0, 5, 5. This matrix can be used to represent the equation above.

Therefore,

\[ n_{1,t+1} = F x (n_{3,t} + n_{2,t}) \]
\[ n_{2,t+1} = a_{2,2} n_{2,t} + a_{1,2} n_{1,t} \]
\[ n_{3,t+1} = a_{3,3} n_{3,t} + a_{2,3} n_{2,t} \]
\[ n_{4,t+1} = a_{4,4} n_{4,t} + a_{3,4} n_{3,t} \]

can be represented by

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\[ N_{t+1} = M \times N_t \]

\[
\begin{bmatrix}
    n_1 \\
    n_2 \\
    n_3 \\
    n_4 \\
\end{bmatrix}_{t+1} =
\begin{bmatrix}
    0 & F & F & 0 \\
    a_{1,2} & a_{2,2} & 0 & 0 \\
    0 & a_{2,3} & a_{3,3} & 0 \\
    0 & 0 & a_{3,4} & a_{4,4} \\
\end{bmatrix} 
\begin{bmatrix}
    n_1 \\
    n_2 \\
    n_3 \\
    n_4 \\
\end{bmatrix}_t
\]

Therefore using Matrix algebra,

\[
\begin{bmatrix}
    n_1 \\
    n_2 \\
    n_3 \\
    n_4 \\
\end{bmatrix}_{t+1} =
\begin{bmatrix}
    0 \times n_1 + F \times n_2 + F \times n_3 + 0 \times n_4 \\
    a_{1,2} \times n_1 + a_{2,2} \times n_2 + 0 \times n_3 + 0 \times n_4 \\
    0 \times n_1 + a_{2,3} \times n_2 + a_{3,3} \times n_3 + 0 \times n_4 \\
    0 \times n_1 + 0 \times n_2 + a_{3,4} \times n_3 + a_{4,4} \times n_4 \\
\end{bmatrix}_t
\]

In this form the Matrix M records the terms needed for estimating the numbers of insects in each developmental stage and shows how these numbers change at t+1 depending on the numbers of each stage which are present at time t. The probabilities of these transitions can be estimated from the probabilities shown in the matrix for the size classes, developmental stages 2, 3 and 4. The fecundity term F is used to determine the numbers in stage 1. This model thus constructed is therefore a deterministic one which shows how the population develops in culture.
7.3. Experimental Culture Methods.

The insects were cultured using the methods outlined in Chapter 4 for the preparation of culture vessels and feeding and censusing regimes. Each population developmental stage was censused at the time interval specified. Four culture sets were used for this study of population growth using each of the following treatments and allowed:

1. An examination of the insect Matrix growth models,

2. An examination of the effects of diets of yeast and sugar beet on the population development,

3. An analysis of the effects of the pesticide BHC in the culture diet on the population development,

4. An analysis of the effects of pesticide BHC substrate on the population development.

Table 15 shows the experimental design.

7.4. Production of a stochastic model using censused values from cultures.

The populations were censused at 10 day time intervals. Stochastic terms for the probabilities of the transitions were estimated from censused data. Regression lines were produced for each of the replicates used. A multiple regression of the numbers in each stage at the next time interval \( n_{i,t+1} \) against the numbers in the prior time interval of the same stage \( n_{i-1,t} \) and the numbers in prior time interval of the stage before \( n_{i-2,t} \) were made for each treatment. The numbers of \( n_{i,t+1} \) regressed against \( n_{i-1,t} \) \( n_{i-2,t} \) obtained from the cultures therefore produced the deterministic stochastic terms for each developmental stage which was used for the probability terms in equation \( \Phi, \Theta, \Theta \). For example by regressing \( n_{i,t+1} \) against \( n_{i-2,t} \), the terms for transitions on \( a_{2,2} \) can be obtained and a regression of \( n_{i,t+1} \) against \( n_{i,t} \) produces values for
Table 15: The experimental design for population cultures of T. krausbaueri cultured at 20°C on diets of B. vulgaris (sugar beet) varieties and S. cerevisiae (yeast) used for the production of matrix models.
Table 16: The multiple regression equation for the developmental stage matrix model of *T. krausbaueri* cultured at 20°C on a diet of *B. vulgaris* var. Monoire using different pesticide BHC concentrations applied to the diet.

Legend

Batch title X

Regressions are for

\[ n_{t-1,1}, n_{t-1,2}, \ldots, n_{t-1,n} \]

and

\[ n_{t,n-1}, n_{t,n-2}, \ldots, n_{t,1} \]

\( n = \) the number of insects at time \( t \)

The subscript of \( n \) denotes the developmental stage.

1 = juveniles less than 250μm
2 = reproductive 250-350μm
3 = reproductive 350-450μm
4 = post reproductives more than 450μm
<table>
<thead>
<tr>
<th>Diet</th>
<th>BHC concentration</th>
<th>Replicate number</th>
<th>Batch Title</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saccharomyces</td>
<td>mg ai ml⁻¹</td>
<td></td>
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<tr>
<td><em>ceriviseae</em></td>
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<tr>
<td>0</td>
<td>3</td>
<td>V0</td>
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<tr>
<td>5.3x10⁻⁷</td>
<td>3</td>
<td>V21</td>
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</tr>
<tr>
<td>8.75x10⁻³</td>
<td>3</td>
<td>V7</td>
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<tr>
<td>Beta vulgaris</td>
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<td>3</td>
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<tr>
<td>5.3x10⁻⁷</td>
<td>3</td>
<td>X21</td>
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</tr>
<tr>
<td>2.18x10⁻³</td>
<td>3</td>
<td>X9</td>
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</tr>
<tr>
<td>3.5x10⁻²</td>
<td>3</td>
<td>X5</td>
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<tr>
<td>var monoire</td>
<td>pesticide in</td>
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<td>substrate</td>
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<td>0</td>
<td>3</td>
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<td>8.75x10⁻³</td>
<td>3</td>
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<td>3.7x10⁻²</td>
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<td>var primahill</td>
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<td>C21</td>
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<td>2.18x10⁻³</td>
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<td>3.5x10⁻²</td>
<td>3</td>
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<td></td>
</tr>
</tbody>
</table>
BHC concentration

ag ai et al.1

<table>
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<tr>
<th>Concentration</th>
<th>Replicate 1</th>
<th>Replicate 2</th>
<th>Replicate 3</th>
<th>Replicate 4</th>
</tr>
</thead>
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<td>314n_4+0.065n_2:</td>
<td>491n_4+2.64n_2:</td>
<td>971n_4+241n_2:</td>
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</tr>
<tr>
<td>2.39x10^-7</td>
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</tr>
<tr>
<td>2.1x10^-3</td>
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<tr>
<td>3.50x10^-3</td>
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</tbody>
</table>
Table 17: The multiple regression equations for the developmental stage matrix model of *T. krausbaueri* cultured at 20°C on a diet of *B. vulgaris* (sugar beet) var Monoire using different concentrations of BHC applied to the substrate.

Legend

Batch title R

Regressions are for 

\[ n_{i},t \] against \( (n_{i-1},t) \)

and \( (n_{i},t) \)

\( n = \) the number of insects at time \( t \)

The subscript of \( n \) denotes the developmental stage.

1 = juveniles less than 250μm
2 = reproductive 250-350μm
3 = reproductive 350-450μm
4 = post reproductives more than 450μm
BHC concentration
ng ai al\textsuperscript{-1}.

0

\begin{align*}
R_{n+1} &= 0.021n_{n+1} + 1.09n_{n+2} : R_{n+1} = 0.554n_{n+1} + 1.144n_{n+2} \\
R_{n+1} &= 0.275n_{n+1} + 0.490n_{n+2} : R_{n+1} = 0.706n_{n+1} + 0.043n_{n+2} \\
R_{n+1} &= 0.840n_{n+1} + 0.455n_{n+2} : R_{n+1} = 0.252n_{n+1} + 0.283n_{n+2} \\
R_{n+1} &= 0.495n_{n+1} + 0.783n_{n+2} : R_{n+1} = 0.411n_{n+1} + 0.229n_{n+2} \\
R_{n+1} &= -0.87 \times 10^{-3}n_{n+1} + 0.248n_{n+2} : R_{n+1} = -0.188n_{n+1} + 0.723n_{n+2} \\
R_{n+1} &= 0.585n_{n+1} + 0.336n_{n+2} : R_{n+1} = -0.125n_{n+1} + 1.20n_{n+2} \\
R_{n+1} &= -0.083n_{n+1} + 1.23n_{n+2} : R_{n+1} = -0.720n_{n+1} - 0.010n_{n+2} \\
R_{n+1} &= -0.031n_{n+1} - 0.853n_{n+2} : R_{n+1} = 0.565n_{n+1} + 1.17n_{n+2}
\end{align*}
Table 18: The multiple regression equation for the developmental stage matrix model of *T. krausbaueri* cultured at 20°C on a diet of *B. vulgaris* (sugar beet) var Primahill using different pesticide BHC concentrations applied to the diet.

Legend

experiment code C

Regressions are for

\[ n_t, ..., \text{ against } (n_{t-1}, ..., n_{t-r}) \]

\[ \text{and } (n_{t-1}, ..., n_{t-1}) \]

\( n \) = the number of insects at time \( t \)

The subscript of \( n \) denotes the developmental stage.

1 = juveniles less than 250\( \mu m \)

2 = reproductive 250-350\( \mu m \)

3 = reproductive 350-450\( \mu m \)

4 = post reproductive more than 450\( \mu m \)
<table>
<thead>
<tr>
<th>SHC concentration (ag. ai. sl⁻¹)</th>
<th>replicate</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image_url" alt="Image of text" /></td>
<td></td>
</tr>
</tbody>
</table>
Table 19: The multiple regression equation for the developmental stage matrix model of T. krausbaueri cultured at 20°C on a diet of S. cerevisiae using different pesticide BHC concentrations applied to the diet.

Legend

Batch title V

Regressions are for

\[ n_{i,t+1} \] against \( \langle n_{i-1,t} \rangle \)

and \( \langle n_{i,t} \rangle \)

\( n = \) the number of insects at time \( t \)

The subscript of \( n \) denotes the developmental stage.

1 = juveniles less than 250μm
2 = reproductive 250-350μm
3 = reproductive 350-450μm
4 = post reproductives more than 450μm
BHC concentration

\[ n_{2t+1} = 0.973 n_{2t} + 0.283 n_{3t}; \quad n_{3t+1} = 4.12 n_{3t} - 2.11 n_{2t}; \quad n_{2t+1} = -3.09 n_{2t} + 2.63 n_{3t} \]

\[ n_{2t+1} = 0.527 n_{2t} + 1.20 n_{3t}; \quad n_{3t+1} = -0.90 n_{3t} + 2.01 n_{2t}; \quad n_{2t+1} = -0.47 n_{2t} + 3.39 n_{3t} \]

\[ n_{2t+1} = 1.89 n_{2t} - 0.756 n_{3t}; \quad n_{3t+1} = 3.53 n_{3t} + 4.65 n_{2t}; \quad n_{2t+1} = -0.043 n_{2t} + 3.73 n_{3t} \]

\[ n_{2t+1} = 0.866 n_{2t} + 0.015 n_{3t}; \quad n_{3t+1} = 0.633 n_{3t} + 3.38 n_{2t}; \quad n_{2t+1} = 0.645 n_{2t} + 0.914 n_{3t} \]

\[ n_{2t+1} = 0.702 n_{2t} + 0.027 n_{3t}; \quad n_{3t+1} = 2.14 n_{3t} + 4.92 n_{2t}; \quad n_{2t+1} = 0.580 n_{2t} + 0.381 n_{3t} \]

\[ n_{2t+1} = 1.66 n_{2t} - 1.54 n_{3t}; \quad n_{3t+1} = 2.10 n_{3t} + 7.81 n_{2t}; \quad n_{2t+1} = 1.07 n_{2t} + 2.93 n_{3t} \]

\[ n_{2t+1} = 0.395 n_{2t} + 0.371 n_{3t}; \quad n_{3t+1} = 0.675 n_{3t} + 0.707 n_{2t}; \quad n_{2t+1} = -0.438 n_{2t} + 1.37 n_{3t} \]

\[ n_{2t+1} = 0.370 n_{2t} + 0.937 n_{3t}; \quad n_{3t+1} = 0.905 n_{3t} + 3.33 n_{2t}; \quad n_{2t+1} = 0.326 n_{2t} + 6.2 n_{3t} \]

\[ n_{2t+1} = 0.508 n_{2t} - 0.033 n_{3t}; \quad n_{3t+1} = 1.50 n_{3t} + 1.43 n_{2t}; \quad n_{2t+1} = 1.560 n_{2t} + 6.35 n_{3t} \]
In order to produce a population model a fecundity term must be introduced into the model as this is needed for the recruitment of insects into stage $n_1$. The derivation of suitable fecundity estimates are discussed in this chapter in relevant sections.

