POPULATION DYNAMICS OF THE SEEDFLY, *PEGOHYLEMYIA JACOBAEAE* (HARDY) (DIPTERA: ANTHOMYIIDAE), AND ITS POTENTIAL AS A BIOLOGICAL CONTROL AGENT OF RAGWORT, *SENECIO JACOBAEA* L.

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Plate 1 Ragwort seedfly adult

ABSTRACT

The aim of this study was to assess the effectiveness of a seedfly, Pegohylemyia jacobaeae (Diptera: Anthomyiidae) as a biological control agent of ragwort, Senecio jacobaea. Seedfly populations were sampled from October to April in 1982/83 and 1983/84 at two sites in the central North Island, New Zealand. Supplementary laboratory experiments were conducted to clarify aspects of the seedfly/ragwort interaction.

In the field a six week pre-oviposition period was recorded before ragwort flowered. The absence of ragwort flowers had no effect on ovary development in laboratory reared flies but the pre-oviposition period predicted by a day degree summation model was shorter than that observed in the field.

The extended pre-oviposition period resulted in competition for oviposition sites when ragwort first flowered, with consequent low fecundity and multiple oviposition. This competition was higher in the second year due to a tenfold increase in the number of flies emerging compared with the previous year. The total number of ragwort seedheads was similar in both years but inflorescence development was faster in 1983/84. A combination of increased seedfly population, increased competition for oviposition sites and improved synchrony between

emergence and ragwort flowering in 1983/84 resulted in a twofold increase in infestation levels compared to 1982/83.

Estimates of seedfly mortality within the seedhead were 33% and 60% in 1982/83 and 1983/84 respectively but were affected by the variable length of the third larval instar. Laboratory and field data indicated that pupating third instar larvae leave the seedhead in conditions of high surface moisture and prolonged dry conditions resulted in high mortality. Pupal mortality ranged from 14.3 to 57% but this was also affected by estimates of third instar larvae. Pupal diapause is initiated at temperatures above 15-20C and in the central North Island seedfly rarely diapause in winter.

Seedfly infestation levels ranged from 10% (1982/83) to 20% (1983/84) and up to 200 seedheads/m^2 escaped predation. Ragwort seeds are long-lived, have a high germinating capacity, and uneaten seeds from seedfly infested seedheads were viable. It was concluded that at the study sites the seedfly's impact on the ragwort population was negligible.

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CHAPTER ONE: INTRODUCTION

1.1 Introduction

Ragwort, *Senecio jacobaea* L., is a common weed throughout New Zealand and is a problem in waste areas, along roadsides, railway lines, on derelict agricultural land, forest margins and on over-grazed, poorly managed pastures. It was classified as noxious plant soon after its discovery in New Zealand because of its toxicity to stock. A prolific seeding plant it also reproduces vegetatively in response to mechanical damage, herbicide treatment or environmental stress.

A biological control programme for ragwort was initiated in the 1920s and 1930s with the introduction of two seedfly (*Pegohylemyia*) species and the cinnabar moth (*Tyria jacobaeae* L.). Hoy (1964), however, deferred further research on this when he stated that "the advent of hormone sprays offers a simple alternative to biocontrol of ragwort and no further efforts in this field are at present contemplated." In 1982, the D.S.I.R. again considered the introduction of new biological control agents of ragwort and redistribution of existing ones. The importance of

obtaining basic information on the effectiveness and distribution of present populations was also realised. This study was therefore initiated to determine how the interaction between P.jacobaeae and its host affected the seedfly's potential as a control agent of ragwort. The remainder of this chapter describes the life history of ragwort and the variety of control measures currently in use in New Zealand. The two ragwort seedfly species are described and published information on their life cycles and effectiveness as biological control agents of ragwort is presented.

1.2 The host plant

1.2.1 Distribution

Ragwort, Senecio jacobaea L. is a member of the largest genus of the family Compositae. Members of this genus range from herbs to shrubs and are found throughout the world. Few are of economic importance but a number are weeds.

Ragwort was first noted in New Zealand near Dunedin in 1874 (Thomson, 1922). A native dune plant of Europe and Asia, it was probably introduced as a contaminant of crop seed. It spread quickly throughout New Zealand and is abundant on light disturbed calcareous soils, organic rich alluvium, light loams and clays. It can be found in most areas receiving more than 800 mm rain per annum (Poole and Cairns, 1940).

1.2.2 Biology and life history

Although ragwort is commonly considered a biennial which dies

after flowering it frequently behaves as an annual or a perennial. Plants can be either single-stemmed or much branched from the base. The stems are 0·5-2 metres high, branching above the middle to give a flat topped dense compound corymb with as many as 2500 capitulae (Poole and Cairns, 1940). A capitulum contains on average 70 achenes (Cameron, 1935), each producing a single seed.

When in bud the involucral bracts are folded over the flowers. Each bract is dark tipped and the massed tips make a dark spot at the centre of the flat topped bud. The stigmas emerge before the anthers. The flowers have a faint odour and are visited by a large number of insects. Nectar is present and the honey bee, Apis mellifera L., collects this but not the pollen (Harper and Wood, 1957). Pollen presentation occurs from 8am to 5pm with peak periods at 10am and noon for ray and disc florets respectively (Harper and Wood, 1957). In a single capitulum anthers continue to dehisce over a period of 4-9 days. Fertilisation may also occur on cut flowers that are still fresh (Poole and Cairns, 1940).

Attached to the top of the disc achenes is a pappus approximately 5mm in length. Its effectiveness is increased in conditions of high wind velocity and low relative humidity (Cameron, 1935). The general consensus is, however, that the pappus does little to aid wind dispersal and the majority of the seeds fall near the plant (Sheldon and Burrows, 1973 and Smallfield, 1970). Poole and Cairns (1940) found that the seed shadow was of a negative exponential form and they estimated that the highest amount of

seed to become windborne was 0.5%.

No viable seed was voided by sparrows and Zebra finches when fed ragwort seeds (Poole and Cairns, 1940) but achenes eaten by sheep pass through the digestive system undamaged and germinate in dung (Eadie and Robinson, 1953). Animals frequently have seed tangled in hair or wool and ragwort dispersal can often be traced to stock movements.

Infestations also follow water courses. Poole (1938b) found that ragwort seeds readily germinated in water. Although the seeds initially sank when the pericarp split they rose to the surface when the cotyledons fully opened. Ragwort seeds have a high germinating capacity under suitable conditions. Cameron (1935) reported 80% viability of seeds germinated on damp filter paper at 15C. Poole and Cairns (1940) working with New Zealand material found germination in the laboratory varied from 50-86% and Kelsey (1955) records an average germination of 70% (range 58-96%).

