Aspects of the ecology of *Tyria jacobaeae.* (L.). A defoliator of Ragwort in New Zealand.

A thesis presented in partial fulfilment
of the requirements for the degree
of

Master of Science
in **Zoology** at
Massey University

Warwick Gray Beban
1991

TABLE OF CONTENTS.

ABSTRACT.

Tyria jacobaeae L. (Lepidoptera: Arctiidae) was introduced to New Zealand as a biological control agent for ragwort *Senecio jacobaea* (L.), a poisonous pasture weed. This study investigated the diapause, pupal survival, population ecology and impact of *T. jacobaeae* on ragwort populations in the Wairarapa. Particular emphasis was placed on those aspects influencing the ability of *T. jacobaeae* to control ragwort.

T. jacobaeae enters obligatory pupal diapause over the winter months. The temperature requirements of *T. jacobaeae* pupae were investigated under controlled and natural conditions. Diapause development was completed after approximately 105 under field conditions and 70 days at 2°C. The minimum temperature for post diapause development indicated pupae were unlikely to enter post diapause quiescence following diapause development in the Wairarapa. The production of two generations of *T. jacobaeae* in a single season will be of little benefit, however storage of quiescent pupae for delayed release is feasible. Pupal survival was largely determined by exposure and substrate under natural conditions.

Strong density dependent mortality was detected among caged larvae, and increased larval density reduced pupal dimensions, weight and potential fecundity. No evidence of the diseases known to infect *T. jacobaeae* overseas was observed.

Natural *T. jacobaeae* populations showed no controlling influence on the ragwort population studied. High larval mortality, a patchy distribution over the host population and rapid ragwort regrowth reduced the effectiveness of T. jacobaeae as a biological control agent. At the most intensively studied site the *T. jacobaeae* population appears to have stabilised at a level below that required for ragwort control. The presence of *T. jacobaeae* was well synchronised with ragwort flowering in the field, and *T. jacobaeae* seems to have adapted to the climatic conditions of the Wairarapa.

ACKNOWLEDGEMENTS.

I wish to express my sincere gratitude to Drs. I. Stringer, Massey University, and P. McGregor, DSIR, for their encouragement, supervision and patience over the course of this study. Thank you both.

I would also like to particularly thank:

- Stephen Pilkington for his assistance with the photography and production of the final copy of this thesis.

- My family: my parents Rock and Judy Beban and brother Grant, for the continued interest, support and encouragement that I am most grateful for.

- The Taylor Family: Thank you for all you have done for me.

- Robyn Taylor: while I wrote this thesis, Robyn did almost everything else. I am grateful for Robyns patience, understanding and constant support.

- To the staff and students of the Botany and Zoology department at Massey University: thank-you for your friendship and encouragement

LIST OF FIGURES.

LIST OF PLATES.

INTRODUCTION

(1.1) Introduction.

Ragwort, *Senecio jacobaea* L. (Compositae), was first recorded in New Zealand near Dunedin in 1874 (Thomson 1922). The plant was accidentally introduced, possibly as a seed contaminant (Radcliffe 1969). It spread rapidly north and established well in areas with rainfall exceeding 890mm per year (Poole and Cairns 1940). Ragwort quickly became a serious pasture weed and was first declared noxious in 1900 (Thomson 1922).

Ragwort is an aggressive weed, reproducing prolifically both from seed and by vegetative growth. Concern over the presence of ragwort in New Zealand pasture stems from two features of the plant's ecology:

(1) It competes with pasture plants for space and resources, often forming dense populations and reducing the stock carrying capacity of land.

(2) Pyrrolizidine alkaloids in its tissues are toxic if ingested by livestock such as cattle, deer, horses and to a lesser extent sheep.

Control of ragwort was initially attempted by herbicidal sprays, mowing of infested paddocks and the labour intensive method of chipping plants. Early workers were optimistic that the cinnabar moth *Tyria jacobaeae* L. (Lepidoptera: Arctiidae) could control ragwort in New Zealand (Miller 1929). *T. jacobaeae* was attractive as a biological control agent because the larval stage is monophagous and periodically defoliates ragwort plants (Cameron 1935). This led to an early attempt at biological control with the importation and release of *T. jacobaeae* into New Zealand between 1929 and 1932 (Miller 1970).

In other countries much information was available on *T. jacobaeae* and its interactions with *S. jacobaea*, however, information on the ecology of *T. jacobaeae* under New Zealand conditions was limited (Miller 1929, 1970). In addition, the effectiveness of *T. jacobaeae* as a long term control agent had not been ascertained. Little research has been undertaken to obtain quantitative data on *T. jacobaeae* and its relationship with ragwort in New Zealand. Much of the published work comprises casual observations (Wise 1952; Meads 1973), reviews of general biology and the introduction and establishment of *T. jacobaeae* in this country (Helson 1974; Syrett 1983, 1989). Important gaps in current knowledge include studies of the insects phenology, mortality and impact on ragwort populations in New Zealand conditions, which are very different from those where *T. jacobaeae* exists naturally.

My research encompassed several aspects of the ecology of *T. jacobaeae* in New Zealand, aimed at evaluating its ability to control ragwort. I concentrated on two areas of the moth's ecology that affect its role as a biological control agent. These were the insect's population ecology and its diapause.

(1.2) Biology of *T. jacobaeae.*

T. jacobaeae has a univoltine life cycle, over wintering as diapausing pupae (Plate 1). Following this obligatory diapause adults emerge in New Zealand during spring, some as early as August (Miller 1970) (Plate 2). Adult numbers slowly increase over September and October and the majority of the population emerges over November and December. Adult emergence in the native range is generally well synchronised. Myers (1979) showed that food limitation in the preceding summer did not select for earlier moth emergence. Instead she concluded that adult emergence is synchronized with ragwort flowering. This conclusion seems plausible, considering the close relationship between *T. jacobaeae* and ragwort.

Females mate once and thereafter are unattractive to males (Rose 1978). The female may live for two to three weeks in the field and larger moths generally live longer than smaller ones (Dempster 1971a). The number of eggs laid between individual females and females in different habitats can be quite variable. Dempster (1982) obtained up to 600 eggs from one female under laboratory conditions and considered this to be the maximum potential fecundity. Generally 90 - 265 eggs are laid under New Zealand conditions (Miller 1970). Female weight at emergence is related to both fecundity and longevity (Dempster 1971a), while the weight of the emerging adult is in turn affected by larval weight at pupation. This is a function of the amount and quality of food available to developing larvae, and this is affected by both larval and ragwort density.

(1.2.1) Introduction and establishment.

The native range of *T. jacobaeae* covers much of Europe, excluding the far north, and eastward into Asia (Dempster 1982). *T. jacobaeae* has been introduced by man to control ragwort in Canada, America, Australia and New Zealand (Harris *et al.* 1975; Frick and Halloway 1964; Bornemissza 1966; Miller 1929, 1970).

Plate 1. *T. jacobaeae* pupae Length approximately 11mm, width approximately 5mm.

Plate 2. Adult *T. jacobaeae* (male).

T. jacobaeae was imported to New Zealand from England as pupae and eggs between 1926 and 1931 (Miller 1970), but the eggs failed to hatch (Miller 1970). During initial releases in New Zealand some 3,400,000 eggs obtained from New Zealand bred adults were mainly distributed in Nelson, Auckland, Taranaki, Wairarapa and Southland between 1929 and 1932 (Helson 1974).

Subsequently, populations of *T. jacobaeae* established, but later disappeared from many areas. Large numbers of *T. jacobaeae* were reported from Horahora, on the Waikato River, in 1941 (Syrett 1983) and an adult was found in the Wairarapa at Masterton in 1951 (Wise 1952). *T. jacobaeae* is now present over most of the Wairarapa, as far north as Dannevirke. It is now found in Wellington and Westward in the Manawatu and in the South Island in Westland (pers. obs.1990; Syrett 1989).

Since 1982 there have been renewed efforts to redistribute *T. jacobaeae*. Re-releases of insects collected from the Wairarapa were made at nearly 20 sites throughout New Zealand but with mixed results. The success of long term establishment at the re-release sites has not been ascertained, however, numbers are increasing at several sites in Westland (Syrett 1984, 1989). Factors affecting establishment of *T. jacobaeae* in this country are not fully understood.

(1.2.2) Oviposition.

The size of egg batches varies widely with a mean of 30 - 40 eggs/batch (Plate 3). Dempster (1982) noted that up to 150 eggs may be laid in a single cluster. He also reported that the mean number per cluster varied between years and populations, ranging from 19.2 - 43.1 eggs/batch over 10 years at Weeting Heath, England (Dempster 1982). Myers and Campbell (1976b) found 25.6 - 58.1 eggs per batch for different localities in North America during the same year. They also suggested dispersal of larvae is related to plant spacing and showed that egg batch size was equal to, or slightly larger than, the number of larvae that could be supported by an average sized food plant. In addition, when plant density was high, egg batches were more clumped and individual batches were smaller than on comparable plants in low density populations.

Dempster (1982) however, disputed the conclusions of Myers and Campbell (1976b). He claimed that both the statistical analysis and interpretation of their results were inappropriate. He concluded that the patterns of dispersion observed in field populations are because larger ragwort plants receive more eggs and because of the agonistic reaction of later instar larvae to one another. While Dempster's populations at Weeting Heath may have behaved differently from those in North America, Myers and Campbell's paper does appear unconvincing. Certainly, Dempster's (1982) explanation is simpler and does not assume the plasticity of *T. jacobaeae* behaviour suggested by Myers and Campbell.

Richards and Myers (1980) found that egg weight decreases over the oviposition period. Heavier eggs are more likely to hatch, so eggs laid later are less likely to hatch. Hatching occurs 4 - 20 days after oviposition and is influenced by ambient temperature (Rose 1978). Under normal New Zealand field conditions eggs hatch after approximately 13 days. Eggs require 64.1 day degrees above 11°C for full development (Harman, Dymock and Syrett 1988).

(1.2.3) Larvae.

First instar larvae are gregarious, clumping together around the egg batch. Their grey/green colour is cryptic against ragwort leaves. Second instars are characteristically banded with black and yellow (Plate 4). There are 5 larval instars, and total development takes between 26 and 34 days under field conditions (Cameron 1935; Miller 1970; Dempster 1982). Development from egg to pupa takes 383.1 ± 5.9 day-degrees above 11°C (Harman, Dymock and Syrett 1988).

Early instar mortality can be very high. Dempster (1982) stated that, generally, 50% to 80% of larvae die between hatching and the end of the second instar. At his Weeting Heath site between 32% and 85% of larvae died by the end of the second instar and he attributed this mortality largely to arthropod predators, which caused 28.6% - 89.1% (mean 56.9%) mortality over 9 years. His earlier studies (Dempster 1971) estimated that total mortality from egg to adult ranged from 80.6% to 99.99% at Weeting Heath.

Plate 3. Eggs of *T. jacobaeae* laid on the underside of a basal leaf. Note bright yellow colour of eggs, prior to hatching eggs appear dark grey.

Plate 4. *T. jacobaeae* larva on the flowers of ragwort.

The only published information on larval mortality in New Zealand was that of Miller (1970) who found that parasitism by *Pales casta* (Hutton) (Diptera: Tachinidae) affected 53.19% to 78.12% of larvae. The native shining cuckoo (*Lamprococcyx lucidus*) and the common, introduced house sparrow (*Passer domesticus*) prey on the moth, while the cuckoo and perhaps the starling (*Sternus vulgaris*) eat larvae (Miller 1970). Miller (1970) also recorded that newly formed, soft pupae are attacked by *Echthromorpha intricatoria* (F.), but his estimate of the rate of parasitism as "moderate " is, unfortunately, meaningless.

As larvae develop, their distribution on the plant changes. After initially clustering on the lower leaves, they move up the plant to feed preferentially on the capitula and flowers (Plate 5). They become less gregarious and begin to behave antagonistically toward each other. Van der Meijden (1976) calculated Lloyd's (1967) measurement of mean crowding, m^* (*mean number per individual of other individuals in same quadrat*) for natural populations in Holland. At the end of the first instar m^* per leaf dropped rapidly. This reduction continued at a slower rate for older instars. While spacing undoubtedly does increase, attempts to quantify this may produce overestimates because of high mortality during the first instar. Fourth and fifth instar larvae are more likely than earlier instars to move between plants. This inter-plant movement often occurs before the plant is defoliated, and the rate of movement increases with increasing plant damage (van der Meijden 1976).

Larvae store the poisonous alkaloids that they ingested from eating ragwort foliage. This, and their bright colour, ensures some protection against vertebrate predators. Aplin and Rothschild (1972) found that all six of the alkaloids contained in ragwort foliage were present in *T. jacobaeae* pupae. Formanowicz and Brodie (1985) showed that some vertebrate predators learned to avoid larvae after earlier attempts at feeding.

Newly hatched larvae weigh about 0.2 - 0.3mg (Dempster 1982) while fifth instar larvae must weigh at least 140 - 150mg to pupate successfully (Dempster 1971; van der Meijden 1976). Absolute weight gain is greatest during the fifth instar which lasts about twice as long as any other instar.

Plate 5. *T. jacobaeae* larvae feeding on ragwort capitula. Note the stripping of foliage and damage to the capitula (Kaipororo Road 1989/90).

(1.2.4) Feeding habits.

T. jacobaeae is monophagous and in this respect it is ideal for the biological control of ragwort. Females will lay eggs on plants other than ragwort, with groundsel (*Senecio vulgaris*) being the most common alternative. However, ragwort appears to be the only plant that supports larval growth. Parker (1959) showed through no-choice starvation tests that many plant species, some of which *T. jacobaeae* larvae had been observed on, were either unattractive to the larvae, or did not allow normal growth. Preference and oviposition tests were carried out in New Zealand on a wide range of vegetable, crop and pasture plants (Miller 1970). In these starvation tests larvae avoided many of the plants tested and ate only a few. Those larvae that did feed on plants other than ragwort were unable to continue normal development. Miller (1970) also noted that oviposition occurred on some of the plants tested, especially when ragwort flowers were present, but emerging larvae died on all except groundsel.

(1.3) Biology of *Senecio jacobaea.*

The size and vigour of the individual ragwort plant varies widely and depends on soil type. Dempster (1971a) records ragwort at Weeting Heath, an area of poor sandy soil and limiting rainfall, generally produced only one flowering stem some 20 - 30cm in height. Under more favourable conditions a plant may produce a dozen stems and reach 180cm in height (Poole and Cairns 1940; Schmidl 1972).

(1.3.1) Distribution.

The native range of Ragwort, *Senecio jacobaea* (Compositae), includes the British Isles, Europe, Asia minor and Siberia (Harper and Wood 1957). Ragwort has been accidentally introduced by man to North and South America, South Africa, Canada, Australia and New Zealand. It is a plant of open well drained sites in medium to light textured soils of medium to high acidity (pH 3.95 - 8.2 in England Harper (1958)). Its distribution in New Zealand is determined by soil type and the requirement of a minimum annual rainfall of 890mm (Poole and Cairns 1940). Ragwort may be absent from areas where the water table is high (Harper and Wood 1957; van der Meijden 1974), or where summer drought kills young seedlings (van der Meijden 1971; Wardle 1987). These requirements have allowed ragwort to establish in New Zealand over most of the North Island, except for some limited areas around the Manawatu and Wanganui Districts and southern Hawkes Bay. In the South Island ragwort is absent from most of Canterbury and Otago. Ragwort is particularly common throughout the wetter regions of the North Island and its spread has been encouraged by the interactions of physical, biotic and management factors (Wardle 1987).

(1.3.2) Pest status.

The established ragwort rosette competes strongly with most pasture plants, including clover, and only tall herbage such as a hay crop will compete with and control ragwort (Harper 1958). The pyrrolizadine alkaloids contained within ragwort tissue are toxic to livestock, particularly cattle and horses, if ingested. Ragwort is probably the major cause of plant poisoning to livestock in New Zealand (Mortimer and White 1975).

Pyrrolizadine alkaloids may also affect human health. Certain liver ailments and diseases common to developing countries have been linked to the consumption of food and medicines prepared from plants containing pyrrolizadine alkaloids (Denzier *et al.* 1977). Cereal grains contaminated with seed from alkaloid containing plants have caused epidemics of poisoning in 4 countries (WHO Health and Safety Guide No. 26). Denzier *et al.* (1977) isolated pyrrolizadine alkaloids from honey containing ragwort nectar, and pointed out that these alkaloids are potentially carcinogenic, mutagenic and teratogenic.

In New Zealand ragwort is currently classified as a class B noxious weed. Under the Noxious Plants Act ragwort must be eliminated from the 20m strip inside farm boundaries. In practice, in many areas this law is not strictly enforced.

(1.3.3) Seed production.

Seed production can vary between 1,000 and 250,000 seeds per plant at different locations (Cameron 1935; Harper and Wood 1957; Schmidl 1972; van der Meijden and van der Waals-Kooi 1979). Ragwort grown at Ruakura, Hamilton produced 50,000 to 150,000 seeds per plant (Poole and Cairns 1940). Each capitulum contained on average 55 seeds with average plants producing between 1,000 and 2,500 capitula per season and particularly vigorous plants producing nearer 5,000. Bornemissza (1966) reported 14 to 1,936 capitula per plant in Australia, and Cameron (1935) found 68 to 2,489 capitula per plant in England, with an average of 70 seeds per capitulum.

Ragwort produces two types of seed, ray and disc. Ray seed is formed around the edge of the capitulum, it takes longer to germinate and it has a lower percentage germination than disc seed. Ray seed is shed later than disc seed, it does not have dispersal structures and its protective pericarp is thicker than that of disc seed (McEvoy 1984b). Disc seed is produced in the centre of the capitulum, is lighter than ray seed, and is adapted for dispersal. McEvoy (1984b) suggested that this dimorphism spreads germination in time and space. Ragwort is clearly well adapted to maintain populations within a sward and dispersing to colonise new areas.

(1.3.4) Dormancy and germination.

Ragwort seed requires light for germination (van der Meijden and van der Waals-Kooi 1979) but may remain dormant for 8 years (Harper 1958). Thompson and Makepeace (1983) found 99% of ragwort seed buried between 0 and 2cm deep was not viable after 4 to 6 years. Seed buried deeper than 4cm retained 1% viability after 10 to 16 years. Covering seed with 1 cm or more of soil can prevent germination (Cameron 1935, van der Meijden 1979). Seed held under laboratory conditions at 15°C showed 80% germination, and most had germinated after 8 days with some germinating after 4 days (Cameron 1935). Poole and Cairns (1940) found 50% - 86% germination and Kelsey (1955) recorded 58% - 96% germination with a mean of 70%. Under field conditions seed produced during the summer germinates in autumn, although germination in some seed may be delayed until the following spring. Germination of buried dormant seed is often induced by disturbance bringing the seed close to the surface.

(1.3.5) Dispersal.

Ragwort disc seed is well suited to wind borne dispersal. A pappus measuring some 4mm in length is attached to the top of the disc seed. The effectiveness of the pappus is increased in low relative humidity and high wind velocity (Cameron 1935). However, despite these adaptations, seed dispersal is poor. Poole and Cairns (1940) found that most seed fell within 10m of the parent plant and they estimated that only 0.5% of seed becomes wind borne. McEvoy and Cox (1987) found 31% of seed travelled only 1m and 89% travelled 5m or less. No seed was collected more than 14m from the source. McEvoy and Cox (1987) concluded that although long distance dispersal of seed was possible, actual dispersal is poor because of local conditions of humidity, wind and vegetation structure. Sheldon and Burrows (1973) concluded that under temperate conditions aerial dispersal of seed was only possible if the seed was carried high on convection currents.

Ragwort seed can be dispersed by surface water. Seed may germinate in freshwater (Poole 1938) and the cotyledonous seedling survive in excess of 2 months (Poole and Cairns 1940). Ragwort seedlings are often found in stream beds indicating possible carriage downstream (Poole and Cairns 1940).

(1.3.6) Establishment.

Germination generally occurs only in the absence of vegetative cover (van der Meijden and van der Waals-Kooi 1979) and seedling survival is low in long grass or a closed sward. Cameron (1935) found that ragwort seedlings could not establish in long grass or short, dense turf but in open soil he found 2,308,680 seedlings per acre. Crawley and Nachapong (1985) also determined seedling recruitment was greatly reduced in dense vegetation.

The density of ragwort seedlings is often higher in openings left by the death of a mature plant (Harris *et al.* 1978; McEvoy 1984a). These gaps are important in allowing germination and seedling establishment thus allowing continued recruitment in an otherwise closed sward (Plate 6). Ragwort also establishes well, and acts as an early successional plant, where the soil has been disturbed by overgrazing, stock trampling or pasture suppression (Wardle 1987).

(1.3.7) Vegetative and reproductive stages.

In the first year of growth, a rosette 12 - 15cm in diameter, is formed. In New Zealand the rosette may reach 30cm in diameter where competition is low and soil fertility optimal (Poole and Cairns 1940). Ragwort is usually biennial and under favourable conditions the rosette increases in size and produces flowering stalks in its second year. However, plants must reach minimum threshold size before they flower (van der Meijden and van der Waals-Kooi 1979), so they may remain as rosettes for several years under sub-optimal conditions until they are large enough to flower. The mature plant generally dies after flowering. In New Zealand more than 90% of mature plants die if allowed to flower and seed without interference (Thompson 1980). However, in England, Islam and Crawley (1983) found that only 25% of the plants studied died immediately after flowering, while up to 44% of plants regenerate after flowering (Forbes 1977).

Ragwort may also be annual, triennial or perennial. In Australia 2% of studied plants were annuals and 39% were perennials (Schmidl 1972). At three sites in the North Island of New Zealand no plants were annuals, between 5% and 20% were biennials, 4% - 20% were triennials and 1% - 5% survived as non-flowering third year rosettes (Thompson 1985).

A perennial habit may occur following damage to the plant. This may be common on agricultural land where defoliation through mowing, grazing or insect feeding often occurs.

Plate 6. Ragwort seedlings established within a break in the sward. Seedling density may be very high in such breaks.

Ragwort can reproduce vegetatively, and in a closed sward in Canada ragwort was found to largely persist in this manner (Harris *et al.* 1978). Vegetative reproduction occurs from buds on either the root stock and/or the crown. Portions of root will readily sprout and form shoots (Poole and Cairns 1940) and a plant can regenerate from a root fragment of less than 1.5cm in length (Harper and Wood 1957). Regeneration from roots is particularly vigorous in rosette plants. This form of reproduction may occur following flowering of an undamaged biennial (Cairns 1938), but is likely to be stimulated by any form of physical damage.

(1.3.9) Toxicity.

Ragwort is toxic because it contains at least six pyrrolizidine alkaloids: jacobine, jacozine, jacoline, senecionine, seneciphylline and integerrimine (Johnson 1978). The total concentration of pyrrolizadine alkaloids in dried ragwort foliage ranges from 0.11% - 0.18% (Aplin, Benn and Rothschild 1968; Buckmaster, Cheeke and Shull 1976; Dickinson *et al.* 1976). Alkaloid concentration in dried flowers is 0.15% - 0.3% (Denzier *et al.* 1977).

Cattle and horses avoid ragwort if sufficient alternative food is available. However, during periods of drought or overgrazing ragwort may be readily grazed and mature cattle occasionally develop a lethal addiction to the plant (Aston and Bruce 1933). Ragwort retains its toxicity upon drying, so poisoning of stock may occur following ingestion of contaminated silage or hay. Symptoms of alkaloid poisoning in stock are known as 'Winton disease' in New Zealand. Its incidence is rather sporadic but could affect up to 5% of stock per year.

Cattle with ragwort poisoning may show a loss of condition, diarrhoea, hyperexcitability and coma. Horses may show unsteadiness, aimless wandering, ataxia and dark urine. Immature sheep develop symptoms similar to those shown by cattle but this is often confused with facial eczema (Mortimer and White 1975).

A characteristic of ragwort poisoning is that the development of symptoms and eventual death may not occur until 1 to 5 months after ingestion of the lethal dose. Symptoms may appear only a week before death. Continued ingestion of alkaloids has cumulative effects. Mattocks (1968) injected pyrrolizadine alkaloids and found that they were converted to pyrroles which the poisoned animal partly excretes in urine, although some remained strongly bound to tissue in the lung and liver. The rate of metabolism of alkaloids to the toxic pyrroles by microsomal enzymes varies greatly in cattle (Johnson 1978). The deleterious effects of pyrrolizadine alkaloids occur only when enough hepatocytes are destroyed and not

regenerated, or when damaged hepatocytes are further stressed. This partly explains the delay observed between the ingestion of the lethal dose and the onset of symptoms.

The most commonly observed tissue damage is the formation of liver lesions. These may be megalocytosis (enlarged cells) and fibrosis (formation of fibrous tissue). Pyrrolizadine poisoning also contributes to chronic liver poisoning as the liver of a poisoned animal may show an increased affinity for, and storage of, copper (Swick, White and Cheeke 1982).

(1.4) Methods of ragwort control.

(1.4.1) Chemical control.

Sodium chlorate was widely used for ragwort control (Harper 1958; Radcliffe 1969). Spot or blanket treatment of this chemical gave reasonable control, but incomplete translocation throughout the root system often led to regrowth from root fragments (Poole and Cairns 1940).

The introduction of hormonal herbicides gave more satisfactory control. young plants at the rosette stage are killed by application of 2,4-D but late rosette, budding or flowering plants are more resistant (Black 1976). 2,4-D is more effective than MCPA, which is also widely used (Forbes 1974, 1977b) but a second application of 2,4-D is often required for effective control (Armstrong 1973). These herbicides however, seriously damage clovers (Honore, Rahman and Dyson 1980; Forbes 1982). This opens gaps in the sward, allowing ragwort seedlings to establish rapidly. 2,4-D is also known to increase the concentration of alkaloid stored in plant tissue while increasing the palatability of the plant to stock by concentrating water soluble carbohydrates in the foliage (Irvine, Forbes and Draper 1977).

An alternative method for ragwort control was developed in New Zealand by Matthews and Thompson (1977). The "Matthews Technique" allows mature plants, which are notoriously difficult to kill by normal methods (Ivens 1979; Wardle 1987), to flower and seed after which 90% of these plants die (Thompson 1980). Seedlings that subsequently establish are treated with 2,4-D ester. Spring application of 2,4-D below levels that inhibit clover is sufficient to control ragwort seedlings in pasture (Matthews and Thompson 1977).

(1.4.2) Control with sheep.

Sheep are relatively resistant to pyrrolizadine poisoning and have often been used in attempts to control ragwort. Sheep apparently have a lower capacity to metabolise pyrrolizadine alkaloids into the harmful pyrroles (Swick *et al.* 1983b). Sheep grazing reduced the density and size of ragwort plants and either prevented or considerably reduced flowering in Australia (Amor, Lane and Jackson 1983). Mean ground cover of ragwort in ryegrass/white clover/cocksfoot in Victoria, Australia, was 5% - 6% in ungrazed pasture and 1.7% - 2% in sheep grazed pasture, but the statistical significance of this could not be determined. Poole and Cairns (1940) found that sheep grazing eliminated flowering and reduced the ragwort population to rosettes of approximately 10cm in diameter.

While sheep may be relatively resistant to pyrrolizadine alkaloids the effects of recurrent ingestion are cumulative and detrimental consequences may not be observed for some time.

(1.4.3) Mechanical removal.

Control of ragwort through the physical removal of the plant has proved largely ineffective. Chipping is generally unsuccessful because ragwort can regenerate from small fragments of root (Poole and Cairns 1940; Islam and Crawley 1983). Crawley and Nachapong (1985) suggest some degree of control may be achieved by mowing the primary flowers above a level that results in the opening up of the sward. Mowing is often impractical in hill country or where ragwort density is high, and cut plants often survive and regenerate. However, Bornemissza (1966) found a critical period of 1 - 2 weeks during late flowering when mowing killed many plants because they had insufficient reserves to recover.

(1.4.4) Insect control.

Ragwort hosts a large number of insect species within its native range. Smith (1980) recorded almost 200 species as visitors or associates on ragwort in England. When ragwort established in countries outside its native range its normal insect fauna was absent. Because native insects in these countries could not control ragwort, proposed biological control programmes required ragwort feeding insects from the weeds native range.

Several native New Zealand insects feed on ragwort. Cameron (1935) recorded two species, the magpie moth (*Nyctemera annulata*) (Boisduval) (Lepidoptera: Arctiidae), a seed and leaf feeder, and *Patagoniodes farinaria* (Turner) (Lepidoptera: Pyralidae), a stem and crown borer, as having some potential as control agents. Two other species, *Melanagromyza senecionella* (Spencer) (Diptera: Agromyzidae), a stem borer, and the leaf miner *Chromatomyia syngenesiae* (Hardy) (Diptera: Agromyzidae) are common associates of ragwort in New Zealand but have little effect (Syrett 1989).

N. annulata is the most conspicuous of the native species. Larvae feed in a similar manner to larvae of *T. jacobaeae*, on the leaves and seeds of the plant. Larvae of *N. annulata* occasionally reach high densities and can then cause considerable defoliation (Miller 1929, 1970). Long term control of ragwort by this moth is unlikely because frequent parasitism of larvae by a braconid, *Microplitis sp.*, and to a lesser extent two tachinid parasites, *Pales nyctemeriana* (Hudson)and *P. casta* (Hutton) heavily reduce its impact on ragwort populations (Miller 1970).

When attempts at biological control of ragwort in New Zealand began, a second promising insect was imported. The ragwort seedfly, *Botanophila seneciella* (Meade) (Diptera: Anthomyiidae) was released at several sites during 1936 and 1937. Female *B. seneciella* oviposit between the bases of the florets on ragwort capitula (Miller 1970). Larvae feed on the immature seed and part of the receptacle (Cameron 1935). Attempts to establish *B. seneciella* in New Zealand produced mixed results. Kelsey (1955) found 91% infestation of early flowers, 42% infestation of maincrop flowers and no attack of late flowers. He estimated that *B. seneciella* reduced seed production by 85% during his study. Dymock (1985), however concluded that within her area of study *B. seneciella* had little effect on ragwort populations. This was due to high pupal mortality, competition for early flowers and the large proportion of ragwort seed that escaped damage.