7.5. The Leslie Matrix model and the use of a spreadsheet to monitor changes in population size and structure.

The matrix model used for the insect population growth can be described by:

$$
\begin{bmatrix}
    n_1, \\
    n_2, \\
    n_3, \\
    n_4,
\end{bmatrix}_{t+1} =
\begin{bmatrix}
    0 & F & F & 0 \\
    a_{1,2} & a_{2,2} & 0 & 0 \\
    0 & a_{2,3} & a_{3,3} & 0 \\
    0 & 0 & a_{3,4} & a_{4,4}
\end{bmatrix}
\begin{bmatrix}
    n_1, \\
    n_2, \\
    n_3, \\
    n_4
\end{bmatrix}_{t}
$$

This model uses the following equations for the numbers of insects in each developmental stage.

$$
\begin{align*}
    n_{1,t+1} &= F(n_1,2t + n_3,t) \\
    n_{2,t+1} &= a_{2,2} n_{2,t} + a_{1,2} n_{1,t} \\
    n_{3,t+1} &= a_{3,3} n_{3,t} + a_{2,3} n_{2,t} \\
    n_{4,t+1} &= a_{4,4} n_{4,t} + a_{3,4} n_{3,t}
\end{align*}
$$

The model was developed in the previous chapter 7.2 and the regression equations for the models are presented in Table 16-19. The model can be run using a spreadsheet program prepared for an Amstrad
pcw 8256, 8512, 9512 and compatibles to estimate population changes and to predict population development.

A spreadsheet is able to define uniquely every cell within the matrix model created by the equations above. How the numbers of insects of each insect size class, developmental stage change can therefore be monitored. The spreadsheet can therefore be used to estimate the numbers of insects in each of the size classes (1-4) after specified time intervals. The spreadsheet can be run to predict how the population will develop and what the population developmental stage distribution is in each time interval. It can also be used to assist in decision making for pest control strategies.

7.5.1. General use of spreadsheet.

The spreadsheet programme for each cell used in the spreadsheet is shown in Appendix 4.

Table 20 describes how data are inputted into the programme for running the models. Each cell of the spreadsheet is coded by a row number and a column letter (005C, 011B etc).

Column A (Headings).

Cell 001A and 002A record the code for the model type replicate etc.

Cell 005A records the code for the numbers in the size class (developmental stage) i.e for stage 4 = \( n_4 \), 007A developmental stage 3\( (n_3) \), 011 developmental stage 2 \( (n_2) \) and 015 developmental stage 1 \( (n_1) \).

Cell 020 (fec) records the code for the fecundity of the population and cell 023 the code for the total number of insects in the population \( (N) \).
Legend.

001, 002, ......0023 = row heading.
A,B, ..............L = column heading
V,X,Y,Z = insect numbers.
1,2,3,4 = insect developmental stages.
a = probability of transitions between developmental stages.
fec = fecundity
R = intrinsic growth rate.
R = finite population growth rate
N = number of insects in stage i at time t+1, t+2 etc.
N = total population numbers.

Brackets show results from culture censuses.
<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
<th>I</th>
<th>J</th>
<th>K</th>
<th>L</th>
</tr>
</thead>
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<td>t</td>
<td>stoch</td>
<td>cell</td>
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<td>cell</td>
<td>t+2</td>
<td>cell</td>
<td>t+3</td>
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<td></td>
</tr>
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<td>enter</td>
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<td>sum</td>
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<td>---</td>
<td>---</td>
<td>( )</td>
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<tr>
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<td>X</td>
<td>a4,3</td>
<td>Wa4,3</td>
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<td>Ya3,3</td>
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<tr>
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<td>Y</td>
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<td>Ya3,2</td>
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<tr>
<td>020</td>
<td>fec</td>
<td>(A⁻)Y</td>
<td>n1t+1/n3t+n2t ( )</td>
<td>---</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>023</td>
<td>W</td>
<td>W+X+Y+Z</td>
<td>----- ( )</td>
<td>---</td>
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</tr>
</tbody>
</table>
Data from culture censuses are entered in column B t (enter), and represent the initial values obtained in cultures relating to insect numbers and fecundities at time t. Thus cell 011B will give the number of insects of stage 2 at time t (n_{2t}). In Table 19, this is recorded as Y.

Cell 023B records the total number of insects in the population at time t.

Column C (Stochastic variable input from difference growth equations)

Column C (stoch enter) records values from stochastic estimates representing the probabilities of insect transitions obtained from the difference regression equations from Tables 15-18. In the example in Table 19, these probabilities are given as they appear in the equations \( \phi, \theta, \sigma, \phi \) which are the transition probabilities used for the Matrix models. Therefore, the probability relationships from the deterministic model are entered into the spreadsheet and cell 009C records \( \phi_{3,3} \) and cell 011C records \( \phi_{3,2} \), etc.

Cell 020C records the fecundity term for the population. This value is obtained from the A term cell (015F) obtained from the numbers of \( n_1 \) (juveniles) at time \( t+1 \) in population cultures divided by the sum of X and Y, the numbers of reproductive insects \( (n_x + n_0) \).

Therefore this term is an F which gives the values at time \( t+1 \) of \( (F = n_{1,t+1}/n_x+n_0) \).

Column E (cell prdct. spreadsheet program input).

These values are calculated by the spreadsheet program.

For example cell 005E records \( W_{4,4} \), the product of the number of insects in developmental stage 4 and the transition probability in the time interval based on stage 4. Cell 007E records \( W_{4,3} \), the product of the number of insects in developmental stage 4 and the transition probability based on the transitions from developmental stage 3.
Column F (t+1) spreadsheet programme input.

This column records the insect numbers in each developmental stage at time t+1. For \( n_a \), \( n_d \), and \( n_s \) this is a sum of the values computed in Column E. For example, \( n_{a+1} = W_{a+1} + W_{d+1} = n_{a+1} + n_{d+1} + n_{s+1} \).

The numbers in \( n_i \) at \( t+1 \) obtained from \( n_{i+2}/n_{i+1} + n_{i+1} \).

The figures recorded in brackets under column F, G, H, etc. are the values obtained from running the spreadsheet after specified time intervals. Therefore F represents the estimated numbers at \( t_2 \), G, the numbers at \( t_3 \) and H the numbers at \( t_4 \). These values can be compared where possible to the numbers obtained from population culture censuses. Where this is done population census numbers are given in brackets.

Once the relationship between cells has been established, the spreadsheet programs can be run by inputing the appropriate values into columns B and C. This allows prediction of the numbers in insect populations for as long as is required since the spreadsheet can be set up to monitor population changes in any time period. For this study however a comparison of numbers to the period \( t+9 \) was made.

The time intervals used were the census times of 10 days (\( t+9 \) therefore corresponds to 90 days in culture). The sensitivity of the fecundity term can also be examined using the spreadsheet.

7.5.2. Development of Models.

Using the results available four types of model can be produced each has a specific but restricted use.

The model types are described here and results from cultures using the appropriate models are presented in further sections.

MODEL 1: Stochastic with variable fecundity to estimate model stability.
The fecundity terms used in this model involve the use of the F estimates which correspond to
\[ F = \frac{n_{t+1}}{n_{t+2}} + n_{t+3} \]
for each time interval. These values are obtained from computations from culture censuses and estimated for each time interval.

Table 21a provides an example of the use of the spreadsheet and shows a spreadsheet for a replicate r03 (a culture on sugar beet without pesticide application.)

Here population data were input into the model following the steps outlined above and the program was run to t₉ (90 days). The figures in brackets are the actual results from the culture census and are compared with the model predictions. A good simulation of the populations' behaviour is obtained. Because culture censuses were made up to 90 days the model can be compared directly with the culture census values. For example Column AD(t+9) shows the population structure after 90 days. The model predicts a value of 13 for n₂₆, at t₉ the actual number from culture census is 12. The model predicts a value of 3 for n₃₅, the value from the culture census is 13. The model also predicts a value of 50 for n₁₃₅ and the value from the culture census is 38. The total population numbers N₉ at t₉ are 65 from the model prediction and 63 from the culture census.

The drawback to this model type is that it is limited by the population values used from culture censuses because fecundity values from the census are used in running the model. Although it can be used in estimating how a population containing a different ratio of n₁:n₂:n₃:n₄ at t will develop under the specified conditions, it is not possible to predict how the model will perform in time intervals beyond t₉, where census values are not available. A different approach is therefore required to allow prediction beyond the census time intervals. This involves a mean fecundity term which is explained in the model 2 below.

**MODEL 2:** Stochastic model with mean constant fecundity term
Table 21a: An example of the use of a spreadsheet.

Legend.

001, 002, .......0023  = row heading.
A,B, ............L    = column heading
V,1,Y,Z             = insect numbers.
1,2,3,4.             = insect developmental stages.
a                = probability of transitions between developmental stages.
    fec             = fecundity
    R                = intrinsic growth rate.
    R              = finite population growth rate
    n_0_0         = number of insects in stage i at time t+1, t+2 etc.
    N               = total population numbers.

Brackets show results from culture censuses.
<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
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<th>F</th>
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<tbody>
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<td>A4</td>
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**MODEL 1**

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**RESULTS**

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</table>

**DISCUSSION**

- The results show a significant increase in cell nt+4 compared to cell nt+1.
- Further analysis is needed to understand the underlying mechanisms.

**CONCLUSION**

- The data support the hypothesis that cell nt+4 is crucial for the observed effect.
- Further experiments are recommended to validate these findings.
This model is identical to model 1 except that a mean fecundity term is used. This term is entered into cell 020B and is used to obtain the numbers which develop into n1 in time intervals studied.

\[ F = \frac{n_{t+1}}{n_{t+2}} + n_{2t} \]

A mean value is obtained from fecundity estimates from the cultures studied. This mean value should therefore predict culture population numbers within time intervals. The mean fecundity value is then adjusted so that it predicts population numbers for subsequent time intervals when the model is run using this value. If the term predicts the censused populations fecundity accurately, it can then be used to predict population development in subsequent time intervals. Table 21b shows the results for a population culture fed on sugar beet without pesticide application. Here the population was censused to t+2 and censused values are given in brackets. At t+2, the numbers predicted by the mean fecundity estimate of 2.2 are \( n_{4t+2} = 3 \) compared with 0 in culture census, \( n_{2t+2} = 20 \) compared with 20 from culture census, \( n_{3t+2} = 15 \) compared with 11 in culture, \( n_{1t+2} = 50 \) compared with 58 in culture and \( N_{t+2} = 87 \) compared with 89 in culture. Since this model with the adjusted mean fecundity term predicts accurately the population's development, it can now be used to predict the population numbers up to 90 days. The values for t+9 are \( n_{4t+9} = 74, n_{3t+9} = 1560, n_{2t+9} = 751 \) and \( n_{1t+9} = 2850 \) and \( N_{t} = 5325 \). There is therefore also a predictive element to this model based on the successful prediction of the population development in t+1 and t+2.

The sensitivity of this model can therefore be tested by changing the fecundity terms (B20) for other replicates to estimate how this affects the development of populations.

MODEL 3: Stochastic predictive models using mean stochastic parameters from treatment replicate equations.

This model uses the population statistics which were determined in chapter 5 to produce a fecundity term which can be used for population simulations.
Table 21b: An example of the use of a spreadsheet. MODEL 2.

Legend.

001, 002, ......0023 = row heading.
A,B, .............L = column heading
W, I, Y, Z = insect numbers.
1, 2, 3, 4, = insect developmental stages.
a = probability of transitions between developmental stages.
fec = fecundity
R= = intrinsic growth rate.  
R = finite population growth rate
n. = number of insects in stage i at time t+1, t+2 etc.
N = total population numbers.

Brackets show results from culture censuses.
### Model 2

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Model 2

[Table continued...]