High temperature, low soil moisture and low relative air humidity reduced germination success in experiments conducted by Van der Meijden and Van der Waals-Kooi (1979). They found that achenes possess innate dormancy but dormancy may be induced by adverse conditions such as frost and drought. Green (1937) observed that after the bracts of the capitulum have rolled back to allow dispersal of the disc achenes they recurve upwards to form a cup retaining the ray achenes. This can be linked to the dimorphism of achenes described by McEvoy (1984). He found that disc and ray

florets yield achenes of different dormancies: disc achenes germinate quickly with high germination success; ray achenes exhibit low percentage and delayed germination. This, he suggests, spreads germination in space and time as those seeds carried away may take advantage of chance exogenous disturbances by germinating quickly. These risks are balanced by those seeds which germinate at the comparably safer rosette openings and also explains how ragwort populations persist in the absence of environmental disturbances.

Light is required for germination and a soil covering greater than 4mm in thickness results in enforced dormancy (van der Meijden and van der Waals-Kooi, 1979). Absence of soil covering retards germination for a time but Poole and Cairns (1940) found that seed sown on the soil surface gave the same ultimate germination as seed sown under a very thin sprinkling of soil. Long term seed viability trials are currently underway at Ruakura Agriculture Research Centre and preliminary results show that viability increases with the depth that the seeds have been buried (Alex Thompson pers.comm, 1984). From initial results Thompson and Makepeace (1983) estimate seed viability to decline to 1% in 4-5 years within 0-2 cm of the surface layer and 10-16 years below 4cm soil depth.

In the field germination success is also affected by availability of germination sites. Cameron (1935) showed that 2% of seed germinated when sown on cut grass compared to 53% on bare soil. McEvoy (1984) recorded higher seedling densities in rosette

openings than in the vegetation immediately surrounding the opening. He attributes this either to the establishment probability being possibly higher inside the rosettes perimeter and/or to differences in sowing density. Maximum germination occurs in autumn following the main seedfall (Poole, 1938a). The first true leaf appears about a month after germination but only a few leaves develop in the winter months. By mid December small rosettes have formed. These overwinter as low vegetative rosettes, 5-15cm in diameter, with broad, horizontally orientated leaves. These generally bolt and flower during the early summer of the second year of growth. The probability that a plant will flower increases with the diameter of the rosette at the start of the flowering season (van der Meijden and van der Waals-Kooi, 1979).

There are many known variations of the biennial life cycle described above. When Schmidl (1972) grew *S.jacobaea* plants from seed and planted them in ungrazed grassland in Victoria, Australia, 2% of those that flowered were annuals, 52% biennials and 46% perennials. Forbes (1977) constructed a model of population flux in a hypothetical population in which germination, maturation and death were constant from year to year. The model predicted that of the plants that flowered 8% were annuals, 39% biennials and 53% perennials.

Regeneration occurs from root buds, from buds in the axils just above ground level or from the crown (Radcliffe, 1969). Plants may regenerate within two months from root fragments less than 2cm

in length but roots of rosettes form buds more readily (37% of root fragments) than those of flowering plants (10%) (Poole and Cairns, 1940). Cairns (1938) attributes the high regenerative capacity of ragwort roots to a non-functional endodermis and development of pericyclic phellogen which results in rapid formation of new tissues.

Perennial growth can be induced by other forms of stress but this is not readily detectable as seedlings are easily confused with rosettes that have arisen vegetatively. The latter are difficult to identify because the connection with the parent plant soon decays. Thompson (1977) concluded that infestations which persisted after herbicide treatment were composed largely of regrowth plants. Islam and Crawley (1983) found that over 75% of plants that had flowered produced shoots in the following spring but 42% of these had suffered severe defoliation by cinnabar moth. Delayed growth in rosettes due to drought in the second summer prevented flowering in a population of ragwort observed by Poole and Cairns (1940). Radcliffe (1969) states that rosettes may persist for many years before flowering when strongly repressed by competition and both Cairns (1938) and Radcliffe (1969) warn that plants dying down after flowering may produce vegetative shoots from their roots.

1.2.3 Toxicity and weed status.

Ragwort contains pyrrolizidine alkaloids responsible for chronic liver damage in cattle and horses. Dickonson and King (1978) noted the highest alkaloid content in flowers and roots while

White (1969) reported 0·2-0·3% alkaloid content in above ground parts and 0·03% in the roots of New Zealand plants. Toxicity may also increase up to flowering time (Connor, 1977). Rabbits do not eat ragwort, (Harper and Wood, 1957), but sheep and goats are often used to control the weed. Sheep were observed by Poole and Cairns (1940) to show a preference for the plant after they had acquired a taste for it. Many of the ill effects suffered subsequently by sheep are not always attributed to alkaloid poisoning which has similar symptoms to facial eczema (Mortimer and White, 1975). The toxic alkaloids are not lost on drying and deaths of cattle and horses may result after eating hay or silage containing ragwort (Dempster, 1982). Honey from ragwort infested areas is reported to be dark coloured and tainted (Thomson, 1922) and can contain alkaloids (Deinzer et al., 1977). Milk from cows and goats fed ragwort also contained alkaloids (Dickonson and King, 1978). The effects on humans are not known.

By 1900 ragwort had been placed on the schedule of noxious weeds in New Zealand (Radcliffe, 1969) primarily on the basis of its toxicity but its conspicuousness may also contribute to its weed status. Economic damage has never been calculated directly in terms of lost pasture and animal production but by costs of control measures (Swarbrick, 1983).

1.3 Ragwort control measures

1.3.1 Herbicide treatment

Application of herbicides seldom, if ever, gives permanent control of established ragwort infestations. 2,4-D is the most widely

used spray in New Zealand for its control and although is not as effective as dicamba or picloram it is less damaging to pasture (Thompson, 1974, 1977).

Ragwort palatibility can be increased by herbicide application resulting in further stock losses (Cameron, 1935 and Thompson, 1974).

1.3.2 Mechanical removal

Mowing ragwort plants checks seeding but does not prevent regrowth. Cutting plants in flower promotes strong regrowth from the crown and roots regardless of the cutting height above ground (Cairns, 1938). Pulling out flowering plants results in some regeneration from root fragments and while fire destroys seed and many plants some regeneration from root fragments may occur. There is considerable regeneration from seed and root fragments after ploughing but quick establishment of a dense sward reduces recolonization. It has been suggested that fertilising pasture promotes a dense sward and decreases the chances of seedling establishment (Bill Makepeace, pers.comm.1982). Farmers must balance the costs of improving pasture against the costs of removing conspicuous plants which they are required by law to do. This often results in cheaper short term measures such as mowing or ploughing being resorted to. The application of costly herbicides which weaken pastures does little to solve the problem.

Sheep grazing prevents flowering and reduces ragwort density but high sheep numbers are necessary to ensure ragwort plants are

grazed and some stock losses occur as mentioned above.