While there are a number of conventional methods available to control ragwort they are either expensive, inefficient or simply ineffective. Several of the methods may reduce ragwort biomass or density but complete control of the weed by conventional methods is difficult and time consuming.

(1.4.5) Control by *T. jacobaeae*.

The effect of *T. jacobaeae* on ragwort populations is strongly affected by environmental conditions that influence the plants ability to survive defoliation. Islam and Crawley (1983) concluded that compensation for damage caused by *T. jacobaeae* was determined more by the size of the plant than the number of feeding larvae or the timing of attack. However, Cox and McEvoy (1983) showed that moisture limited plant compensation under both experimental and natural conditions. With increasing irrigation the amount of secondary growth, the number of nodes, and the number of capitula all increased following defoliation. Cox and McEvoy (1983) concluded that the full potential of *T. jacobaeae* as a biological control agent could only be realised in years of below average rainfall.

This view is supported by Dempster and Lakhani's (1978) results. Their mathematical model of fluctuations in the abundance of *T. jacobaeae* populations suggested that larval numbers and adult fecundity depended on the biomass of food available. Differences in summer rainfall accounted for 95% of the annual variation observed in ragwort plant numbers at Weeting Heath, England. Therefore, it seems that fluctuations in the abundance of *T. jacobaeae* populations were determined by the biomass of ragwort, which in turn was influenced by summer rainfall.

Dempster (1975) concluded the major factors determining the effect of *T. jacobaeae* on ragwort were climate, soil conditions and vegetation structure. These factors determine the ability of the plant to recover from defoliation. Stimac and Isaacson (1976) consider the success and survival of *T. jacobaeae* to be functions of two factors. These are firstly, site specific conditions such as soil fertility, climate and insect mortality factors, and secondly, plant response to defoliation which is significantly influenced by site specific conditions.

Ragwort appears well adapted to survive periodic defoliation. Rosettes can produce vegetative regrowth from damaged crowns or root stock within 2 weeks of total defoliation (Stimac and Isaacson 1978). Cameron (1935) found by cutting ragwort plants that a vigorously growing plant under good growing conditions may produce a secondary crop of seeds equal to 34.7% of the original potential. However, he also found that if growing conditions were less than ideal, no seeds were produced after defoliation. Bornemissza (1966) determined that overall seed production was reduced by 98% following defoliation in Australia.

Crawley and Nachapong (1985) found a statistically significant drop in germination of secondary seeds (78.8%) when compared to germination of seed produced in the primary capitula (86.6%). Regrowth seeds were also lighter (0.26mg vs 0.41mg) but establishment on bare soil was equal to that from primary seed. Schmidl (1972) found 52% viability of secondary seed compared with 84% from normal seed in Victoria, Australia. The differences in plant response to defoliation in these various studies is best explained by variation in the environmental conditions under which the experiments were conducted.

Despite the effects of *T. jacobaeae* larvae on individual plants, their influence on ragwort populations is often insignificant. Dempster and Lakhani (1979) found that defoliation had a negligible effect on plant numbers in the next year. Myers' (1976) work appears to support this view. She found that environmental factors such as weather and soil type were the main cause of variation in ragwort numbers and this in turn controlled the dynamics of *T. jacobaeae*. Similarly, Crawley and Gillman (1989) showed that *T. jacobaeae* populations were limited by the food plant but ragwort was not herbivore limited.

In contrast, some reports do exist of *T. jacobaeae* controlling ragwort populations. Hawkes (1968) recorded establishment of *T. jacobaeae* in most of the areas where it was released in California and that within a 1 ha test plot almost 100% of flowers were consumed by larvae each season between 1963 and 1966. Ragwort density in this plot was apparently lower than in areas where *T. jacobaeae* was not present, but this was not statistically validated. Nagel and Isaacson (1974) studied *T. jacobaeae* in Western Oregon at 4 sites over a 4 year period. They found a significant reduction in flowering plant densities, increased aggregation of plants and a two thirds reduction in total plant biomass at all 4 sites. They suggested that ragwort was being controlled, as the level of defoliation had risen from 50% to 70% over the period of the study. Cameron (1935) reported that *T. jacobaeae* reduced recruitment to only a few seedlings after attacking a ragwort population covering approximately 5ha and numbering over 1,300,000 plants. Secondary growth did not occur because growing conditions were unfavourable. Cameron concluded that *T. jacobaeae* had effectively controlled this ragwort population.

In a Dutch sand dune system *T. jacobaeae* reduced the relative percentage cover of ragwort by 54% in 3 years when compared to sub populations free of *T. jacobaeae* (van der Meijden 1978). In California *t. jacobaeae* reduced the number and size of flowering ragwort stems from approximately 75cm in height to rosettes only 5 - 6cm in height (Hawkes and Johnson 1978).

The most spectacular success of *T. jacobaeae* as an agent for ragwort control was in Canada. While most populations of ragwort were little affected by *T. jacobaeae*, east coast populations were completely defoliated and plant densities declined rapidly. Harris *et al.* (1976) showed that clipped plants were more sensitive than unclipped plants to low temperature (-22°C) and that this sensitivity was greatest during the rapid regrowth after defoliation. On average, once in every three years defoliated ragwort plants could not recover before the onset of frosts, and these plants were killed.

Stimac and Isaacson (1976) considered the potential for control of ragwort by *T. jacobaeae* in Oregon to be higher than in England, part of the native range, by comparing data from Weeting Heath. They suggested three reasons, firstly, regrowth of ragwort in Oregon is rapid, leading to the availability of food for later developing larvae. Secondly, in Oregon the major mortality factors acting on the moth are density dependent. Lastly, late instar larvae and pupae are less affected by parasites and predators. Mortality amongst these stages is as low as 15% for some Oregon populations. Dempster (1975) determined through *k*-factor analysis that mortality amongst the larvae and pupae was the most significant factor affecting population stability. The survival of *T. jacobaeae* in Australia was severely limited because of predation by the scorpian fly *Harpobittacus nigriceps* (Selys) (Currie and Fyfe 1938; Bornemissza 1966). Bornemissza (1966) concluded *H. nigriceps* could eliminate populations of *T. jacobaeae* in 1 - 3 seasons and would prevent the spread of the moth from any liberation centre.

These studies suggest that *T. jacobaeae* can only exert control if ragwort populations are stressed and *T. jacobaeae* populations do not suffer heavy predation or parasitism. Control of ragwort by *T. jacobaeae* is therefore possible, and has occurred, when these conditions have been fulfilled.

GENERAL METHODS.

(2.1) Description of the study sites.

The study sites were selected on the basis of personal observation and information supplied by the local Noxious Plants Officer. Each site was known to host both *T. jacobaeae* and ragwort.

(2.1.1) Hukanui (NZMS reference T25 366682).

This site was a field measuring approximately 300m x 200m. It was situated 1km west of the Hukanui settlement, along Pukehoi Road, close to the eastern foot of the Tararua ranges. Ragwort plants, while numerous, were widely distributed over the study area.

The area was moderately grazed by beef cattle over the course of the summer but the animals appeared to have an aversion to ragwort as the plants were not grazed as far as I could tell. The scattered ragwort distribution may have been a result of grazing by sheep at an earlier date.

Winter conditions were extremely cold and wet. The cinnabar moth is present at this site at a reasonably low density and appears to have only recently colonised this area. One 20m x 20m quadrat was constructed at this site, and *T. jacobaeae* studied here during the 1989/90 season.

(2.1.2) Eketahuna (NZMS reference T25 355586).

Here my study was conducted on a field measuring 400m x 150m. This site was situated approximately 4km to the west of the Eketahuna township, along Nireaha Road. The field was bordered at its western side by a shelter belt formed from mature pines. In the previous summer, 1988/1989, this field was covered by a large ragwort population with a density at the beginning of that summer of approximately 1 flowering plant / m^2. The ragwort population supported a huge number of *T. jacobaeae* larvae which defoliated every plant in the field by late January, 1989. Many late hatching larvae died from starvation, although a great number survived to pupate. The row of pines, and the debris beneath them, provided numerous pupation sites.

During the summer of this study, 1989/1990, there was a total of only 6 plants in the entire field. The site remained ungrazed for the duration of this study. Here there was a very small ragwort population and a potentially large *T. jacobaeae* population. The prospects for dispersal of the moth were limited as ragwort had been eradicated from the countryside immediately surrounding the field.

(2.1.3) Kaipororo Road (NZMS reference T25 308516).

This site was a field, approximately 400m x 200m, bordered on two sides by native bush, one side by a maturing pine plantation and the other by the Makakahi River (Plate 7). The field was situated across the river around 3km along Kaipororo Road, which leaves SH3 2.5km north of Mount Bruce. The ragwort distribution was more uniform than at the other sites. The land was planted in young pines and all stock was excluded from the area. This area has a long history of *T. jacobaeae*-ragwort interaction following the moths rediscovery in the Wairarapa. It also appears likely that *T. jacobaeae* has become distributed throughout the Wairarapa from this area. This site was the most intensively studied because of it's more typical ragwort distribution and the large area available to work in. As the area was planted with young pine trees there was no disturbance of the ragwort through mechanical or chemical control. Here 5 quadrats, each measuring 20m x 20m, were constructed and marked and a total of 25 ragwort plants sampled over both the 1989/90 and 1990/91 seasons.

(2.2) Pupal collection.

All pupae that were required for experimental work were collected from the Eketahuna site. Pupae were present in the area beneath the pine shelter belt in very large numbers. The pines were fenced on both sides to exclude stock, and consequently the pupae remained almost totally undisturbed. The soil beneath the trees was a dense clay, covered with a thick layer of dried pine needles and sticks. Many large branches and logs were scattered around the area, while in some areas the detritus had been blown away exposing bare clay. Pupae were found throughout the detritus, under decaying logs, within crevices in bark, and in the soil, with some even lying unprotected on bare ground. Pupae were found most readily in decaying wood. By breaking open rotting logs and branches large numbers were found in the soft wood and in channels presumably formed by other insects.

Plate 7. Kaipororo Road study site. This picture was taken before ragwort began to bolt and flower. Note long, dense grasses.

PUPAL SURVIVAL

(3.1) Introduction.

Mature *T. jacobaeae* larvae leave their host plant to pupate in the upper layers of soil, under stones or logs, in detritus, in cavities in bark or in rotting wood. These sites afford protection from adverse weather and predators. I also found pupae resting fully exposed on bare soil.

Previous reports of pupal mortality (Cameron 1935; Bornemissza 1966; Dempster 1982) have identified parasites, fungal pathogens, arthropods and vertebrate predators as agents of mortality. However, pupal survival in relation to substrate or the position of pupae in that substrate does not appear to have been investigated. Here I present an account of an experiment to test the effects of substrate and exposure on pupal mortality.

(3.2) Methods.

Frames measuring 1000mm x 500mm were constructed from 75mm x 25mm wood. A wooden partition was fixed across the centre to form a pair of 500mm x 500mm trays. Curtain netting material (mesh approximately 20 per cm^2) formed the bottom of each tray. They were then filled with a 40mm deep layer of one of the following substrates:

(1) Sand: coarse horticultural grade river sand.

(2) Potting mix: mixture of 50% pumice and 50% peat.

(3) Bare: pupae were placed directly onto the netting floor covering the base of the trays.

(4) Detritus: the dried pine needles and sticks that covered the ground at the base of the row of pine trees at the Eketahuna site.

(5) Clay: the dense clay that surrounded the base of the pines at the Eketahuna site.

Thirty pupae collected at the Eketahuna site in early April were added to each compartment of the trays. Pupae were buried in one compartment and left exposed in the other, for the trays containing sand, potting mix and clay. All pupae were exposed in the "bare" trays and were considered buried in the trays of detritus because they would not stay exposed on the surface.

The trays were positioned under pine trees at the Eketahuna site within 1m of each other. Chicken wire, of mesh diameter 10mm, was secured over the trays to prevent disturbance from large vertebrates such as possums *(Trichosurus vulpecula)* but this still allowed invertebrate predators and mice *(Mus musculus)* access to the pupae.

The trays were left undisturbed until early October when adult emergence was imminent. Clear plastic sheeting was then secured over them to trap all emerging adults. The trays were checked weekly after the first adult moths appeared in the field. The plastic protected dead and alive moths from scavenging insects, birds and weather. Adults were removed from the trays when counted to avoid being recorded twice.

(3.3) Results.

Newly formed *T. jacobaeae* pupae were often seen fully exposed on the substrate surface at the Eketahuna site. Since it was unlikely these pupae could have been blown or washed free from some other position, it appears some larvae pupate in exposed areas, and do not find, or seek, more adequate protection.

The number of successfully emerged moths from each of the treatments is given in Table 3.1 and plotted in Figure 3.1.

Mortality was significantly affected by pupal position. Buried pupae survived better than pupae that were exposed on the surface (G-test (Sokal and Rolf 1981); Buried: $G = 28.72$, $P < 0.001$; Exposed: $G = 21.56$, $P < 0.001$). Analysis of the influence of substrate on survival showed that for sand, the position of the pupae strongly affected pupal survival ($G = 14.70$, $P < 0.001$). Survival of pupae in potting mix and clay was not significantly affected by the substrate.

Figure 3.1 Percentage adult emergence in relation to substrate and pupal position.

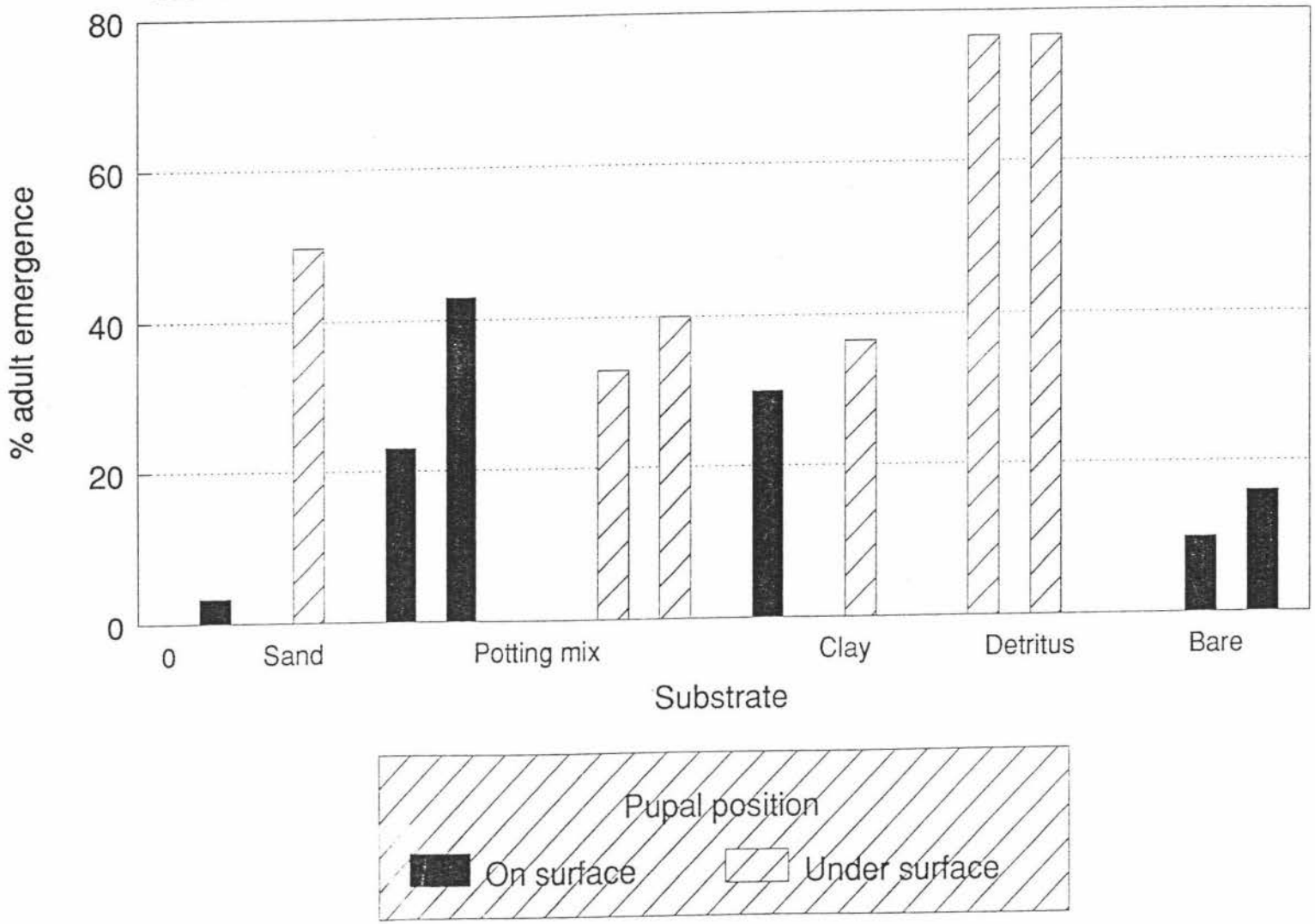


Table 3.1 Effect of substrate and exposure on pupal survival.
Numbers = number of adults emerged; figures in parentheses = % emergence.

Substrate	On surface	Buried
Sand	1 (3.3)	15 (50)
Potting mix		
rep. 1	7 (23)	12 (40)
rep. 2	13 (43)	10 (33)
Bare		
compartment 1	3 (10)	-------
compartment 2	5 (16)	-------
Detritus		
compartment 1	------	23 (76.6)
compartment 2	------	23 (76.6)
Clay	9 (30)	11 (36.6)

(3.4) Discussion.

Mortality of *T. jacobaeae* pupae is high under both natural and experimental conditions. Dempster (1971a, 1975) estimated that at Weeting Heath, England, between 51.4% and 96.1% of fully grown larvae that leave the host plant to pupate were killed within the first 6-8 weeks of pupal life. He attributed most early pupal mortality at to predation by moles (*Talpa europaea*) and field mice (*Apodemus sylvaticus*). He confirmed that both moles and field mice ate *T. jacobaeae* pupae under laboratory conditions. After this initially high mortality, however, the mortality rate is low for the rest of the stadium.

Bornemissza (1966) also reported high pupal mortality, ranging from 45% to 95% over 2 years for insects from 3 different provenance, under natural conditions in Victoria, Australia. By manipulating pupal exposure to natural rainfall, he showed that pupal mortality was not affected by soil moisture. In contrast, Dempster (1971a) showed that prolonged contact with water killed all pupae. While these results appear contradictory, *T. jacobaeae* pupae can absorb water to avoid desiccation. The pupae in Bornemisszas' trial were exposed to a range of moisture levels. Some pupae were sheltered from natural rainfall, while at the other extreme

pupae were exposed to rainfall that was then prevented from evaporating. Dempsters' result is not surprising if pupae were allowed to become water logged and soften. I therefore feel that *T. jacobaeae* larvae are more sensitive to excessive moisture than is indicated by Bornemissza. Dempster (1972a) concluded that, in England, *T. jacobaeae* is restricted to free draining areas, although van der Meijden (1976) considered this not to be so in Holland.

Cameron (1935) found mortality of 65% for pupae placed under stones, 69% for those under moss, and 90% for pupae on the soil surface. Mortality in my study was extremely variable between treatments and ranged from 96.7% for pupae on the surface of sand, to only 23.4% for pupae placed in detritus. This latter estimate of mortality is probably approaching the minimum likely for *T. jacobaeae* under natural conditions in New Zealand.

I found that pupal mortality was significantly influenced by substrate type. The low mortality of pupae in detritus may relate to the physical properties of that substrate. The dense mat of pine needles and sticks would provide protection from predators while allowing air to circulate around the pupae, drying them and allowing unrestricted respiration. Pupae placed on the "bare" surface were more vulnerable to predation and adverse weather. The low level of adult emergence indicates that one, or both, of these factors acted to increase mortality.

The relatively high level of adult emergence (50%) for pupae buried in sand suggests that this gave reasonable protection from predation and weather, probably due to its density. High mortality of pupae on the surface of sand may again be caused by predators or weather. Predation may have been enhanced, as the pupae were conspicuous on this surface.

The negligible difference between mortality in clay and potting mix is predictable and while the potting mix allowed better drainage and air movement around the pupae, the clay was very dense providing good protection for buried pupae. Pupae exposed on clay could settle part way into the surface, affording increased protection.

Pupal mortality was significantly related to the pupal position. Exposed pupae were obviously more susceptible to predation. Windecker (1939) found certain vertebrate predators that were known to avoid eating *T. jacobaeae*, would accept pupae less than 8 weeks old. Miller (1970) reported two bird species preying on the adult, and one or two birds that eat larvae in New Zealand. There is no record of vertebrate predation of pupae in this country and I observed no evidence of

it during this study. Therefore losses of pupae to vertebrates are probably insignificant. However several other potential sources of mortality were identified. I often found groups of Darkling Beetles (*Mimopeus opaculus*) (Coleoptera: Tenebrionidae) under logs and in detritus near *T. jacobaeae* pupae. On several occasions these beetles were seen grouped around clusters of neatly opened, empty, pupal cases of *T. jacobaeae*. Arthropods were not excluded from the trays containing pupae, so losses of pupae to the predacious arthropods, i.e. *Megadromus capito* (White) (Coleoptera: Carabidae), seen in the area may have been significant . Wilkinson (1965) showed that establishment of *T. jacobaeae* in British Columbia failed because of predation by ground beetles on newly formed pupae.

Cameron (1935) found that 16% - 20% of pupae were killed annually through fungi. A fungal infection, later identified as a species of *Paecilomyces* affected between 5 and 10% of all pupae. Infected pupae were often encountered during the fortnightly collections of pupae for the diapause trials. Of the 20 - 30 pupae collected, usually at least one or two showed fungal infections. Regrettably, records were not kept of the actual numbers, however, I feel 5% to 10% is a reliable estimate. The fungi was saprophytic and no pupae infected with it produced adults. Bornemissza (1966) found between 2% and 6% of pupae were killed by fungal infection in Australia.

Isaacson (1973) suggested several mortality factors that may cause emergence failure: an early factor causing hollow puparia; fungal infection; and a late factor causing death after adults have formed. Bornemissza (1966) found that mortality in the absence of predation ranged between 30% and 35%, mostly through the action of fungi and unexplained death.

The detritus treatment most closely approximated field conditions in my study. Therefore, the emergence rate of pupae in detritus (76.6%) estimates pupal survival under natural conditions in the Wairarapa although it probably slightly underestimates mortality because the pupae were protected from physical disturbance such as stock trampling. It is possible that the absence from New Zealand of many predators known to cause pupal mortality in other countries could reduce mortality during the pupal stage here.

DIAPAUSE.

(4.1) Introduction.

T. jacobaeae is univoltine and over winters as diapausing pupae. Diapause is obligatory and lasts approximately 270 days in Europe (Bornemissza 1961) limiting *T. jacobaeae* to a single generation per year. Van Zoelen and Kusters (1986) reported that *T. jacobaeae* pupae pass through an initial period of diapause development, or physiogenesis, during the first 3 - 4 months of exposure to cold, followed by post diapause quiescence which synchronises adult emergence. As temperatures rise morphogenesis is initiated and post diapause development continues. This is the normal pattern for hibernal diapause (Tauber and Tauber 1976, 1986).

The result of pupal diapause in the native range is a highly synchronised adult emergence which carries through to larval development. Manipulation of the pupal development period may therefore produce earlier or later emerging adults, and lengthen the period when adults and larvae are available for study (van Zoelen and Kusters 1986).

I believe that manipulating pupal hibernation to produce some adults that emerge later than those under natural field conditions could enhance the effectiveness of *T. jacobaeae* as a control agent by prolonging larval attack on ragwort. The increased stress suffered by the plants may increase the mortality rate in ragwort populations. This is likely because stress caused by environmental conditions has apparently increased the effectiveness of *T. jacobaeae* overseas (Cameron 1935; Harris *et al.* 1978; Cox and McEvoy 1983).

Little information is available on the process of pupal development in natural *T. jacobaeae* populations and nothing is published concerning temperature requirements for diapause development of *T. jacobaeae* under New Zealand conditions. Information is available from studies of diapause in this species under controlled conditions (Bornemissza 1961; van Zoelen and Kusters 1986) but this has not been correlated with field studies. My aim was to determine from laboratory studies the chilling requirements of *T. jacobaeae* for completion of diapause development in New Zealand, and to relate this to the occurrence and timing of the successive stages outlined by van Zoelen and Kusters (1986), for a field population of *T. jacobaeae*.

(4.2) Methods.

(4.2.1) Controlled chilling experiments.

Pupae collected from the Eketahuna study site in early April were placed at random in groups of 10 into perspex specimen vials (5cm x 6cm) each containing a 2cm x 2cm x 1cm piece of moistened moss to reduce desiccation. They were then chilled at either 2°C or -15°C for varying periods before being transferred to a controlled temperature cabinet at 17.5 ± 0.5°C.

Two groups of 32 pupae, collected soon after pupation in late February, were held at 17.5°C as controls. These pupae received no chilling. Pupae were checked regularly throughout the experiment. When adult moths began to emerge the frequency of checking was increased to every 1-2 days.

(4.2.2) Field chilling experiment.

Twenty to thirty pupae were collected every two weeks from the Eketahuna site during the winter. Pupae were obtained from as many different locations within this study area as possible to minimise effects of differential mortality and development between pupation sites.

Each group of pupae was transferred to a screw-topped perspex specimen vial (5cm diameter x 6cm high) containing a 2cm x 2cm x 1cm piece of moistened moss to reduce desiccation. All vials were stored in a controlled temperature cabinet at 17.5 ± 0.5°C. The pupae collected as controls for the laboratory experiments also served as the controls in this experiment. To prevent fungal infections all pupae were initially washed briefly in a 5% solution of sodium hydroxide. This was discontinued when it was realised that fungi did adversely affect control pupae.

Pupae were checked weekly until the first adult emerged. Thereafter they were checked every 1-2 days.

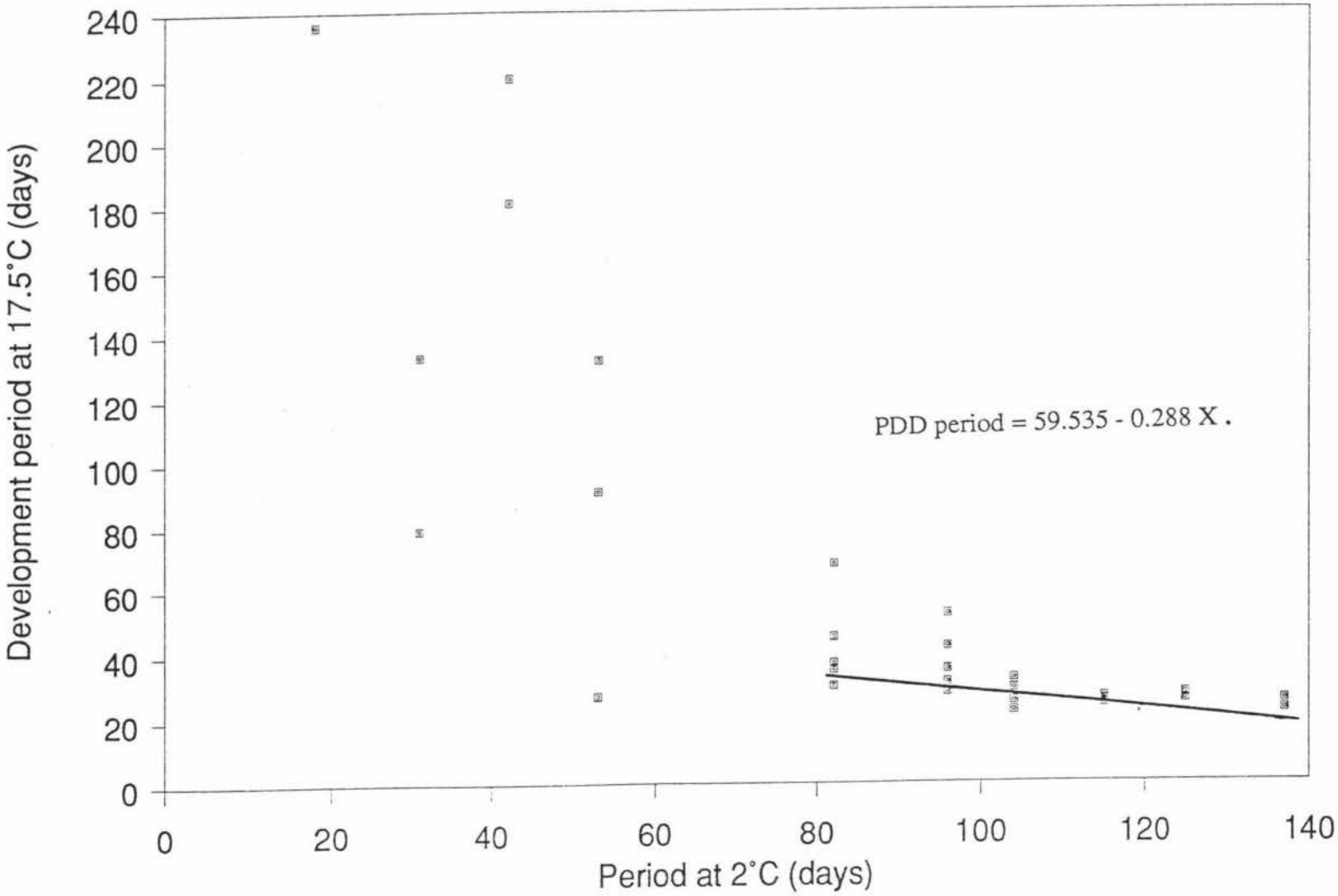
(4.3) Results.

(4.3.1) Controlled chilling experiments.

(4.3.1.1) 2°C Treatment.