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Note: All values are in arbitrary units.
the intrinsic rate of population increase and the R value (R = $e^{\lambda t}$) a finite estimate of the rate of increase were estimated from population cultures. Finite estimates are specific for population replicates. The F values were then estimated by running the model so that $N_{t+1}/N_t$ gives the R value for population increase.

The model also uses population censuses of the developmental stage distribution of insects (Chapter 3) as the values entered in column B for the numbers of insects in each developmental stage at time t. These values are 50: 25:15:9 for the stages 1:2:3:4. It is therefore a more reliable estimate as it uses insect developmental stage numbers in established populations. Thus the population spreadsheet can be run to predict the $F(t+20)$ term from the R values.

The use of this model therefore involves further development of MODEL 2 by addition of row 24 and 25 which are used to estimate the fecundity term in O20B which in turn is used to run the spreadsheet. Cell O24B records the Rm value and the R value is recorded in Row 25.

Where mean treatments are used the mean Rm value is also used and recorded in B29. The population's fecundity term is then adjusted to ensure that at $N_{t+9}$, the population achieves its R value.

This spreadsheet therefore consists of oscillations in the population developmental stage numbers until a stable population structure and finite growth rate R (row 25) has been obtained. Begon and Mortimer (1986) have recorded this series of oscillations as characteristic of a continuously breeding population with geometrical increase.

Two examples of the use of this model are illustrated in Fig 22a and 22b. These are models of the same replicate but they differ in that two different F terms (2.0 and 1.10) have been used. Oscillations in the populations growth can be seen in row 025. R, the finite growth rate, changes as the population develops in Table 22a from 1.32 at $t+1$ to 1.20 at $t+3$ to a final constant value of 1.21 at $t+4$ to $t+9$.

Clearly for this example the required R value of 1.03 (0025B) obtained from the Rm value of 0.03, will not be achieved because the population F term is too high (2.0). When the fecundity term is adjusted however the effect on R values can be seen. This effect is

168
An example of the use of a spreadsheet. MODEL 3.

Legend.

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<tr>
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<td>column heading</td>
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</tr>
<tr>
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<td>insect developmental stages.</td>
</tr>
<tr>
<td>fec</td>
<td>probability of transitions between developmental stages.</td>
</tr>
<tr>
<td>R_m.</td>
<td>fecundity</td>
</tr>
<tr>
<td>R</td>
<td>intrinsic growth rate.</td>
</tr>
<tr>
<td>N_i</td>
<td>finite population growth rate.</td>
</tr>
<tr>
<td>n_i</td>
<td>number of insects in stage i at time t+1, t+2 etc.</td>
</tr>
<tr>
<td>N</td>
<td>total population numbers.</td>
</tr>
</tbody>
</table>

Brackets show results from culture censuses.
<table>
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The table contains data organized in columns and rows. Each column represents a different parameter or value set, and each row provides specific data points across these parameters.
Table 22b: An example of the use of a spreadsheet. MODEL 3.

Legend.

001, 002, .......0023 = row heading.
A,B, ..............L = column heading
V,X,Y,Z = insect numbers,
l,2,3,4, = insect developmental stages,
a = probability of transitions between developmental stage.
fec = fecundity
R.. = intrinsic growth rate.
R = finite population growth rate
n,.. = number of insects in stage i at time t+1, t+2 etc.
N = total population numbers.

Brackets show results from culture censuses.
shown in Table 23b. An F value of 1.1 will therefore also provide oscillations in the populations growth rate 0.95 at t+1, 1.12 at t+2 and 1.03 at t+3 to t+9. However the value of 1.03 is achieved at t+3. Therefore the selected F term (1.1) is the right one for the model and predicts a Nt value of 132 at t+9.

MODEL 4.

This model is identical to model 3 except that instead of using the population developmental stage ratios of 50:56:15:9, for stages 1:2:3:4 in column B (n enter), a calculation of the numbers of insects after application of BHC pesticide based on the developmental stage specific LC50 values obtained in Chapter 5 is used. This calculation and input is made from results of the application of BHC pesticide to T. krausbaueri. This model is therefore a synthesis of all the relevant available data obtained in this thesis on T. krausbaueri and can be used to determine how population will be affected by application of a potentially lethal pesticide dose during the development of a population under specified conditions.

Further discussion and use of the model is presented in Chapter 7.6.
7.6 The use of Leslie Matrix population growth models to examine the effects of EHC on *T. krausbaueri*.

The results presented here use the models described in chapter 7.5 (Models 2, 3 and 4). Although producing Model 1 was an important step in the modelling process it was not used in this section because of the limitations to this model which have already been discussed.

Model 2 was used to produce a spreadsheet for replicates of treatments which allowed comparisons to be made with the development of population censuses from cultures. The spreadsheets for one replicate in each treatment are presented here. Populations were obtained from cultures which gave a good $R^2$ value. Similar spreadsheets can be produced for other replicates from the regression equations presented in Table 16-19.

Table 23 shows a series of replicates treated with pesticide and cultured on a diet of Sugar beet var Monore at 20°C. At $t+2$ the simulation compares favourably with culture censuses presented in brackets. In the simulation $n_2 = 20$ compared with 20 from censusing, $n_2 = 15$ compared with 11 in culture, $n_1 = 50$ compared with 58 in culture and with $N_t$ value of 87 compared with 89 in culture. The simulation predicts that $N_t$ at $t+9 = 5235$.

With the concentration of pesticide in the diet increased to $5.34 \times 10^{-7}$ mg ai ml$^{-1}$ (Table 23b), comparisons with census values made to $t+3$ gave 22 in census compared with a value from simulation of 12, for $n_2$, 16 from census compared with value of 34 from model simulation for $n_2$ and 101 compared with 89 from simulation for $n_1$. The total population number counts (Nt) compared favourably at $t+3$ with a value of 134 from the model and 139 from the culture census. $N_t$ values predicted from the model at $t+9$ were 7941 which is larger than for the replicate described earlier which did not use pesticide and suggests some compensatory population growth in response to the
Spreadsheets for replicates of treatments of cultures of T. krausbaueri on Sugar beet S. vulgaris var. Monoiré with BHC applied to the diet at concentrations of

a) 0 mg ai ml$^{-1}$.  
b) 5.34x10$^{-7}$ mg ai ml$^{-1}$.  
c) 2.18x10$^{-3}$ mg ai ml$^{-1}$.  
d) 3.5x10$^{-2}$ mg ai ml$^{-1}$.  

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<p>|       | A         | B         | C         | D         | E         | F         | G         | H         | I         | J         | K         | L         | M         | N         | O         | P         |
|-------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| 001   | cell      | ni+5      | cell      | nt+6      | cell      | nt+7      | cell      | nt+8      | cell      | nt+9      |           |           |           |           |           |
| 002   |           |           |           |           |           |           |           |           |           |           |           |           |           |           |           |
| 003   | 12.40     | 0.31      | 3.72      | 4.91 (7)  | 1.52      | 2.62 (8)  | 0.97      | 2.35      | 0.79      | 4.21      |           |           |           |           |           |
| 006   | 17.00     | 0.97      | 1.19      | 16.46 (21)| 1.28      | 19.67 (29)| 1.38      | 50.11     | 3.51      | 91.43     |           |           |           |           |           |
| 009   | 0.42      | 7.12      | 7.14      | 8.24      | 21.00     |           |           |           |           |           |           |           |           |           |           |
| 010   | 4.00      | 2.84      | 11.36     | 4.29 (5)  | 11.53     | 14.74 (11)| 41.97     | 24.49     | 78.44     | 29.75     |           |           |           |           |           |
| 012   | 0.87      | 3.48      | 3.65      | 12.83     | 21.56     |           |           |           |           |           |           |           |           |           |           |
| 014   | 3.00      | 0.24      | 0.72      | 46.20 (28)| 11.09     | 49.99 (58)| 11.90     | 76.71     | 10.17     | 164.81    |           |           |           |           |           |
| 020   | 2.20      |           |           |           |           |           |           |           |           |           |           |           |           |           |           |
| 021   |           |           |           |           |           |           |           |           |           |           |           |           |           |           |           |
| 022   | 36.90     |           |           |           |           |           |           |           |           |           |           |           |           |           |           |
| 023   |           |           |           |           |           |           |           |           |           |           |           |           |           |           |           |
| 031   |           |           |           |           |           |           |           |           |           |           |           |           |           |           |           |
| 034   |           |           |           |           |           |           |           |           |           |           |           |           |           |           |           |
| 044   | 4.30     | 6.70      | 2.39      | 12.97     | 4.42      | 23.19     | 7.19      | 41.52     | 12.56     | 74.26     |           |           |           |           |           |
| 045   | 6.40     | 151.20    | 18.50     | 273.89    | 19.17     | 494.65    | 34.63     | 875.65    | 61.20     | 1555.64   |           |           |           |           |           |
| 050   | 39.31     | 63.35     | 114.76    |           | 297.26    | 366.90    |           |           |           |           |           |           |           |           |           |
| 051   | 112.39    | 74.13     | 210.54    | 133.76    | 379.98    | 235.35    | 668.25    | 428.00    | 1192.73   | 759.83    |           |           |           |           |           |
| 052   | 34.86     | 64.50     | 116.37    |           | 284.75    | 365.40    |           |           |           |           |           |           |           |           |           |
| 053   | 39.55     | 220.60    | 69.26     | 455.72    | 118.98    | 856.05    | 215.24    | 1665.99   | 385.84    | 2054.41   |           |           |           |           |           |
| 058   | 521.64    | 916.36    | 1650.43   | 2943.44   | 5225.19   |           |           |           |           |           |           |           |           |           |           |</p>
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16.02      | 14.47     | 0.85      | 11.70     | 0.94
application of pesticide. When the pesticide concentration was increased further to $2.18 \times 10^{-3} \text{ mg ml}^{-1}$, (Table 23c) comparisons of culture census and simulation made at $t+3$ were, 10 of $n_0$ compared with 10 in culture, 8 of $n_2$ compared with 10 in culture, 28 of $n$ compared with 24 in culture and $N_t$ values of 64 in culture compared with 45 by the model simulation. At $t+9$ however the population showed a decline with $N_t$ values reduced to 29. This suggests that with the application of this pesticide concentration to the diet, the population would decline after this time period.

With the highest pesticide concentration applied $3.5 \times 10^{-2} \text{ mg ml}^{-1}$, (Table 23d) at $t+9$ 9 insects were expected to survive from the simulation of population development, and the comparison with population censuses was good at $t+1$, with census values of 0, 4, 3, 14 and 20 for $n_0$, $n_2$, $n$, and $N_t$ comparing with 1, 3, 15 and 18 from the model simulation. However, the $F$ term used for this simulation was high (3.7) which suggests that the small number of $n_2$ which had survived to $t+1$ were actively reproducing although the longevity of juveniles produced under these conditions could barely sustain the population levels to $t+9$.

Model 3 was used to construct the treatment models for the populations cultured on diets of yeast and sugar beet with pesticide application either to the diet or the substrate. The values for regression equations used in the model were mean values obtained from treatment replicates.

The output for the production of the matrix model and the printout for the spreadsheets for replicate treatments are shown in the Appendix section. The size class population changes for the treatments are shown.

A comparison can be made between pesticide application in the substrate and its effect on population numbers. Appendix 5a shows the matrix model constructed for this data set with no pesticide application. Appendix 5b shows the spreadsheet. With pesticide applied at the concentration of $3.37 \times 10^{-3} \text{ mg ml}^{-1}$, the matrix
model is shown in Appendix 6a and the spreadsheet in Appendix 6b. The fecundity term used this pesticide concentration was 1.4 compared with 1.1 where pesticide was absent. This again suggests that the presence of pesticide BHC at low concentrations results in an increase in fecundity. Using the same numbers of insects at time t, the model shows that at t+9 when a stable population has been established, there will be 37 of developmental stage $n_2$, 29, $n_3$, 68 $n_4$, and 133 $N_5$ compared with 20 $n_2$, 23 $n_3$, 60 $n_4$, and 101 $N_5$. The $N_5$ numbers are only slightly affected by the application of the pesticide after t+9 (30 days), due mainly to increased reproduction since the numbers of $n_2$ are more than twice those with the pesticide applied. The pesticide therefore also reduced the longevity of $n_2$.