1.3.3 Insects as biological control agents of ragwort

Over 65 insect species from five different orders have been recorded on ragwort (Harper and Wood, 1957). When it was introduced into North America, Argentina, Australia and New Zealand, ragwort was not accompanied by its native fauna but it was expected that native Senecio species may provide a source of endemic insects which would take advantage of a new host.

Miller (1970) cites six species with potential to control ragwort in New Zealand but none of them are native. These include three Lepidopteran species, two Diptera and an aphid. The cut worm Ariathisa comma (Walk.) (Noctuidae) damages juvenile ragwort but is a pest of cultivated plants. The pyralid stem borer Homeosoma vagella Zell. also infests a high proportion of plants but does not prevent flowering (Cottier, 1931). The noctuid Nyctemera annulata Bd. commonly known as the magpie moth, is the best known insect found on ragwort in New Zealand. The larva, which is often confused with the cinnabar moth, feeds on ragwort foliage but seldom reaches high densities. It also feeds on native species of Senecio, Brachyglottis, groundsel and cineraria (Miller, 1970). There are no published data on the life history of the magpie moth although it was found to sequester ragwort alkaloids (Benn et al., 1979). It is attacked by three parasites; the ichneumonid Echthromorpha intricatoria (Fabr.) which oviposits in the pupae and two tachinids, Cerosomya nyctemeriana (Huds.) and C.casta(Hutt) which parasitize the larvae. The Dipteran stem

borer, Agromyza aeneiventris Fln., is common on ragwort (Miller, 1970) but has little effect. A Dipteran leaf miner, Phytomyza atricornis Mg., rarely damages ragwort plants in the field but high densities occur in the sheltered conditions of the glasshouse and insectary (Kelsey, 1937 and pers.obs.) where it may kill the plants. The aphid, Brachycaudus helichyrysi (Kltb.) which clumps flowers together with its honey dew may have some effect on seed dispersal (Miller, 1970).

Several insects have been released in New Zealand specifically as biological control agents of ragwort. The most conspicuous of these is the cinnabar moth, Tyria jacobaeae L. (Lepidoptera: Arctiidae). It is univoltine throughout its range with an obligatory diapause in the pupal stage. Although liberated throughout New Zealand from 1929 to 1932 populations persisted only in the south of the North Island (Miller, 1970).

As a control agent of ragwort the cinnabar moth has had mixed success overseas. In the Netherlands there have been local extinctions of both the moth and ragwort (van der Meijden, 1976) while at Weeting Heath in England both plant and insect populations experience high amplitude fluctuations with no control at low plant densities (Dempster, 1982). In Oregon, USA, the weed has been maintained at relatively low densities by cinnabar moth over a five year period (Stimac and Isaacson, 1976). but in British Columbia, Canada, moth populations are stabilising at levels below that needed for complete defoliation (Harris et al., 1976).

The ragwort flea beetle, Longitarsus jacobaeae Wat. (Coleoptera: Curculionidae), was liberated in New Zealand during 1983 with further releases planned (P.Syrett, pers.comm.1984). There are two biotypes. The Swiss strain has a facultative egg diapause and the Italian strain has a facultative adult aestivation period (Syrett, 1983). The beetle attacks the roots of ragwort during winter and spring and it is hoped that it may complement the attack of Tyria jacobaeae which is active in summer.

1.4 Ragwort seedfly

1.4.1 Description

Pegohylemyia jacobaeae (Hardy) and P.seneciella (Meade) are two similar European anthomyiid flies. Both are commonly called ragwort seedflies because their larvae develop in flower heads of ragwort. Miller (1970) describes P.seneciella as a small, dull greyish- pubescent insect; darker in the male, and 4-5mm long. Collin (1936) states that P.jacobaeae adults are slightly larger averaging 6mm in length compared to 4-5mm for P.seneciella. The two species are more reliably distinguished by differences in shape and hair arrangement of the ovipositor in females and the hypopygium and fifth abdominal sternite in males (Holloway, 1983). The underside of the costal vein in P.jacobaeae also has an additional row of evenly spaced hairs (Holloway, 1983).

1.4.2 Liberation and establishment in New Zealand

Both species of Pegohylemyia were imported into New Zealand from England between 1928 and 1939 (Miller, 1970) but field recoveries of Pegohylemyia throughout New Zealand in 1981 and 1982 have all

been of P.jacobaeae (Holloway, 1983).

Seedfly were transported to New Zealand as pupae and released as adults. In February 1936, 612 insects were released at the Cawthron Institute, Nelson in the South Island and 1,378 near Putaruru in the North Island. During autumn and from late winter to early summer 1937, approx 92,470 flies were liberated, 80,000 of them at Putaruru and the remainder at Coromandel, Matamata, Tirau, Opotiki, Ohinemuri, Paeroa, and Te Awamutu and again in Nelson. These came from the 7th to 10th consignments from England and only P.seneciella specimens were preserved from these (Holloway, 1983). Unfortunately no record of the proportions of the two species released was kept and no distinction was made between them in follow up observations.

Seedfly populations were initially out of synchrony with conditions in the Southern Hemisphere and liberation at a site at Ngongotaha near Rotorua in autumn 1940 was followed by an observed winter infestation in June 1940 and a further generation in the next summer.

Infestations persisted at the Cawthron Institute, at Tirau and Putaruru until 1944/45 and at Ngongotaha until at least 1942 but no flies were found there in 1950 (Kelsey, 1955). He found, however, a thriving population at Redwoods Forest, Ngatira, the offspring of 36 adults released there in February 1937.

In 1984 seedfly was present only in the central North Island, Bay

of Plenty and the southern Waikato (Fig.1.1).