Pupae chilled for 10 days at 2°C did not complete their development when placed at 17.5°C. Thereafter the time required to complete development at 17.5°C decreased with longer periods of chilling (Figure 4.1). Chilling for more than 104 days at 2°C caused only a gradual reduction in subsequent period of development at 17.5°C. The relationship between development at 17.5°C and the period of chilling

Figure 4.1 Pupal development at 17.5°C in relation to the period of previous



was clearly non-linear. There appeared to be two separate responses to exposure to 17.5°C following different lengths of chilling. Firstly, pupae chilled for less than 70 days showed extremely variable development periods at 17.5°C. Secondly, pupae chilled for longer than 70 days had a more uniform, shortened period of development. The transition between these two forms of response occurred over a short period between 53 and 82 days of chilling.

Regressions of development time at 17.5°C on chilling period were fitted to each of these two phases. The regression up to and including 53 days was not significant (development period = 257.616 - 2.987 days chilled, $r^2 = 0.166$, $p = 0.173$), but that fitted on and after 82 days was highly significant (development period = 59.535 - 0.288 days chilled, $r^2 = 0.323$, $p < 0.001$). Also the proportion of adults that emerged within each treatment increased with increasing prior chilling to a maximum of 80% after pupae were chilled for 125 days (Figure 4.2). The linear relationship between the length of chilling and pupation success was significant (rate = 5.047 + 0.502 days chilled, $r^2 = 0.641$, $p < 0.005$).

There was also a significant negative relationship between the range of adult emergence and the length of chilling (Figure 4.3) (range = 153.8 - 1.316 days chilled, $r^2 = 0.516$, $p < 0.001$).

(4.3.1.2) -15°C Treatment.

Few pupae successfully eclosed after exposure to -15°C. After 1 hour's chilling 40% eventually emerged as adults (mean development time at 17.5°C was 166 days) and 1 adult emerged 157 days after 3 hours of chilling. No pupae chilled for 2 hours or more than 3 hours completed development.

(4.3.1.3) Estimation of the minimum threshold temperature for post diapause development.

Diapause development was estimated to be completed after about 70 days of chilling at 2°C. This value lies in the transition period between the two phases of development at 17.5°C. Using the regression representing the post diapause development period (PDD period) at 17.5°C, the post diapause development period after 70 days of chilling is:

$$\text{PDD period}_{17.5°C} = 59.535 - (0.288 \times 70 \text{ days})$$
$$= 39.375 \text{ days.}$$

Figure 4.2 Relationship between % adult emergence and the period of previous chilling.

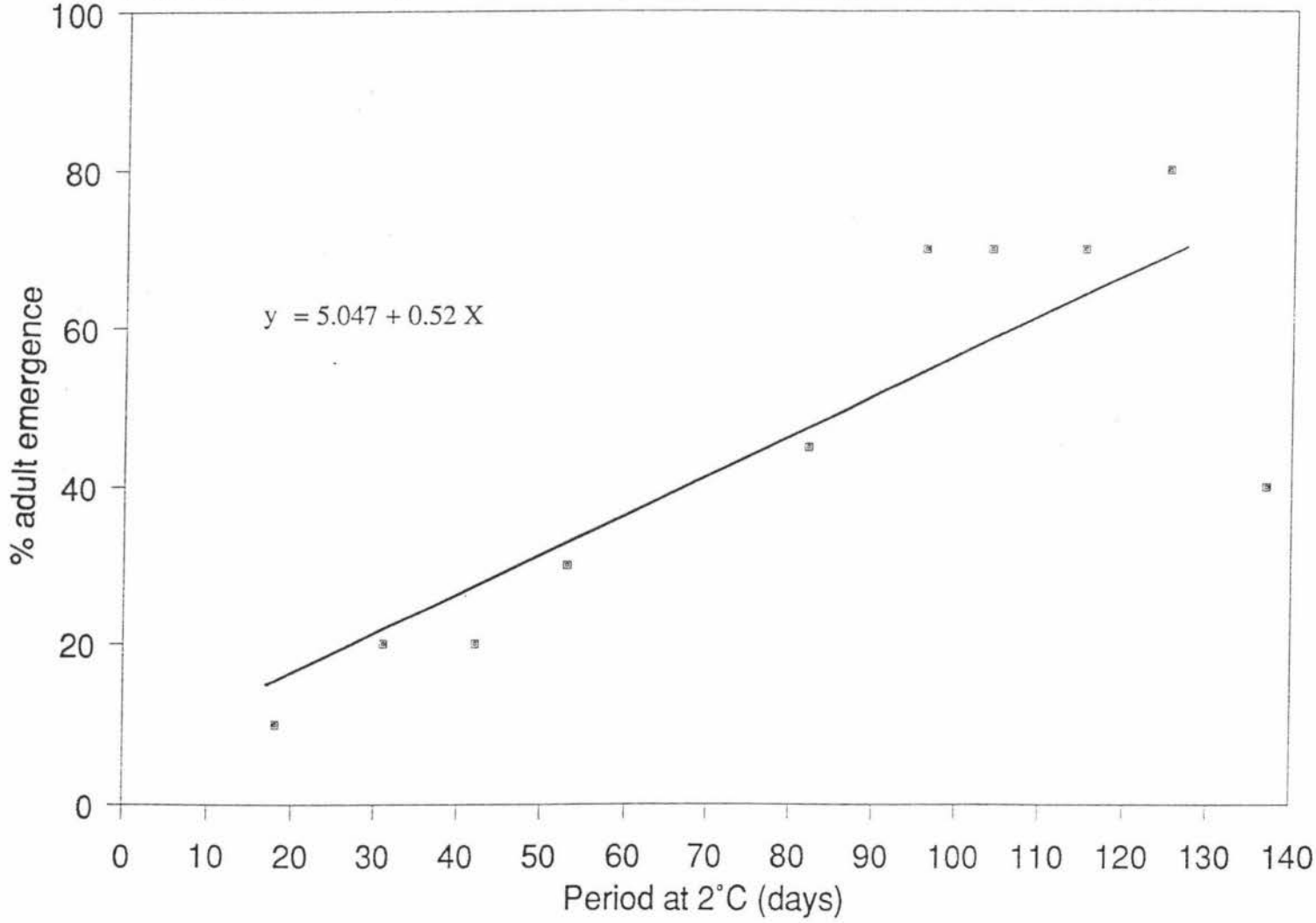
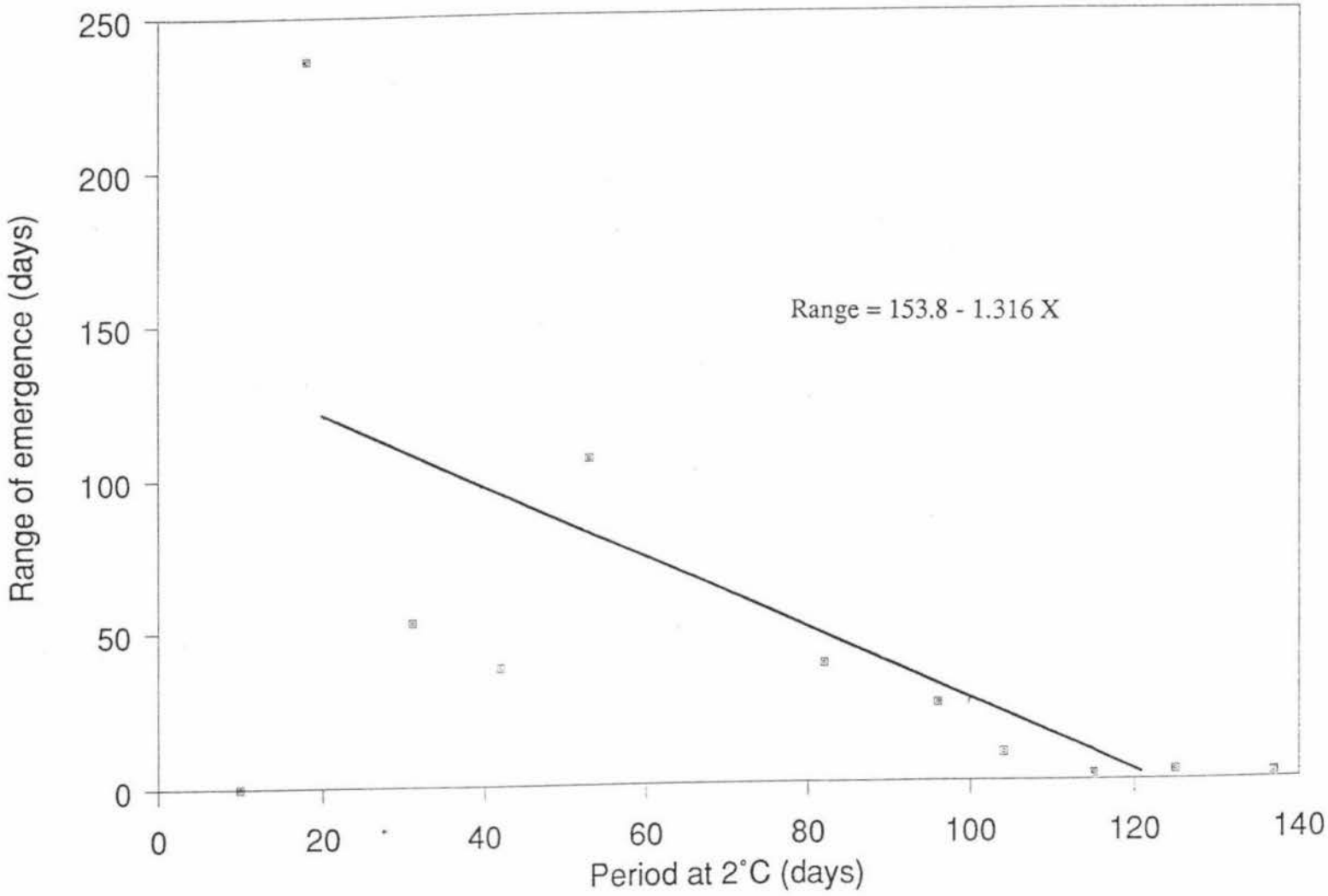


Figure 4.3 Relationship between the range of emergence and the period of previous chilling.



and the PDD rate at 17.5°C is:

$$\text{PDD rate}_{17.5°C} = 1/39.375$$
$$= 2.5397 \times 10^{-2}$$

Pupae chilled for 137 days at 2°C require 59.535 - (0.288 x 137 days) = 20.079 days at 17.5°C. Thus, pupae chilled for the extra 67 days at 2°C completed a proportion equal to $1 - ((2.5397 \times 10^{-2})\ (20.079)) = 4.9005 \times 10^{-1}$ of their development during the extra period at 2°C. Therefore, their daily PDD rate at 2°C was:

$$\text{PDd rate}_{2°C} = 4.9005 \times 10^{-1}/67$$
$$= 7.3142 \times 10^{-3}$$

Thus, there are now 2 points on a straight line relating PDD rate to temperature so the equation of this line can be calculated as:

$$\text{PDD rate} = 4.9809 \times 10^{-3} - (1.1666 \times 10^{-3} \times \text{temperature})$$

Therefore, when PDD rate equals zero, the temperature at which no development occurs is:

$$(-4.9809 \times 10^{-3})/(1.1666 \times 10^{-3})$$
$$= -4.2696°C$$
$$= -4.27°C$$

To check the accuracy of this estimate, we can suppose there is an error of 14 days on either side of the estimated time for the completion of diapause development, i.e. 70 ± 14 days, so the earliest and latest values are 56 and 84 days. After 56 days chilling:

$$\text{PDD period}_{17.5°C} = 59.535 + (0.288 \times 56 \text{ days chilled})$$
$$= 43.407 \text{ days}$$

giving: $\text{PDD rate}_{17.5°C} = 2.3038 \times 10^{-2}$

Pupae chilled for a 137 days at 2°C required on average 20.079 days to complete development at 17.5°C and therefore completed a proportion equal to 1 - $((2.3038 \times 10^{-2}) \times (20.079)) = 5.3741 \times 10^{-1}$ of their development at 2°C.

so:

$$\text{PDD rate}_{2°C} = 5.3741 \times 10^{-1} / 81$$
$$= 6.6348 \times 10^{-3}$$

Thus, PDD rate = $4.4741 \times 10^{-3} + (1.0803 \times 10^{-3} \times \text{temperature})$

So, the threshold temperature for post diapause development equals:

$$(-4.4741 \times 10^{-3}) / (1.0803 \times 10^{-3})$$
$$= -4.1415°C$$
$$= -4.14°C$$

Following 84 days of chilling at 2°C:

$$\text{PDD period}_{17.5°C} = 59.535 - (0.288 \times 84 \text{ days chilled})$$
$$= 35.343 \text{ days}$$

giving: $\text{PDD rate}_{17.5°C} = 2.8294 \times 10^{-3}$

Pupae chilled for an extra 53 days (137 total) at 2°C completed 1 - $((2.8294 \times 10^{-2}) \times (20.079)) = 4.3188 \times 10^{-1}$ of their development at 2°C. So:

$$\text{PDD rate}_{2°C} = 4.1176 \times 10^{-1} / 53$$
$$= 8.1487 \times 10^{-3}$$

Hence, PDD rate = $5.5493 \times 10^{-3} + (1.2997 \times 10^{-3} \times \text{temperature})$

So, the threshold temperature for post diapause development equals:

$$(-5.5493 \times 10^{-3}) / (1.2997 \times 10^{-3})$$
$$= -4.2697°C$$
$$= -4.27°C$$

Thus, by assuming that diapause development ended between 56 and 84 days at 2°C, then the threshold for post diapause development is between -4.14 and -4.27°C.

(4.3.2) Field chilling experiment.

The time required to complete pupal development at 17.5°C after removal from the field varied with the length of exposure to ambient temperatures (Figure 4.4). Development times at 17.5°C for pupae collected before the 13/6/89 (105 days after pupation) were very variable and few adults emerged. Development periods of pupae collected after this date were much less variable. These averaged 65 days by the 13/6/89 and decreased to an average of only 7.5 days for pupae collected immediately prior to adult emergence in the field (collected on the 7/11/89, 253 days as pupae). For analysis the date of collection was converted to the number of days after 1/3/89 as this was the approximate date by when all larvae had pupated.

The relationship between pupal development period at 17.5°C and exposure to ambient temperatures was non-linear. There were clearly two overlapping phases of pupal development at 17.5°C and these depended on the length of exposure to field conditions. The transitional period included pupae that had experienced 105 to 119 days under field conditions, and data from these samples was included in both regressions. The line relating the development periods of pupae collected before and including 119 days, and collection date, was significant (dev. period = 270.064 - 1.772 collection date, $r^2 = 0.605$, $p < 0.000$) as was the line fitted through the development periods of pupae collected after and including 105 days (dev. period = 106.812 - 0.405 collection date, $r^2 = 0.638$, $p < 0.001$).

The proportion of pupae that produced adults was positively correlated with increased exposure to field conditions (Figure 4.5) (Emergence rate = -6.474 + 0.382 date, $r^2 = .810$, $p < 0.001$). All pupae collected approximately 2 months after pupation (on the 30/3/89) failed to complete development and there was an increase in the proportion of successful pupations to a maximum of 96% for those collected on the 10/10/89 (226 days after estimated pupation). Following this the percentage of adult emergence decreased again to 60% for pupae collected on the 7/11/89, immediately before adult emergence began in the field.

Pupae collected after 105 days (on the 13/6/89) had the shortest mean total development period, i.e. days chilled + days warmed, of 170 ± 6.6 days, although only 29% of adults emerged. In contrast, the mean total development period for those collected after 119 days (on the 27/6/89) was 186 ± 6.4 days, with 55% adult emergence.

Figure 4.4 Pupal development at 17.5°C in relation to exposure to ambient temperature.

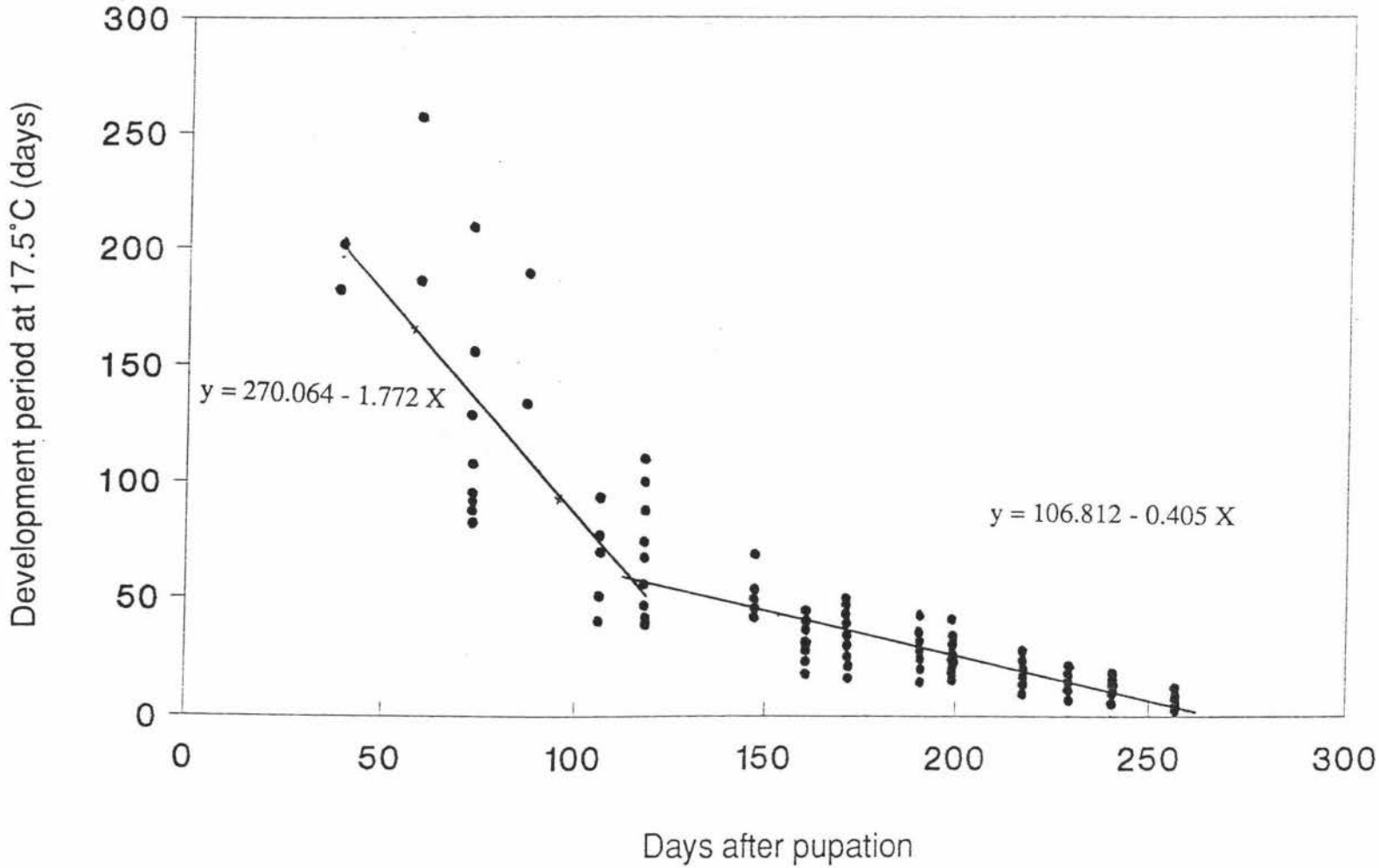


Figure 4.5 Relationship between % adult emergence and exposure to ambient temperature.

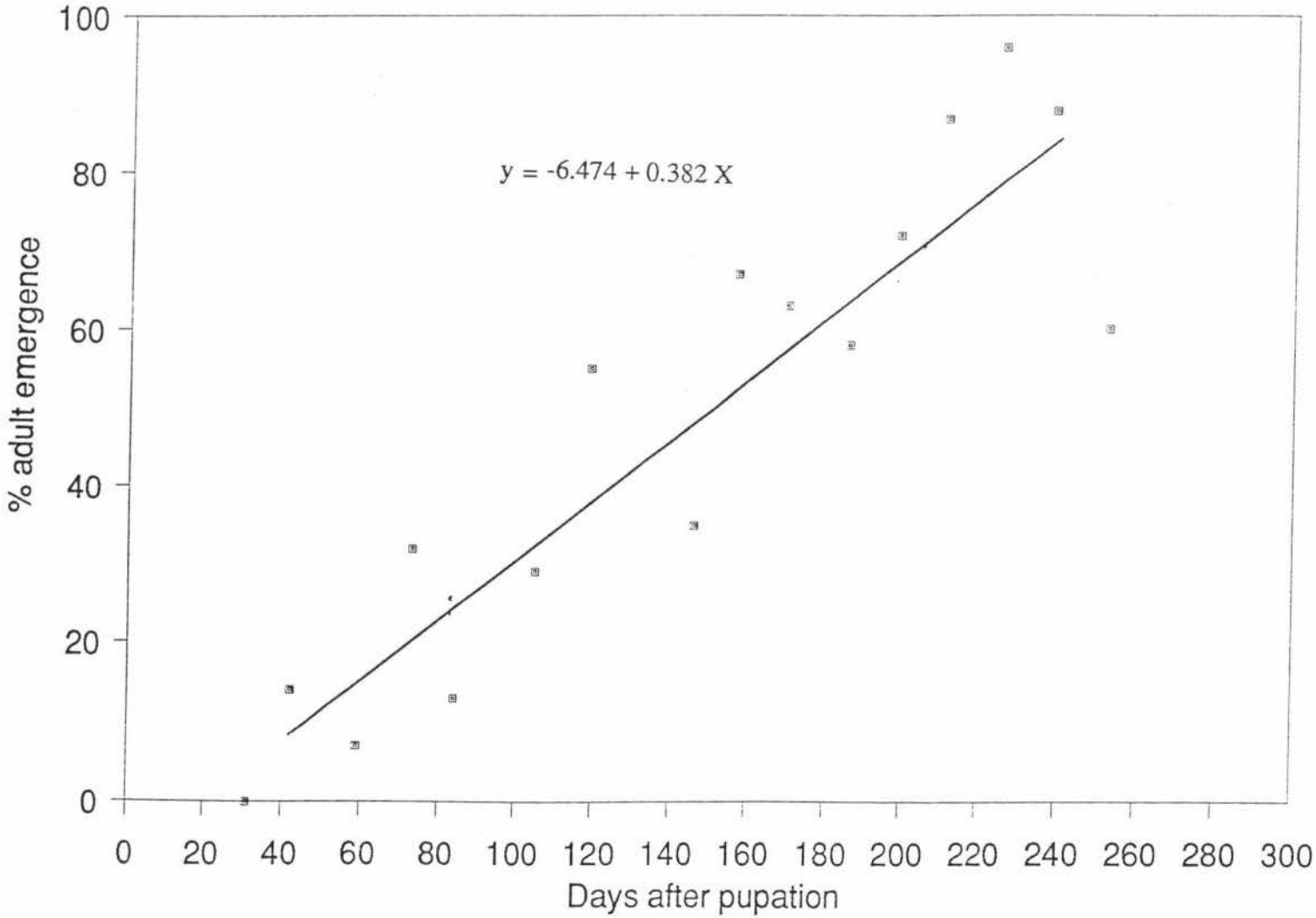
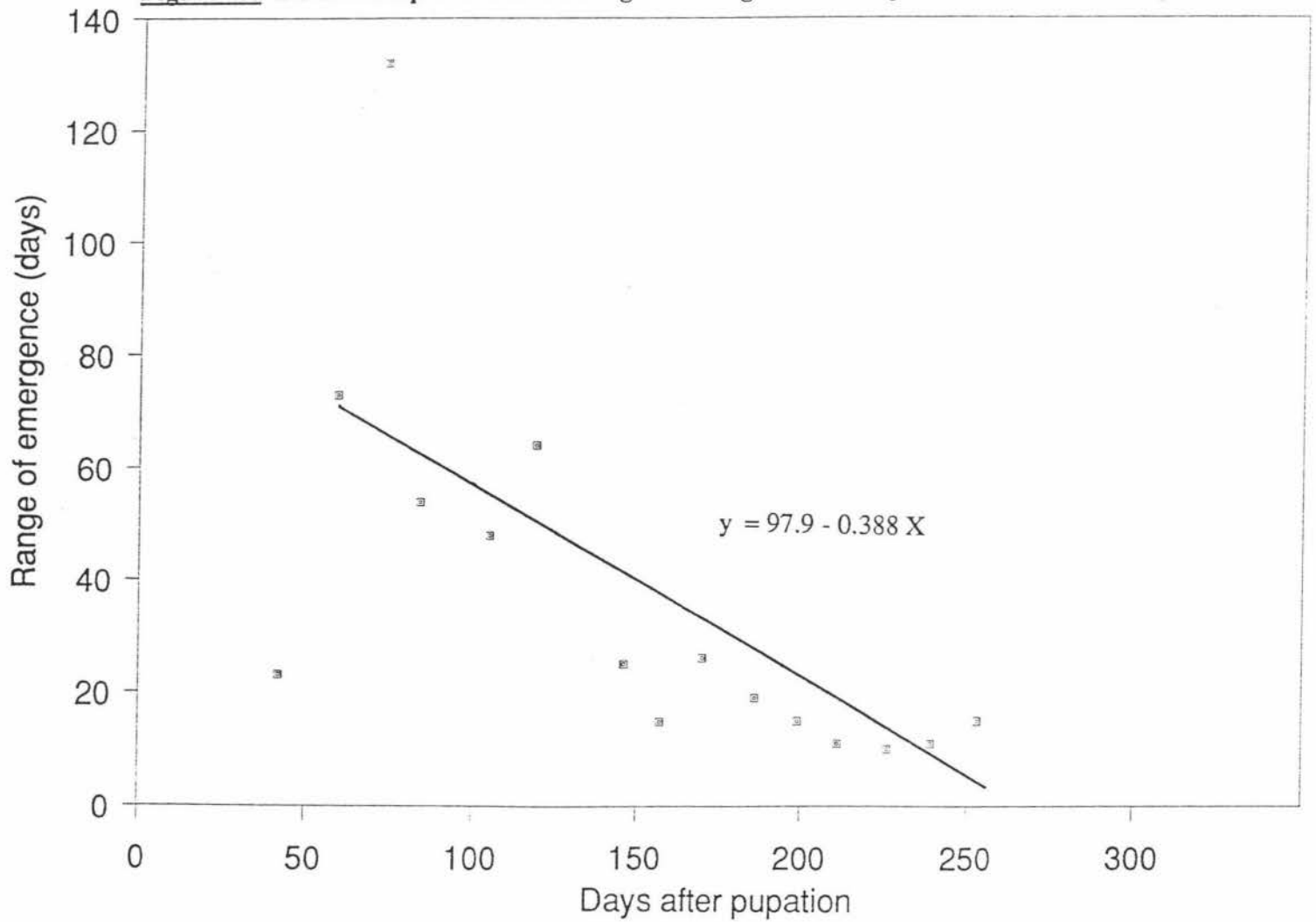


Figure 4.6 Relationship between the range of emergence and exposure to ambient temperature.



The time range over which adults emerged, or the degree of synchronisation of adult emergence, improved with increasing exposure to field temperatures (Figure 4.6). This range diminished from 132 days for pupae collected on the 11/5/89 (73 days after pupation), to 10 days for pupae collected on the 10/10/89 (226 days after pupation). The one anomalous eclosion for pupae collected on the 1/8/89 where the last adult emerged some 118 days after the other 15 increased the range from 15 to 133 days and increased the mean pupal development period at 17.5°C. Despite this there was a significant negative linear relationship between increasing exposure to ambient temperature and range of adult emergence (range = 97.9 - 0.338 date, r^2 = .260, $p < 0.030$).

(4.4) Discussion.

My field collection and laboratory experiments support the view that diapause termination is accelerated by exposure to cold. Sufficient chilling terminated diapause and initiated post diapause development at a rate proportional to temperature. In both experiments the period of post diapause development at 17.5°C and the range of times over which adults emerged were reduced, while the proportion of adults emerging increased, with longer periods of chilling.

Stimuli that induce and maintain diapause in *T. jacobaeae* are not fully understood. The effects of photoperiod were not investigated as I frequently found pupae buried in the upper layers of soil or deep within rotting logs where they would receive no light. Philogene (1975) showed that the photoperiod experienced by developing larvae did not influence the timing, onset or intensity of diapause, so it is unlikely that photoperiod is responsible for either the induction or maintenance of diapause.

Isolating a single environmental stimulus as the major diapause regulating factor may be misleading. Temperature or photoperiod often only regulate the rate of diapause development (Tauber and Tauber 1976) and the response observed in diapausing insects to environmental stimuli may in fact be a reaction to several interrelated environmental characteristics. However, in the absence of any other information on diapause in *T. jacobaeae* it is reasonable to assume that temperature is the most significant factor influencing diapause development.

Pupae used in my controlled chilling experiments were exposed to field conditions for approximately one month before collection. Initial diapause development is unlikely to have occurred because field temperatures were too high. The average minimum daily temperature between the estimated date of pupation and the date of collection was 10.14°C. Van Zoelen and Kusters (1986) found an initial period of warming did not significantly shorten development period compared to immediately chilled pupae.

Chilling pupae at 2°C simulated conditions of cold, lower on average, than those observed at the Wairarapa field site. Exposure to -15°C showed that very low temperature does not act as a "supernormal" stimulus as it often does with diapause development (Tauber and Tauber 1976).

Insufficient chilling greatly decreased successful eclosion and increased variation in the length of the post diapause development period. The mean post diapause development period stabilised after around 70 days of chilling at 2°C, indicating a general requirement of *T. jacobaeae* pupae for at least 70 days of chilling before the diapause maintenance period is terminated and regular post diapause development can proceed.

It is clear that overwintering pupae progressed through two successive stages. The great variability in development period during the first phase reflects natural variability in the rate of diapause development among pupae. While between 18 and 53 days at 2°C is sufficient for some pupae to complete development, most pupae need longer than this. This variability is later reduced with further chilling. The regression fitted to the second phase represents the rate of post diapause development at 2°C. The reduction in development period with increased chilling at 2°C is gradual, but the significant negative slope indicates that post diapause development occurs at this low temperature.