When insects were cultured on a diet of sugar beet which had BHC applied to it, simulations were used to predict how the populations would develop. On the diet of sugar beet var Primahill the use of the Leslie matrix model for 0 pesticide use (Appendix 7) provided a spreadsheet which showed an increase to 190 from the initial number of 100 insects used. Insects in this spreadsheet would also be expected to stay longer as stage $n_4$ (adults) and a F term of 0.8 was obtained. As the amount of pesticide in the diet was increased to $5.34 \times 10^{-7}$ mg al ml$^{-1}$, the Leslie Matrix model (Appendix 8a) used on the spreadsheet (Appendix 8a) produced 134 of $N_5$ compared with 190 where pesticide had not been applied. There was also a low fecundity term of 0.2. At the highest concentration of BHC $3.5 \times 10^{-2}$ mg al ml$^{-1}$ (Appendix 9a), the $N_5$ numbers were reduced to 116 with a low F term of 0.6.

The above simulations were carried out using the same initial population numbers at each of the developmental stages. Other information from this thesis would however suggest that with pesticide application these ratios change. The results do however show that the populations would be affected by BHC even at the lowest pesticide concentration.
The variety Monolre produced similar results to those above for Primahill. The matrix model for the diet which did not include pesticide (Appendix 10a) gave a spreadsheet (Appendix 10b) which at t+9 had 276 Nt although fecundity in this population was only .01. As the pesticide concentration increased to 5.34x10^{-7} mg ai ml^{-1}, fecundity for the matrix model (Appendix 11a) had to be raised to 0.6 in the spreadsheet (Appendix 11b) but even at this level the numbers of N at t+9 was only 120, less than half the value obtained where there was no pesticide used.

At the higher pesticide concentrations 2.18x10^{-3} mg ai ml^{-1} (Appendix 12) and 3.5x10^{-2} mg ai ml^{-1} (Appendix 13), the Nt numbers were higher (152 and 184). This was achieved with the high F terms of 2.1 and 2.2. This suggests that survivors in the population would detect the pesticide and then increase their fecundity to compensate for the pesticide in their diet but that they would however be unable to achieve the numbers obtained from the simulation without pesticide.

The treatment models constructed for populations cultured on the yeast diet produced contrasting results which predicted large population increases in the culture conditions. When pesticide was excluded from the culture diet, the population model shown in Appendix 14a was obtained and the simulation of this is in Appendix 14b. There was a high probability term for n3 insects remaining in n3 after each time interval. This value of 3.53 led to a reduced fecundity term as more insects would remain in this reproductive stage. The large number of insects in this population produced at t+9 (1859796) in Table 33b should however be viewed in the context of the size of the culture vessels which would be unable to support more than 1,000 insects in the culture environment available. With the concentration of pesticide in the diet of 5.34x10^{-7} mg ai ml^{-1}, there was also a large term of 2.143 for stage 3 remaining in the reproductive stage during the time period studied, (Appendix 15a). Again numbers at t+9 were large (41029) with a low F term of 0.1 (Appendix 15b). With the highest pesticide concentration however of 8.75x10^{-3} mg ai ml^{-1}. 176
(Appendix 16a), a higher fecundity term of 0.27 was recorded. The population was however expected to increase only to 113 from 100 at t, with larger numbers of stage 3 present.

Table 24 shows the model predictions for populations each originating with the same number of individuals. BHC application reduced the numbers of insects in the developmental stages at time t+9 in all the different culture conditions. For populations fed on the variety Monoire there was an abundance of juvenile stage 1 predicted at the higher pesticide concentrations of $2.18 \times 10^{-2}$ mg ai ml$^{-1}$ and $3.5 \times 10^{-2}$ mg ai ml$^{-1}$ whilst stage 3 were prevalent when pesticide was not present. This pattern was not as clear for populations fed on the Primahilli variety which nevertheless showed reduced numbers as the pesticide concentration increased. When pesticide was applied to the substrate, at $3.37 \times 10^{-5}$ mg ai ml$^{-1}$, the Nt value at t+9 was 101, less than the numbers produced when pesticide was applied to the diet at higher concentrations. Toxicity from the substrate therefore produces a marked sublethal effect.

The figures obtained with yeast in the diet were however over predictions of the populations' development. When pesticide was applied to the diet at $8.75 \times 10^{-3}$ mg ai ml$^{-1}$, where numbers were also reduced to 112 at t+9.

The final model presented in Table 25 was constructed using the Spearman Karber stage specific toxicity values obtained from chapter 5 for sugar beet var Monoire cultures. The mean LC$_{50}$ values were $2.45 \times 10^{-2}$ mg ai ml$^{-1}$ for developmental stage 1, $4.54 \times 10^{-2}$ mg ai ml$^{-1}$ for developmental stage 2, and $2.85 \times 10^{-2}$ mg ai ml$^{-1}$ for stage 3.

Assuming that pesticide was applied at the rate of $2.54 \times 10^{-2}$ mg ai ml$^{-1}$ to a population made up of 9:14:25:50 for stage 4:3:2:1, the population structure would be changed to 0:8:24:25. These figures were therefore entered into n in the model. When the population model spreadsheet was run, the numbers of n, n$_2$, n$_3$, n$_4$ at t+9 of 12:140:60:2 and an N$_a$ value of 215. If the population is simulated
Table 24: Prediction of numbers of *T. krausbaueri* in each developmental stage (n1-n4) after 90 days (t9) using model type 3. All populations are simulated using the same number of $n_1$ (50) $n_2$ (25) $n_3$ (15) $n_4$ (9) $N$ (100) at time $t$. 
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Table 25: The treatment Leslie Matrix model of *T. krausbaueri* cultured at 20°C on a diet of *Sugar beet* *vulgaris* var *Monolore*.

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0.299 & 1.07 & 0 & 0 \\
0 & 1.69 & 0.353 & 0 \\
0 & 0 & 0.065 & 0.314 \\
\end{bmatrix}
\begin{bmatrix}
1_t \\
1_{t+1} \\
1_{t+2} \\
1_{t+3} \\
\end{bmatrix}
= 
\begin{bmatrix}
N_1 \\
N_2 \\
N_3 \\
N_4 \\
\end{bmatrix}
\]

Spreadsheet of

The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of *Sugar beet* (*Beta vulgaris* var *monolore*) using 2.54x10^-4 mg ai ml^-1 pesticide applied at t

The change within the population developmental stage structure in each time interval are shown.

Regression equations used for the model.

\( n_{t+1} = 0.314n_t + 0.065n_{t-1} \)
\( n_{t+1} = 0.353n_t + 1.69n_{t-1} \)
\( n_{t+1} = 1.07n_t + 2.98n_{t-1} \)

Fecundity \( (F = 0.01) \)

Legend.

experiment batch title XO
fec = fecundity
\( R_m = \) intrinsic growth rate.
\( R = \) finite population growth rate.
\( n_{t+1} = \) number of insects in stage 1 at time t, t+1, t+2 etc.
\( N = \) Total population number.
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using the initial ratios of 9:14:26:50, however the population numbers $N_t$ at $t+9$ are 276. The effect of $2.45 \times 10^{-4}$ mg ml$^{-1}$ on the population therefore only reduced the population numbers by 60 in this analysis after 90 days.
General Discussion.

The production of a deterministic model for the development of *T. krausbaueri* in culture showed how the population would behave in culture, and how insects would pass from one size class developmental stage to another. It also identifies the different size classes used and the fecundity (F) in the population. The fecundity term used was found to depend on the numbers of insects in size class 2 and 3. The introduction of a stochastic element into the model allowed the estimation of probabilities of the transitions between the insect size classes, developmental stages to be made and using values obtained from culture census to produce these relationships by multiple regression techniques. It was then possible to produce replicate models for cultures of populations fed on *B. vulgaris* and *S. cerevisiae* with and without pesticide application and from this to construct treatment models based on the means from replicate models. These models were then further examined with the computer programsimulation to simulate and predict how populations would develop under a range of diets and BHC concentrations.

The validity of the model was tested by comparisons with the values obtained from the population studies from Chapter 5 which monitored the development of the numbers of insects in the 4 size classes over a specified time period.

Four types of models were produced for computer simulation and validation with the populations of *T. krausbaueri* cultured in this study.

Model 1. This model was used to measure population growth and allowed direct comparison with censuses where the values for population fecundity were available.

Model 2. this model used an F term to monitor population fecundity chosen so the the population growth simulated censused values from
culture. The F term was then used to predict population growth in further time intervals.

Model 3 This model used Rm and R values to determine population doubling times and growth rates and the F term was adjusted to predict the R and Rm values for the population under specified conditions which were obtained from Chapter 5. This estimate of F was therefore based on a population statistic which was estimated for each population.

Model 4. This model is a further development of the models above (1-3). In addition the LC50 values obtained in chapter 5 which were found to depend on insect size classes were incorporated into the model to determine the effect of BHC field dose on population numbers.

The Leslie Matrix (1948) deterministic model developed in this chapter used the relationships between the four size classes, developmental stages of the insect populations. This type of model was used by Longstaff 1974, 1976, to monitor changes in the numbers of insects in populations of Coliembola. Longstaff's models constructed for members of the genera Sinella, Onychlus and Hypogastura used an arbitrary definition of developmental stages (size classes) to divide insect populations into classes which could then be modelled successfully.

Longstaff's 1974 model however examined the relationship between fecundity and time and fecundity and population density. F values for all replicates for each culture condition were plotted against time and population density to describe the fecundity function. With this approach Longstaff (1974) was able to use a fecundity function in the his Matrix model.

In this study however a large population density leading to overcrowding did not occur or appear to affect population fecundity with time during the interval studied. The culture F term used was therefore n0+n1/n1+1 reflecting the effect of the reproductive stages on fecundity.
In addition other population statistics the R and Rm values which were obtained from population studies in Chapter 5 at different environmental conditions were used to describe the populations growth rate based on the fecundity and longevity of individuals in the more precise models presented here. This also eliminated the need to produce a fecundity function.

Using the population models produced above the change in size of populations of *T. krausbaueri* can be computed validated and simulated using a spreadsheet to follow individual population size class changes. Simulation of population models where the birth and mortality statistics are constant (Begon and Mortimer 1986) over time provide a precise way of determining the changing population size. The assumption that populations are unlimited by space and that the elements of the transition matrix are constant have also been made and in these populations the $R_m$ statistic relating to cultures of individual species under specified conditions of temperature relative humidity and diet (Krebs 1978) have also been made.

Under field conditions these assumptions will have to be reexamined since migration from the population and changes in diet temperature and relative humidity will inevitably occur and change the profile of population development to some extent.

The models produced and used were valuable because they allow a predictive element to be incorporated into the populations, comparing behaviour under specified conditions which can be contrasted with other population behaviour so that decisions about pest control, based on the likelihood and extent of pest development can be made.

The additional sensitivity of the models occurs from their stepwise construction which allows available information about populations, to be used. Information on population fecundity can be incorporated into Model 1 and the structure of a field population (ratio of juveniles reproductives and post reproductives or the size classes they belong to can be incorporated into all the models at time $t$ before the model is run.

The specific toxicity of size classes can also be used in these models and this has been shown to depend on the size class of insects
when tested with the Spearman Karber (Hamilton et al 1977). LC₅₀ tests. The modelling step of pesticide introduction can be made at any time in the population simulation and its effect on population development can be immediately made.

In the field BHC is applied at the rate of 1.1 kg ha⁻¹ either to the top soil or incorporated into the soil by liquid or granular application. Once applied, the pesticide is incorporated into the soil and permeates the soil to reach the target pest. T. krausbaueri can be found in the top soil levels. The movement of the pest in the soil is small (Chapter 3 and 4), and this will serve to concentrate T krausbaueri in areas which are diet rich (Brown 1981, Curry and Purvis 1982). Determination of factors such as the leachability and movement of the pesticide BHC in the many different soil types used for Sugar beet cultivation (Holmes 1979) also affect the process of the pesticide achieving contact with the pest.

The degradation of the pesticide in soil and the concentration of the applied BHC which will eventually be in contact with the pest can be measured by methods such as exhaustive soil sampling techniques and pest population censuses on a temporal basis. Such specific information once obtained from field studies can however be incorporated into the Matrix model in the same way as the long and short term population studies with the application of pesticide have been used in this thesis, to assist in the validation of the models produced.

Some pesticide concentrations of BHC (Chapter 5 and 6) have been shown to cause injury, and death to T. krausbaueri and B vulgaris.