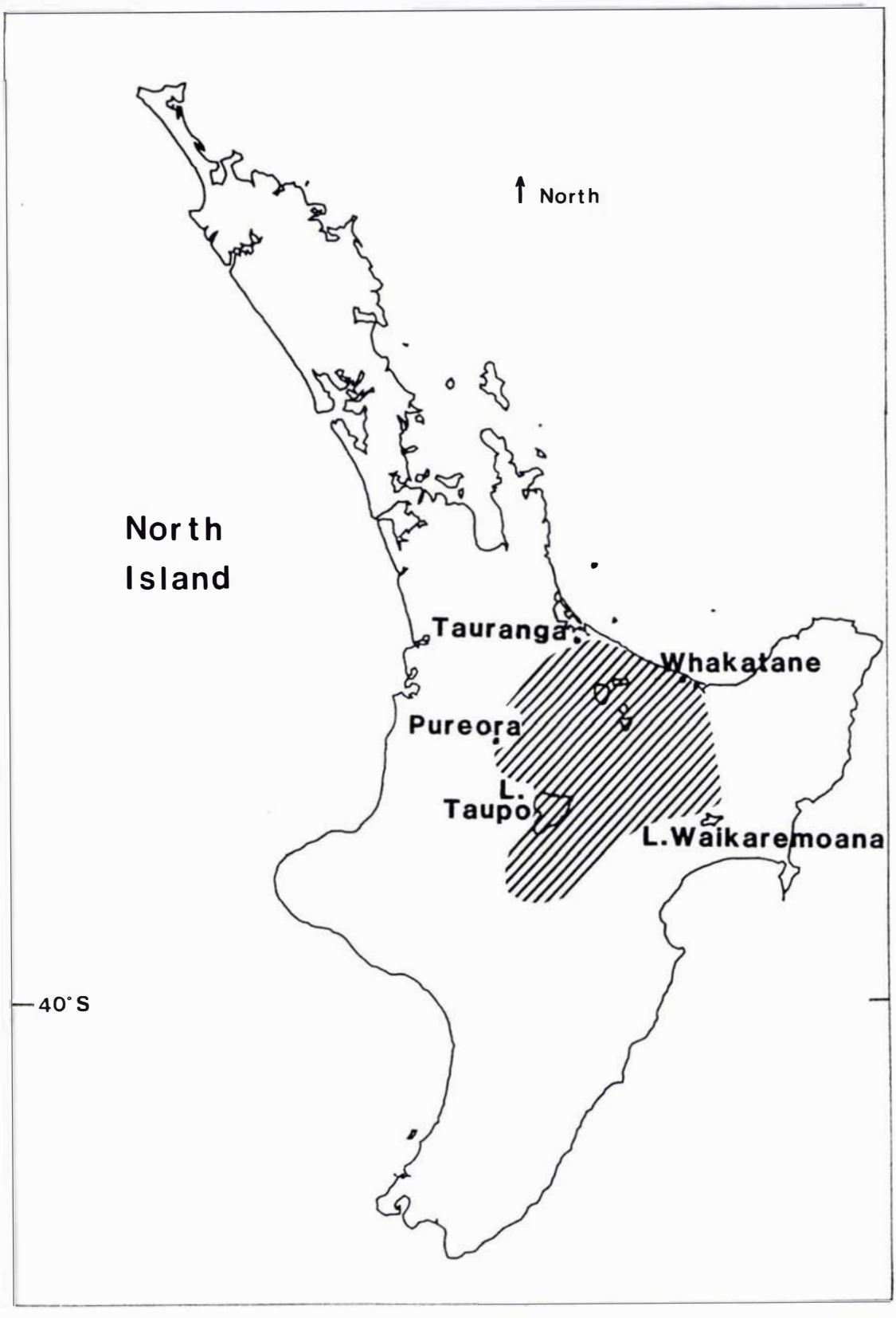
1.4.3 Life history

The life cycle of the ragwort seedflies has been described by Cameron (1935), Miller (1970) and Frick and Andres (1967). The seedfly pupa overwinters in the soil and adults emerge in spring as ragwort buds are developing. The eggs are laid down among the florets or alongside the green bracts. Only one larva develops per seedhead even though several eggs may be laid. First instar larvae are found inside individual developing florets but may move from one floret to another and can be detected by chewed windows in the wall of the floret (pers.obs.). Neither the egg nor the early first instar are visible externally. Damage becomes visible as browning of the florets caused by late first instar and second instar larvae feeding. Later the florets are displaced by the feeding larva and the pappus becomes prematurely extruded and matted together by larval secretion. Signs of larval damage differ in the two species. The early sign of a dark spot in the centre of the disc is more common in Oregon where only P.seneciella have established and the pappus, although not extruded as far, is covered with a white, sticky exudate not seen in New Zealand (P.Syrett, pers.comm.1984). Third instar larvae of P.jacobaeae observed leaving the plant during this study were not attached to a thread but dropped freely or crawled down the stem.

Some information on seedfly life history was obtained in New Zealand from flies imported for biological control (Miller, 1970) but no distinction was made between the two species. The longest

Figure 1.1 Seedfly distribution in 1984

Surveyed by P.Syrett and J.Dymock



adult life span recorded was 44 days. The time from oviposition to larvae leaving the flowers ranged from 36 days to 94 days depending on the temperature and larvae pupated within five days of leaving the seedhead. The pupal stage ranged from 130-240 days.

1.4.4 Effectiveness as a biological control agent of ragwort

Cameron (1935) reported that Pegohylemyia infested approximately 8-9% of the capitula in southern England and 33-34% in northern Scotland with 75% of the seed in the capitulum destroyed in both areas. He also noted that the northern range of P.jacobaeae extended much further north than Tyria in the British Isles and suggests that this advantage may be useful in higher and colder regions, where it may be impossible to establish Tyria. In New Zealand, Kelsey (1955) reported that 91% of the florets of early flowers and 43% of those in the main flowering period were infested by seedfly at Redwoods Forest in 1949/50 while 60-98% of the early crop and 8-71% of the main crop was infested in 1953/54. Kelsey (1955) also found that the average number of seed surviving from infested capitula was 12, (range 0-22) but these failed to germinate.

Some information on larval and pupal mortality was obtained from flies collected from Redwoods Forest for shipment to Australia (Hoy, 1958). Of 33 dead larvae examined 32 were infected by nematodes of the genus Rhabditis and one larva had been invaded by a fungus. Fourteen out of 21 pupae examined were parasitized by a fungus, 2 by Rhabditis species and in 2 the cause of death was

unknown. Most of the nematode species were saprophytic so that flies infected had died from other causes. According to Hoy (1960) the flies arrived in Australia in good condition and three quarters of them emerged successfully. He concluded that little internal damage had occurred during the of retrieval of pupae by sieving because the number of deformed flies that emerged was low.

Seedfly released in Australia in the 1930s and 1950s failed to establish (Waterhouse, 1967) but those released by Frick in California in 1967 were well established by 1968 and 1969 (Frick, 1969). Andres and Davis (1973) found that this release site had been inadvertently mown but the fly was recovered close by in 1976 and more releases were planned (Andres et al, 1976). P.seneciella is now also established in Oregon (Isaacson and Ehrensing, 1977) after initial difficulties. Seedfly is hard to locate in the years immediately following release but usually reappears in the vicinity several years later (P.Syrett, pers.comm.1984).

1.5 Objectives of the present study

Field populations of seedfly and ragwort were studied during the summers of 1982/83 and 1983/84. The field sites are described and the sampling methods and data collected are presented in the following chapter. The field observations were supplemented with laboratory studies which are described in Chapter 3. This involved experimental manipulation of the pre-oviposition period to determine the relationship between oviposition site availability and infestation levels. In addition, egg and larval development rates obtained under controlled conditions were used

to construct survivorship curves. Chapter 4 draws on the information obtained in the laboratory to construct a model of the seedfly pre-oviposition period and development within the seedhead. This model was compared with the field population to check the synchrony of various stages of seedfly life history with its host. Throughout the chapters the results are compared with published information on other anthomyiid flies. However, information on seed eating anthomyiids is scant, with research concentrated mainly on those flies of economic importance. The majority of these are root feeders which have differing life history strategies. Some are less host specific than seedflies and others have more than one generation per year. However, their taxonomic relationship to ragwort seedfly warrants their inclusion for comparative purposes. The final chapter is a discussion of the factors which influenced seedfly infestation levels of ragwort during the study period and the seedfly's role in the biological control of ragwort.