Van Zoelen and Kusters (1986) consider that artificial extension of adult and larval availability may be achieved by either preventing the induction of diapause or by the early termination of diapause. My results show that diapause can sometimes be terminated after approximately 70 days of chilling, but that this is detrimental to the proportion of adults that successfully emerge and the range of emergence. Chilling for 96 days produced the shortest mean development period of 131 ± 3.3 days in conjunction with emergence exceeding 50% (70% after 96 days at 2°C).

Van Zoelen and Kusters (1986) found chilling at 5°C for at least 120 days produced the highest proportion of emerging adults and the shortest total development time (162 days). Results from my experiment indicate a shorter total development period (131 days), although the use of a lower chilling temperature (2°C) may be responsible for this.

The production of two generations per year to increase control seems not to be a valid option because of the inherent time lapse between generations. Even this minimum period of 131 days between generations exceeds the period of ragwort flowering and seed production, so a second generation would have no effect on ragwort reproduction in that year, and would be exposed to the lower temperatures of autumn and early winter. A more realistic means of extending the presence of *T. jacobaeae* in the field, thereby increasing the level of control, may be to delay eclosion by storing quiescent pupae. If some manipulation of the time of adult eclosion is desired, then storage of pupae at 2°C appears to slow further development until elevated temperature are experienced. Storing pupae at around -4.2°C should arrest development until warmer temperatures are again experienced. Upon exposure to higher temperatures after chilling, the period of warming required will be proportional to the length of chilling. Bornemissza (1961) similarly found lower mortality when diapause was extended rather than shortened, but he also reported that fecundity was reduced after long periods in diapause.

I found no estimate of the temperature threshold for post diapause development in the published literature and this appears to be the first attempt at its calculation. The accuracy of the estimate is influenced by two factors. Firstly, error in the regression of development time at 17.5°C on the period of chilling at 2°C, for the period of post diapause development will greatly affect the estimate. However, this regression appears reliable because of the large number of emergence dates on which the regression was modelled. The moderate r^2 value again reflects natural variability within the pupae. The second assumption is that the relationship between post-diapause development rate and temperature is linear. This method of calculating the temperature threshold is still widely used, despite criticism of its reliability. A sigmoid function has predicted development rates more accurately than a linear model (Stinner, Gutierrez and Butler 1974). However, Kitching (1977) suggested that the linear function adequately described the development/temperature relationship under most temperatures encountered in the field.

Therefore, while there may be some error in my estimate, it does correlate well with the habit of *T. jacobaeae* in its native range. Pupal hibernation continues over late autumn and throughout winter in England and Europe, therefore pupae are exposed to very low temperatures in many areas under natural conditions. Because insects often undergo seasonal changes in their ability to withstand cold, Tauber and Tauber (1986) divide cold hardiness into two categories: non-diapause cold hardiness and diapause-associated cold hardiness. Insects in the latter category are only resistant to injury or death from certain levels of cold during the diapausing state, and *T. jacobaeae* meets this condition. The estimated threshold temperature for post diapause development of between -4.14 and -4.27°C indicates that *T. jacobaeae* is well adapted to survive low temperatures, and may continue post diapause development down to at least -4.27°C. Pupae would enter post diapause quiescence if temperatures fell below the threshold for development, and this is thought to synchronise adult emergence and probably ensures larvae have access to the capitula and flowers of ragwort plants. However, the average monthly minimum temperature over the period of pupation (March-November) during 1989 in the Wairarapa ranged between 10.14 and 0.94°C, with -3.8°C the lowest temperature recorded.

Reports from the moths native range indicate a highly synchronised period of adult emergence lasting approximately 6 weeks in England (Cameron 1935) and about 1 month in Holland (van Zoelen and Kusters 1986). In New Zealand adult moths may be found as early as August (Miller 1970), and numbers slowly increase over the next four months. The period of oviposition, determined from field studies (see Chapter 6), ranged from 27 to 54 days at the sites studied in the Wairarapa and indicated greater synchrony than expected. Therefore, although winter temperatures in the Wairarapa were not low enough to initiate pupal quiescence, they were low enough to slow development in pupae exposed to ambient temperatures and produce some synchrony of pupal development and subsequent adult emergence.

The successive stages of diapause reported by van Zoelen and Kusters (1986) were partially identified in the field population studied. The steeper regression through the earlier and highly variable development periods appears to represent diapause development under field conditions, while the flatter line models post diapause development and morphogenesis. This demonstrates that post diapause development steadily reduced the development period at 17.5°C as post diapause development and morphogenesis were stimulated by rising temperatures in the field. Because development periods for pupae collected at 105 and 119 days, representing

the transition period between the two processes, were included in both regressions, then the regressions are conservative. The slope showing diapause development would steepen, while that showing post diapause development would flatten further, if data from these collection dates was excluded.

The rapid stabilisation of mean development period to around 65 days at 17.5°C for pupae collected following 105 days of pupation indicates that diapause development was completed around this date. Normally post diapause quiescence would last through the coldest weeks of the winter in the native range. However, natural populations of *T. jacobaeae* are not likely to undergo quiescence in New Zealand.

The decrease in adult emergence success to 60% for pupae collected at the beginning of adult emergence in the field may result from a biased sample. If some adults had already emerged, the sample would have contained proportionately more inviable pupae.

Diapause development appears to have been completed after about 105 days of pupation in the Wairarapa. Upon termination of this phase, post diapause development continues at an accelerating rate with increasing temperature for approximately 150 days, until post diapause development is completed and adult emergence begins in natural populations.

DENSITY DEPENDENT MORTALITY AND VARIABILITY OF PUPAL SIZE IN RELATION TO LARVAL DENSITY.

(5.1) Introduction.

A common and obvious effect of high densities of *T. jacobaeae* larvae is to completely defoliate ragwort populations, causing widespread starvation among immature larvae. However high larval densities may also have other effects on the stability of *T. jacobaeae* populations. Dempster (1982) identified three density dependent processes acting on populations of *T. jacobaeae*. Firstly he described a delayed density dependent relationship between larval density and female fecundity in the following year. Secondly he showed that larval and pupal mortality was influenced by available ragwort shoot biomass. Total larval mortality showed a significant and non-linear relationship with larval density through intraspecific competition. Lastly he demonstrated significant density dependent emigration of moths from areas of high moth density.

Larvae show little behavioural adaptation to reduce the effects of food shortage. Increased interplant movement may occur as competition for food increases (van der Meijden 1976) but this behaviour may lead to higher mortality among migrating larvae (Crawley and Gillman 1990).

Most information on density dependence in *T. jacobaeae* (Dempster 1982) has been obtained through observation of natural populations. Factors like predation or migration of larvae between plants can make these studies complex and difficult to interpret. To surmount some of these problems I used cage trials to study the effects of larval density on larval survival and the size of resulting pupae. This approach also allowed me to quantify plant damage in relation to larval numbers. This is difficult to estimate in the field, again because of predation and migration. Bornemissza (1966) conducted trials in Australia with caged larvae but reported very high levels of mortality.

(5.2) Methods.

Ragwort plants and *T. jacobaeae* larvae were enclosed within 100cm x 60cm x 60cm cages made from 25mm x 25mm wood covered in curtain netting (mesh 20 per cm^2) on all sides except the bottom (Plate 8). The cages were placed outside on gravel, which allowed free drainage. An automatic irrigation system watered the plants twice daily and meant that the cages could be left undisturbed.

Plate 8. The cages constructed to house *T. jacobaeae* larvae in position at Massey University.

(5.2.1) Experiment one.

Experiment one began on the 11/1/90. Eight flowering ragwort plants of similar size (mean above ground fresh weight was estimated at 1500g after weighing plants of similar size) were collected and potted. The cages were arranged into 4 pairs with each pair having plants matched as closely as possible. Second and third instar larvae were placed on the plants at densities of 50, 35, 20 and 10 larvae per plant so that the plants in each pair received the same number of larvae. All larvae used were collected from the Kaipororo Road site on the 9/1/89 and were fed on cut ragwort leaves until the 11/1/89 when they were placed in the cages. Second and third instar larvae were chosen because of difficulties involved in collecting first instar without injuring them, while fourth and fifth instars were too advanced to provide a reasonable period of time on the plants. Using only second and third instar larvae also approximated the age characteristics of a single cohort developing over a similar period of time.

The larvae were left to feed and develop on the plants for 4 weeks, a sufficient time to complete development. At the end of this period, the cages were removed and living larvae and pupae were collected and counted.

(5.2.2) Experiment two.

The second experiment began on 14/2/90. Large rosette plants that were not flowering at the start of the experiment (mean above ground fresh weight estimated as 1800g) were used. Second and third instar *T. jacobaeae* larvae were collected from the Kaipororo Road site three days before the trial and fed on cut leaves until they were transferred to the cages. The cages and plants were set up as in experiment one.

Larvae were left on the plants for twenty two days (14/2/90-6/3/90), after which the cages were removed. Living and dead larvae and pupae were collected from each cage and numbers recorded. Pupae were weighed to 0.0001g, and their length and width measured to the nearest 0.5mm with Vernier callipers.

At the conclusion of both experiments each plant was scored on the following scale of capitula damage:

1 = No damage

2 = Capitula grazed: mildly attacked with little damage

3 = Capitula damaged: at least 50% of capitula heavily damaged

4 = Capitula destroyed: no capitula remaining

Defoliation was also assessed by visual estimation of the foliage removed. The categories were:

1 = No damage
2 = 25% defoliation (25% of foliage eaten)
3 = 50% defoliation
4 = 75% defoliation
5 = 100% defoliation (no green foliage remaining)

(5.3) Results.

The foliage and flowers of the plants used in these experiments were approximately 40% of total above ground fresh weight, while the stems contribute approximately 60% of above ground fresh weight. Therefore the plants used provided about 600g in experiment one, and 720g in experiment two, of foliage and flowers per plant. This represents the net weight of food available to larvae.

(5.3.1) Experiment one.

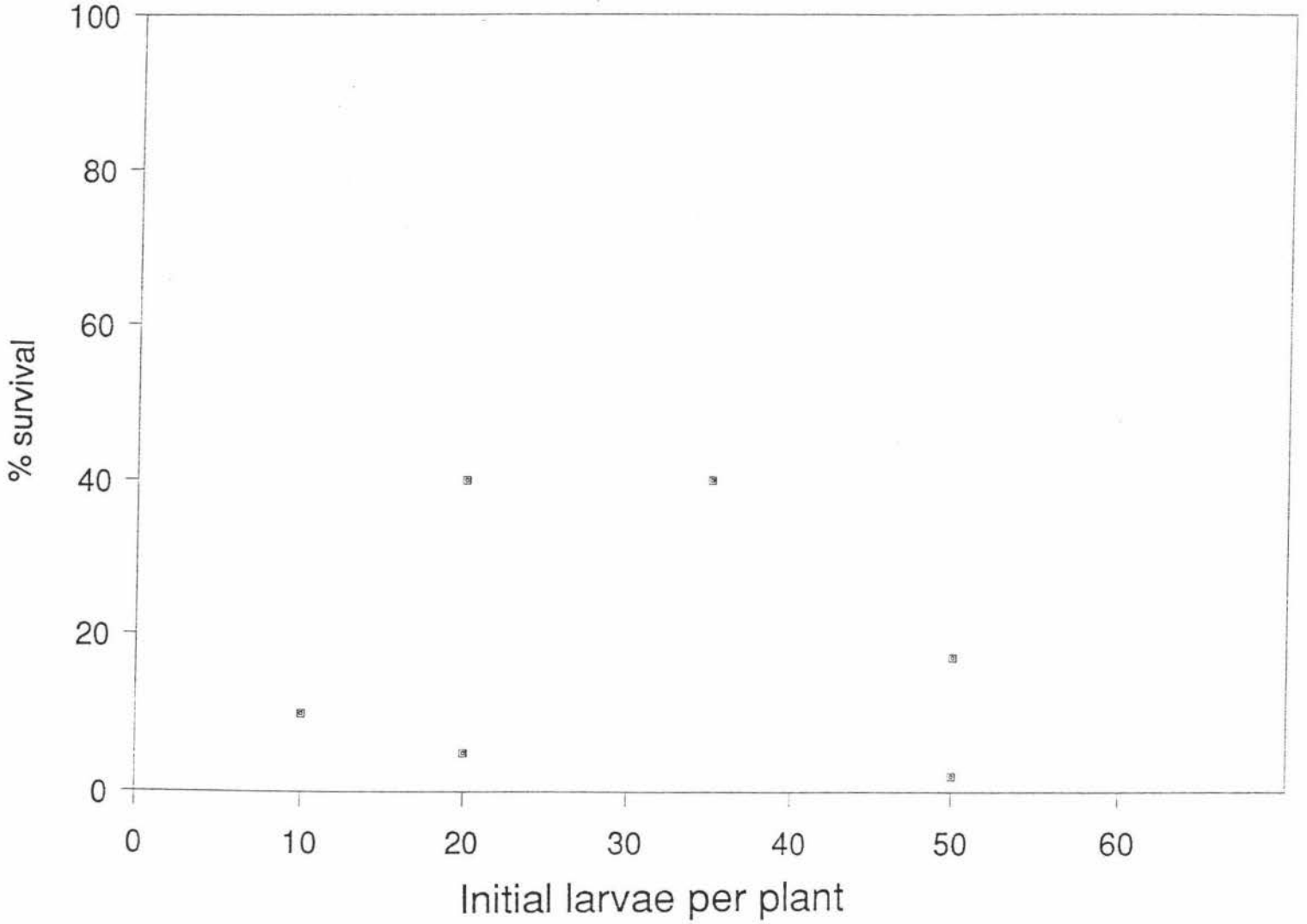
Successful pupation was low at all densities (Figure 5.1). As expected plant damage increased with increasing larval density (Table 5.1).

Table 5.1. Effect of larval density on ragwort damage (Experiment one).

Larvae per plant	Replicate	Capitula damage score	Defoliation score
50	a	4	5
50	b	4	5
35	a	4	5
35	b	4	5
20	a	3	3
20	b	4	4
10	a	3	2
10	b	2	2

The high mortality was apparently caused by starvation. There was no predation and no parasitism, and at no stage did I see evidence of disease.

Figure 5.1 Survival in relation to initial larval density (Experiment 1).



(5.3.2) Experiment two.

The larger plants in this second trial provided more foliage for the larvae so mortality was much lower (Figure 5.2). Plant damage showed a similar relationship to larval density as in experiment one (Table 5.2).

Table 5.2 The effect of larval density on ragwort damage (Experiment two).

Larvae per plant	Replicate	Capitula damage score	Defoliation score
50	a	4	5
50	b	4	5
30	a	4	5
30	b	4	5
15	a	3	4
15	b	2	3
10	a	2	2
10	b	2	3

(5.3.2.1) Density dependence.

k-values were calculated for each density in both experiments by the method of Varley and Gradwell (1960), such that:

$$k = \ln (\text{initial density/final density})$$

k-values per plant were calculated from the initial density of larvae and the final density of pupae. Smith's (1973) method was used to test for density dependent mortality. *k*-values for each density were plotted against their respective untransformed initial densities and a regression of *k*-value on initial density fitted (Figure 5.3). The regression fitted to the data from experiment one was not significant ($p = 0.702$). However, for experiment two the regression was highly significant ($P < 0.001$, $r^2 = .904$) suggesting strong density dependent mortality.

Figure 5.2 Survival in relation to initial larval density (Experiment 2).

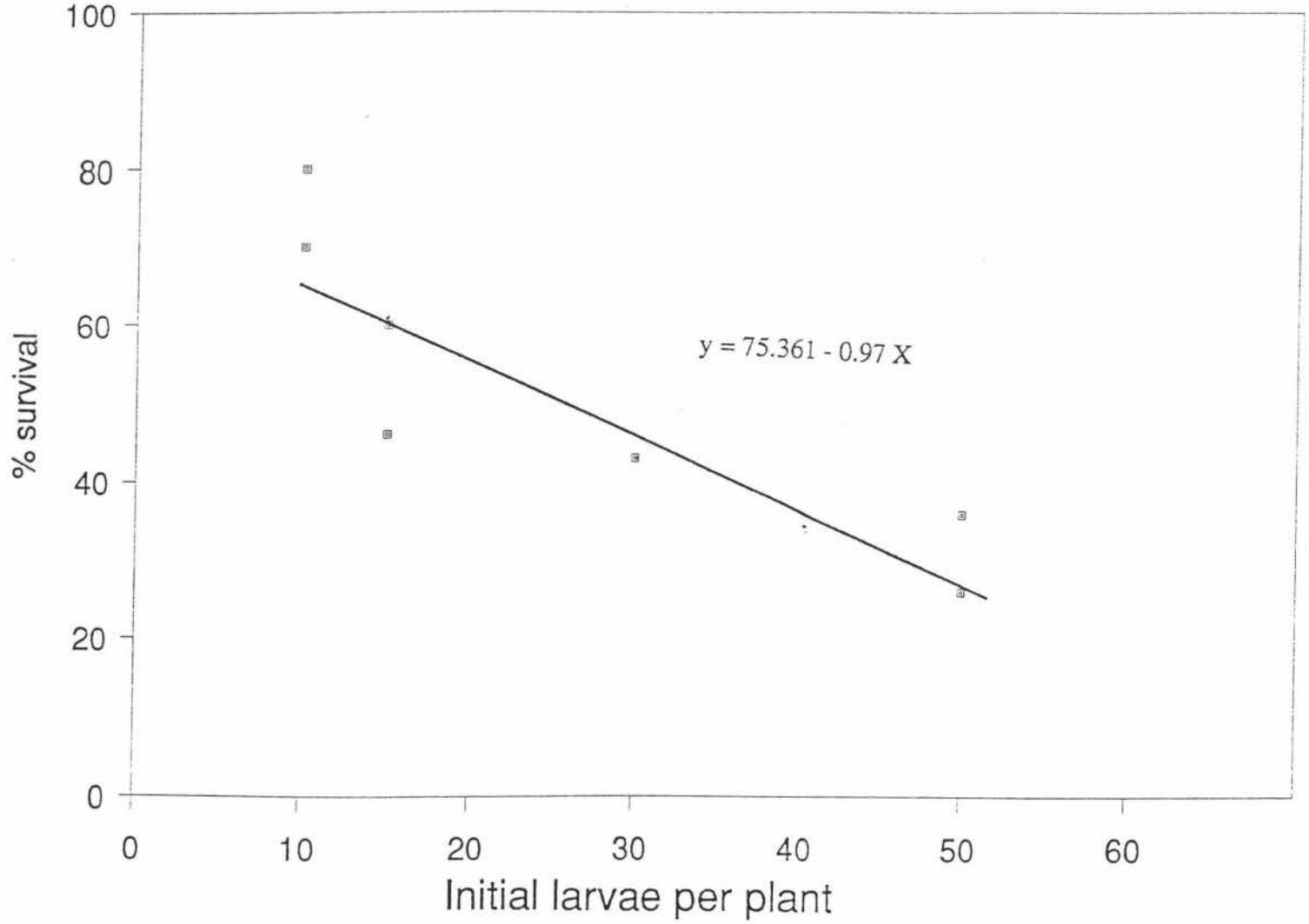
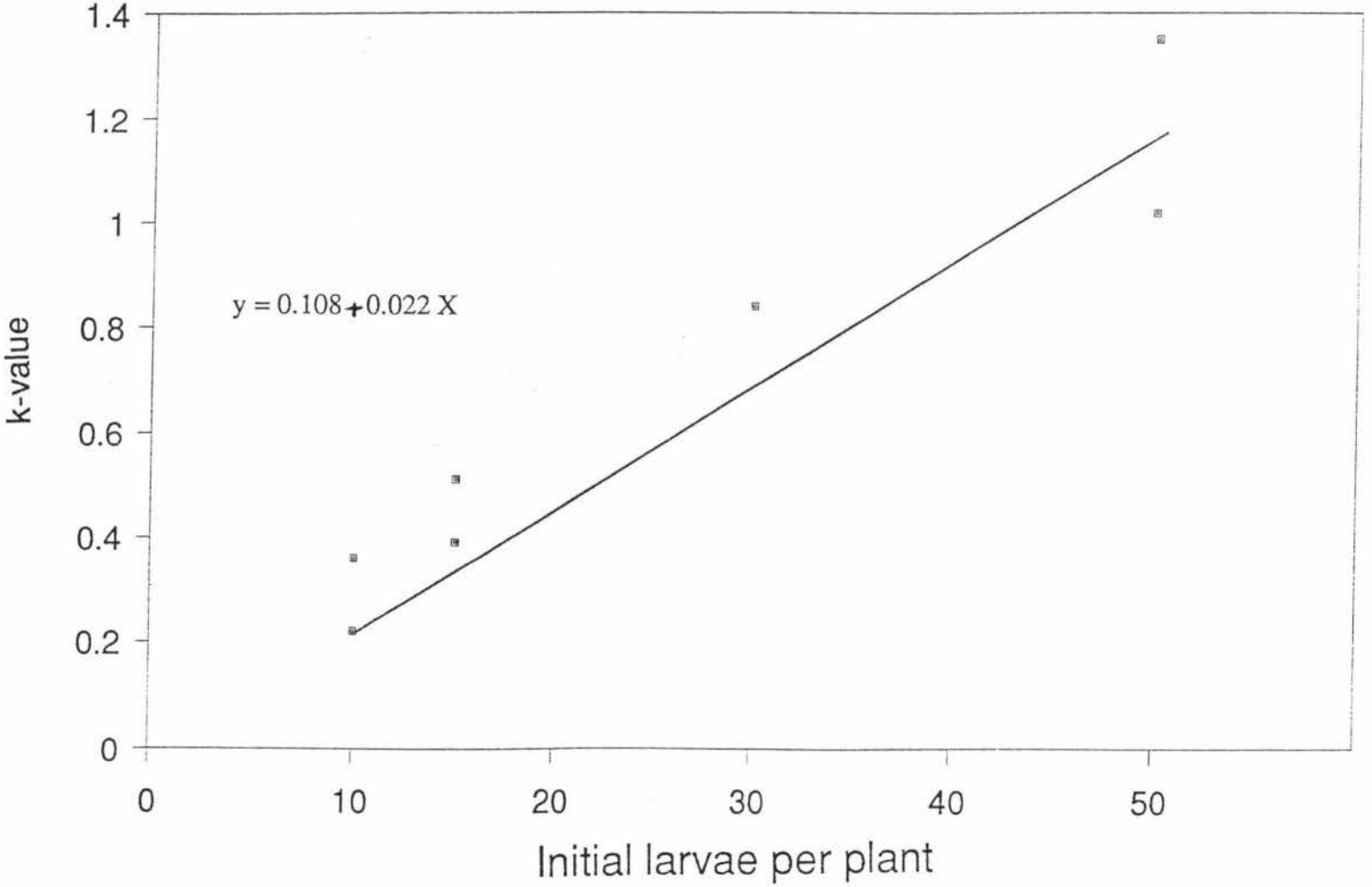


Figure 5.3 *k*- value in relation to initial larval density (Experiment 2).



(5.3.2.2) Pupal dimensions.

Dimensions of pupae in relation to larval density for experiment two are given in Table 5.3.

Parameters of pupal size were inversely related to larval density (length = 1.246 - 0.003 density, $r^2 = 0.186$, $P < 0.001$) (Figure 5.4), (width = 0.533 - 0.001 density, $r^2 = 0.136$, $P < 0.001$) (Figure 5.4), (weight = 0.199 - 0.001density, $r^2 = 0.188$, $P < 0.001$) (Figure 5.5).

Table 5.3. Effect of larval density on pupal dimensions at different densities (Experiment two).

Larvae per plant	Mean length (cm)	Mean width (cm)	Mean weight (g)
50	1.15	0.49	0.0644
50	1.17	0.48	0.0719
30	1.21	0.54	0.0922
30	1.18	0.52	0.0956
15	1.23	0.57	0.1183
15	1.22	0.55	0.0935
10	1.24	0.56	0.1178
10	0.56	0.56	0.1191

Using the equation given by Dempster (1971) the potential fecundity of female moths was estimated from their pupal widths, thus:

$$n = 253.69 + 2463 (D - 0.4948)$$

n = expected fecundity
D = observed mean pupal width

Figure 5.4 Relationship between pupal dimensions and initial larval density.

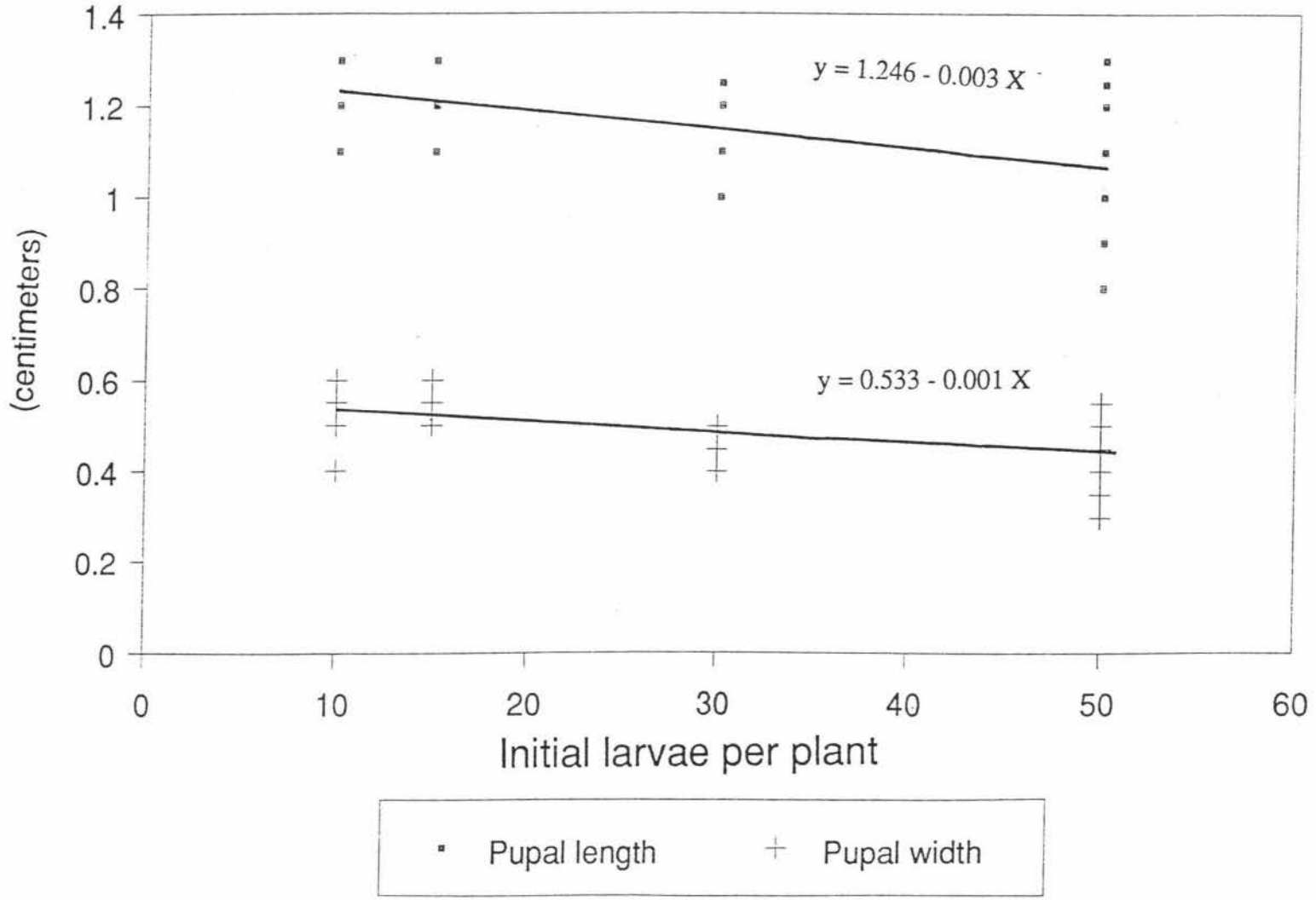
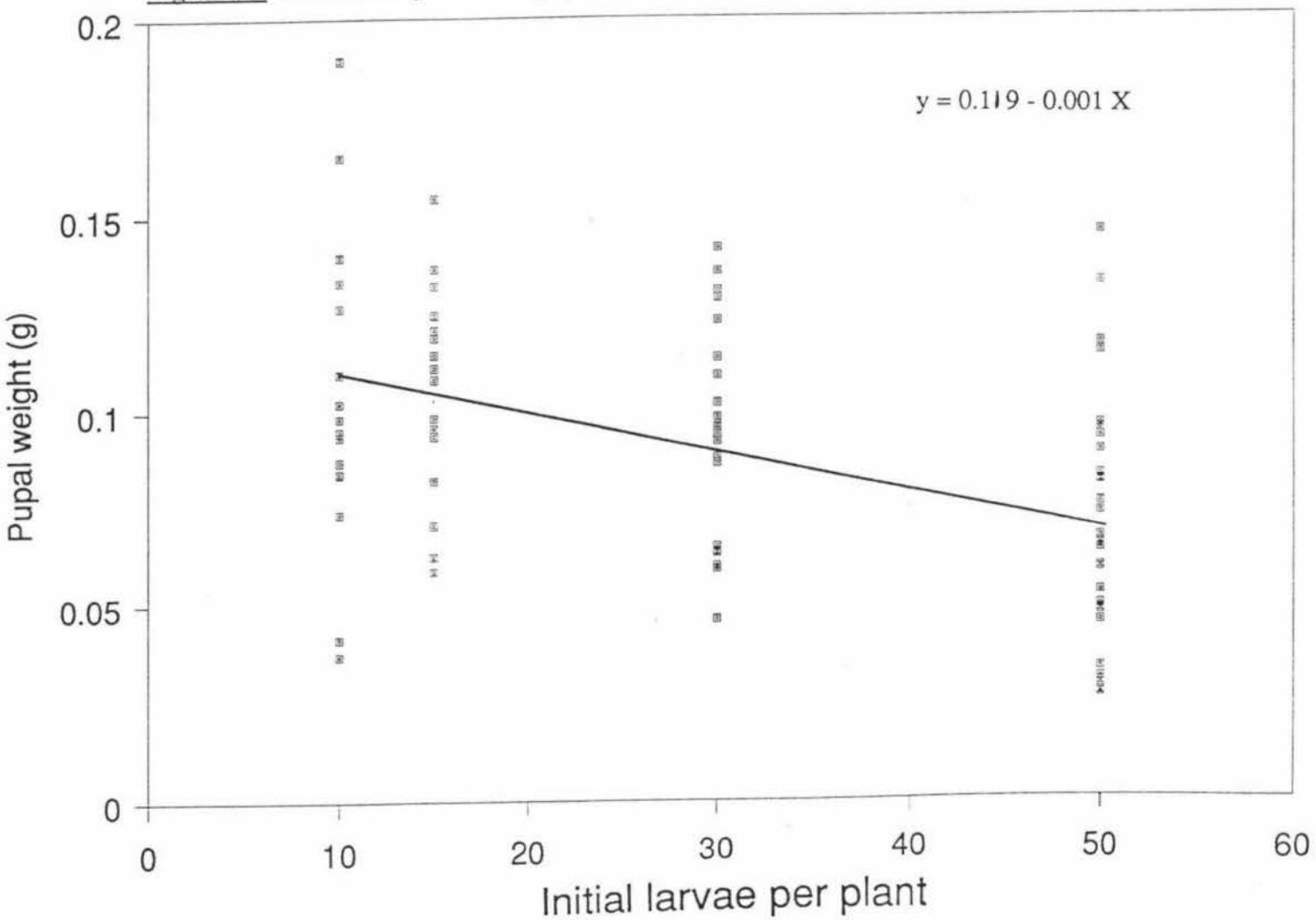


Figure 5.5 Relationship between pupal weight and initial larval density.