Where a pesticide concentration of 3.3x10⁻⁸ mg m⁻³ was applied to the culture substrate, a sublethal effect was obtained with populations surviving, but failing to develop or increase in numbers (N=101) at t=9 with N at t=100, for culture simulations.

At higher concentrations of BHC applied to substrate, populations declined and failed to develop. This occurred even though the LC₅₀ values for the insect by contact were of the order of 10⁻³. Chapter 5). Continued exposure to pesticide therefore resulted in a greater
reduction in the populations development than would be predicted by the LC₉₀, alone and LC₉₀ values might form the basis for determining the rate at which pesticide is applied (Mathews 1979).

The application of pesticide in the diet of *T. krausbaueri* formed the basis of further examinations of pest development. Where the diet of *T. krausbaueri* was limited to sugar beet due to cultural practices in the field and with restricted migration into the soil, insects would feed exclusively on sugar beet which would contain some BHC if soils had been treated with pesticide. How the population would then develop was examined. The population development was greater in insects feeding on the monoire variety with populations developing to 277 at t9 compared with 190 for primahill (*N* =100 at t). As the pesticide concentration increased in the diet, the population size was reduced although this was not always a direct relationship. Control of the pest by a reduction in the population numbers was be achieved in the simulation when sugar beet grown in pesticide containing at the low rate of 5.34x10⁻⁷ mg ai ml⁻¹.

The introduction of the pesticide in the yeast diet however required the highest concentration of 8.75x10⁻³ mg ai ml⁻¹ to control populations (*N* =112 at t9). The models of cultures of populations where *S. cerevisiae* was the diet appeared to predict population explosions which would not be supported in culture vessels. It is also likely that space will limit population developments to this level in field conditions.
8. Final Discussion

The development of strategies for the control of harmful agricultural pests depends on the identification and quantification of several key relationships. The correct identification of the pest, assessment of its numbers in the field, the use of correct information on the pests' biological, behavioural, developmental and population growth processes, will also provide a basis for developing a control strategy. The identification of the vulnerable crop growth stages, and the evolution of a pest control rationale with a biological control agent which is not injurious to crop also needs to be established to develop control strategies. A continuous refinement of evolved control strategies using predicting and forecasting techniques to ensure that strategies can be modified in response to changes in the relationship between pest, crop and pesticide is then vital if control strategies are to have repeated success.

This thesis has examined the above relationships for a widely grown agricultural crop Sugar beet (*B. vulgaris*), which is cultivated with the use of the pesticide Gamma benzene hexachloride (BHC). This is a pesticide applied both as a seed dressing treatment or as an overall crop treatment which is incorporated into the soil, to control soil pests which include the springtail *T. krausbaueri*.

Identifying the insect

The first identification of the Onychiuridae as an insect family which had close association with sugar beet seedlings was made by Winner (1959) when *O. campatus* was identified in sugar beet fields. Winner (1967), Heijbroek (1971), Dunning (1972), Baker and Dunning (1975), Ulber (1978), Feeny (1979), Hansen Curry and Purvis (1981), added to the list of harmful Onychiurid species. This list currently includes: *O armatus*, *T. krausbaueri*, *T. quadrispina*, *O fimatus*, *O ghidini*, which contribute to making up the 30 or so Collembola species found in agricultural soils (Brown 1983).
O. armatus and T. krausbaueri were found to be the most abundant species in sugar beet fields by Ulber (1978) and Curry and Purvis (1981) who also found that there were larger numbers of T. krausbaueri than O. armatus in the early stages B. vulgaris germination and growth. These onychiuridae insects form part of a soil pest complex which also contains millipedes (Blaniulus sp.) symphilids (Scutigerella sp.) pygmy beetle (Atomaria linearis), and wire worms (Agriotes sp). The Onychuridae are however the most widespread of the potential pests that inhabit agricultural soils on which B vulgaris is grown (Baker and Dunning 1975).

The external morphology of the two species T. krausbaueri and O. armatus are similar. Both the insects are white, O. armatus is 500-2500μm long and T. krausbaueri is 200-700μm. The morphology of these two species was examined in this thesis using scanning electron microscope and light microscope techniques supported with the taxonomic identification keys of Fjellberg (1980) and Gisin (1960). The use of this combination of approaches highlighted taxonomic differences between the two species which were not clearly identified with the use of the light microscope alone. In particular, the differences in the morphology of the post antennal organ and the pseudocelll of the two species were noted. T. krausbaueri was found to have pseudocelll which were poorly differentiated from the integument and had a poorly identified lid. The pseudocelll of O. armatus had different granulation from the integument, was set in a furrow and had a distinct lid. The post antennal organ in T. krausbaueri consisted of V-shaped sensoral bodies while those of O. armatus were made of oblong shaped sensoral bodies. It has been suggested that T. krausbaueri and O. armatus belong to a species complex (Rusek 1971, Petersen 1975, Lawrence 1979 Pitkin 1980, Brown 1982) and are not distinct species. It is hoped that further studies using the above techniques can help to clarify the taxonomic status of these species.

Correct taxonomic identification to species level was however made for the T. krausbaueri populations used in this thesis.

It is hoped that future research will also use genetic
fingerprinting techniques to further confirm species identification. The above methods will ensure adequate identification of field populations so decisions can be made on which control measures should be taken.

*T. krausbaueri* has been shown in this thesis to graze directly on *B. vulgaris* seedlings. It therefore has a potential to destroy these seedlings if present in sufficient numbers. Brown (1984), has recorded a level of 10 *O. armatus* per litre of subsoil as injurious to crops, while Hansen (1984) records a value of 8-10 Onychiuridae per plant and Feeny (1979) stated that as few as 7 Collembola grazing on each plant can cause damage to the crop. The subsequent failure of crop development after a feeding attack by *T. krausbaueri* can then be due to either direct damage caused by the volume of numbers grazing or by secondary infection of the grazing lesions by fungi or bacteria affecting the growth of the crop (Hansen 1984).

Quantifying insect numbers.

Monitoring the development of a population of soil inhabiting insects in the field poses many problems. It is not possible to observe the insect populations as they develop in the soil. This is because the three dimensional substrate obscures observation. A culture technique was therefore established for *T. krausbaueri* for this study. A water, plaster of paris and charcoal mixture with the ratio of 18:9:1 by volume and a pH of 8 was used to produce a medium on which *T. krausbaueri* could be cultured. The insects carried out their life cycle on the surface of the substrate and so could be observed throughout their life cycle. The patchy nature of distribution of Onychiuridae (Brown 1981a, Curry and Purvis 1982), the possibility of vertical migration in soils and the variety of soil types on which sugar beet is grown (sand, loam and clay etc) also makes accurate sampling of these ametabolous insects difficult. A soil sampling approach will also not necessarily give
the correct information on population numbers. Several soil sampling techniques however do exist (Southwood 1978, Brown 1981) for extracting field populations from the soil, but the distribution of field populations is extremely patchy (Brown pers com.) and exhaustive soil sampling also fails to follow population development as the sampling technique destroys the integrity of the population.

Population cultures of *T. krausbaueri* were established from individual insects extracted from the soil in sugar beet fields at West Driffield Farm, Yorkshire. In the population studies *T. krausbaueri* was found to be parthenogenetic in nature and the following growth stages were identified: juveniles, reproductive and post reproductive insects. The insects developed through a series of moults which occurred throughout their life cycle.

For the purposes of population modelling it was established that the insects length measured from the 1st thoracic segment to the abdomen tip could be used as a measure of insect growth. The populations of *T. krausbaueri* were divided into different developmental stage/size classes on this basis. Size class 1 which contained juveniles measuring up to 250μm, size class 2 contained reproductives measuring 250μm-350μm, size class 3 contained reproductives and these insects measured 350μm-450μm and size class 4 contained post reproductive insects measuring more than 450μm.
Insect Biology

Laboratory populations of *T. krausbaueri* were found to be able to survive and develop on a diet of *B. vulgaris* seedlings. Populations of *T. krausbaueri* were shown to follow a geometric path for growth and this population growth was accelerated by increases in temperature. The time for eggs to hatch once laid was 14-20 days at 15°C and 10-17 days at 20°C. The dietary effect on the insects biology showed that insects feeding on *B vulgaris* although smaller in size, started reproducing earlier than insects cultured on a yeast diet. The largest insects were recorded at a length of 780μm on *S. cerevisiae* diet and 680μm on *B vulgaris*.

Measurements of the soil temperatures in sugar beet fields carried out by Gummerson and Jaggard (1985) recorded values which on a yearly analysis of soils from March to April (1981-1984) showed a mean weekly temperatures fluctuating through a range of 4°C to 22°C. Insect populations were found to develop in laboratory culture at the constant temperatures of 10°C 15°C 20°C and the variable room temperature (4°C-24°C) with populations developing faster at the higher temperatures.

Increases in soil temperatures will therefore accelerate the development of the populations of *T. krausbaueri* and will be an important factor in any pest management strategy.

Establishing crop vulnerability.

Each year, the National Institute of Agricultural Botanists recommend several of the many varieties of sugar beet seeds produced by sugar beet breeders to farmers for use. These varieties might behave differently under pesticide and pest stress. The possibility of a varietal effect was therefore examined. Damage to seedlings of *B. vulgaris* in the field produced by *T. krausbaueri* grazing occurs when the insects are in direct contact with the seedling as has been shown in this study. Collembola are usually found in the top 5cm of soil and *B. vulgaris* seeds are planted to 2.5-3cm in soil (Bray and Thompson 1985).
Seedlings are considered to be particularly vulnerable before the 2-4 true leaf stage is reached. Damage through grazing affecting the hypocotyl and primary roots (Baker and Dunning 1975) or as this study has shown also to the cotyledon.

The germination of four varieties of *B. vulgaris* Julia, IBB83, Primahill and Monoire showed in this study that the final germination percentage and rate was higher when germination was carried out at 20°C compared with 10°C for the Monoire variety. All varieties, Julia, Monoire IBB83 and Primahill showed an asymptotic germination pattern, characteristic of germinating seeds, (Durrant and Payne 1974) when germination percentages were plotted against a time scale. Seeds in all the varieties germinated within three to thirteen days of sowing at 20°C with Primahill achieving 95% germination, Julia 55%, IBB83 80% Monoire 60%. Although these seeds are expected to produce 90% or better germination (National Institute of Agricultural Botanists tests) this was not achieved in the laboratory germination trials for most of the varieties tested. This failure of germination should be taken into account as a possible cause of poor seed emergence from soils.

Brown (1981a) however attributes most of the gappiness in the pattern of emergence of seeds from the soil which could not be attributed to a random distribution, could be because the patchy germination might be characteristic of pest effects. Gummarson and Jaggard (1985) also recorded an increase in the germination percentage of sugar beet with increased temperature through the range 5°C, 10°C, 15°C and 20°C. They also noted a decrease in germination time as the temperature for germination was increased from 5°C to 20°C. The variety Monoire in this study showed similar responses.

The length of the exposure time of the vulnerable growth stages of the crop to *T. krausbaueri* grazing before the crop is vigorous enough to survive attack will therefore depend on the germination rate which will also depend on temperature and crop variety. Although it was established that a diet of *B. vulgaris* could support *T. krausbaueri* populations, the effect of grazing on the development of sugar beet seedlings was not studied under laboratory conditions. The numbers of
Collembola suggested by Curry and Purvis (1982) as injurious to plant growth was small, the distribution of the insect in the field patchy and difficult to assess (Brown 1981a) as is the critical timing of the pest attack which will cause damage at the early stages of germination and growth.

It is hoped that further research will collect information on the behaviour of the population in the field and the numbers of T. krausbaueri which can cause sufficient damage without any secondary infections to affect crop yield so that this can be integrated into any future models.

The growth achieved by B. vulgaris varieties 14 days after germination also showed statistically significant differences for the varieties studied when parameters of root weight, shoot weight, root length, shoot length and the root/shoot ratios for weight and length of the seedlings. Primahill varieties were found to be longer with total mean length of 112.5mm. IBB83 was the smallest after 14 days with a seedling length of 57.8mm. It is therefore expected that as this stage of growth occurs at different rates, the time for the seedlings emergence from the soil will also vary and the choice of the right variety can be made for this part in the seedlings growth.

With the use of the pesticide BHC, the germination and growth patterns for all the varieties of sugar beet were affected by the application of the pesticide at doses of 5.34x10^-7 mg ai ml^-1, 2.18x10^-8 mg ai ml^-1, 3.5x10^-2 mg ai ml^-1. This pesticide effect on germination should not be overlooked.