CHAPTER TWO: FIELD STUDIES

2.1 Introduction

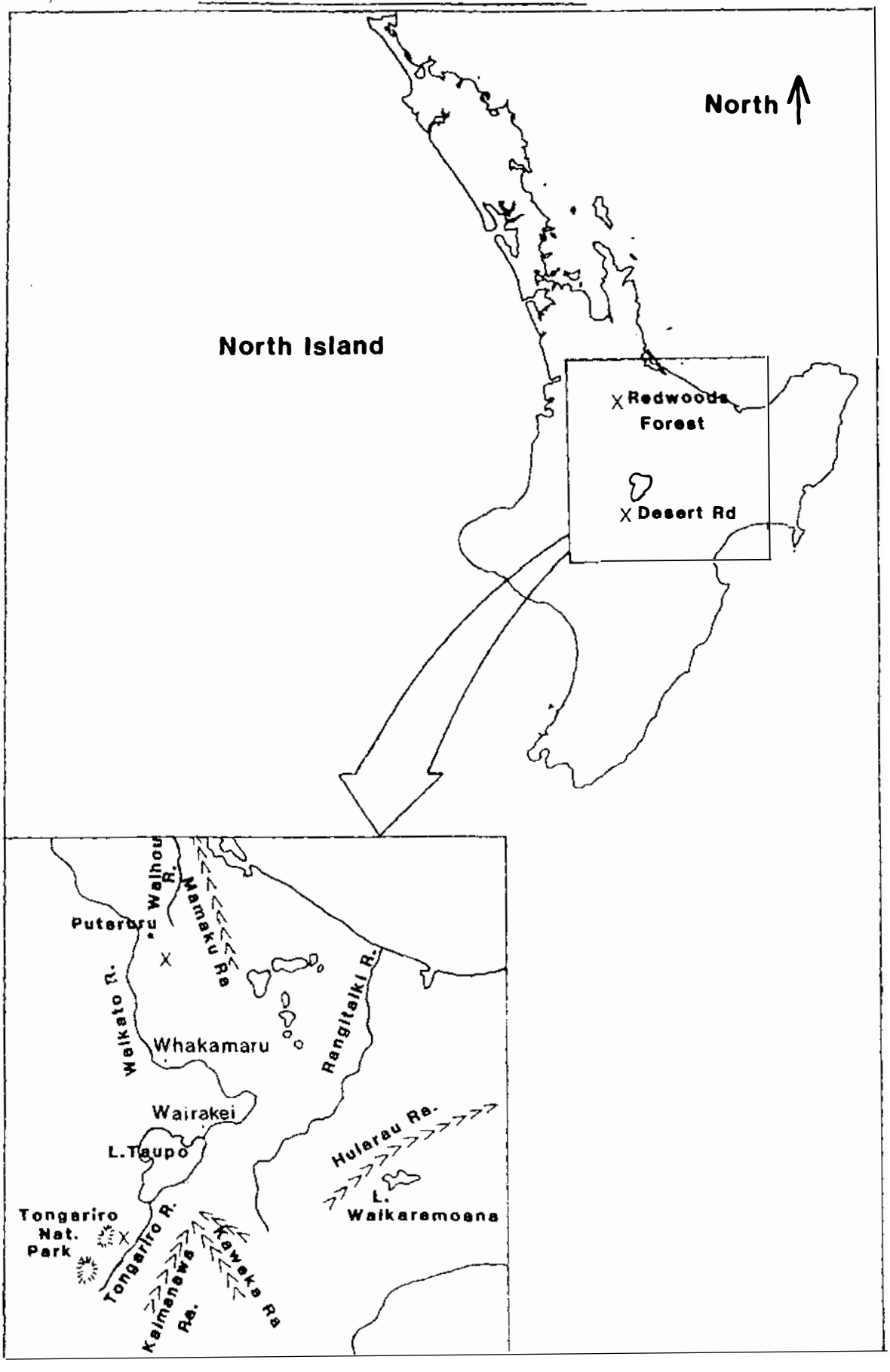
Two seedfly populations were sampled in the field over two successive summers to obtain information on their life history and infestation levels of ragwort. The field sites chosen (Fig.2.1) were representative of the climatic conditions experienced by the seedfly in New Zealand. Research effort was concentrated at the lower altitude, warmer Redwoods Forest site while a more exposed area at the Desert Rd was the site of less intense data collection. The latter was used for comparing the phenology of the populations at the two sites. The sites selected were protected from interference by grazing animals, other weed control operations and curious people.

2.2 The field sites

2.2.1 The Redwoods Forest site

This was a 6•2 hectare site situated 10km SE of Putaruru, North Island, New Zealand (N.Z.M.S.1, N75, Grid Reference Area 350120). It is part of Redwoods Forest owned by New Zealand Forest Products Limited Kinleith. The area was formerly unproductive for dairy

Figure 2.1 Location of the field sites



farming due to cobalt deficiency and was originally the site of a trial plantation of redwoods (Sequoia species). Stands of Pinus radiata Don., Eucalyptus regnans F.Muell. and E.delegatensis R.T.Bak. were planted in the 1940s and 1950s (Fig.2.2). The site was leased for grazing from 1/10/59 to 1/10/79 and pines were planted at the "Pines Plot" and the steeper "Road Plot" in 1981/82. The "Poles Plot" was a grassland strip providing clearance for double pole power lines (Fig.2.3 and Plate 2).

Geology, soil type and topography

The area is part of the Mamaku Plateau and was formed in the Pleistocene when large ignimbrite floods from the Rotorua area poured northwest and north to Tirau and Tauranga. Subsequent erosion has partially stripped away the soft upper layers of the ignimbrite sheets exposing the harder rocks below, forming the rolling country and rocky outcrops typical of the region. The yellow-brown pumice soils of the area are derived from the Taupo rhyolitic ash showers of 1800 B.P.(Gibbs, 1965). The site is 226m above sea level and forms part of the catchment of the Waihou River which flows north to the Hauraki Plains.

Climate

Meteorological data from 1931-1983 were obtained from Kinleith, 10kms southwest of the Redwoods Forest field site. The mean monthly temperature for this period ranged from 17•5C in February to 6•9C in July. The mean annual rainfall was 1544mm and there was an average of 172 raindays per year. Winds are predominantly from

the west and southwest.