Estimates of expected fecundity are based on the mean female pupal width for each larval density (Table 5.4).

Table 5.4. Expected fecundity of female pupae from larvae raised at different densities, based on pupal width.

Larvae/plant	Mean Width	Expected Fecundity
50	0.445	131.0
30	0.460	168.0
15	0.500	266.0
10	0.530	340.0

(5.4) Discussion.

T. jacobaeae larvae collected from the Kaipororo Road site showed no signs of either the microsporidian disease (Hawkes 1973) or the nuclear polyhedrosis virus (Bornemissza 1966) that infect *T. jacobaeae* larvae overseas. In contrast to Bornemissza (1966) it appears that larvae, from the Kaipororo Road site at least, may be confined during development with no deleterious effects from disease. As larvae at this site were apparently disease free this encourages the hope that *T. jacobaeae* redistributed elsewhere in New Zealand from the Wairarapa (Syrett 1987) are also free of diseases that may reduce the insect's effectiveness as a biological control agent.

Bornemissza (1966) estimated that more than 15 larvae per plant could completely defoliate a "medium sized" plant of 25g dry weight, which corresponded to an initial density of 25 larvae per plant. I found that an initial density of 30 second and third instar larvae, or about 4.2 larvae per 100g of live foliage and flowers, can cause complete defoliation and stripping of the capitula and flowers. Larvae raised at 30 per plant in experiment two showed 43% survival in both replicates, resulting in a final density of 13 pupae per plant which correlates well with Bornemisszas' (1966) results. My results show that an initial density of 2.1 larvae per 100g of foliage and flowers prevented flowering and severely damaged at least 50% of the capitula. The results of my investigation of natural *T. jacobaeae* populations (see Chapter 4) indicate that fourth instar larvae are largely

responsible for defoliation. I found from the field study that plants hosting more than 16 fourth instar larvae had flowers and capitula completely removed, and at 31 or more fourth instar larvae per plant defoliated all but the largest ragwort plants. Therefore, the number of larvae needed to cause damage similar to that seen in my cage experiments is slightly higher among field populations. However, plants growing under more natural conditions can more easily compensate for damage.

My results show that New Zealand populations of *T. jacobaeae* appear to suffer from limited availability of food in similar ways to populations elsewhere. Starvation is a key factor in that determines fluctuations in population size of *T. jacobaeae* in England (Dempster 1975) and total larval mortality is positively correlated with larval density in a non-linear manner (Dempster 1982).

Density dependent mortality was clearly demonstrated in this study. In experiment one, any density dependent effects were masked by the high mortality. Because predation, parasitism, disease and mortality associated with migration did not occur during my experiments, mortality must have been solely determined by competition for food, causing starvation. This poor survival in experiment one was caused by the use of flowering plants that had little foliage. In experiment two food was severely limiting only at a larval density above 4.2 larvae per 100g foliage and at higher larval densities starvation caused greater mortality.

Several studies have investigated the performance of *T. jacobaeae* larvae in relation to the part of the plant they ate. The rate of larval development, pupal size and the proportion of emerging adults are all higher for larvae fed flowers compared to larvae fed only on leaves (van der Meijden 1976; Rose 1978; Dempster 1982). Capitula were damaged to some degree at all larval densities investigated during my study. Early hatching larvae with access to the capitula should therefore develop faster than those larvae forced by intraspecific competition to eat only foliage.

The density dependent reduction in pupal dimensions and weight found in experiment two agrees with Dempster's (1971) results for English stock, and with van der Meijden's (1976) results for Dutch populations. The fecundity of the female moth is strongly correlated with her weight at emergence which in turn is related to pupal width (Dempster 1971). Dempster considered pupal width a more convenient parameter from which to estimate potential fecundity. Mean pupal width has been found to be significantly different for larvae raised at different densities (Dempster 1971).

Dempster (1971) found delayed density dependent reduction in female fecundity after a year of high larval density. However his *k*-factor analysis indicated that reduction in natality (the combined effects of variation in fecundity, adult mortality and dispersal) had little effect on the trend of K, i.e. that variable natality was not a major cause of fluctuations in *T. jacobaeae* population size.

I found that an initial larval density greater than 10 per plant reduced mean female pupal width and therefore potential fecundity. This occurred despite the apparent excess of food in the 10 and 15 larvae per plant treatments. Therefore the reduction in pupal width may have been caused by the agonistic behaviour of larvae, which interrupts normal feeding and growth when no migration is possible. Dempster (1971) referred to this behaviour as "mutual interference". However, competition for capitula and flowers, even at low densities, may reduce the average quality of food available to larvae and reduce pupal dimensions (van der Meijden 1976). At higher densities the optimal weight for pupation in my trials was almost certainly not reached because of intense intraspecific competition for food, so pupal width was considerably reduced.

These cage experiments prevent predation and migration, which are both likely to affect mortality in a density dependent manner. Thus, the strength of density dependence may be underestimated. Despite this, my study showed strong density dependent mortality of larvae suggesting that this is an important process in field populations.

FIELD POPULATION STUDY.

(6.1) Introduction.

T. jacobaeae larvae periodically defoliate ragwort at some localities in New Zealand, whereas they persist only at low densities elsewhere and have little influence on the ragwort population. Much has been published on the population dynamics of both *T. jacobaeae* and ragwort, and the interactions between these species in other countries. Cameron's (1935) initial work in England on the suitability of *T. jacobaeae* as a control agent for ragwort in New Zealand provided an excellent general investigation of the moth's ecology and provided information about its potential to control ragwort. Dempster (1971, 1982) investigated the population ecology of the moth and its interactions with ragwort on dry, sandy soils in England. Isaacson (1973) produced a lifetable for the moth in Oregon and Crawley and Gillman (1989) investigated the population dynamics of *T. jacobaeae* and ragwort in grassland at Silwood Park, Berkshire. There have also been reports on the effectiveness of this moth as a control agent in Australia (Bornemissza 1966), the Netherlands (van der Meijden and Waals-Kooi 1979) and Canada (Harris *et al.* 1978; Myers 1980).

Much of the information obtained from these studies may not apply to New Zealand conditions. Differences in climate, farming techniques and pressure from predation, parasitism and disease mean that the interactions between *T. jacobaeae* and ragwort are unlikely to be the same in different countries. There is very little information available on the population processes of *T. jacobaeae*, or its influence on ragwort in this country (Miller 1970).

An intensive study was therefore undertaken of the phenology, mortality and interaction of *T. jacobaeae* with ragwort in the Wairarapa, where it is maintaining viable populations. My study focused on the pattern of oviposition seen in natural populations as well as the change in numbers and survival of larvae on marked plants over the larval growth period. The damage to ragwort plants and the mortality among ragwort populations caused by larval feeding was also investigated. My aim was to identify factors that regulate *T. jacobaeae* populations and affect the ability of *T. jacobaeae* to control ragwort in New Zealand.

(6.2) Methods.

(6.2.1) Development of the sampling program.

The aim of the sampling program was to estimate quantitative changes in the following variables with time:

(a) Oviposition.

(b) Larval numbers.

(c) Damage to the host plant and the plant's response to damage.

Accuracy is maximised in a sampling program designed to estimate changes in variables by retaining the same basic sample units throughout the program. In this case the basic sample unit was a preselected ragwort plant. Data are therefore obtained for individual plants and the *T. jacobaeae* population directly associated with those plants. This provides an accurate account of changes on the individual plants and allows estimation of changes within the plant and the insect populations as a whole at that site, provided the sample is large enough.

Certain assumptions are necessary with this form of sampling program that, if valid, provide more reliable information. Firstly, the plants selected for regular examination must accurately represent the whole plant population. Thus they must be selected randomly so that their selection is unbiased. Secondly, mortality of both plants and insects must be independent of the position of an individual within the study area.

This method removes the bias that may result if sampled plants were reselected at each sample date. Potential bias may be related to plant size, number of eggs and/or larvae on the plant or the level of defoliation of the plant. However, if plants are randomly selected before these variables changed then potential bias eliminated.

(6.2.2) Sample plant selection.

Detailed descriptions of the study sites are given in the General Methods section. At each site ragwort plants were randomly selected and marked with a numbered stake driven into the ground beside each plant. For the Kaipororo Road site 5 plants within each quadrat were selected and marked in this manner, giving a total of 25 plants. Five plants were marked at each the Hukanui and Eketahuna sites.

(6.2.3) Estimation of ragwort density.

Ragwort density during the 1989/90 and 1990/91 seasons was estimated from direct counts of the plants within each of the five 20m x 20m quadrats at the Kaipororo Road site. The same method was used at the Hukanui site, although here there was only one 20m x 20m quadrat. At the Eketahuna site the 6 plants present were within 5m of each other but plant density was estimated by the number of plants contained within the entire field, so as not to overestimate density.

This method of obtaining ragwort density does not accurately estimate total plant density, as only those plants large enough to allow identification were counted. Seedlings (i.e. <10cm diameter) were not recorded because of the difficulty in identifying and counting them. This has no bearing on the accuracy of *T. jacobaeae* population estimates because the estimate of plant density is based on plants of sufficient size to attract ovipositing female moths and migrating larvae. It is therefore a true estimate of potential host plant density.

(6.2.4) Measurement of plant dimensions.

The diameter and height of each marked plant was recorded weekly. Diameter measurements were taken across the widest point of the plant while height was measured from ground level to the highest point.

(6.2.5) Recording egg batches and larval numbers.

In the first year of the field study adult moths were observed flying on the 4/11/89 and regular weekly sampling began on the 9/11/89. In the second year regular weekly sampling began on the 3/11/90. The same sample dates were retained during the 1990/91 season as in the 1989/90 season. On each occasion the sampled ragwort plants were searched leaf by leaf for eggs and larvae. The number of eggs contained within each egg batch observed was recorded, and new batches were identified on each sample date.

When eggs began to hatch two potential sources of sampling error became apparent. Firstly, newly hatched larvae are gregarious on the leaf supporting the egg batch. Consequently, with a large number of very small and inconspicuous larvae clustered together, much care was required to obtain an accurate count. These larvae were counted several times and if counts differed they were averaged.

The second source of error occurred when larvae were disturbed by movement of the plant or even by the shadow of the observer. If disturbed the larvae would drop to the ground on a thin silk thread. Extreme care was therefore necessary when these larvae were present. This behaviour did not result in the same errors for older, more brightly coloured larvae because they could be counted without causing undue disturbance. Counts of first instar larvae may therefore be underestimates.

The number of larvae of each instar present on the marked plants was recorded weekly. Instars were subjectively determined, usually by size, and particularly head capsule width.

(6.2.6) Plant damage.

Once larvae began to inflict visible damage to sample plants, the level of damage was recorded. Plants with their flowers and capitula entirely eaten were recorded as "Capitula Destroyed". If little or no photosynthetic leaf material remained the plant was recorded as "Defoliated".

Regrowth was recorded as "Some Regrowth", indicating secondary growth had begun, or as "Full Regrowth", where the plant had recovered and produced abundant secondary foliage. Plants that flowered after defoliation were recorded as "Secondary Flowering".

(6.2.7) Estimation of pupal density.

The density of surviving pupae was determined at the Kaipororo Road site immediately before the expected date of adult emergence. Soil samples measuring 0.25m x 0.25m were taken to a depth of approximately 10cm. Twenty four of these samples were taken on 4/11/90 and a further 24 on the 14/11/90. The soil samples were removed and thoroughly hand sorted for living pupae.

(6.3) Results.

(6.3.1) Stage frequency analysis.

A modification of Southwood's (1978) method of stage-frequency analysis was used to estimate total numbers of eggs and larvae at each site from data collected during weekly sampling. The original method involves graphical estimation of the area under the stage-frequency curve, which is divided by the mean development time for that life stage. The area under the stage-frequency curve is estimated as:

$$A = 0.5\sum_{i=1}^{k}\{(h_i - h_{i-1})(n_i + n_{i-1})$$

where there are k sampling occasions with h_i being the ith of these and n_i animals are recorded in the instar on occasion i.

If d = the mean development time for the stage, then the number of individuals passing through the stage is:

$$N = A/d$$

Sawyer and Haynes (1984) suggested that stage frequency curves should be plotted against a physiological time scale, i.e. day-degrees, to allow for the dependence of development rate on temperature. Therefore the reciprocal of the slope of the regression of development rate on temperature, b, equals d_p, i.e $d_p = 1/b$.

The number of animals passing through that stage is calculated from:

$$N = 0.5\sum_{i=1}^{k}\{(hp_i - hp_{i-1})(n_i + n_{i-1})\}/d_p$$

where hp_i is the time in day-degrees at which the ith sample was taken. Day-degrees were calculated from temperature records supplied by the New Zealand Meteorological Service for the Mount Bruce Station. Average daily temperatures at Eketahuna were within 0.5°C of Mount Bruce, so Mount Bruce records were also used for this site. The physiological temperature requirements for eggs and each instar were obtained from Harman, Dymock and Syrett (1988).

The numbers of eggs and larvae entering each instar calculated by this latter method and are given in Table 6.1.

Table 6.1. Total number of individuals per quadrat per site for 1989/90 and 1990/91, estimated by Southwood's method (Sawyer and Haynes 1984).

	Instar					
	Eggs	First	Second	Third	Fourth	Fifth
Kaipororo Road (1989/90)						
Quadrat One	2558	830	1878	477	112	27
Quadrat Two	2236	957	699	283	29	17
Quadrat Three	6583	1917	2357	985	190	49
quadrat Four	4717	1865	729	447	134	7
Quadrat Five	3403	1131	714	303	41	30
Kaipororo Road (1990/91)						
Quadrat One	3106	1589	1439	1020	482	89
Quadrat Two	1628	850	587	756	380	32
Quadrat Three	757	235	235	110	68	9
Quadrat Four	1347	623	394	294	74	10
Quadrat Five	1121	536	619	222	139	25
Eketahuna (1989/90)	4126	866	1808	1573	419	26
Hukanui (1989/90)	1593	---	---	---	---	---

(6.3.2) Estimation of ragwort density.

The number of plants per 20m x 20m quadrat was recorded for each quadrat individually, and the estimated average ragwort density at each site is given in Table 6.2.

Table 6.2. Average ragwort density at study sites.

Site		Total no.	Plant density/ m^2
Kaipororo Road	1989/90	73	0.037
	1990/91	217	0.110
Hukanui	1989/90	12	0.030
Eketahuna	1989/90	6	0.0001

(6.3.3) Oviposition.

Egg batches were always laid on the underside of the basal leaves of the ragwort plant. Each batch was laid singly on a leaf, and no leaves carried more than one batch. Egg batch size was extremely variable, ranging from a single egg to 179 eggs. A summary of data collected is presented in Table 6.3, and the frequency distributions of egg batch sizes for Kaipororo Road are given in Figure 6.1 a + b.

Figure 6.1a Frequency of batch sizes at Kaipororo Road (1989/90).

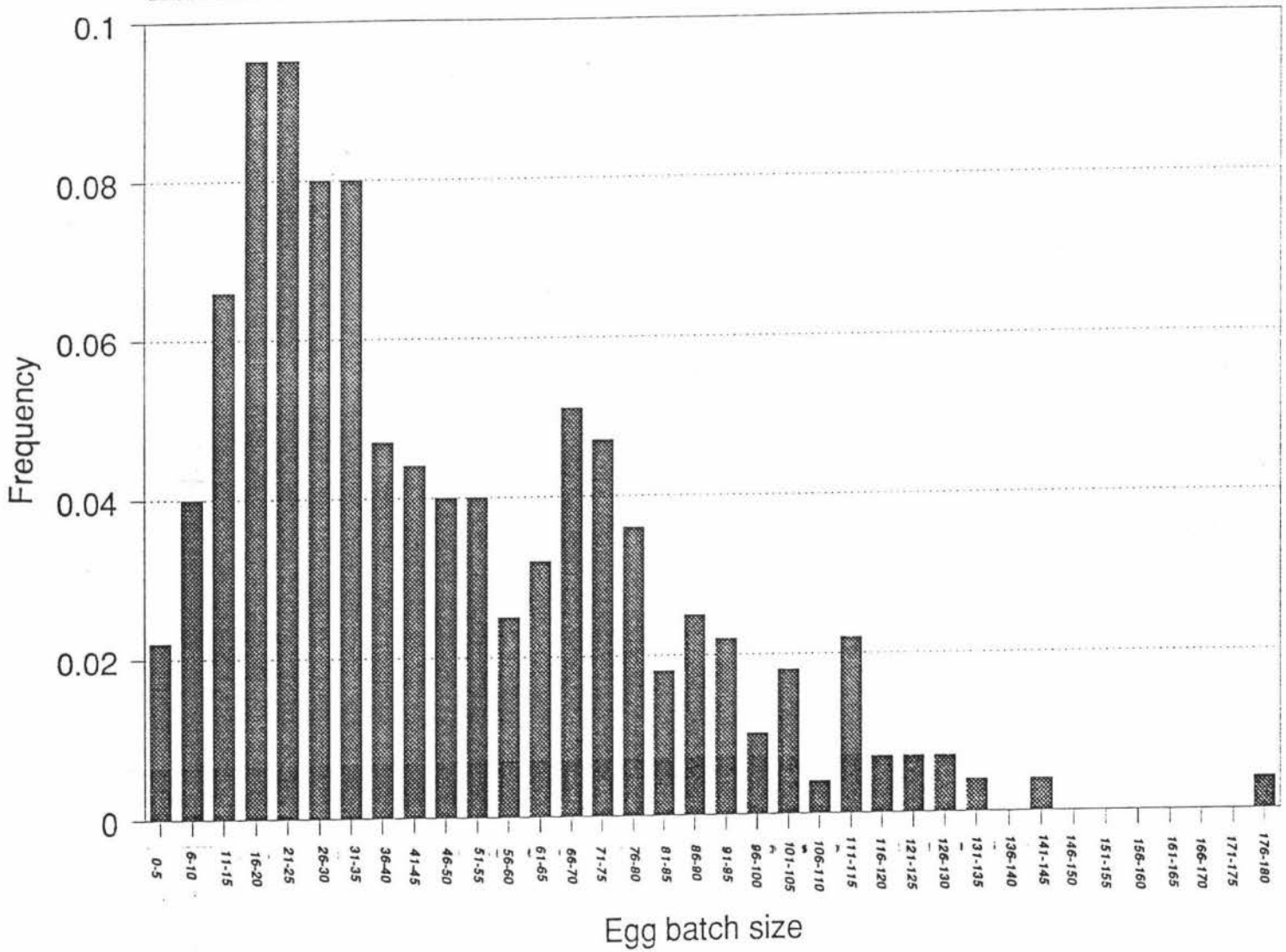


Figure 6.1b Frequency of batch sizes at Kaipororo Road (1990/91).

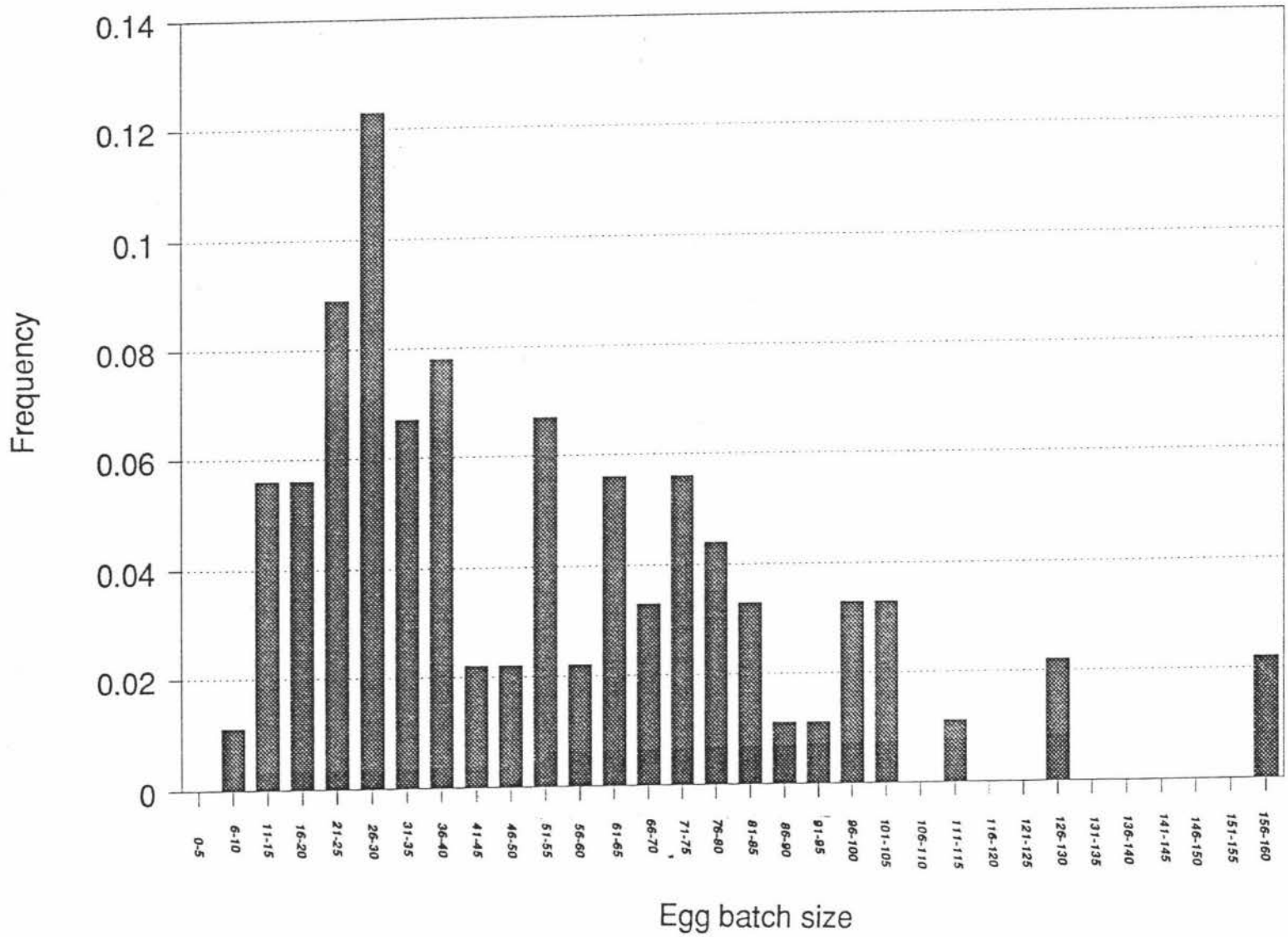


Table 6.3. **Oviposition data for 1989/90 and 1990/91 seasons (untransformed data).**

Site	Mean no. eggs per batch	Mean no. eggs per plant	Mean no. batches per plant	Observed oviposition period(days)
Eketahuna	47.2 ± 3.8	570	12	27
Kaipororo				
(1989/90)	47.2 ± 1.9	517	11	54
(1990/91)	53.2 ± 3.6	183	4	46
Hukanui	58.5 ± 9.4	222	4	34

Plots of the frequency of transformed and untransformed batch sizes indicated a bimodal distribution. This was investigated with the "KMM" program (McLachlan and Basford 1988) which fits a mixture of normal distributions with either equal or arbitrary covariance matrices to two-mode two-way data. The program was run using the square root transformed data from the Kaipororo Road site for 1989/90 and 1990/91 separately. For the 1989/90 data the program could not fit two or more normal curves that fitted the data significantly better than a single normal curve, hence the distribution was not proved to be other than unimodal. For the 1990/91 data two normal curves fitted the data significantly better than either a single or three normal curves, thereby identifying a bimodal distribution. The program fitted curves with means of 4.93 (approximately 24.3 eggs per batch) and 8.27 (approximately 68.4 eggs per batch) with variances of 0.92 and 3.32 respectively, with 46% of batches assigned to the first distribution and 54% to the second.

(6.3.3.1) Oviposition phenology.

The pattern of oviposition over time for the three sites is given in Figure 6.2. In the 1989/90 season at Kaipororo Road 6.7% of the total number of eggs observed on sampled plants were already present by 9/11/89 when sampling commenced. The highest rate of oviposition was between 14/11/89 and 21/11/89 when 23.3% of all eggs were laid. All eggs were laid by 2/1/90. One live female was found near the last egg batch laid (on 2/1/90) and this was the last living adult observed in the field. One or more egg batches were observed on 88% of sampled plants at this site. In the following season, 1990/91, eggs were first recorded on the 3/11/90, when 0.04% of all eggs laid were present. Forty percent were laid by the 5/12/90 and 100% were laid by the 9/1/91. One or more egg batches were observed on 96% of sampled plants in this season.

Half the total number of eggs observed at the Hukanui Road study site in 1989/90 were present on the 9/11/89 and 89.7% of eggs were laid by the 28/11/89. None were laid after the 12/12/89 at this site and all sampled plants were observed to host eggs.

At the Eketahuna site 16.3% of the total number of eggs observed were present on sampled plants by 9/11/89 and 48.1% of all eggs observed at this site were laid by the 14/11/89. No further eggs were laid after the 5/12/89 and all sampled plants hosted eggs.

(6.3.3.2) Egg batch size in relation to plant size and date.

For regression analysis the data on egg batch size for both years were square root transformed to better fit a normal distribution and stabilise the variances. The influence of plant diameter, plant height and date of oviposition on observed batch size was determined for each site by partial correlation analysis. To compensate for the dynamic nature of plant dimensions through time, date was held constant. Egg batch size for both years at Kaipororo Road in relation to each of these variables is given in Figures 6.3 a+b, 6.4.a+b and 6.5 a+b, and egg batch size in relation to date at Eketahuna in 6.5 c.

(6.3.3.3.) 1989/90.

There was no significant correlation between either plant diameter or plant height and batch size per plant at all sites. Regression analysis of the square root of egg batch size against sample date indicated a significant negative relationship at both the Kaipororo Road site ($\sqrt{}$batch size = 7.162 - 0.043 date, $r^2 = 0.038$, $p < 0.001$) and the Eketahuna site ($\sqrt{}$batch size = 7.430 - 0.095 date, $r^2 = 0.098$, $p < 0.008$).

Figure 6.2 Cumulative % of eggs laid in relation to sample date (using stage frequency adjusted data).

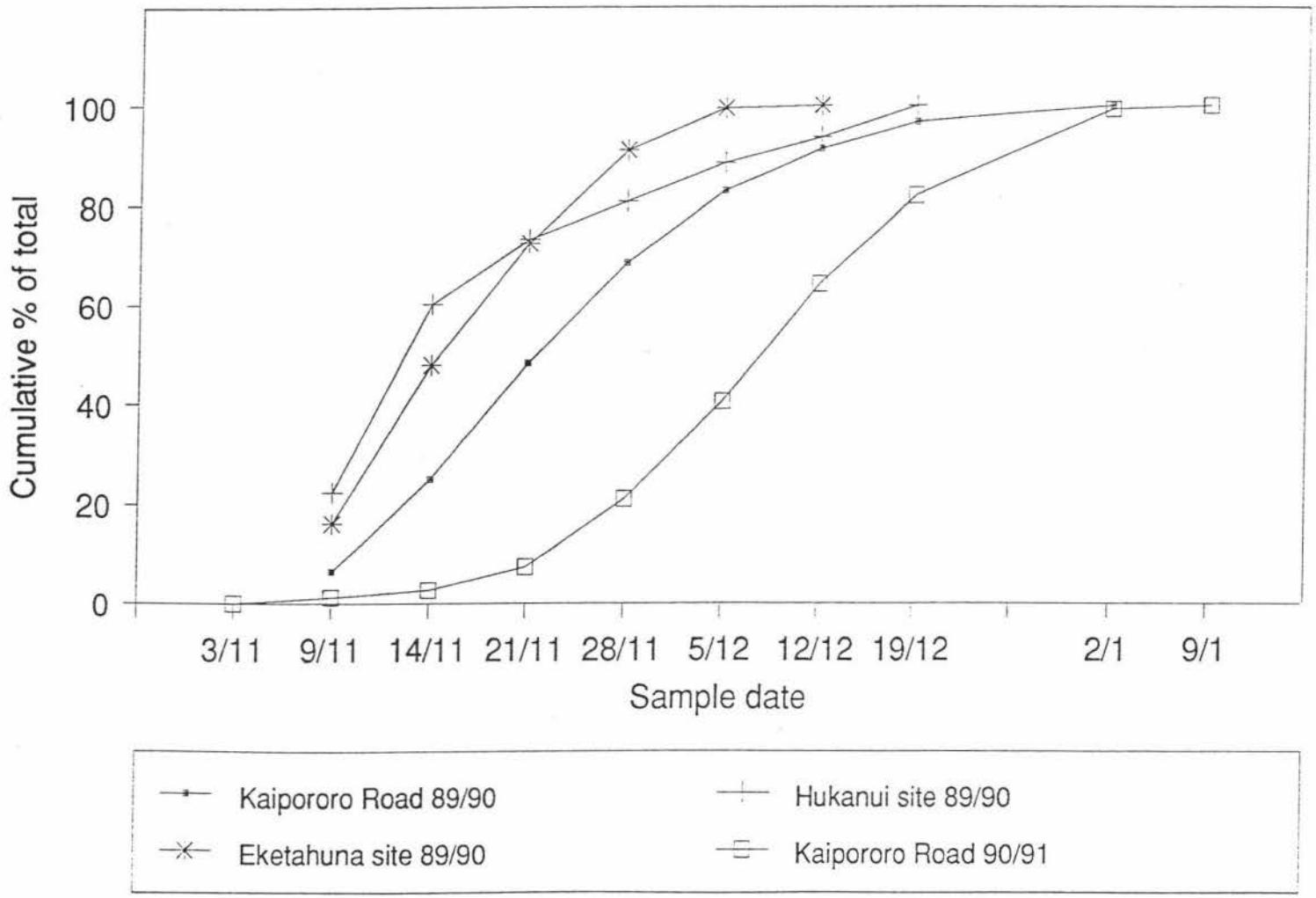


Figure 6.3a The number of eggs per batch in relation to the diameter of the host plant. Kaipororo Road 1989/90.