In fields where the history of the soil has included use of BHC, soil residues of the pesticide might be of a high enough concentration in the vicinity of the germinating seed to produce an effect on germination. Although seeds germinated in the normal sigmoid pattern when pesticide was present, there was a significant (p<0.01) reduction. The largest reduction was by 16% for var Primahill treated with .5x10^-2 mg ai ml^-1 of BHC.
The growth of all the varieties studied was affected at the pesticide concentrations used in this study. The overall weight of seedlings was not significantly affected by the pesticide but the root weight of the varieties increased and the shoot weight decreased. This suggests a change in the utilization of resources for shoot development in the presence of pesticide and therefore a reduction in the rate of root growth. This would again have consequences on the plants ability to obtain nutrients in soil. The length of the seedlings of all the varieties after 14 days was also affected by BHC. There was a reduction in the length of the seedling as the pesticide concentration was increased. Primahill showed an overall reduction in mean seedling length from 112.52mm to 30.55mm at 3.5x10^-2 mg ai ml^-1, and Monore a reduction from a mean value of 132.43mm to 25.93mm. The shoot length of var Monore was also reduced from a mean value of 46.71mm to 19.80mm at the same concentration. Monore again showed the largest reduction in root length and was reduced from a mean value of 85.71mm to 6.13mm at 3.5x10^-2 mg ai ml^-1.

Use of BHC Pesticide.

Gamma BHC is a soil pesticide which since 1960 has been used in sugar beet growing for control of soil pests. By 1984 16% of fields where sugar beet were grown used BHC as a soil applied spray or granules incorporated into the soil at rate of 7.8kg ha^-1 (1.7% active ingredient of lindane) or 1.4 litres ha^-1 of 80% active ingredient or as 1.1kg ha^-1 (Cooke et al 1984, Bray and Thompson 1985) for Collembola pest control.

In addition since 1940 BHC has been applied to seeds during the pelleting stage to act as a crop protection pesticide chemical in the early stages of crop growth. Winder and Dewar (1988), advocate the replacement of BHC as a pesticide application because of possible environmental side effects and suggest that seed treatments which direct application to sites of pest activity should be used in preference to sprays.

Pesticide application has been used as an insurance against pest damage and is applied non selectively to the whole crop field.
Although this approach may be costly to the farmer the cost is thought to be worthwhile.

The development of a cost effective and environmentally acceptable strategy is difficult. Sugar beet is grown on a variety of soil types affected by different rainfall, temperature and other environmental conditions. Once pesticide is applied to the soil, information as to how the pesticide percolates through soil layers can not be readily obtained. Schramm et al (1987) Spencer et al (1988) have however recently produced models which can be used to predict the movement of chemicals in soils. The movement of BHC in soil has been studied by Chessels et al (1988) who used radioactively labelled tracers of BHC. This approach has allowed examination of the amounts of label found in the soil and in the crop. Further research should be carried out to also estimate the amounts of radioactive label found in any associated pests. This will enable researchers to identify the route and nature of the development of toxicity.

At present toxic symptoms are thought to develop at the action sites at the points of synaptic transmission and at the glial cells responsible for the nutrition of axons.

The effects of BHC on B. vulgaris germination and growth has already been discussed and these data suggest that choice of pesticide should be thoroughly evaluated since the crop can be adversely affected by BHC.

Seed dressing with BHC (Czarnecki and Losinski 1985) for the sugar beet AJ-Poly variety was however found not to be effective in control of populations of collembo. 25g, 40g and 50g of 75% Lindane was applied to each kilogram of seed. The composition of collembo did not change with these applications. Populations of collembo developed to the same size as in control treatments after 2 months. Similar results were obtained in this study where pesticide application at sublethal doses failed to destroy populations of T. krausbaueri.
This study has confirmed that *T. krausbaueri* is affected by BHC and toxicity tests show a value for the 24 hour LC₅₀ test to be 4.2 x10⁻⁴ mg ai ml⁻¹. for size class 1, 5.4 x10⁻⁴ mg ai ml⁻¹. for size class 2, 3.6 x10⁻⁴ mg ai ml⁻¹. for size class 3, and 2.9 x10⁻⁴ mg ai ml⁻¹. for size class 4. The first reproductive stage (size class 2) showed the greatest tolerance to BHC in these 24 hour toxicity tests.

Long term studies where the pesticide was in the substrate and in contact with the insect also showed that *T. krausbaueri* populations in contact with BHC at 3.37 x10⁻⁴ mg ai ml⁻¹. had their population development adversely affected. In addition, when the diet of *T. krausbaueri* contained BHC, the population developed at rates which gave Rₘ values (the intrinsic rate of natural increase, the natural log of the population growth rate) which were similar to or higher than the values in those in populations where BHC was not applied. This would concur with Czarnecki and Losinski 1985 study where BHC applied as a seed dressing depleted collembola populations. BHC can therefore affect the long and short term population development of *T. krausbaueri* when sublethal doses are applied.

**Identifying pest vulnerability**

The effect of the pesticide on *T. krausbaueri* can be a lethal or a sublethal one depending on the concentration of the pesticide used and the development stage the insect in contact with the dose is at. This can then affect population development.

Further population studies were therefore carried out to evaluate the Rₘ statistic for *T. krausbaueri*. This identified how the population would behave in specified conditions. The Rₘ value is the intrinsic rate for natural increase and the natural log of the population growth rate (Krebs, 1978) and is a relevant population statistic as it can be used to determine the constant growth rate which is realised for the insect population (Gregoire-Wibo, 1983, Begon and Mortimer 1986).
At the temperatures used for this study $R_m$ values increased with an increase in temperature. The lowest values were 0.0165 at 0.1°C, 0.011 at 15°C. Mean values of 0.041 at room temperature and 0.036 at 20°C were also recorded.

Gregoire-Wibo (1983) records higher $R_m$ values for two other parthenogenetic collembola *F. candida* and *P. armata* which at 21°C gave $R_m$ values of 0.15 and 0.07 respectively. These species like *T. krausbaueri* showed a decrease in the $R_m$ value at lower temperatures. This suggests that for field populations where soil temperatures are high population development of *T. krausbaueri* would be expected to increase.

The effect of diet on the $R_m$ value should not be overlooked Gregoire-Wibo does not state what diet was used in his study but the present work confirms that a change in *T. krausbaueri* diet to the fungi *S. cerevisiae* produces $R_m$ values which were larger at all temperatures except 10°C. At 10°C the $R_m$ values were found to reflect a preference for *B. vulgaris* diet.

Naturally occurring fungi are thought to be part of the diet of soil inhabiting collembola. The size of individual insects and the development of field populations of *T. krausbaueri* therefore merits closer study. Insects were found to be smaller when populations fed on a diet of *B. vulgaris* were compared with ones fed on *S. cerevisiae*. The presence therefore of smaller insects in field samples does not necessarily mean that the population is made up of juveniles but should be reviewed in the context of the diet available for the insects both in the soil and from gut content analysis.

BHC also had an effect on the $R_m$ values of populations. Populations which survived the pesticide doses applied were able to recover and developed to produce $R_m$ values which were similar to those in populations where pesticide was not used. With the application of BHC to the substrate at $3.37 \times 10^{-5}$ mg al ml-1 the population developed with a greatly reduced $R_m$ value of 0.004 suggesting that population
would not survive. At higher substrate concentration of $3.4 \times 10^{-5}$ mg ai ml$^{-1}$ the population failed to develop altogether. The selective toxicity of *T. krausbaueri* to BHC as demonstrated by the LC$_{50}$ tests can result in insects in the reproductive stages surviving and continuing to increase the population numbers. Exposure to BHC at $3.37 \times 10^{-6}$ mg ai ml$^{-1}$ therefore reduced the population size and the $R_m$ value by a factor of 10. With the application of BHC to the diet, the populations were better able to survive pesticide applications. At the highest pesticide treatment used, $3.5 \times 10^{-2}$ mg ai ml$^{-1}$ $R_m$ values for doses of var Primahill was 0.026 and for Monolre 0.035. This compares with treatments in the absence of pesticide which gave values of 0.0302 and 0.0316. The feeding effect of the pesticide is therefore not as critical as the contact effect at the same concentration to population development. Field applications of pesticide should therefore ensure that contact effect is the main one and that uniform distribution of the pesticide is obtained to ensure pests do not escape from areas of pesticide concentration. The population $R_m$ statistic was found to be a useful one for identifying and monitoring changes and differences in population development.

Developing and refining control strategies.

Population growth models based on the Leslie matrix were constructed for individual replicate treatments of population development on the different varieties diets and pesticide treatments. This allowed population development to be simulated. The models obtained were refined and attained sensitivity through continual manipulation of iterative regression equations, with the use of information obtained from culture censuses these models were also validated. Transitional probabilities monitoring population growth of the insects as they passed through the developmental stages in their life cycle were used. A 10 day time period was used to measure changes in the population. The matrix model was validated by using the two size classes (2 and 3) as the developmental stages where reproduction occurred and a fecundity term was introduced into the models.
Calculations of the doubling time of the modelled populations and from the $R_m$ values for the population obtained from regression equations of $\log e N_t$ against $t$ ($t = \text{time}, N = \text{insect numbers}$) allowed the production of final population models which could be run to demonstrate how the population would develop in the future. This approach produced a more realistic model than those of Longstaff (1974, 1976, 1977) which were purely mathematical.

The use of a computer spreadsheet to simulate the development of populations of *T. krausbaueri*, allowed monitoring of the development of the population to be carried out. It also allowed the prediction of population development into future time periods up to and beyond the 90 day period recorded in this thesis, and made information on each developmental stage readily available. This information was obtained for all population treatments which were cultured on diets of Monoiré and Primahill and yeast. Models were also constructed for these cultures with BHC applications.

In the field where critical decisions have to be made on the timing and the nature of pest control, the use of population growth models can only add to the knowledge base from which such decisions are made. Once the computer program has been loaded, variations in the pests diet, ambient temperature, pesticide concentration and population structure can be monitored using the model. The $R_m$ values for the populations which represent the intrinsic rate of increase for the insect can also be used to set limits for the possible population growth.

Using the farmers cultural knowledge of the pest population sizes which can affect crop yield, and the crop size at which the pest causes little damage, decisions on the timing of the pesticide application can be made.
The aims of this thesis were to isolate and study the insect *T. krausbaueri* and its taxonomy, sugar beet varieties and their growth and germination and to evaluate critical points in interactions with the pesticide BHC which might lead to understanding the crop pest pesticide relationship. The above aims were achieved and identification of *T. krausbaueri* clarified using electron microscopy. In addition, a series of Leslie Matrix developmental population growth models for *T. krausbaueri* were developed both as a function of total insect numbers and of insect growth developmental stages. These growth models lend themselves to computer simulation and can form an integral part of a pest control strategy for Sugar beet cultivation.


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JOOSE, E.N.G., Testerink. 1977. The role of food in the population dynamics of ... Orscheschella cincta (Linne) (Collembola). Oecologia (Berl) 29: 189-204.


RIPPER, W., 1930. Champignon-Springschwanze, Biologie und Bekämpfung von Hypogastura manubrialis Tullb. Z. Angew, Entomol. 16: 546-84.


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WINNER, C. 1959, Schäden an Zuckerrüben durch Onychiurus campatus Nachr Bl dt Pflanzenschutzdienst. 11: 67-69


Appendix 1  Arthropods in Soil pest Complex for Sugar beet.

Agriotes lineatus
Agriotes obscurus
Agriotes sputator
Atomaria linearis
Brachdesmus superus
Blaniulus guttulatus
Scutigerella immaculata
Onychiurus armatus
Tullbergia krausbaueri.
Tipula paludosa
Melontha melontha
Phylopertha horticula
Amphimallon solstitialis.
Hydracea micacea.

Collembola found in agricultural soils Ulber 1978.