Vegetation

The dominant pasture species in both areas of recent pine plantation and the Poles Plot were Yorkshire fog (Holcus lanatus L.) and cocksfoot (Dactylis glomerata L.). The other grasses present included brown top (Agrostis tenuis Sibth.), perennial ryegrass (Lolium perenne L.) and prairie grass (Bromus catharticus L.). Lotus pedunculatus L. was common as were creeping and giant buttercup (Ranunculus repens L.) and (R.acris L.). Dock (Rumex obtusifolius L.), broad and narrow leaved plantain (Plantago major L. and P.lanceolata L.), blackberry (Rubus fruticosus L.) and catsear (Hypochoeris radicata L.) were also present.

2.2.2 The Desert Road site

This 100m^2 site is also part of a grassland strip providing clearance for power pylons. It is situated in manuka shrubland in Tongariro National Park, North Island, N.Z., 0•5kms north of the Oturere trig on State Highway 1 (Desert Rd) (N.Z.M.S.1, N112, Grid Reference Area 255785) (Fig.2.4 and Plate 3).

Geology, soil type and topography

Pyroclastic deposits of the Desert Rd area consist of Tongariro ash overlain by dark Mangatawai andesitic ash deposited by Mt. Ngauruhoe during its growth in the early Pleistocene (Gibbs, 1965). The area, at an altitude of 850m, is drained to the east by the

Makahikitoa Stream.

Climate

Meteorological data for the area was obtained from Waiouru 800m a.s.l.(Fig.24) (N.Z. Meteorological Service, 1983). For the period 1966-1980 the mean annual rainfall was 1096 mm with an average of 145 raindays per year. The mean daily maximum was 13•7 C in February and 3•6 C in July. There was on average 96 frost days and 19•5 snow days per year.

Vegetation

Brown top (Agrostis tenuis) and prairie grass (Bromus catharticus) together with catsear (Hypochoeris radicata L.) and hawksbeard (Crepis capillaris L.) were the dominant plants. The surrounding vegetation was predominantly manuka (Leptospermum scoparium Forst.) and the low, herbaceous shrubs, Cassinia fulvida Hook., Coriaria pteridoides Oliver and Gaultheria antipoda Forst. were also present.

2.3 Methods and Equipment

2.3.1 Sampling frequency

Fly populations were sampled fortnightly at both sites from October to April. This sampling frequency was constrained by available travel funds. Temperature was monitored hourly at Redwoods Forest by a Grant temperature recorder. The temperature sensitive probe was placed among the seedheads one metre above the ground. At the Desert Rd site a thermohygrograph was placed at

Plate 2 Redwoods Forest field site showing Pines Plot in the foreground and double-pole electricity wires of the Poles Plot in the distance

Plate 3 Desert Road field site with emergence traps, surrounding manuka scrub and overhead power wires