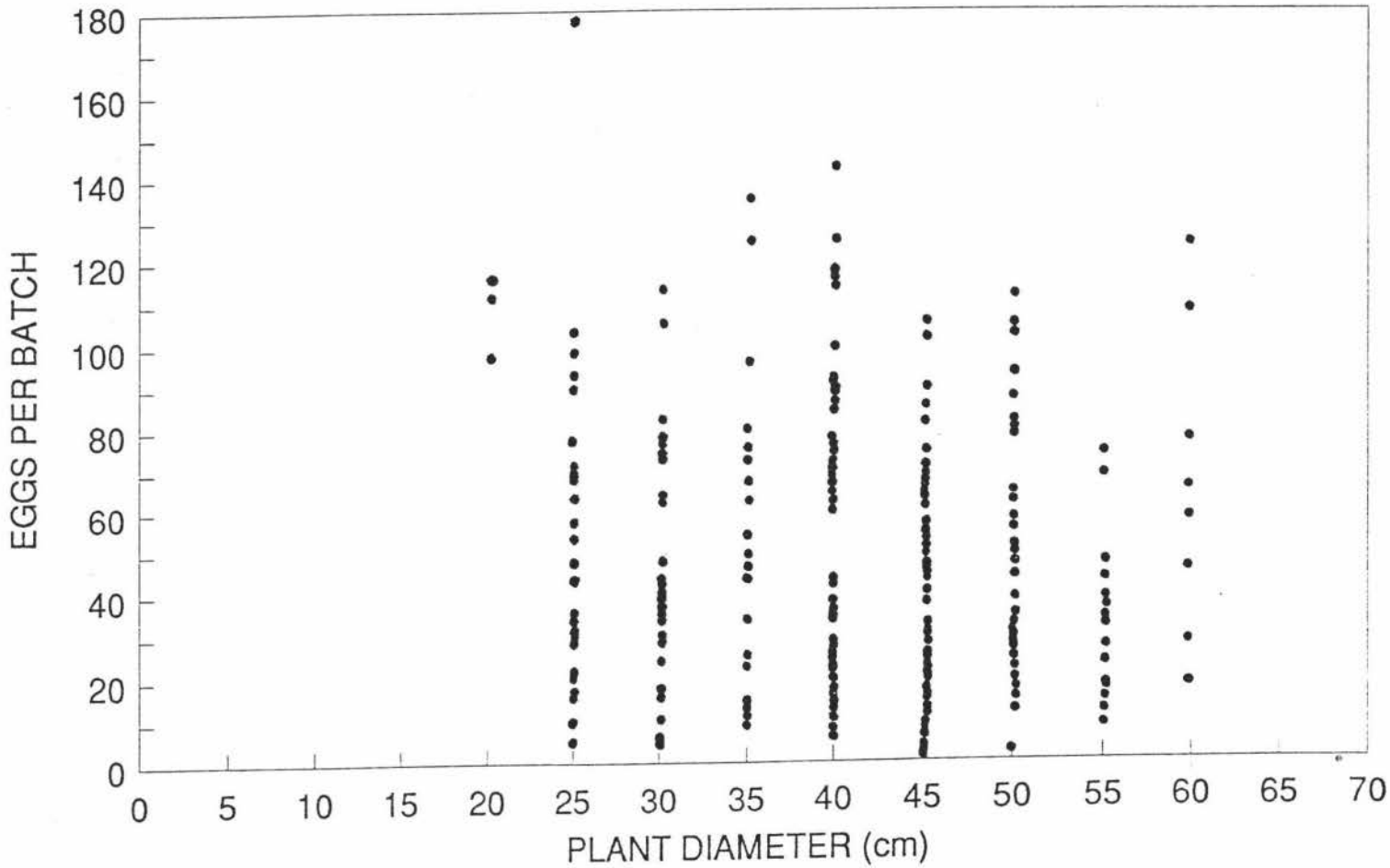


Figure 6.3b The number of eggs per batch in relation to the diameter of the host plant. Kaipororo Road 1990/91.

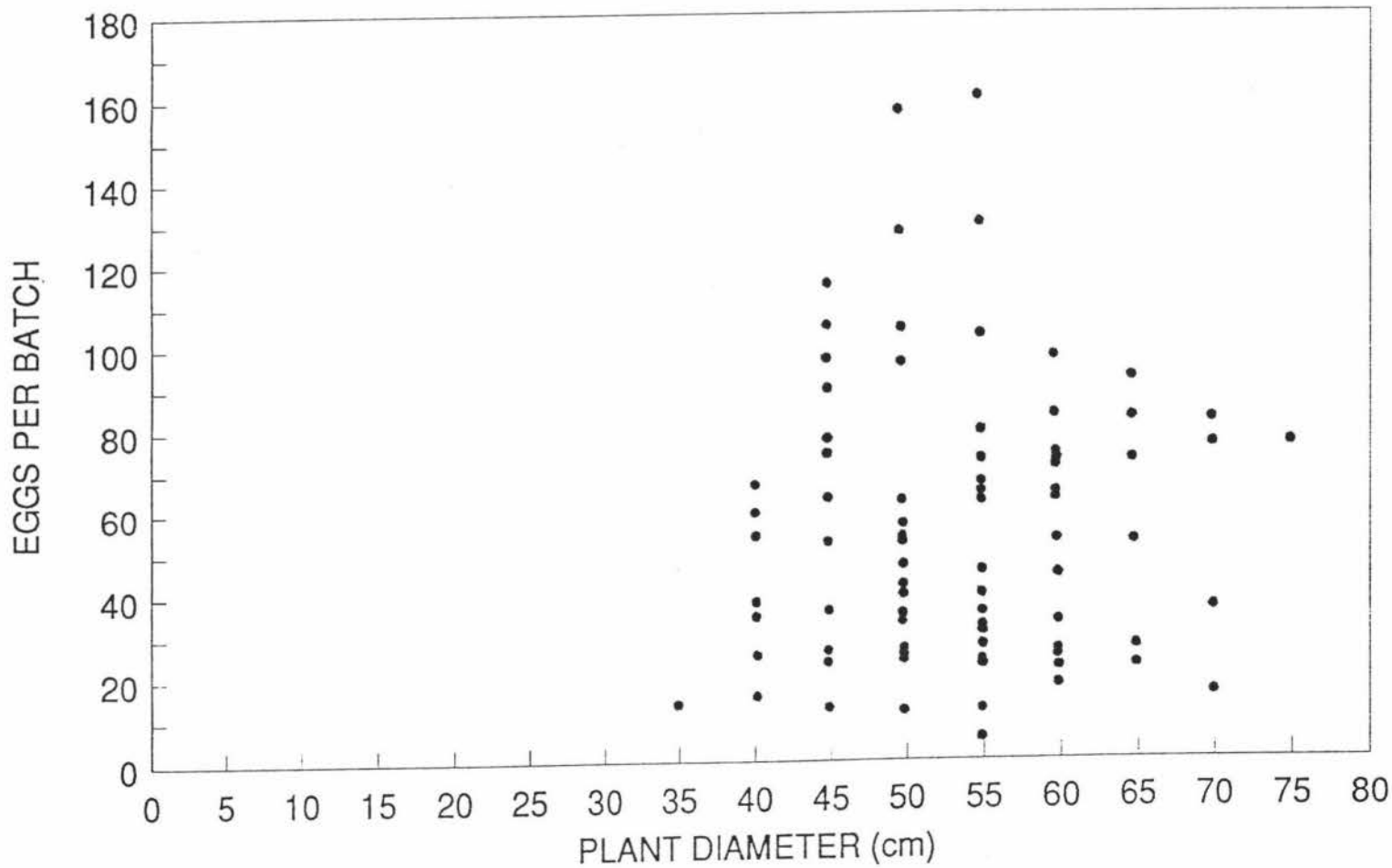


Figure 6.4a The number of eggs per batch in relation to the height of the host plant. Kaipororo Road 1989/90

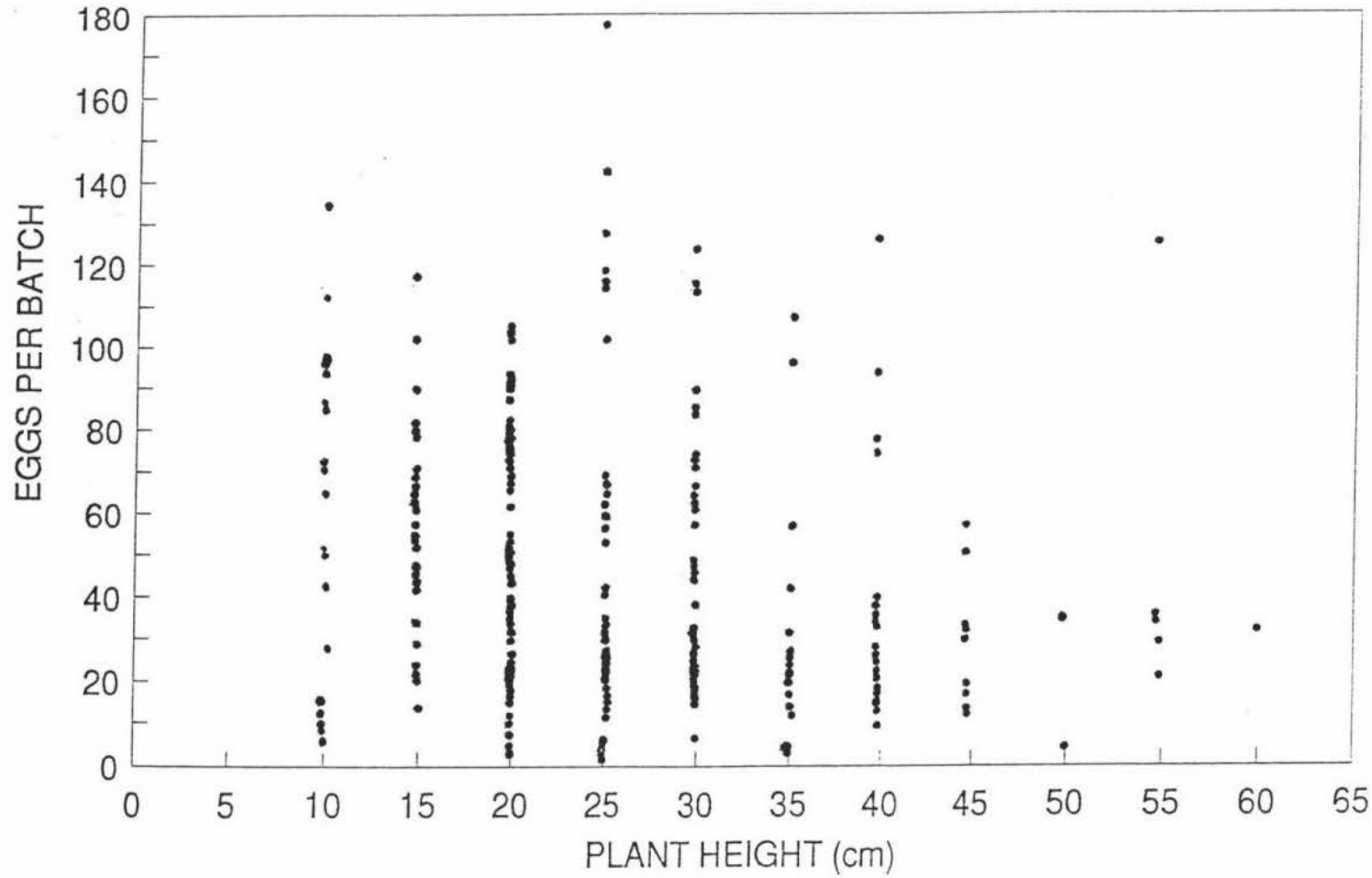


Figure 6.4b The number of eggs per batch in relation to the height of the host plant. Kaipororo Road 1990/91

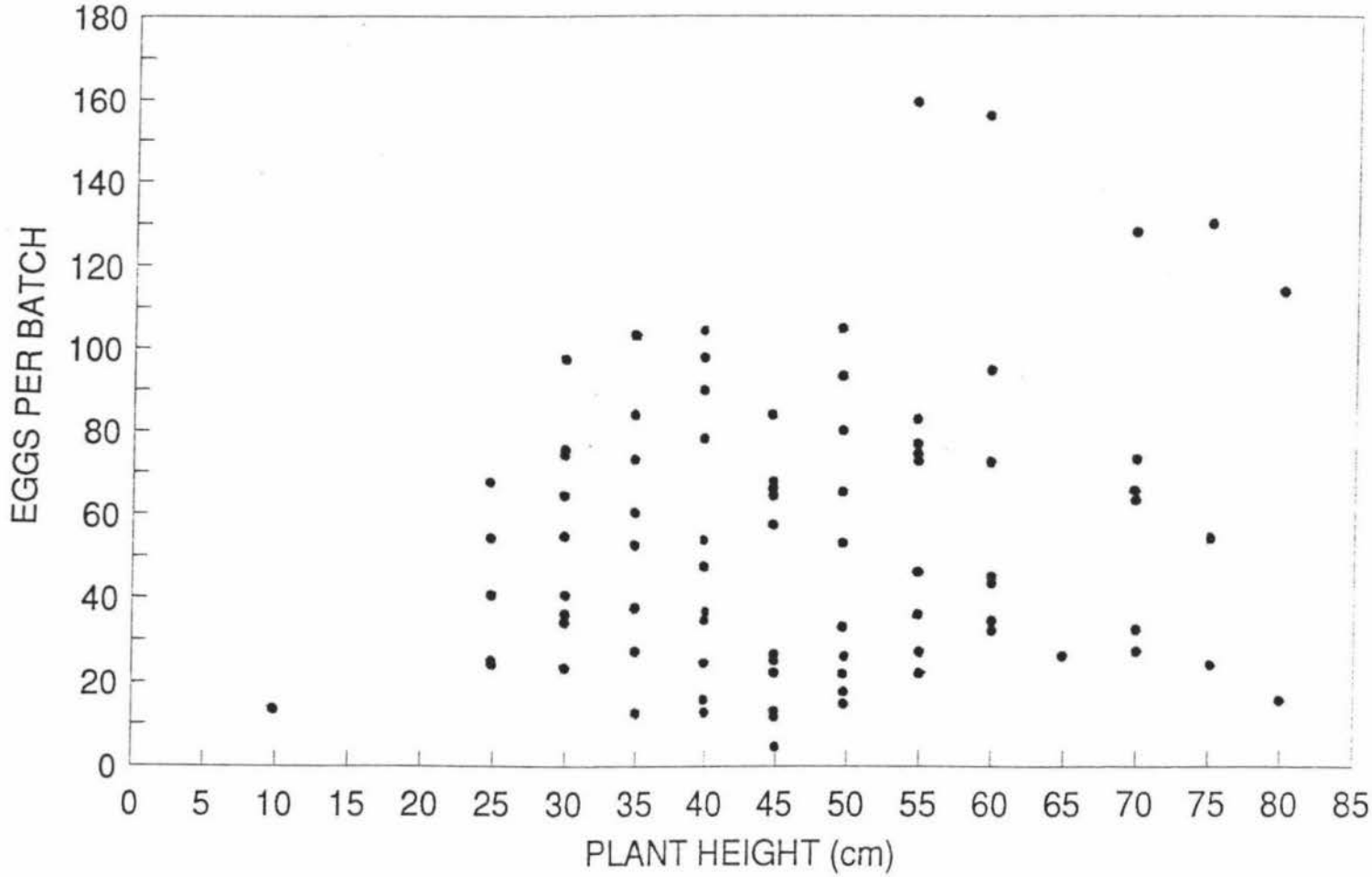


Figure 6.5a Egg batch size in relation to sample date.

Kaipororo Road 1989/90

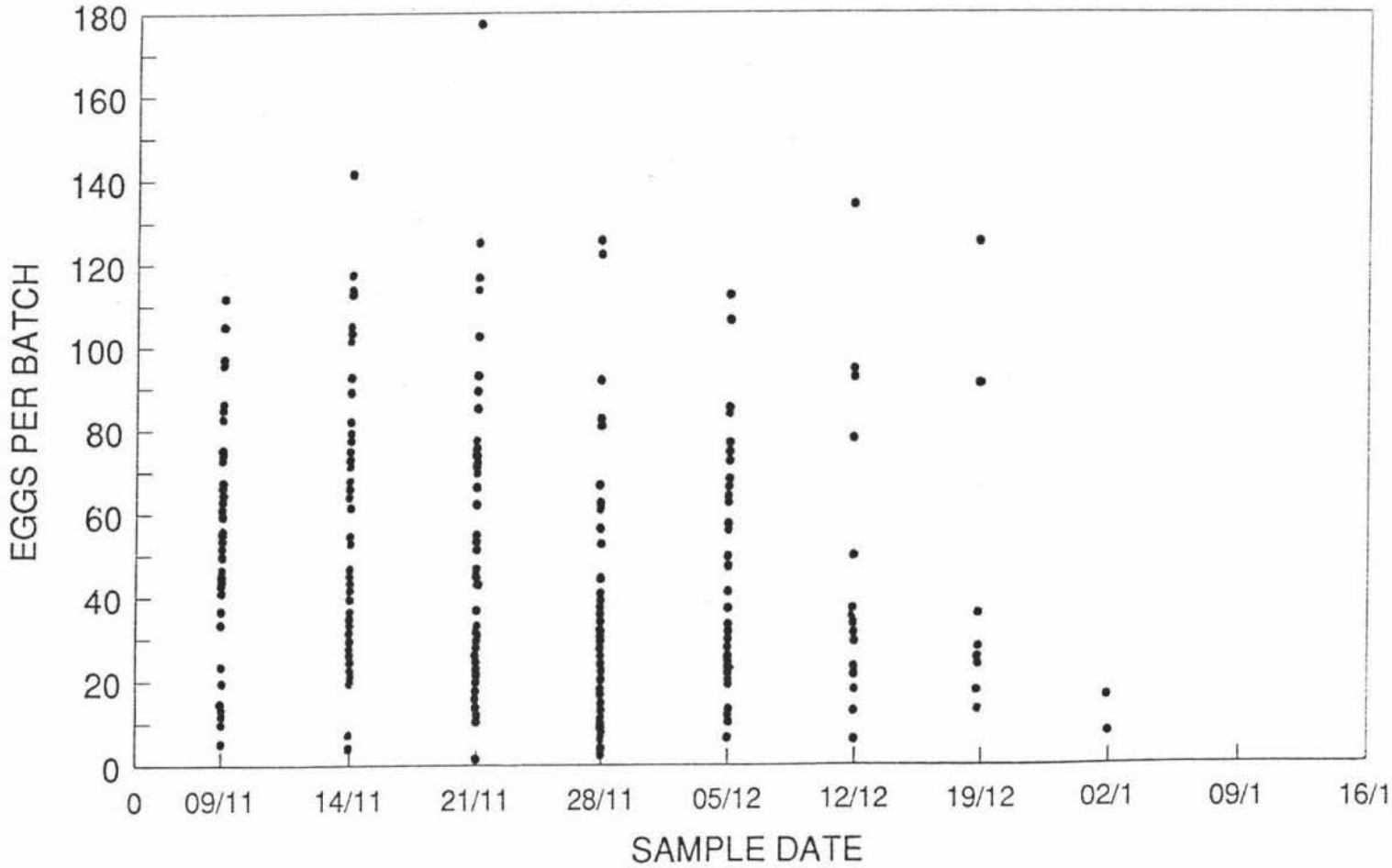
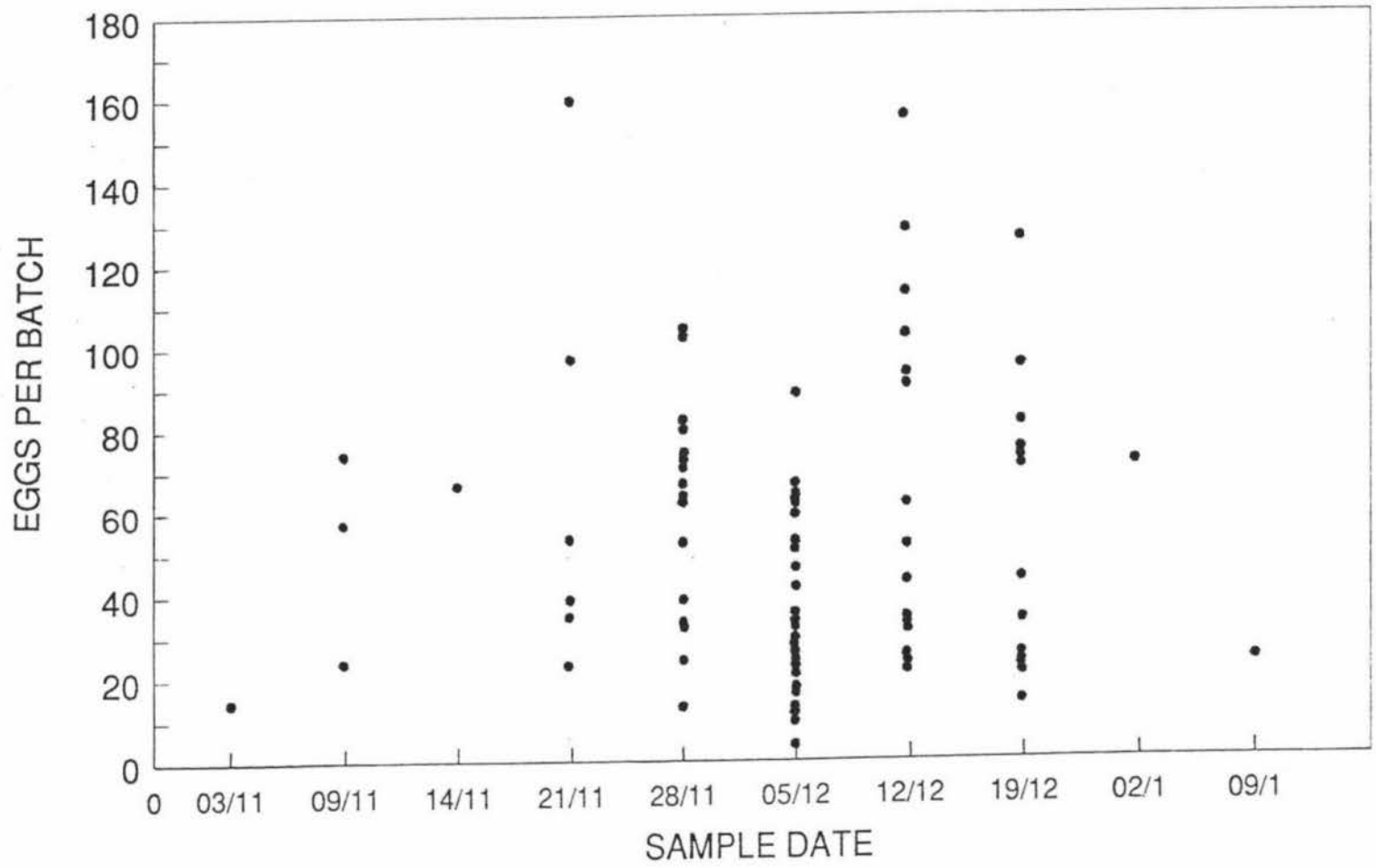


Figure 6.5b Egg batch size in relation to sample date.

Kaipororo Road 1990/91



A multiple regression was performed to determine the effect of date on eggbatch size for all 3 sites. This indicated that without the conflicting influence of plant dimensions, date showed a highly significant negative correlation with eggbatch size ($p < 0.001$) while the effects of site were not significant ($p = 0.607$).

(6.3.3.4) 1990/91.

The was no significant correlation between either plant diameter or plant height and egg batch size at the Kaipororo Road site. Regression analysis of batch size against sample date also indicated no significant relationship ($p = 0.702$).

(6.3.4) Larval phenology and mortality.

(6.3.4.1) Larval phenology.

The abundance of each instar with time is given for Kaipororo Road during 1989/90 and 1990/91 in Figures 6.6 a+b, and for the Eketahuna site in Figure 6.7. At Kaipororo Road first instar larvae first appeared in the 1990/91 season approximately three weeks later than in 1989/90 and fifth instar larvae were present for an additional month in comparison to 1989/90. First instar larvae were recorded on 92% of sampled plants in 1989/90 and 72% in 1990/91. During 1989/90 all plants were observed to host first instar larvae at the Eketahuna site whereas 80% did so at the Hukanui site. The Hukanui site was mowed by the farmer around 19/12/89 so larval data from this site was excluded from analysis.

(6.3.4.2) Larval mortality

Mortality was calculated as the difference in numbers between instars (Table 6.4). Total mortality, calculated as the difference between the estimates of egg numbers and fifth instar numbers was 99.9% at the Kaipororo Road site in 1989/90 and 97.9% in 1990/90. Results for the Eketahuna site demonstrate the difficulty in obtaining accurate counts of first instar larvae, and shows the resulting underestimate of their numbers. The mortality between the egg stage and first instar was therefore overestimated as demonstrated by the 108.7% increase in numbers between the first instar and the second instar. Total mortality was 98.5% at this site.

Figure 6.6a Cumulative percentage curve for *T. jacobaeae* in relation to sample date.

Kaipororo Road 1989/90

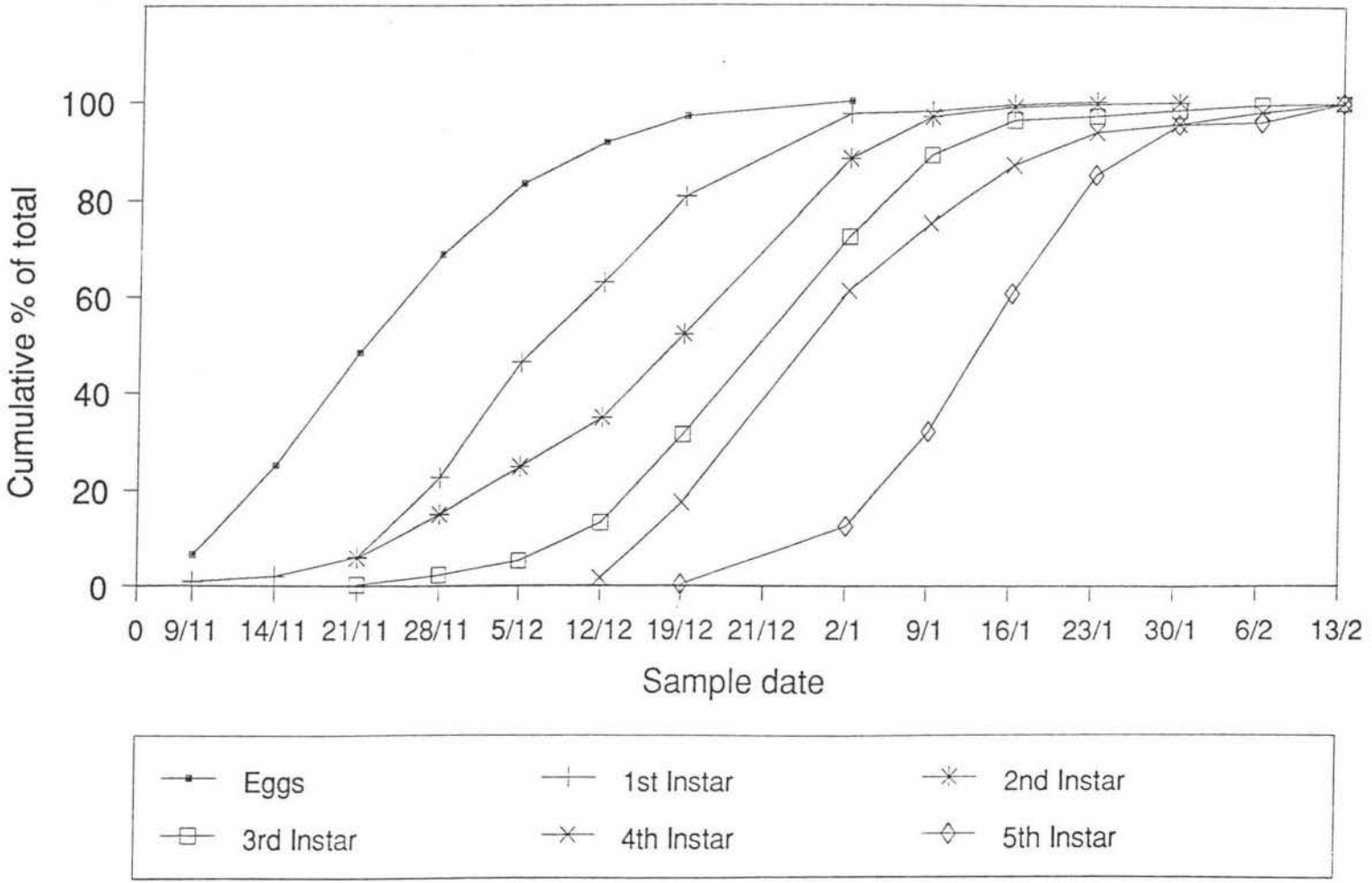


Figure 6.6b Cumulative percentage curve for *T. jacobaeae* in relation to sample date.