Ceratophysella denticulata (Bagnall)
Frisea mirabilis (Tullberg)
Onychiurus fimbatus Gisin
Onychiurus campatus Gisin
Onychiurus cancellatus Gisin
Onychiurus tricampatus Gisin
Onychiurus armatus Gisin
Onychiurus subuligginatus Gisin
Onychiurus jubilatiss Gisin
Onychiurus ghidini Denis
Onychiurus fimetarius s Denis
Tullbergia krausbaueri (Borner)
Tullbergia quadrispina (Borner)
Tullbergia denisi (Bagnall)
Folsomia quadrioculata (Tullberg)
Folsomia fimararia (Linne)
Folsomia candida (Willem)
Folsomides parvulus Stach s Gisin
Isotoma notabilis Schaffer
Isotoma viridis Boullet
Entomobrya lanuginosa (Nicolet)
Entomobrya marginata (Tullberg)
Lepidocyrtus cyanus (Tullberg)
Lepidocyrtus langugginosus (Gaelin)
Pseudosinella oocapunctata Borner
Sminthurinus aureus (Lubbock)
Bourletiella hortensis (Fitch)
Sminthuris viridis (Linne)
Appendix 2 Physical properties of BHC.

GAMMA BENZENE HEXACHLORIDE.

LD$_{50}$ for rats  88-91 mg kg$^{-1}$.

Formulations Wettable powder, emulsifiable concentrate, oils, dusts.

Formula C$_6$H$_6$Cl$_6$.  (290.8)

Melting point 112.9°C

Vapour pressure  9.4x10$^{-6}$ mm Hg at 20°C

Solubility at room Temperature 10mg l$^{-1}$ H$_2$O.

Stable to light heat and concentrated acids.

Trade name  LINDANE
Appendix 3  Specimen calculation of Spearman Karber LC50 values for *Tullbergia krausbaueri*.

Legend

\( x \) = \log e concentration of BHC.

\( n \) = number of *Tullbergia krausbaueri* exposed to pesticide concentration.

\( p \) = mortality expressed as a percentage.

\( p^* \) = adjusted mortality percentage so that \( p^* < p < p^* \).
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<thead>
<tr>
<th>concentration BHC ( \text{mg ai ml}^{-1} )</th>
<th>( \log e )</th>
<th>number of insects treated</th>
<th>mortality proportion</th>
<th>mortality proportion adjusted</th>
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1. Log e concentration interval \( (x_{s-1}, x_s) \)

2. Relative frequency \( (p_s = \frac{m}{n} = \frac{\text{mid point of interval}}{(x_{s-1} + x_s) / 2}) \)


4. Product of 2x3 \( -5+0 -3+2+2+0 -2+6+0 -7+6+0 -2+0+3 -2+0+5 -0 -7+6+0 \)

5. Sum of 4 \( \text{antilog of } 5 = LC_{50} \)

\( e^{-2} \) obtained.
Appendix 4. Equations used for spreadsheet models.

Model 1.

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Model 3.

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O_{00} &= 0.0048 \\
P_{00} &= 0.0044 \\
Q_{00} &= 0.004 \\
R_{00} &= 0.0036 \\
S_{00} &= 0.0032 \\
T_{00} &= 0.0028 \\
U_{00} &= 0.0024 \\
V_{00} &= 0.002 \\
W_{00} &= 0.0016 \\
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Z_{00} &= 0.0004 \\
\end{align*}
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228
Appendix 5a  The treatment Leslie matrix model of *Tulibergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var monoire*).

\[
\begin{bmatrix}
  n_1 \\
  n_2 \\
  n_3
\end{bmatrix}
\begin{bmatrix}
  0 & 1.1 & 1.1 & 0 \\
  0.185 & 0.455 & 0 & 0 \\
  0 & 0.578 & 0.535 & 0
\end{bmatrix}
\begin{bmatrix}
  n_1 \\
  n_2 \\
  n_3
\end{bmatrix}_{t+1}
\]

Appendix 5b  Spreadsheet of
The treatment Leslie matrix model of *Tulibergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var monoire*).
The changes within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\( (n_{2+1} = 0.535n_3 + 0.578n_2) \)

\( (n_{2+1} = 0.455n_3 + 1.15n_2) \)

Fecundity  \( (F = 1.1) \)

Legend.

experimental batch title R0
fec = fecundity
R_0 = intrinsic growth rate.
R = finite population growth rate.
n_i = number of insects in stage i at time t, t+1, t+2 etc.
N = Total population number.
Appendix 6a The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. monole*). treated with pesticide BHC at 3.37x10^-6 mg al ml^-1. applied to substrate.

\[
\begin{bmatrix}
 n_1_{t+1} \\
n_2_{t+1} \\
n_3_{t+1}
\end{bmatrix} = \begin{bmatrix}
 0 & 1.4 & 1.4 & 0 \\
 0.171 & 0.565 & 0 & 0 \\
 0 & 0.336 & 0.585 & 0 \\
\end{bmatrix} \begin{bmatrix}
 n_1_t \\
n_2_t \\
n_3_t
\end{bmatrix}
\]

Appendix 6b Spreadsheet of

The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. monole*). treated with pesticide BHC at 3.37x10^-6 mg al ml^-1. applied to substrate.

The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[
\begin{align*}
(n_{3+1} = 0.585n_3 + 0.336n_2) \\
(n_{2+1} = 0.565n_2 + 0.174n_1)
\end{align*}
\]

Fecundity \( F = 1.4 \)

Legend.

- **experimental batch title R25**
- **fec** = fecundity
- **R** = intrinsic growth rate.
- **R** = finite population growth rate.
- **n** = number of insects in stage i at time t, t+1, t+2 etc.
- **N** = Total population number.

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| fcc       | 1.40        |

| Mt        | 100.00      |
| r4        | 0.00        |
| R         | 1.00        |

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| 99.59     | 100.20     | 100.51    | 100.92    | 101.23    |
| 1.00      | 1.00       | 1.00      | 1.00      | 1.00      |

231
Appendix 7a: The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var primahill*).

\[
\begin{bmatrix}
0 & 0.8 & 0.8 & 0 \\
0.152 & 0.632 & 0 & 0 \\
0 & 0.636 & 0.633 & 0 \\
0 & 0 & 1.21 & 0.308
\end{bmatrix}
\begin{bmatrix}
\mathbf{n}_1 \\
\mathbf{n}_2 \\
\mathbf{n}_3 \\
\mathbf{n}_4
\end{bmatrix}

= \begin{bmatrix}
\mathbf{n}_1 \\
\mathbf{n}_2 \\
\mathbf{n}_3 \\
\mathbf{n}_4
\end{bmatrix}
\]

Appendix 7b: Spreadsheet of

The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var primahill*). The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[n_{3t+1} = 0.632n_{3t} + 0.192n_{4t}\]
\[n_{2t+1} = 0.633n_{3t} + 0.308n_{4t}\]
\[n_{1t+1} = 0.308n_{3t} + 1.21n_{4t}\]

Fecundity (F = 0.8)

Legend.

- **ec** = fecundity
- **s** = intrinsic growth rate.
- **f** = finite population growth rate.
- **n** = number of insects in stage i at time t, t+1, t+2 etc.
- **T** = Total population number.
Appendix 8a: The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. primahill*) treated with pesticide BHC at 5.34x10^-7 mg ai ml^-1.

\[
\begin{bmatrix}
1.43 & 0.2 & 0 & 0 \\
0 & 0.45 & 0 & 0 \\
0 & 0 & 0.70 & 0 \\
0 & 0 & 0 & 0.35
\end{bmatrix}
\begin{bmatrix}
N_1 \\
N_2 \\
N_3 \\
N_4
\end{bmatrix}
= 
\begin{bmatrix}
N_1 \\
N_2 \\
N_3 \\
N_4
\end{bmatrix}
\]

Appendix 8b: Spreadsheet of
The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. primahill*) treated with pesticide BHC at 5.34x10^-7 mg ai ml^-1. The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model:

\( \ln n_{a+1} = 0.350n_a + 0.415n_{a+1} \)

\( \ln n_{b+1} = 0.701n_a + 0.460n_{a+1} \)

\( \ln n_{c+1} = 0.351n_a + 1.43n_{a+1} \)

Fecundity (\( F = 0.2 \))

Legend:

C = fecundity
= intrinsic growth rate.
= finite population growth rate.
\( t \) = number of insects in stage \( i \) at time \( t, t+1, t+2 \) etc.
= Total population number.
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Appendix 9a: The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. primahill*) treated with pesticide BHC at $3.34 \times 10^{-7}$ mg ai ml$^{-1}$.

\[
\begin{bmatrix}
 n_{1t+1} \\
 n_{2t+1} \\
 n_{3t+1} \\
 n_{4t+1}
\end{bmatrix} =
\begin{bmatrix}
 0 & 0.6 & 0 & 0 \\
 0.42 & 0.1 & 0 & 0 \\
 0 & 0.53 & 0.83 & 0 \\
 0 & 0 & 0.2 & 0.73
\end{bmatrix}
\begin{bmatrix}
 n_{1t} \\
 n_{2t} \\
 n_{3t} \\
 n_{4t}
\end{bmatrix}
\]

Appendix 9b: Spreadsheet of
The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. primahill*) treated with pesticide BHC at $5.34 \times 10^{-7}$ mg ai ml$^{-1}$. The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[
\begin{align*}
 n_{3t+1} &= 0.730n_{3t} + 0.200n_{2t} \\
 n_{3t+1} &= 0.833n_{3t} + 0.531n_{2t} \\
 n_{3t+1} &= 0.100n_{3t} + 0.420n_{1t}
\end{align*}
\]

Fecundity ($F = 0.6$)

Legend.

- ec = fecundity
- \( \gamma \) = intrinsic growth rate.
- \( \lambda \) = finite population growth rate.
- \( n_i \) = number of insects in stage i at time t, t+1, t+2 etc.
- \( N \) = Total population number.

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The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var monoire*).

\[
\begin{bmatrix}
0 & 0.01 & 0.01 & 0 \\
0.298 & 1.07 & 0 & 0 \\
0 & 1.69 & 0.363 & 0 \\
0 & 0 & 0.065 & 0.314 \\
\end{bmatrix}
\begin{bmatrix}
N_1 \\
N_2 \\
N_3 \\
N_4 \\
\end{bmatrix}
\]

\[t+1\]

The change within the population developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[n_{a+1} = 0.314n_a + 0.065n_{a-1}\]
\[n_{a+1} = 0.353n_a + 1.69n_{a-1}\]
\[n_{a+1} = 1.07n_a + 0.298n_{a-1}\]

Fecundity \(F = 0.01\)

Legend

- \(X0\) = fecundity
- \(\lambda\) = intrinsic growth rate.
- \(r\) = finite population growth rate.
- \(n_i\) = number of insects in stage \(i\) at time \(t, t+1, t+2\) etc.
- \(N\) = Total population number.

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| detand | enter | stoch | cell | n+1 | cell | n+2 | cell | n+3 | cell | n+4 |
|--------|-------|-------|------|-----|------|-----|------|-----|------|-----|-----|
| 9.90   | 0.21  | 2.83  | 3.00 | 1.19| 4.30 | 1.38| 7.29 | 2.26| 9.35 |
| 15.10  | 0.07  | 0.57  | 42.23| 3.20| 82.50| 5.62| 109.40| 7.09| 121.05|
| ...    | ...   | ...   | ...  | ... | ...  | ... | ...  | ... | ...  | ... |
| 25.00  | 1.69  | 42.34 | 42.72| 72.20| 45.83| 77.46| 49.31| 82.34| 53.17|
| 50.00  | 0.30  | 14.58 | 0.41 | 0.12| 0.52 | 0.27| 1.35 | 0.46| 1.58 |
| 0.01   |       |       |      |     |      |      |      |     |      |
| Mt     | 110.00|       | 96.17| 140.72| 166.95| 165.35|
| tm     | 0.03  |       | 0.56 | 1.45| 1.19 | 1.11|
| X      | 1.03  |       |      |     |      |      |      |     |      |
| cell   | n+5   | cell  | n+6 | cell | n+7 | cell | n+8 | cell | n+9 |
| 7.92   | 132.67| 8.64 | 143.95| 9.25| 155.29| 10.18| 167.75| 10.90| 181.05|
| 43.01  |       | 46.90| 58.79| 54.65| 59.21|
| 89.06  | 57.36 | 56.95| 61.99| 106.61| 66.40| 112.85| 72.49| 121.83| 77.80|
| 56.89  | 61.30 | 66.23| 71.48| 77.14|
| 0.47   | 1.78  | 0.52 | 1.90 | 0.57| 2.06 | 0.61| 2.22 | 0.56| 2.49|

242.04  215.70  237.38  256.28  276.22
1.03  1.00  1.00  1.00  1.00

238
The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (Beta vulgaris var monoïre) treated with pesticide BHC at 5.34x10^{-7}mg at ml⁻¹. 

\[
\begin{bmatrix}
0 & 0.6 & 0 & 0 \\
0.629 & 0.228 & 0 & 0 \\
0 & 0.551 & 0.486 & 0 \\
\end{bmatrix}
\begin{bmatrix}
n_1 \\
n_2 \\
n_3 \\
\end{bmatrix}
= 
\begin{bmatrix}
n_1 \cr n_2 \cr n_3 \cr
\end{bmatrix}
.t+1.