Figure 2.2 Area Map of Redwoods Forest field site

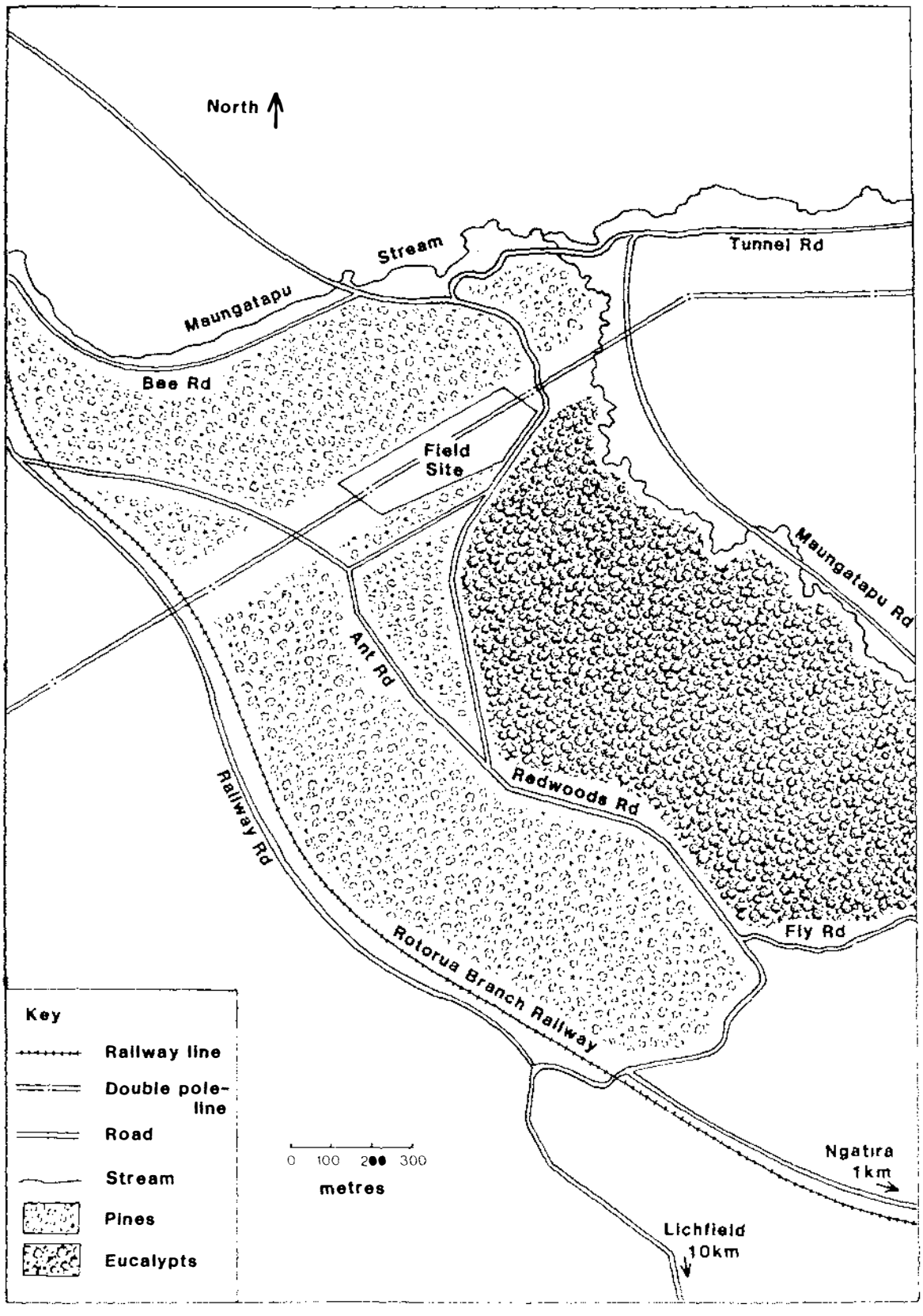


Figure 2.3 Map of Redwoods Forest site

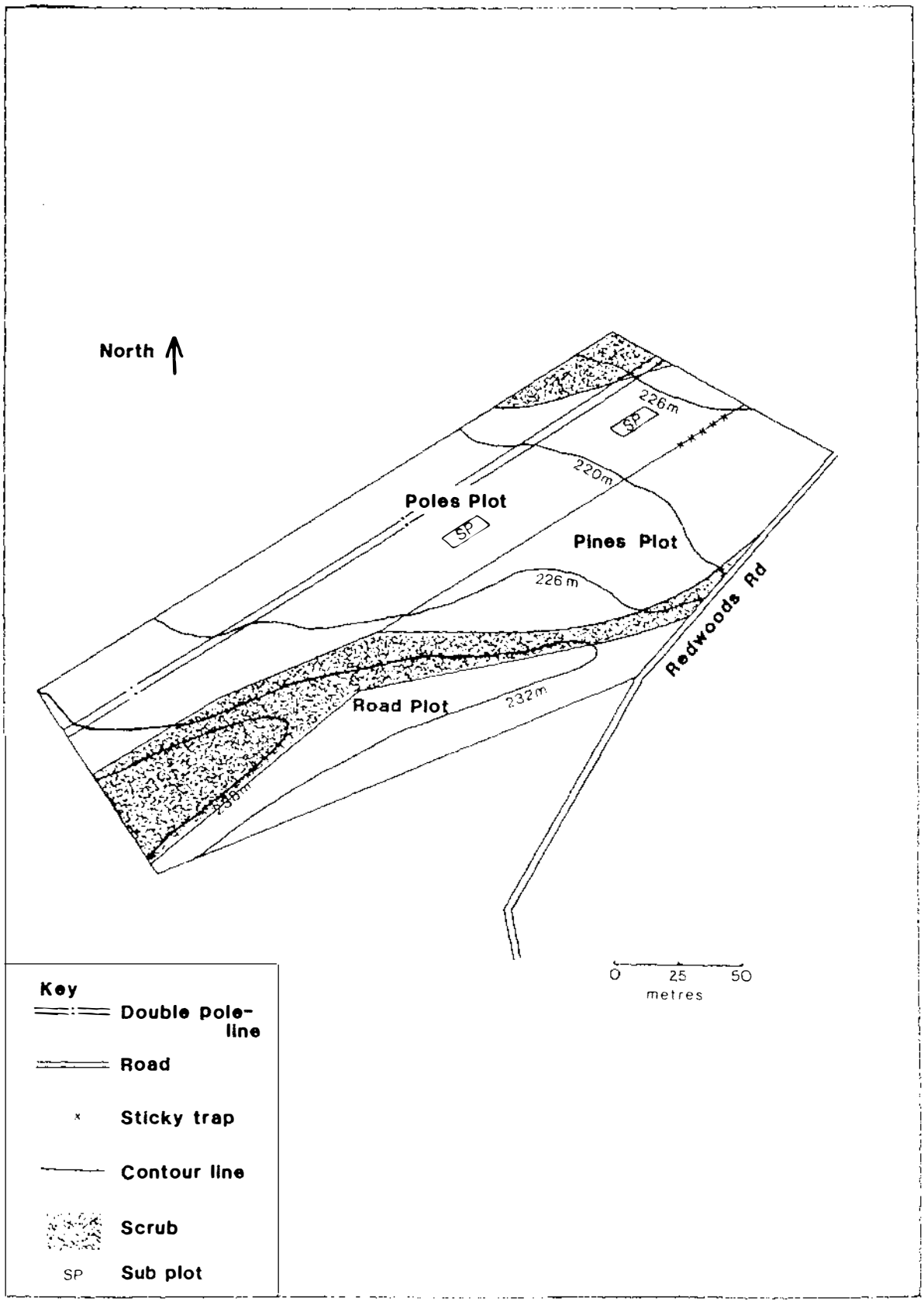
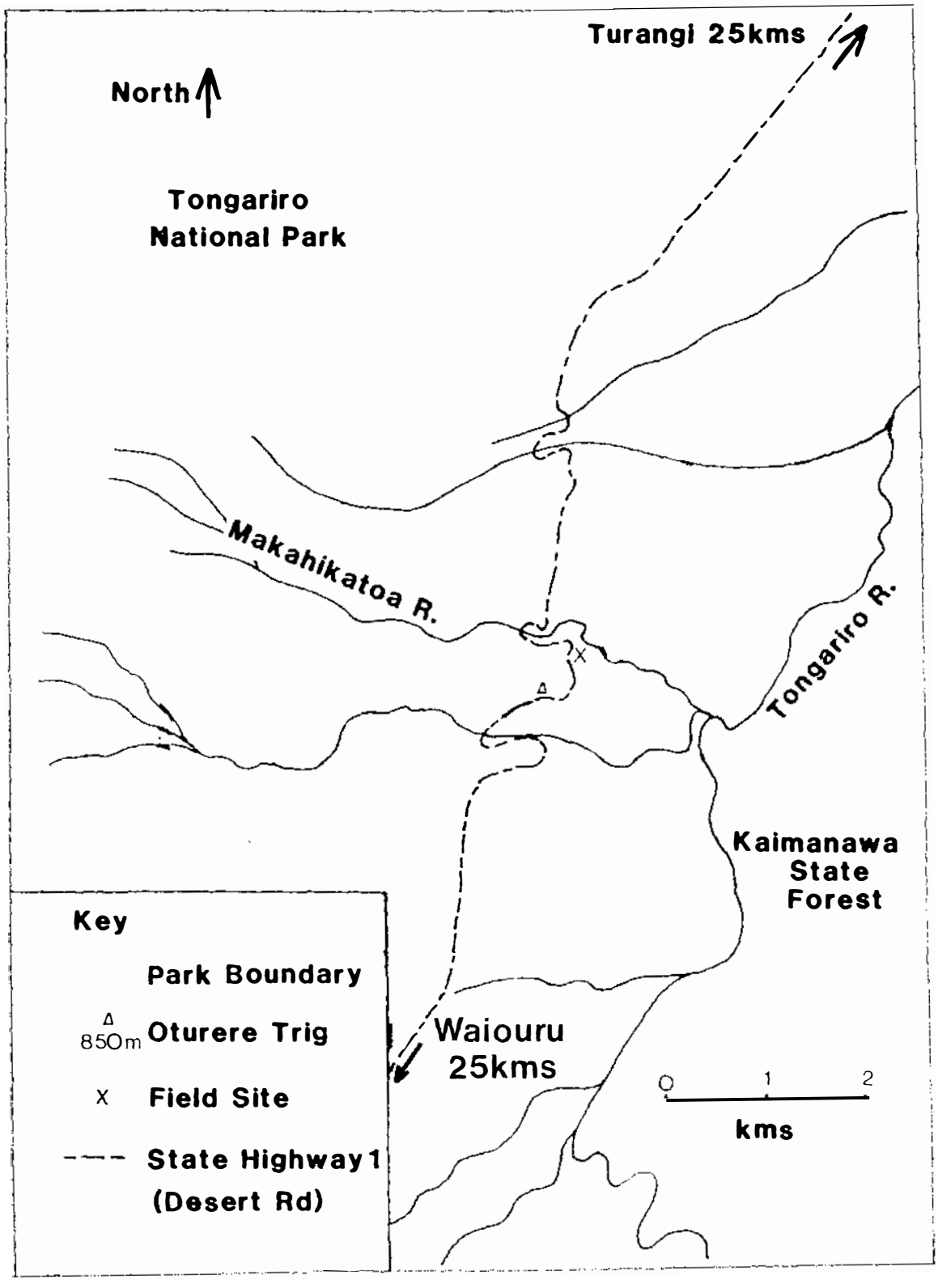