Kaipororo Road 1990/91

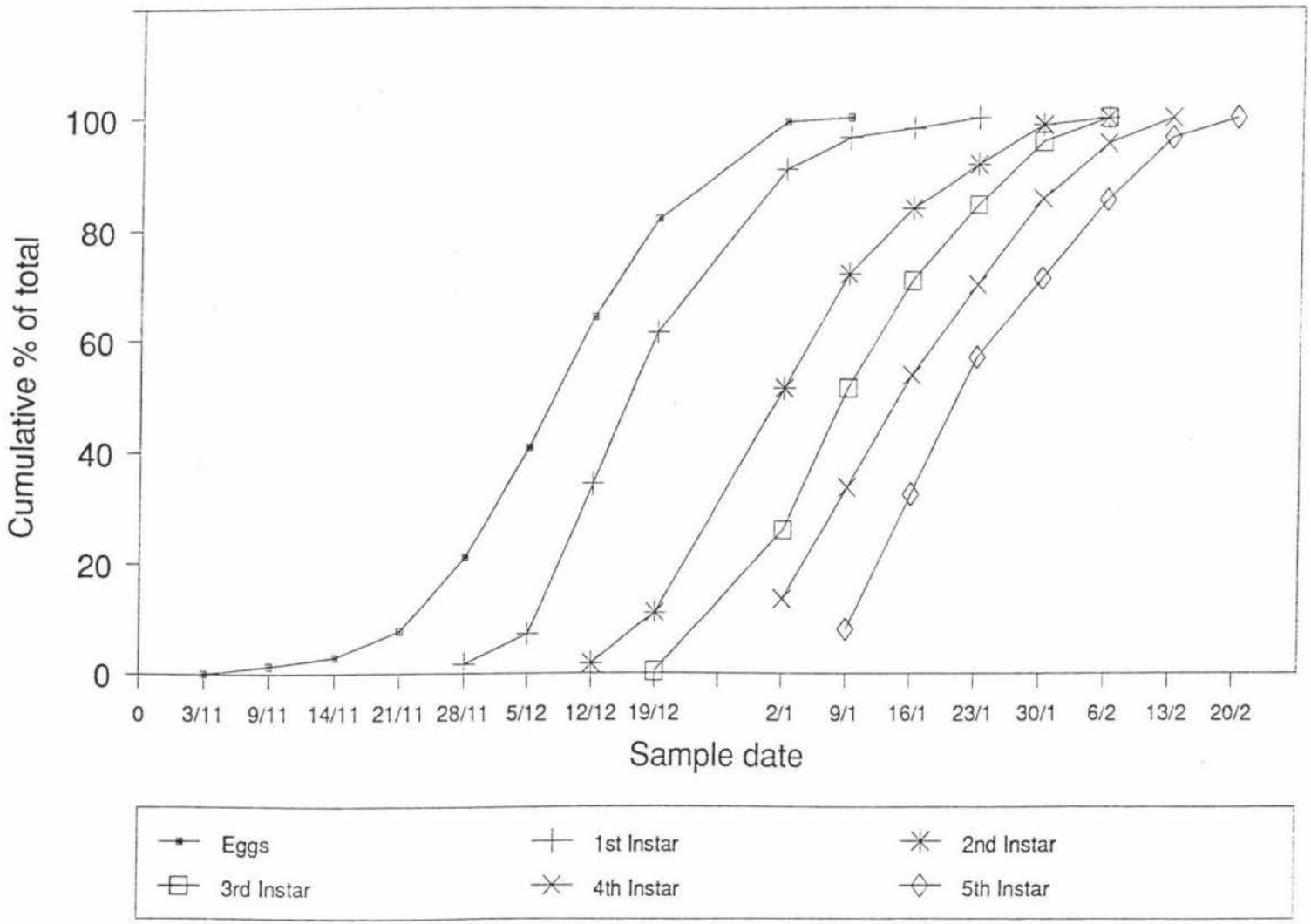


Figure 6.7 Cumulative percentage curve for *T. jacobaeae* in relation to sample date.

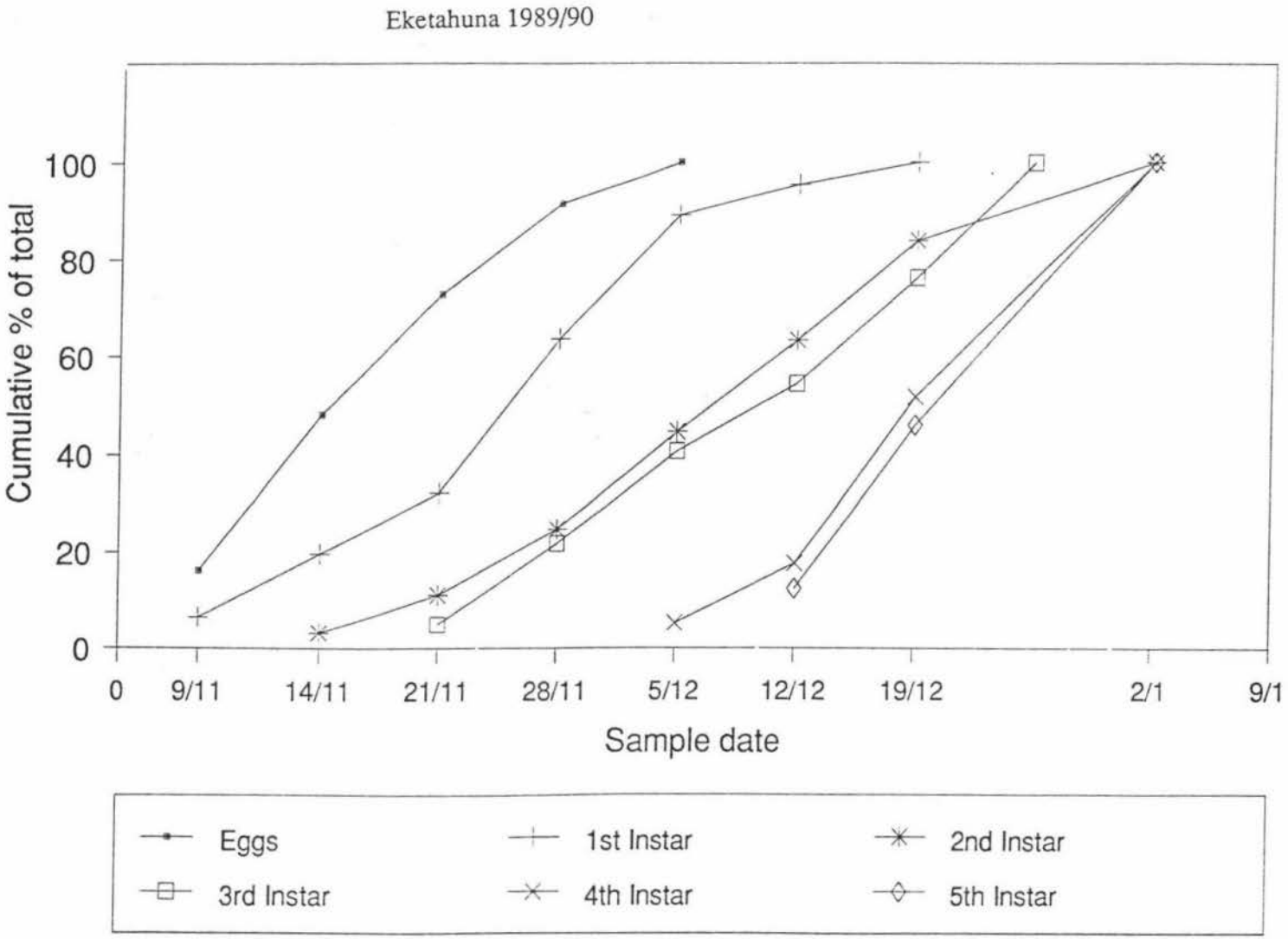


Table 6.4. Estimated mortality of *T. jacobaeae* between successive stages. + indicates an increase in numbers between successive stages.

Site	Interval				
	Eggs-1st	1st-2nd	2nd-3rd	3rd-4th	4th-5th
Kaipororo Road					
(1989/90)	65.5%	4.8%	60.8%	79.7%	74.3%
(1990/91)	51.8%	14.6%	26.6%	52.4%	85.5%
Eketahuna					
(1989/90)	70.0%	+108.7%	12.9%	73.3%	93.8%

(6.3.4.3) Key factor analysis.

To identify key stage mortalities, data from the Kaipororo Road and the single Eketahuna quadrat were combined for 1989/90 to increase the number of points on which the regressions were modelled, and data for the Kaipororo Road site used alone for 1990/91, when comparing changes in the number of individuals entering the successive stages. Key stage mortalities were estimated using the method of Barlow, French and Pearson (1986). This is derived from the method of Manly (1977, 1979). The analysis identifies the key stage as that with the highest value of :

$$A_i = b^2_{i+1}\, b^2_{i+2} \ldots b^2 MSD_i$$

where there are n stages (i), b_i = the coefficient of the regression of log density of stage i on log density of stage i-1 and MSD_i = mean square deviation from that regression.

Fourth instars contributed most to spatial variability in mortality during both the 1989/90 and 1990/91 seasons (Tables 6.5 and 6.6).

Table 6.5 Key factor analysis from the combined data from the Kaipororo Road and Eketahuna sites (1989/90).

Interval	b	MSD	A
Egg-1st instar	0.750	0.452	0
1st-2nd instar	-0.068	0.003	0
2nd-3rd instar	-0.944	1.447	0.026
3rd-4th instar	1.362	4.292	0.042
4th-5th instar	0.099	0.048	0.048

Table 6.6 Key factor analysis for Kaipororo Road (1990/91).

Interval	b	MSD	A
Egg-1st instar	1.312	1.885	1.573
1st-2nd instar	0.892	1.561	1.637
2nd-3rd instar	1.156	2.396	1.880
3rd-4th instar	0.920	2.788	0.332
4th-5th instar	0.963	3.087	3.087

(6.3.4.4) Density dependence.

Density dependent mortality was investigated using the method of Smith (1973) by fitting regressions to plots of *k*-value on untransformed initial density (Tables 6.7 and 6.8) (See Chapter 5 for discussion of methods). Due to the conservatism of the test (Smith 1973), the significance level was set at $\alpha = 0.1$. Data from the Kaipororo Road and Eketahuna sites for 1989/90 were combined.

Table 6.7 Regressions of *k*-value on initial number of *T. jacobaeae* per quadrat (Kaipororo Road and Eketahuna sites combined 1989/90).

Interval	Regression coefficient	p	r^2
Eggs-4th	0.529	0.458	0.000
Eggs	0.909	0.492	0.000
1st instar	-0.502	0.409	0.000
2nd instar	0.696	0.850	0.000
3rd instar	1.924	0.316	0.059
4th instar	0.703	0.106	0.400

Table 6.8 Regression of *k*-value on initial number of *T. jacobaeae* per quadrat (Kaipororo Road 1990/91).

Interval	Regression coefficient	p	r^2
Eggs-4th	2.154	0.618	0.000
Eggs	1.031	0.266	0.176
1st instar	0.100	0.804	0.000
2nd instar	0.535	0.809	0.000
3rd instar	0.683	0.861	0.000
4th instar	1.951	0.898	0.000

No overall density dependent mortality was detectable in *T. jacobaeae* populations during either the 1989/90 or 1990/91 seasons between the egg stage and the fourth instar. Investigation of individual stages also gave no significant density dependence for either season.

(6.3.5) The influence of *T. jacobaeae* larvae on host plants.

Damage to the sampled plants at the Kaipororo Road site in 1989/90 was first recorded on 2/1/90 when 22% of plants examined had their capitula and flowers destroyed. No other animals were present in high enough numbers to cause the damage, which was consistent with *T. jacobaeae* larval feeding. The proportions of plants showing the categories of damage against time for 1989/90 and 1990/91 are shown in Figures 6.8 a+b. Thirteen percent of plants sampled were completely defoliated only 54 days after initial observation of eggs at this site in 1989/90.

Overall, 44% of sampled plants had severely damaged capitula and flowers but 82% of these recovered to produce flowers after secondary growth. Ninety percent of previously defoliated plants were flowering by the 25/2/90.

Severe damage to the capitula and flowers coupled with defoliation affected 36% of sampled plants but 89% of these produced foliage through secondary growth and 78% produced a crop of secondary flowers by the 25/2/90, approximately 1 month after maximum defoliation.

Twenty-two percent of defoliated plants did not produce secondary flowers and 11% did not produce any secondary regrowth. The latter were classified as dead and represented 4% of all plants sampled.

During the 1990/91 season at Kaipororo Road damage to the sampled plants was first recorded on the 2/1/90 when 4% of plants had their capitula destroyed. Maximum capitula damage was recorded on the 30/1/91, when 32% of plants were affected.

Of the 32% of sampled plants with capitula completely eaten by *T. jacobaeae* larvae, 38% produced a crop of secondary flowers by the 13/2/90. Therefore, 20% of all plants sampled were prevented from flowering, and 4% died.

At the Eketahuna site defoliation occurred rapidly during the 1989/90 season so that 40 days after eggs were first observed, 40% of plants were defoliated and all plants were defoliated 54 days after eggs were initially observed with no secondary growth by these plants observed.

Figure 6.8a Percentage of ragwort population in each damage category in relation to sample date.

Kaipororo Road 1989/90

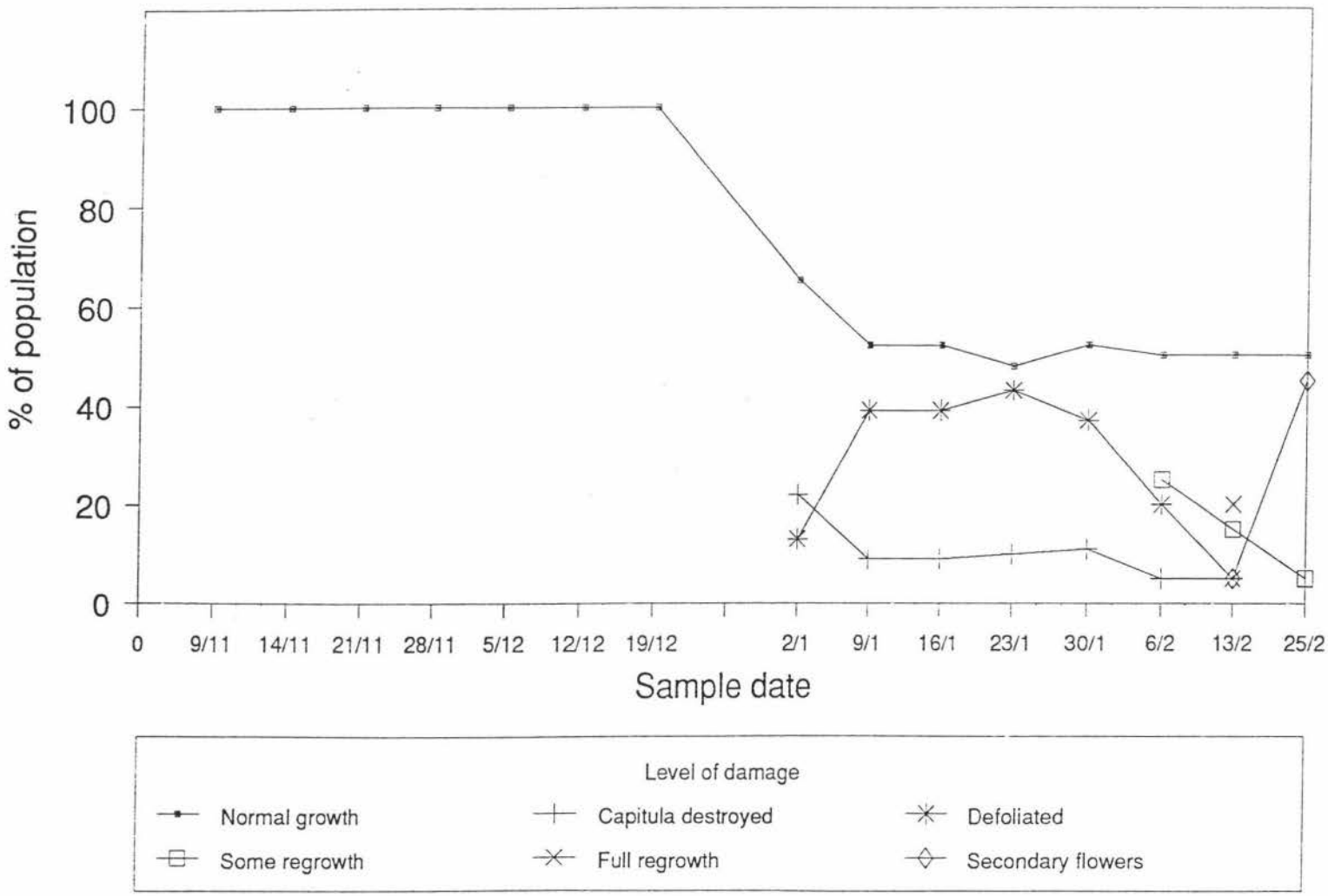
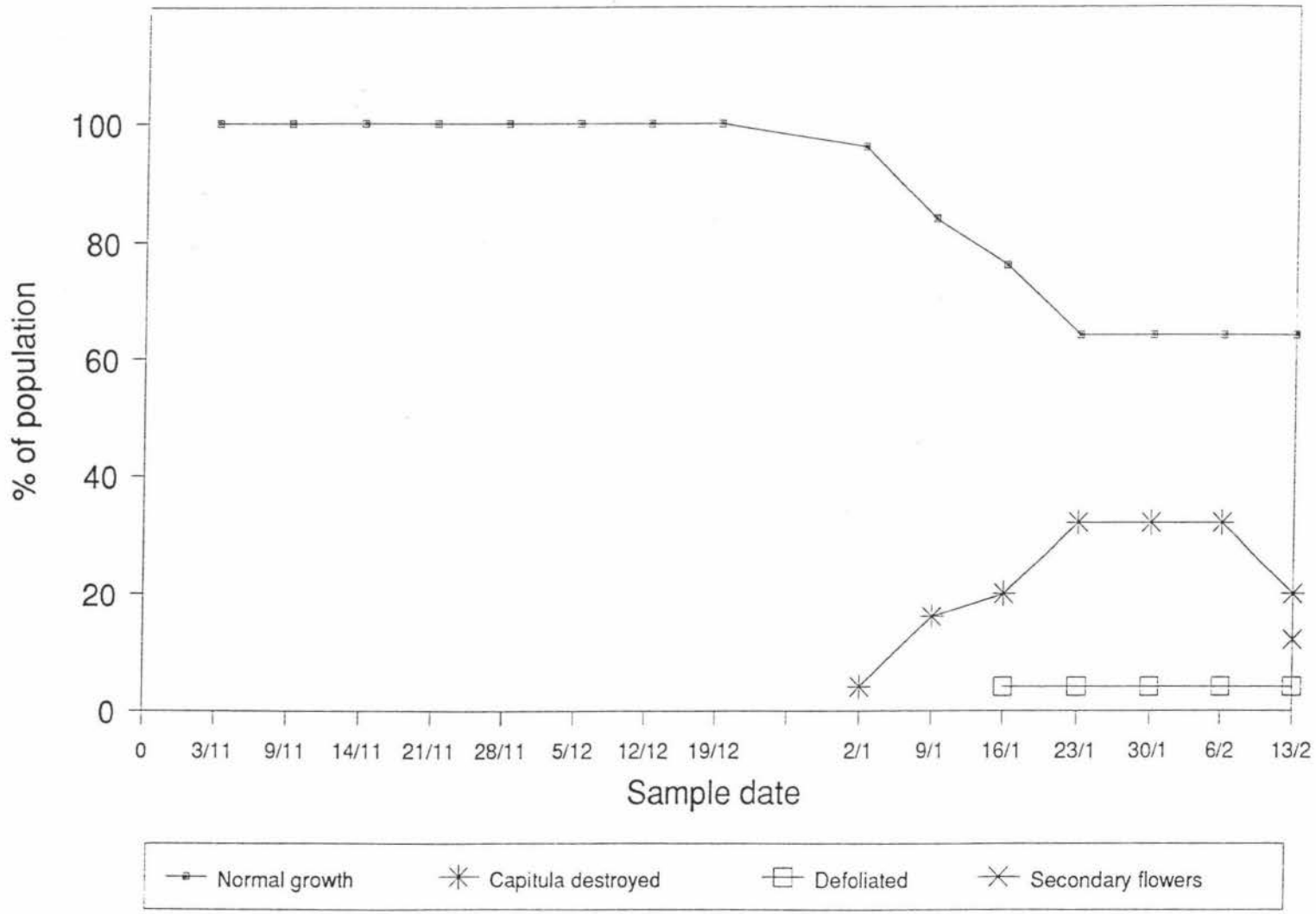


Figure 6.8b Percentage of ragwort population in each damage category in relation to sample date.

Kaipororo Road 1990/91



(6.3.6) Estimate of pupal density

Only one living pupa was recovered from the soil samples giving a pupal density of 0.33 pupae per m^2. In addition a single empty pupal case was found in these soil samples. This case was neatly opened at one end and the contents removed. This pupa was probably from the previous season so it is possible that pupal density at the initiation of diapause was 0.66 pupae per m^2.

(6.4) Discussion.

(6.4.1) Stage-Frequency analysis.

The use of stage-frequency analysis, adjusted for temperature dependent development rate, allowed accurate estimation of the total numbers of *T. jacobaeae* entering each stage from the serial samples taken. The most obvious feature of the results is the increase in larval numbers between the first and second instars for some quadrats. This suggests that the estimated number of first instar at both the Kaipororo Road and Eketahuna sites is conservative.

This method provided more meaningful estimates of *T. jacobaeae* abundance than the use of non-adjusted raw data or by using the method of Southwood (1978). Because samples were recorded at weekly intervals, the number of day-degrees between samples exceeded the temperature requirements for the completion of any of the first four instars but were below that required for completion of the long fifth instar. Had this not been corrected for, the numbers of *T. jacobaeae* would have been underestimated for all stages except for an overestimation of numbers in the fifth instar. By accounting for the temperature dependent rate of development, errors associated with this form of sampling method were substantially reduced.

(6.4.2) Oviposition.

Oviposition on the underside of the basal leaves of the host plant probably reduces desiccation and provides protection from adverse weather conditions such as heavy rain. The position of eggs on the basal leaves also reduces egg mortality caused feeding of older larvae which are normally found on the upper leaves and flowers (van der Meijden 1978). Eggs and older larvae are therefore spatially separated on the plant. Egg batch size varied widely at Kaipororo Road (Figure 6.1) ranging from 1 to 179 eggs per batch in 1989/90 and 6 to 160 in 1990/91. I found no reference to the effect of female size on egg batch size in the published literature on *T. jacobaeae* but if there is, the wide variation in batch size may reflect differences in the size of female moths, and this in turn may reflect differences in larval weight at pupation. Laying larger batches appears to be advantageous. Van

der Meijden (1976) found that the hatching success of eggs in smaller batches was slightly lower than in larger batches under natural conditions. Although I did not assess egg mortality directly, it was clearly very low. Dempster (1971) reported egg mortality of 1.2-13.1% over 5 years at Weeting Heath. I similarly found that a very small number of eggs, probably not exceeding 2% in each season, were inviable at Kaipororo Road over 1989/90 and 1990/91 and only 0.3% of all eggs were lost between samples. Some of these were possibly blown off or failed to adhere to the leaf undersurface. Egg mortality therefore appeared to be an insignificant component of total mortality during my study.

Dempster (1982) reported that the mean batch size ranged between 19.2-43.1 eggs over 10 years at Weeting Heath. Myers and Campbell (1976b) found 25.6-58.1 eggs per batch at different localities in North America during one year. These values are similar to those observed during my study in the Wairarapa. Mean egg batch size varied at the Kaipororo Road site between the two years of study, and at the Hukanui site, where *T. jacobaeae* density was lowest, the mean batch size was larger than at the other sites during the 1989/90 season. However, there was remarkable similarity in the mean batch size between the Eketahuna (47.2 ± 3.8) and Kaipororo Road (47.2 ± 1.9) sites in 1989/90. The mean number of eggs per plant fell considerably in the second season (1990/91) at Kaipororo Road, but the increase in ragwort density in this year resulted in the eggs being distributed over a larger host plant population. The number of eggs per m^2, estimated from the ragwort density and the mean number of eggs per plant during each season, was 19.12 per m^2 in 1989/90 and 20.13 per m^2 in 1990/91. If female fecundity was not significantly different between years then the number of female moths in the second year at least equalled, and probably exceeded, the number in the first year. This suggests that the *T. jacobaeae* population remained at a similar density over the two years of this study despite approximately 99.9% mortality estimated for 1989/90.

Myers and Campbell (1976) suggested that *T. jacobaeae* has the genetic or phenotypic flexibility to adjust egg batch size in relation to variations in ragwort density. Dempster (1982) strongly criticised this hypothesis on the basis that while both egg batch and plant size varied at Weeting Heath, the variations were not correlated. My results suggest that variation in batch size and the number laid per plant may result from variations in mean female fecundity and ragwort density.

The diameter and height of the host plant was found not to influence the size of batches laid on that plant, which is consistent with van der Meijden's (1976) result. Female moths do not appear to actively select larger plants on which to lay their eggs, and the pattern of oviposition in relation to plant size results from larger

plants receiving more eggs, but not larger batches. Low growing rosettes and smaller flowering plants often carried no eggs and usually remained free of larvae. Van der Meijden (1978) suggests that this is a mechanism to reduce the possibility of early food shortage among larvae too immature to migrate successfully. Host plant selection then seems to depend on the chemical composition of the host plant. Van der Meijden, van Zoelen and Soldaat (1989) investigated ovipostion in relation to nitrogen, sugar and alkaloid content of the potential host plant and reported that female moths selected plants with high concentrations of organic nitrogen. Regrowth foliage has been found to be sometimes, although not consistently, preferred by ovipositing females (Wilcox and Crawley 1988). Wilcox and Crawley (1988) found that larvae grew larger on regrowth foliage. Regrowth plants from the previous season were not differentiated during my study, but in light of the patchy distribution of eggs this appears to warrant further investigation.

The analysis of batch size frequency indicated two distinct distributions within the range of egg batch sizes, with a slightly higher frequency of larger batches. The inverse relationship between batch size and date indicates that as a whole the female *T. jacobaeae* population lays progressively smaller batches. This has two explanations. Firstly the newly emerged female lays a series of progressively smaller batches as her potential fecundity is approached. Secondly, as the oviposition period passes, a greater proportion of the plant population will already host eggs and/or larvae. The female may then decrease her batch sizes so the carrying capacity of individual plants is not so greatly exceeded. Richards and Myers (1980) also found that egg weight decreased over the oviposition period and that the lighter eggs showed lower hatching success. Thus the reduction in batch sizes and hatching success results in plants that already host eggs and/or larvae receiving proportionately fewer eggs per additional batch laid against time.

Oviposition during 1990/91 at Kaipororo Road began slightly earlier than in the 1989/90 season (Figure 6.2) and finished later. It was therefore about 2 weeks longer. However, the rate of egg laying was reduced during the first few weeks of laying in 1990/91, and while 50% of all eggs were laid by the 21/11/89 this proportion was not reached until the 8/12/91 in the second year. This variation probably relates to differences in temperature during diapause which affected the rate of pupal development and so delayed oviposition. However synchrony with ragwort flowering was not affected despite the delay in ovipostion. Myers (1979) reported that *T. jacobaeae* has adapted its temperature threshold for emergence at different sites in North America in response to seasonal fluctuations in temperature. Therefore, *T. jacobaeae* remains synchronised with ragwort flowering that may occur over different periods in different regions. It appears that *T. jacobaeae* has

adapted in a similar manner in the Wairarapa, and remains well synchronised with ragwort flowering despite variations in the emergence times of most of the population between years. Reports of poor synchrony with ragwort flowering (Miller 1970) may have originated from areas where *T. jacobaeae* had not adapted to local climatic conditions.

(6.4.3) Larval phenology and mortality.

Larval phenology was consistent between sites but not years. The appearance of first instar larvae in 1990/91 was delayed by 19 days when compared to their appearance in 1989/90. The delay in larval abundance was caused by the slow initial build up of eggs during 1990/91 and the corresponding low number of early larvae were either missed during the early samples or died soon after hatching. Larval abundance was well synchronised to ragwort flowering during 1990/91 with 91% of first instar and 76% of second instar larvae present when 40% of plants were flowering (on the 9/1/91). Because stripping of the capitula affected only 16% of plants by the 9/1/91, synchronisation with ragwort flowering resulted in subsequent instars having access to flowering plants.

Estimated larval mortality was very high at all sites studied (Table 6.4) but compares well with Dempster's (1971) estimates of total mortality. These ranged from 80.6% to 99.99% at Weeting Heath over 4 years. The reasons for high mortality in New Zealand are not obvious. Predation did not appear to be a significant cause of mortality. Dempster (1982) estimated that 32-85% of larvae died by the end of the second instar, largely through the action of arthropod predators. My estimation of 67.3% and 58.8% mortality between the egg and second instar at Kaipororo Road for 1989/90 and 1990/91 respectively indicates high mortality among newly emerged and immature larvae, although the reasons for this are not clear. The weather in the Wairarapa was still cold and wet during the the period of larval hatching in both years of study. Over November and December in 1989, the mean minimum temperature was 9.9°C and 357mm of rain fell and in 1990 the mean minimum temperature was 9.5°C with 260mm of rain over these months. Therefore the adverse weather conditions probably increased larval mortality. I saw predation on larvae only once in two years. In this case I found a common plant bug (Hemiptera: Pentatomidae) feeding on a third instar larva. Schmidl (1972) reported "moderate" losses of larvae to pentatomid bugs in Australia. Parasitism also appeared to be insignificant despite the report by Miller (1970) that between 53.19 and 78.12% of larvae are parasitised by *Pales casta* (Hutton) in New Zealand. I raised and stored many hundreds of larvae and pupae during my study and saw no evidence of parasitism.