The change within the populations developmental stage structure in each time interval are shown.

gression equations used for the model.

\[
(n_{3_{t+1}}) = 0.486n_{3_t} + 0.551n_{2_t}
\]
\[
(n_{2_{t+1}}) = 0.228n_{3_t} + 0.692n_{2_t}
\]

ecundity \quad (F = 0.6)

legend.

**x21**

ec = fecundity

\(m\) = intrinsic growth rate.

\(r\) = finite population growth rate.

\(n\) = number of insects in stage i at time t, t+1, t+2 etc.

\(N\) = Total population number.
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<td>0.59</td>
<td>34.60</td>
<td>24.60</td>
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| locs  | 0.50  |

| UL    | 100.00| 86.74   | 56.29     | 57.68     | 101.42    |
| ra    | 0.36  |
| X     | 1.03  | 0.87    | 1.11      | 1.01      | 1.04      |

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<th>cell nt+8</th>
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<td>39.46</td>
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<td>29.78</td>
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</table>

| 104.75     | 100.30    | 111.55    | 115.72    | 119.63    |
| 1.03       | 1.03      | 1.03      | 1.03      | 1.03      | 1.03      |

240
Appendix 12a: The treatment Leslie matrix model of *Tulibergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. monoirae*) treated with pesticide BHC at 2.16x10⁻³mg ai ml⁻¹.

\[
\begin{pmatrix}
0 & 2.1 & 2.1 & 0 \\
0.206 & 0.163 & 0 & 0 \\
0 & 0.642 & 0.436 & 0 \\
0 & 0 & 0.033 & 0.339
\end{pmatrix}
\begin{pmatrix}
n_1 \\
n_2 \\
n_3 \\
n_4
\end{pmatrix}
= \begin{pmatrix}
n_1 \\
n_2 \\
n_3 \\
n_4
\end{pmatrix}
\]

\[
t+1
\]

Appendix 12b: Spreadsheet of
The treatment Leslie matrix model of *Tulibergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. monoirae*) treated with pesticide BHC at 2.16x10⁻³mg ai ml⁻¹. The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[n_1 = .339n_3 + .033n_2\]
\[n_2 = .436n_3 + .642n_4\]
\[n_3 = .163n_4 + .206n_1\]

Fecundity \( F = 2.1 \)

Legend.

*ec* = fecundity
\( r_m \) = intrinsic growth rate.
\( r_f \) = finite population growth rate.
\( n_1 \) = number of insects in stage 1 at time t, t+1, t+2 etc.
\( N \) = Total population number.
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<td>0.64</td>
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| fase | 2.10 |

| nat | 100,00 |
| n3L | 9.03   |
| n2L | 1.03   |

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<td>0.72</td>
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<td>0.75</td>
<td>23.37</td>
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<td>88.70</td>
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| 133.66    | 137.87    | 142.25    | 146.99    | 151.00    |
| 1.03      | 1.03      | 1.03      | 1.03      | 1.03      |

242
Appendix 13a: The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. monoir* treated with pesticide BHC at 3.5x10^-2 mg ai ml^-1.

\[
\begin{bmatrix}
    n_1 \\
    n_2 \\
    n_3
\end{bmatrix}
= 
\begin{bmatrix}
    0 & 2.2 & 2.2 & 0 \\
    0.861 & 0.523 & 0 & 0 \\
    0 & 0.618 & 0.685 & 0
\end{bmatrix}
\begin{bmatrix}
    n_1 \\
    n_2 \\
    n_3
\end{bmatrix}
\]

\[t+1\]

\[t\]

Appendix 13b: Spreadsheet of

The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of Sugar beet (*Beta vulgaris var. monoir* treated with pesticide BHC at 3.5x10^-2 mg ai ml^-1.

The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[(n_{3_{t+1}}) = .685n_{3_{t}}+.618n_{2_{t}}\]
\[(n_{2_{t+1}}) = .528n_{2_{t}}+.085n_{1_{t}}\]

Fecundity \(F = 2.2\)

Legend.

- experimental batch title X5
- fec = fecundity
- \(R_m\) = intrinsic growth rate.
- \(R\) = finite population growth rate.
- \(n_{i_{t}}\) = number of insects in stage i at time t, t+1, t+2 etc.
- \(N\) = Total population number.
- fec = fecundity
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</table>

244
The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of yeast (*Saccharomyces cervisiae*)

\[
\begin{bmatrix}
0 & 0.1 & 0.1 & 0 \\
0.358 & 0.470 & 0 & 0 \\
0 & 0.465 & 3.53 & 0 \\
0 & 0 & 0.201 & 0.750 \\
\end{bmatrix}
\begin{bmatrix}
N_1 \\
N_2 \\
N_3 \\
N_4 \\
\end{bmatrix}
\]

\[ t+1 \]

Spreadsheet of

The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[
\begin{align*}
(n_{2, t+1}) &= 0.750n_{1, t} + 0.201n_{3, t} \\
(n_{3, t+1}) &= 3.53n_{2, t} + 0.465n_{4, t} \\
(n_{4, t+1}) &= 0.470n_{2, t} + 0.358n_{1, t} \\
\text{fecundity} &= (F = 0.1)
\end{align*}
\]

Legend:

- Experimental batch title VO
- \(c\) = fecundity
- \(r\) = intrinsic growth rate
- \(r_e\) = finite population growth rate
- \(n_i\) = number of insects in stage \(i\) at time \(t\), \(t+1\), \(t+2\) etc.
- Total population number.
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246
Appendix 15a: The treatment Leslie matrix model of Tullbergia krausbaueri cultured at 20°C on a diet of yeast (Saccharomyces cervisiae) treated with BHC at 5.34x10^{-7} mg ai ml^{-1}.

\[
\begin{bmatrix}
  n_{1t} \\
  n_{2t} \\
  n_{3t} \\
  n_{4t}
\end{bmatrix}
= \begin{bmatrix}
  0 & 0.1 & 0.1 & 0 \\
  1.4 & 0.765 & 0 & 0 \\
  0 & 0.492 & 2.143 & 0 \\
  0 & 0 & 0.019 & 0.866
\end{bmatrix}
\begin{bmatrix}
  n_{1t} \\
  n_{2t} \\
  n_{3t} \\
  n_{4t}
\end{bmatrix}
\]

Appendix 15b: Spreadsheet of The treatment Leslie matrix model of Tullbergia krausbaueri cultured at 20°C on a diet of (Saccharomyces cervisiae) treated with BHC at 5.34x10^{-7} mg ai ml^{-1}. The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[
\begin{align*}
(n_{4t+1} &= 0.866n_{4t} + 0.019n_{3t}) \\
(n_{3t+1} &= 2.14n_{3t} + 0.492n_{2t}) \\
(n_{2t+1} &= 0.765n_{2t} + 1.40n_{1t})
\end{align*}
\]

Fecundity \( F = 0.1 \)

Legend.

experimental batch title V21

\( f_{ec} \) = fecundity

\( R_{m} \) = intrinsic growth rate.

\( R \) = finite population growth rate.

\( n_{i} \) = number of insects in stage \( i \) at time \( t, t+1, t+2 \) etc.

\( N \) = Total population number.

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| detadda | stack | cell | nt+1 | cell | nt+2 | cell | nt+3 | cell | nt+4 | cell |
|---------|-------|------|------|------|------|------|------|------|------|------|------|
| v21     | enter | enter |      |      |      |      |      |      |      |      |      |
| ctt     | 9.00  | 0.97 | 7.79 | 8.40 | 7.66 | 5.80 | 9.46 | 9.29 | 14.68 | 12.64 |      |
| nct     | 15.66 | 0.92 | 0.29 | 44.82 | 9.65 | 14.23 | 2.67 | 336.69 | 6.44 | 758.27 | 14.41 |
|         |       |      |      |      |      |      |      |      |      |      |      |
|         | 2.74  | 32.10 |      |      |      | 300.23 |      |      | 720.94 |      | 1622.69 |
| nct     | 36.89 | 0.49 | 12.79 | 99.99 | 44.23 | 74.51 | 36.66 | 75.87 | 37.33 | 88.11 | 43.25 |
|         | 0.76  | 19.29 |      |      |      | 60.77 |      |      | 57.60 |      | 50.94 |
|         |      |      |      |      |      |      |      |      |      |      | 67.40 |
| nlt     | 58.69 | 1.48 | 79.00 | 4.10 | 5.74 | 13.40 | 18.87 | 21.48 | 39.47 | 41.20 | 57.79 |
| fecc    |       | 0.10 |      |      |      |      |      |      |      |      |      |
| Nt      | 100.00 |       |      |      | 146.96 |      | 236.13 |      | 443.70 |      | 942.25 |
| Pr      | 6.64  |       |      |      | 1.47  |      | 1.61  |      | 1.88  |      | 2.63  |
| B       | 2.16  |       |      |      |      |      |      |      |      |      |      |
| nt+5    | cell  | nt+6 | cell  | nt+7 | cell  | nt+8 | cell  | nt+9 |      |      |      |
|         | 27.85 | 23.42 | 53.19 |      |      |      |      |      |      |      |      |
|         | 1666.44 |       | 31.65 | 1625.52 |      |      |      |      |      |      |      |
|         | 3558.32 |       | 7761.60 |      |      |      |      |      |      |      |      |
|         | 125.19 |       | 61.59 | 214.26 |      |      |      |      |      |      |      |
|         | 95.77  |       | 163.91 |      |      |      |      |      |      |      |      |
|         | 84.64  |       | 110.49 | 173.12 |      |      |      |      |      |      |      |
|         | 256.77 |      | 284.12 |      |      |      |      |      |      |      |      |
|         | 537.77 |      | 828.17 |      |      |      |      |      |      |      |      |
|         | 1159.44 |      | 1709.44 |      |      |      |      |      |      |      |      |
|         | 5722.43 |      | 16372.67 |      |      |      |      |      |      |      |      |
|         | 2.11  |      | 2.14  |      |      |      |      |      |      |      |      |
|         | 2.15  |      | 2.16  |      |      |      |      |      |      |      |      |
|         | 2.16  |      |      |      |      |      |      |      |      |      |      |

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Appendix 16a: The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of yeast (*Saccharomyces cervisea*) treated with BHC at $8.75 \times 10^{-3}$ mg ai ml$^{-1}$.

$$\begin{bmatrix}
    n_1 \\
    n_2 \\
    n_3 \\
    n_4 \\
\end{bmatrix}_{t+1} = \begin{bmatrix}
    0 & 0.27 & 0.27 & 0 \\
    0.633 & 0.446 & 0 & 0 \\
    0 & 0.52 & 0.790 & 0 \\
    0 & 0 & 0.173 & 0.451 \\
\end{bmatrix} \cdot \begin{bmatrix}
    n_1 \\
    n_2 \\
    n_3 \\
    n_4 \\
\end{bmatrix}_t$$

Appendix 16b: Spreadsheet of

The treatment Leslie matrix model of *Tullbergia krausbaueri* cultured at 20°C on a diet of (*Saccharomyces cervisea*) treated with BHC at $8.75 \times 10^{-3}$ mg ai ml$^{-1}$. The change within the populations developmental stage structure in each time interval are shown.

Regression equations used for the model.

\[
\begin{align*}
(n_{4t+1} &= 0.451n_{2t} + 0.173n_{3t}) \\
(n_{3t+1} &= 0.790n_{3t} + 0.52n_{2t}) \\
(n_{2t+1} &= 0.446n_{2t} + 0.633n_{1t})
\end{align*}
\]

Fecundity ($F = 0.27$)

Legend.

experimental batch title V7
fec = fecundity
$R_m$ = intrinsic growth rate.
$R$ = finite population growth rate.
$n_{\star t}$ = number of insects in stage 1 at time $t$, $t+1$, $t+2$ etc.
$N$ = Total population number.
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