Pupal density at Kaipororo Road was not high enough to estimate pupal mortality. The minimum expected level of pupal mortality described in Chapter 3 indicated that pupal survival is likely to be reasonably high under New Zealand conditions. Dempster (1982) identified pupal loss as a key factor determining population fluctuations at Weeting Heath, and attributed the high mortality to predation by moles. Pupal loss at the Kaipororo Road site is unlikely to influence population density to a greater degree than the high larval mortality.

(6.4.3.1) Key stage mortalities.

Many methods may be used to identify the key stage mortalities that most influence the variation in total generation mortality. The method of Manly (1977, 1979) was considered by Barlow, French and Pearson (1986) to be the only method that considers the effects of density dependent mortality factors. Because strong density dependent mortality was detected among caged *T. jacobaeae* larvae I considered application of Manly's method to be more appropriate to natural populations of *T. jacobaeae* than the more commonly used techniques of Varley and Gradwell (1960) and Podoler and Rogers (1975). Mortality was high among fourth instar larvae, and the increasing abundance of fourth instar larvae also coincided with increasing plant damage in both years (see section 6.3.5). Therefore, the fourth instar was probably the earliest stage to be affected by intraspecific competition for food. Increasing plant damage also leads to increased migration (van der Meijden 1976). Crawley and Gillman (1989) found that larvae migrating through tall, dense vegetation and those moving from isolated plants suffered higher than average death rates. The high mortality of fourth instars was probably caused in part by migration from the sampled plants. The dense, tall grass and low ragwort density at the Kaipororo Road site presumably reduced the proportion of larvae successfully finding an alternative host plant. This drop in larval numbers supports the contention that migrating larvae were exposed to higher mortality because emigrating larvae were not replaced by immigrating larvae on the sample plants. Further study of *T. jacobaeae* under a range of habitats in New Zealand will provide additional information on the major mortality factors that affect individual populations.

(6.4.3.2) Density dependence.

This analysis (Smith 1973) produces a more statistically reliable estimate of density dependence than other more widely used techniques. The method of Varley and Gradwell (1968), in which *k*-value is regressed against log(initial density), overestimates density dependent effects. This is because log of initial density is present on both sides of the regression equation so that sampling errors in the estimation of initial density (the independent variable) are incorporated into the *k*-value (the dependent value). This inflates the apparent density dependence and invalidates significance tests (Kuno 1971). The overestimation of density dependent effects through sampling error is reduced in Smith's (1973) method because the *k*-value (log(initial density) - log(final density)) is regressed against untransformed initial density. The relationship between initial density and log(initial density) is not close and sampling errors do not reduce the independence of initial density and *k*-value.

Density dependent mortality in field populations apparently occurs at densities above those that result in density dependent mortality among captive populations (Chapter 5). The strong density dependent mortality in caged populations (Chapter 3) occurred at densities comparable to those reached by natural *T. jacobaeae* populations in 1989/90. However density dependent mortality in field populations was probably reduced because ragwort plants were able to compensate better for defoliation under natural conditions. Also, failure to detect density dependent mortality does not prove it does not occur (Southwood 1978), and the detection of density-dependence in unmanipulated natural populations is particularly difficult because of stochastic effects and undersampling (Hassell *et al.* 1987).

(6.4.4) Influence of *T. jacobaeae* on the ragwort population.

Although defoliation affected 36% of sampled plants at Kaipororo Road during 1989/90 only one (4%) did not recover from defoliation. This may have merely reflected natural mortality. The increase in plant density observed in the second year of study indicated that *T. jacobaeae* was not effecting control at this site. However two years of study are insufficient to completely understand this very complex interaction so this conclusion is tentative.

There are several factors that could contribute to this apparent lack of control. Firstly, an initial density of at least 30 second or third instar larvae were required to cause defoliation (see Chapter 5). Although 88% of plants in 1989/90 and 96% of plants in 1990/91 received eggs, 32 and 46% respectively received 100 eggs or less. In 1989/90, 24%, and in 1990/91, 36%, of plants hosted less than 30 larvae of all

instars. Based on mortality between the egg and third instar over both years of the study at Kaipororo Road, an initial egg density of at least 125 per plant is required to attain even the minimum of 30 third instar larvae per plant. Therefore around one third of plants hosted insufficient larvae to cause defoliation while others hosted more than the plant could support. The consequent patchy distribution of *T. jacobaeae* adversely influenced its potential to cause uniform defoliation.

Comparison of the timing of larval damage (Figures 6.8 a+b) and larval abundance (Figure 6.6) shows that the early instars had little influence on ragwort damage, but increasing capitula damage and defoliation coincided with the increase in abundance of fourth and fifth instar larvae. This is reasonable because these larger larval stages ingest more ragwort foliage. However, larval mortality by the end of the third instar was 87.2% in 1989/90 and 70% in 1990/91. Therefore, unless larvae are present at a density high enough for the earlier instars to cause plant damage, the potential for control is considerably reduced through high mortality.

Regrowth following defoliation largely negated the effect of *T. jacobaeae* in 1989/90. Stimac and Isaacson (1978) found regrowth occurred less than two weeks after defoliation in Western Oregon and considered that this reduced starvation among late instar larvae. At the Kaipororo Road site, full regrowth was occurred about three weeks after maximum defoliation. This was too late to enhance larval survival on individual defoliated plants. However, it still allowed secondary flowering and seed production during the same season.

GENERAL CONCLUSIONS.

T. jacobaeae and ragwort display a high degree of co-evolution. Larvae can ingest and store the poisonous alkaloids contained in ragwort tissue, while ragwort is well adapted to survive the periodic defoliation caused by larval feeding. Many studies have concluded (see section 1.4.5) that *T. jacobaeae* only controls ragwort populations when the plants are already stressed. The success of *T. jacobaeae* in other countries has been largely determined by the inability of ragwort to compensate for defoliation. Poole and Cairns (1940) defoliated 10 ragwort plants monthly for 7 months and found that only six were eventually killed. Therefore it is unlikely that a single defoliation per year under normal conditions can control ragwort. The remarkable propagative and regenerative potential of the plant enables it to persist as a serious pasture pest in many parts of the world despite continued attempts at its eradication.

Populations of ragwort and *T. jacobaeae* may remain at equilibrium for long periods (van der Meijden 1970, Dempster 1971). Harris *et al.* (1978) reported the decline of a *T. jacobaeae* population in North America from an initially high density, to a level below that necessary for complete defoliation. This appears to have happened at the Kaipororo Road site where the *T. jacobaeae* population was stable, despite high mortality, but was a level that had no short term effect on plant numbers.

However, *T. jacobaeae* can, and often does, reduce ragwort biomass for several months each year. This reduces the potential for stock poisoning over the summer months when feed is often scarce and stock more likely to graze ragwort. The reasons for the lack of success of *T. jacobaeae* as a biological control agent in this country cannot be fully determined from this study, but certain detrimental factors can be identified. High larval mortality severely limits the potential for defoliation. Factors causing mortality were not apparent, but oviposition and larval hatching did coincide with adverse weather conditions in the Wairarapa and this must cause high initial mortality. The patchy distribution of *T. jacobaeae* on the host population results in some plants remaining almost entirely unaffected by larval feeding, while others are stripped of foliage with high mortality of associated larvae. However, this mortality may be reduced by the presence of ungrazed ragwort plants, which can provide food refuges for *T. jacobaeae* larvae, so enhancing the insects local persistence. Most plants recover from defoliation and quickly produce secondary flowers. So, while a high proportion of the ragwort population is allowed to flower and seed unchecked, then effective control is unlikely to occur.

Additional stress could be induced in ragwort populations by the release of *T. jacobaeae* during the period of ragwort regrowth. While rearing two generations per year is possible, storage of quiescent pupae from the previous season is more realistic. The economics of an approach like this have not yet been investigated, but must be compared to the cost of further development or importation of alternative control agents.

The combined effects of several biological control agents acting on ragwort may lead to more satisfactory control. The ragwort seed fly, *Botanophila jacobaeae* is largely ineffective (Dymock 1985, 1987). Crawley and Pattrasudhi (1988) found strong interspecific competition between *B. jacobaeae* and *T. jacobaeae*, with *T. jacobaeae* substantially reducing recruitment of *B. jacobaeae*. If the ranges of these species begin to overlap in New Zealand then the effectiveness of *B. jacobaeae* will be further reduced.

There is optimism that ragwort flea beetle, *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae) will act as an additional biological control agent for ragwort in New Zealand (Syrett *et al.* 1984; Syrett 1989). *L. jacobaeae* was introduced to New Zealand from Oregon in 1981 where it acts synergistically with *T. jacobaeae* by placing additional stress on the plant during the winter and spring when *T. jacobaeae* is not active (Hawkes and Johnson 1978). The adult beetles feed on the foliage and cause only slight damage, but larvae feed on the roots, thus causing considerable damage to the roots and so deplete the plant's energy reserves. *L. jacobaeae* adapts rapidly to a new environment. When acting with *T. jacobaeae*, *L. jacobaeae* almost completely controlled ragwort in California (Hawkes and Johnson 1978; Hawkes 1981).

In New Zealand *L. jacobaeae* may aid *T. jacobaeae* to reach its full potential as a biological control agent for ragwort. My study shows that the potential of *T. jacobaeae* is presently reduced, in the Wairarapa at least, by high larval mortality, a patchy distribution on the host population and its failure to prevent regrowth of defoliated plants.

REFERENCES.

Aplin, R.T.; Benn, M.H.; Rothschild, M. 1968 Poisonous alkaloids in the body tissues of cinnabar moth (*Callimorpha jacobaeae* L.). *Nature, UK* **219**: 747-748.

Aplin, R.T.; Rothschild, M. 1972 Poisonous alkaloids in the tissues of the garden tiger moth (*Actia caja* L.) and the cinnabar moth (*Tyria(Callimorpha) jacobaeae*) (Lepidoptera) *In* "Toxins of Animal and Plant Origin" (Eds. A de Vries and K. Kochva), pp 579-595. Gordon and Breach, London.

Armstrong, D. 1973 Pasture weed control. *New Zealand Journal of Agriculture romanbold* **126:** 47.

Amor, R.L.; Lane, D.W.; Jackson, K.W. 1983 Observation on the influence of grazing by sheep or cattle on the density and cover of ragwort. *Australian Weeds* **2:** 85-94.

Aston, B.C.; Bruce, J.A. 1933 The chemistry of weed killers. *New Zealand Journal of Agriculture* **46**: 108-109.

Barlow, N.D.; French, R.A.; Pearson, J.F. 1986 Population ecology of *Wiseana cervinata*, a pasture pest in New Zealand. *Journal of Applied Ecology* **23:** 415-431

Black, W.N. 1976 Effects of herbicidal rates and time of application on the control of tansy ragwort in pastures. *Canadian Journal of Plant Science* **56**: 605-610.

Bornemissza, G.F. 1961 Termination of diapause in the cinnabar moth and the reproductive capacity of the resulting females. *Nature* **190:** 936-937.

Bornemissza, G.F. 1966 An attempt to control ragwort in Australia with the cinnabar moth, *Callimorpha jacobaeae* (L.) (Arctiidae: Lepidoptera). *Australian Journal of Zoology* **14**: 201-243.

Buckmaster, G.W.; Cheeke, P.R.; Shull, L.R. 1976 Pyrrolizadine alkaloid poisoning in rats: protective effects of dietary cysteine. *Journal of Animal Science* **43**: 464-473.

Cairns, D. 1938 Vegetative propagation of ragwort. *New Zealand Journal of Science and Technology* **20:** 137a-183a.

Cameron, E. 1935 A study of the natural control of ragwort *(Senecio jacobaea). Journal of Ecology 23;* 265-322.

Cheeke, P.R. 1984 Comparative toxicity and metabolism of pyrrolizadine alkaloids in ruminants and non-ruminant herbivores. *Canadian Journal of animal science* **65** (suppl.), 201-202.

Cox, C.S.; McEvoy, P.B. 1983 Effect of summer moisture stress on the capacity of tansy ragwort *(Senecio jacobaea)* to compensate for defoliation by cinnabar moth *(Tyria jacobaeae). Journal of Applied Ecology* **20:** 225-234.

Crawley, M.J.; Gillman, M.P. 1989 Population dynamics of cinnabar moth and ragwort in grassland. *Journal of Animal Ecology* **58:** 1035-1050.

Crawley, M.J., Nachapong, M. 1985 The establishment of seedlings from primary and regrowth seeds of ragwort *(Senecio jacobaea). Journal of Ecology* **73:** 255-261.

Crawley, M.J.; Pattrasudhi, R. 1988 Interspecific competition between insect herbivores: asymmetric competition between cinnabar moth and ragwort seed-head fly. *Ecological Entomology* **13**: 243-249.

Currie, G.A.; Fyfe, R.V. 1938 The fate of certain European insects introduced into Australia for the contrl of weeds. *J. Coun. Scient. Ind. Res. Aust.* **11:** 289-301.

Dempster, J.P. 1971 The population ecology of the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae). *Oecologia* (Berl.) **7:** 26-67.

Dempster, J.P. 1971a A population study of the cinnabar moth *Tyria (Callimorpha jacobaeae)* L. *Proceedings of the Advanced Study Institute on dynamics of numbers in populations* Oosterbeek 1970 380-389.

Dempster, J.P. 1975 "Animal Population Ecology". Academic Press, London and New York.

Dempster, J.P. 1982 The ecology of the Cinnabar Moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae). *Advances in Ecological Research* **12:** 1-36.

Dempster, J.P.; and Lakhani, K.H. 1979 A population model for cinnabar moth and its food plant ragwort. *Journal of Animal Ecology* **48:** 143-163.

Denzier, M.L.; Thomson, P.A.; Burgett, D.M.; Isaacson; D.L. 1977 Pyrrolizadine alkaloids: their occurence in honey from tansy ragwort (*Senecio jacobaea* L.). *Science* **195**: 497-499.

Dickinson, J.D.; Cooke, M.P.; King, R.R.; Mohamed, P.A. 1976 Milk transfer of pyrrolizadine alkaloids in cattle. *Journal of the American Veterinary Association* **169**: 1192-1196.

Dymock, J.J 1985 Population dynamics of the seedfly *Pegohylemyia jacobaeae* (Hardy) (Diptera: Anthomyiidae), and its potential as a biological control agent of Ragwort, *Senecio jacobaea* L. PhD. Thesis Massey University.

Dymock, J.J. 1987 Population changes of the ragwort seedfly *Pegohylemyia jacobaeae* (Diptera: Anthomyiidae) introduced for biological control of ragwort, *New Zealand Journal of Zoology* **14**: 337-342.

Forbes, J.C. 1974 Spraying and cutting experiments on ragwort (*Senecio jacobaea* L. and *S. aquaticus* Hill). *Proceedings 12th British Weed Control Conference,* 743-750.

Forbes, J.C. 1976b Chemical control of marsh ragwort (*Senecio aquaticus* Huds.) in established grassland. *Weed Research* **17**: 247-250.

Forbes, J.C. 1977 Population flux and mortality in a ragwort (*Senecio jacobaea*) infestation. *Weed Research* **17:** 387-391.

Forbes, J.C. 1982 Evaluating herbicides for selective control of *Senecio jacobaea* in grass/clover swards. *Proceedings of the 35th British Crop Protection Conference - Weeds*, 375-380.

Frick, K.E.; Halloway, J.K. 1964 Establishment of the cinnabar moth, *Tyria jacobaeae*, on tansy ragwort in the western United States. *Journal of Economic Entomology* **57:** 154-154.

Harper, J.L., Wood, W.A. 1957 Biological Flora of the British Isles. *Senecio jacobaea* L. *Journal of Ecology* **45**: 617-637.

Harper, J.L. 1958 The ecology of Ragwort (*Senecio jacobaea*) with especial reference to control. *Herbage Abstracts* **28**(3): 151-157.

Harman, H.M.; Dymock, J.J.; Syrett, P. 1988 Temperature and Development of Cinnabar Moth, *Tyria jacobaea* (L.) (Lepidoptera: Arctiidae), in New Zealand. *Proceedings of the 8th International Symposium on the Biological Control of Weeds, Rome*, 1988.

Harris, P.; Wilkinson, A.T.S, Neary, M.E.; Thompson, L.S.; Finnamore, D. 1975 Establishment in Canada of cinnabar moth *Tyria jacobaeae* (Lepidoptera: Arctiidae) for controlling the weed *Senecio jacobaea Canadian Entomologist* **107:** 913-917.

Harris, P.; Wilkinson, A.T.S.; Thompson, L.S.; Neary, M. 1978 Interaction between the cinnabar moth, *Tyria jacobaeae* L. (Lep.: Artiidae) and ragwort, *Senecio jacobaeae* L. (Compositae) in Canada. *Proceedings of the 4th International Symposium on the Biological Control of Weeds, Gainsville*, 1976, 174- 180.

Harris, P.; Wilkinson, A.T.S.; Myers, J.H. 1981 *Senecio jacobaea* L. tansy ragwort (Compositae). In *Biological Control Programmes gainst Insects and Weeds in Canada 1969-1980.* (Editors Kelleher, J.S.; Hume, M.A.) Farnham Royal, UK; Commonwealth Agriculture Bureaux.

Hawkes, R.B. 1968 The cinnabar moth, *Tyria jacobaeae*, for control of Tansy ragwort. *Journal of Economic Entomology* **61:** 499-501.

Hawkes, R.B. 1973 Natural mortality of cinnabar moth in California. *Annals of the Entomological Society of America* **66**: 137-146.

Hawkes, R.B.; Johnson, G.R. 1978 *Longitarsus jacobaeae* aids moth in the biological control of tansy ragwort. *Proceedings of the 4th International Symposium on the Biological Control of Weeds, Gainsville, 1976,* 193- 196.

Helson, G.A.M. (1974) Beneficial insects - cinnabar moth and ragwort seed fly. *New Zealand Journal of Agriculture* **128**: 56-59.

Honore, E.J.; Rahman, A.; Dyson, C.B. 1980 Effects of winter application of phenoxy herbicides on white clover and pasture production in the lower North Island. *Proceedings of the 33rd New Zealand Weed and Pest Control Conference,* 55-58.

Irvine, H.M.; Forbes, J.C.; Draper, S.R. 1977 Effect of 2,4-D on the soluble carbohydrate content of ragwort (*Senecio jacobaea*) leaves. *Weed Research* **117**: 169-172.

Islam, Z.; Crawley, M.J. 1983 Compensation and regrowth in ragwort (*Senecio jacobaea*) attacked by cinnabar moth (*Tyria jacobaeae*). *Journal of Ecology* **71**: 829-843.

Isaacson, D.L. 1973 A life table for the cinnabar moth, *Tyria jacobaeae*, in Oregon. *Entomophaga* **18:** 291-303.

Isaacson, D.L. 1978 The role of biological agents in integrated control of ragwort. *Proceedings of the 4th International Symposium on the Biological Control of Weeds Gainsville* 1976 189-192.

Ivens, G.W. 1979 Ragwort. *New Zealand Journal of Agriculture*. September (1979).

Johnson, A.E. 1978 Tolerance of cattle to tansy ragwort (*Senecio jacobaea*). *American Journal of Veterinary Research* **43**: 718 - 723.

Kelsey, J.M. 1955 Ragwort seedfly establishment in New Zealand. *New Zealand Journal of Science and Technology* **A 36**: 605-607.

Kitching, R.L. 1977 Time, resources and population dynamics in insects. *Australian Journal of Ecology* **2:** 31-42.

Kuno, E. 1971 Sampling error as a misleading artifact in key factor analysis. *Researches in Population Ecology* **13:** 28-45.

Lloyd, M. 1967 Mean crowding, *Journal of animal ecology* 36: 1-30

Manly, B.F.J. 1977 The determination of key factors from life table data. *Oecologia* **31:** 111-117

Manly, B.F.J. 1979 A note on key factor analysis. *Reasearches in population ecology* **21:** 30-39

Matthews, L.J.; Thompson, A. 1977. Ragwort control through seeding and spraying. *Ruakura farmers' conference proceedings,* 6-7.

Mattocks, A.R. 1968 Toxicity of pyrrolizadine alkaloids. *Nature, London* **217**: 723-728.

McEvoy, P.B. 1984a Dormancy and dispersal of dimorphic achenes of tansy ragwort *Senecio jacobaea* L. (Compositae). *Oecologia* **61**: 160- 168.

McEvoy, P.B. 1984b Seedling dispersion and the persistence of ragwort *Senecio jacobaea* (Compositae) in a grassland dominated by perennial species. *Oikos* **42:** 138-143.

McEvoy, P.B.; Cox, C.S. 1987 Wind dispersal distances in Dimorphic achenes of ragwort, *Senecio jacobaea. Ecology* **68** (6): 2006 - 2015.

McLachlan, G.J.; Basford, K.E. 1988 *Mixture models: Inference and applications to clustering*. Marcel Dekker, Inc: New York.

Meads, M.J. 1973 A note on the cinnabar moth *(Callimorpha jacobaeae)* (Arctiidae) *New Zealand Entomologist* **5** (2): 170 - 171.

Meijden, E. van der. 1971 *Senecio* and *Tyria (Callimorpha)* in a dutch dune area. A study on the interaction between a monophagous consumer and it's host plant. *Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeck, 1970* 390-404.

Meijden, E. van der. 1974 The distribution of *Senecio jacobaea* L. and *Tyria jacobaeae* L. in relation to soil properties. *Acta Botanica Neerlandica* **23:** 681-690.

Meijden, E. van der. 1976 Changes in the distribution pattern of *T. jacobaeae* during the larval period. *Netherlands Journal of Zoology* **26:** 136-161

Meijden, E. van der 1978 Interactions between the cinnabar moth and tansy ragwort (*Senecio jacobaea). Preceedings of the 4th International Symposium on Biological Control of Weeds, Gainsville,* 1976, 159-162.

Meijden, E. van der. 1979 Herbivore exploitation of a fugitive plant species: local survival and extinction of the cinnabar moth and ragwort in a heterogeneous environment. *Oecologia* **42:** 307-323.

Meijden, E. van der; Waals-Kooi, R.E. van der 1979 The population ecology of *Senecio jacobaea* in a sand dune system. 1. Reproductive strategy and the biennial habit. *Journal of Ecology* **67**: 131-153.

Meijden, E. van der.; Bremmelen, M. van., Kooi, R.; Post, B.J. 1984 Nutritional quality and chemical defence in the ragwort-cinnabar moth interaction. *Journal of Animal Ecology* **53:** 443-453.

Meijden, E. van der; Zoelen, A. van; Soldaat, L.L. 1989 Oviposition by the cinnabar moth in relation to nitrogen, sugars and alkaloids of ragwort, *Senecio jacobaea. Oikos* **54:** 337-344.

Miller, D. 1929 Control of ragwort: Experimental work witk cinnabar moth. *New Zealand Journal of Science and Technology* **11:** 112-119.

Miller, D. 1970 Biological control of weeds in New Zealand 1927-48. *Department of Scientific and Industrial Research information series* **74**: 104pp.

Mortimer, P.H.; White, E.P. 1975 Toxicity of some composite (*Senecio*) weeds. *Proceedings of the 29th New Zealand Weed and Pest Control Conference*, 88-91.

Myers, J.H. 1978 Biological control introductions as grandiose field experiments: adaptations of the cinnabar moth to new surroundings. *Proceedings of the 4th International Symposium on Biologcal Control of Weeds, Gainsville, 1976,* 181-188.

Myers, J.H. 1979 The effects of food quantity and quality on emergence time in the cinnabar moth. *Canadian Journal of Zoology* **57**: 1150-1156

Myers, J.H. 1980 Is the insect or the plant the driving force in the cinnabar moth-ragwort system? *Oecologia* **47:** 16-21.

Myers, J.H.; Campbell, B.J. 1976 Distribution and dispersal in populations capable of resource depletion. A field study on cinnabar moth. *Oecologia* (Berl.) **24:** 7-20.

Nagel, W.P.; Isaacson, D.L. 1974 *Tyria jacobaeae* and tansy ragwort in western Oregon. *Journal of Economic Entomology* **67:** 494-496.

Philogene, B.J.R. 1975 Responses of the cinnabar moth *Hypocrita jacobaeae* to various temperature/ photoperiod regimes. *Journal of Insect Physiology* **21:** 1415-1417.

Poole, A.L. 1938b Germination of ragwort in water. *New Zealand Journal of Agriculture* **57**: 95 - 96.

Poole, A.L.; Cairns, D. 1940 1940 Botanical aspects of ragwort (*Senecio jacobaea)* control. *Bulletin of the New Zealand Department of Scientific and Industrial Research.* **82:** 1 - 66.

Prins, A.H., Nell, H.W. 1990 Positive and negative effects of hebivory on the the p[opulation dynamics of *Senecio jacobaea* L. and *Cynoglossum officinale* L. *Oecologia* **83:** 325 - 332.

Radcliff, J.E. 1969 Ragwort control. *New Zealand Journal of Agriculture* **119:** 80-83

Rose, S.D. 1978 Effect of diet on larval development, adult emergence and fecundity of the cinnabar moth, *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae) MSc. Thesis Oregon State University, pp 88.

Richards, L.J.; Myers, J.H. 1980 Maternal influences on the size and emergence time of the cinnabar moth. *Canadian Journal of Zoology* **58:** 1452-1457.

Sawyer, A.J.; Haynes, D.L. 1984 On the nature of errors involved in estimating stage-specific survival rates by Southwoods method for a population with overlapping stages. *Researches on Population Ecology* **26**: 331-351.

Schmidl, L. 1972 Biology and control of ragwort *Senecio jacobaea* L. in Victoria, Australia. *Weed Research* **12**: 37-45.

Schmidl, L. 1972 Studies on the control of ragwort, *Senecio jacobaea* L. with the cinnabar moth *Callimorpha jacobaeae* L. (Arctiidae: Lepidoptera) in Victoria. *Weed Research* **12:** 46-57.

Sheldon, J.C.; Burrows, F.M. 1973 The dispersal effectiveness of the achene pappus of selected Compositae in steady winds with convection. *New Phytologist* **72**: 665-675.

Sokal, R.R.; Rohlf, F.J. 1981 *Biometry*. 2nd Edition. San Francisco, W.H.Freeman and company pp.859.

Smith, C.J. 1980 *Ecology of the English Chalk*. London, UK; Academic Press, pp 573.

Southwood, T.R.E. 1978 *Ecological Methods* 2nd edition London; Chapman and Hall. Pp 524.

Smith, R.H. 1973 The analysis of intra-generational change in animal populations. *Journal of animal ecology* **42:** 611-622.

Stimac, J.L.; Isaacson, D.L. 1978 Cinnabar moth as a biological control of tansy ragwort: comparison of population dynamics in England and Oregon. *Proceedings of the 4th International Symposium on the Biological Ccontrol of Weeds, Gainsville, 1976,* 155-158.

Stinner, R.E.; Gutierrez, A.P.; Butler, G.D. 1974 An algorithm for temperature-dependent growth rate simulation. *Canadian entomologist* **106:** 519-524.

Swick, R.A.; Miranda, C.L.; Cheeke, P.R.; Buhler, D.R. 1983b Effect of phenobarbitol on toxicity of pyrrolizadine (*Senecio*) alkaloids in sheep. *Journal of Animal Science* **56**, 887-894.

Swick, R.A.; White, R.D.; Cheeke, P.R. 1982 Effect of *Senecio jacobaea* and molybdenum on copper in sheep. *Journal of Animal Science*. **55**, Supplement 1, 492-493.

Syrett, P. 1983 Biological control of weeds in New Zealand: a review. *Australian weeds* **2:** 96,101.

Syrett, P.; Scheele, S.M.; Philip, S.M. 1984 Renewed activities in biological control of ragwort. *Proceedings of the 37th New Zealand Weed and Pest Control Conference* 37-41.

Syrett, P.; 1989 *Senecio jacobaea* L. ragwort (Asteraceae) *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987.* Eds. Cameron, P.J.; Hill, R.L.; Bain, J.; Thomas, W.P. CAB International.

Tuaber, M.J.; Tauber, C.A. 1976a Insect seasonality: Diapause maintenance, termination and post diapause development. *Annual Review of Entomology* **21:** 81-107.

Tauber, M.J.; Tauber, C.C. 1986 *Seasonal adaptations of insects*. Oxford University Press, New York. pp 410

Thompson, A. 1980 Ragwort population and control studies. *Proceedings of the 33rd New Zealand Weed and Pest Control Conference*, 59 - 62.

Thompson, A. 1985 Population studies on ragwort (*Senecio jacobaea*). *Proceedings of the 38th New Zealand Weed and Pest Control Conference*, 122-126.

Thomson, G.M. 1922 *The naturalisation of plants and animals in New Zealand* Cambridge.

Varley, G.C.; Gradwell, G.R. 1960 Key factors in population studies. *Journal of animal ecology* **26:** 399-401.

Wardle, D.A. 1987 The ecology of ragwort (*Senecio jacobaea* L.) -a review. *New Zealand Journal of Ecology,* **10:** 67-76.

Windecker, W. 1939 *Euchelia (hypocrita) jacobaeae* L. und das Schutztrachten problem. *Z. Morph. Okol. Tierre.* **35**: **84-138**

Wise, K.J. 1952 A recent ocurrence of the cinnabar moth (*Tyria jacobaeae*) *New Zealand Entomologist* **1** (2): 10.

Zoelen, A.M. van,; Kusters, G.J. 1986 Termination of diapause in the cinnabar moth (*Tyria jacobaeae*) by chilling. *Entomolgia Experimentia et Applicata* **41:** 185-192.