Figure 2.4 Area Map of the Desert Road site



ground level. This recorded temperature continuously for ten days following sampling. Temperature data for the final four days of the sampling interval was obtained from a meteorological station at the Rangipo Power Station 2kms west of the site.

2.3.2 Adults

Adult seedfly were sampled with emergence traps and sticky traps. The former gave an estimate of absolute fly numbers and the latter an estimate of longevity.

Emergence traps

These were 30cm high and sampled an area of 0•2 m^2 (Fig.2.5). The frames were constructed of No.8 fencing wire and covered with green plastic mesh. 125ml "T.V.L." collecting jars with their lids slit were inverted over a 5cm section of plastic tubing glued into the apex of each trap. Ten centimetre wire projections at the base of the frame were pushed into the ground to anchor the trap. The number and position of traps used is summarised in Table 2.1. The traps were distributed randomly by marking out a grid at each plot and selecting the coordinates for the traps from a table of random numbers.

Sticky traps

These consisted of an aluminium cylindrical drum 10cm in diameter and 30cm long (area of 942cm^2), supported on a vertical 1m steel rod attached to a wooden block inside the cylinder (Plate 4). A sheet of clear plastic, wrapped around the drum and held in place

by rubber bands, was covered with an adhesive,"Tack trap[1]". Five of these sticky traps, (two white and three yellow), were placed at Redwoods Forest (Fig.2.3) and two traps (one white and one yellow) at the Desert Rd field site. The plastic sheets were replaced at each sampling date after the number of flies caught had been recorded.

2.3.3 Eggs and larvae

Because of the variability of plant size (Table 2.2) the fly population within seedheads was sampled on a stem basis. Fifty stems were collected at each sampling date from Redwoods Forest and ten from the Desert Rd site. This number of stems was the maximum that could be analysed between sampling dates. Stems were collected at random by moving from plant to plant and taking every nth stem encountered. N was provided by a table of random numbers between 1 and 15. Samples were frozen as soon as possible to prevent any further development of the flies within the capitula. When thawed, the seedheads were dissected under a microscope and the number of eggs and larvae per stem were recorded. Larval instars were determined by measuring the maximum length of their sclerotised mouthparts. These fell into three, clearly defined size groups (Table 2.3) representing the three larval instars.

The number of seedheads per stem was also recorded. Seedheads expected to contain eggs were designated as "buds" and those capable of supporting larvae were termed "capitulae". When eggs and larvae cohabited a seedhead it was also recorded as a

1. Animal Repellents Inc. Georgia USA

capitulum.

2.3.4 Pupae

Pupae were sampled at the Redwoods Forest site using the following two methods:

(i) Soil samples: Soil samples covering the same area as emergence traps and 10cm deep were obtained randomly using the method for selecting the position of emergence traps. These samples were considered to be deep enough to collect all the pupae present because an initial pilot trial of ten $0{\cdot}3m^2$ samples had shown that seedfly pupate in the top 0-5cm layer of soil. Soil from each sample was placed in water so that the orange pupae could be collected as they floated to the surface.

(ii) Collection of pupae at the stem base (autumn 1984 only): Stems wereselected randomly as in 2.3.3. Each stem was tied to an aluminium stake to prevent wind movement. All the additional stems were removed when a stem was selected from a multiple-stemmed plant. A plastic tray, 30cm in diameter and 12cm deep, was slit to centre and fitted around the base of the stem. The slit was then wired together and the tray was filled with moistened sand (Plate 5). The sand was sieved to a grain size of less than 2·5mm so that when sieved again any pupae present could be easily collected. The sand was covered with cut grass to reduce evaporation and "tack trap " was spread around the rim of the tray to prevent any larvae escaping. When the pupae were collected at each sampling date any third instar larvae found were returned to their respective trays.

Plate 4 Sticky trap at Redwoods Forest

Plate 5 Arrangement at Redwoods Forest for collecting third instar larvae. The plant was staked and a tray filled with sand was placed at the base.

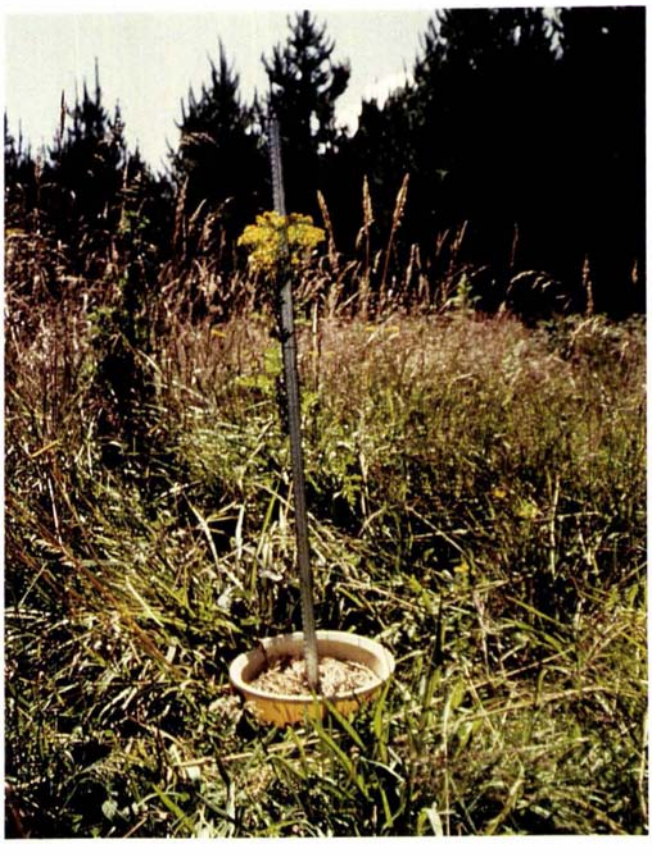


Figure 2.5 Emergence Trap

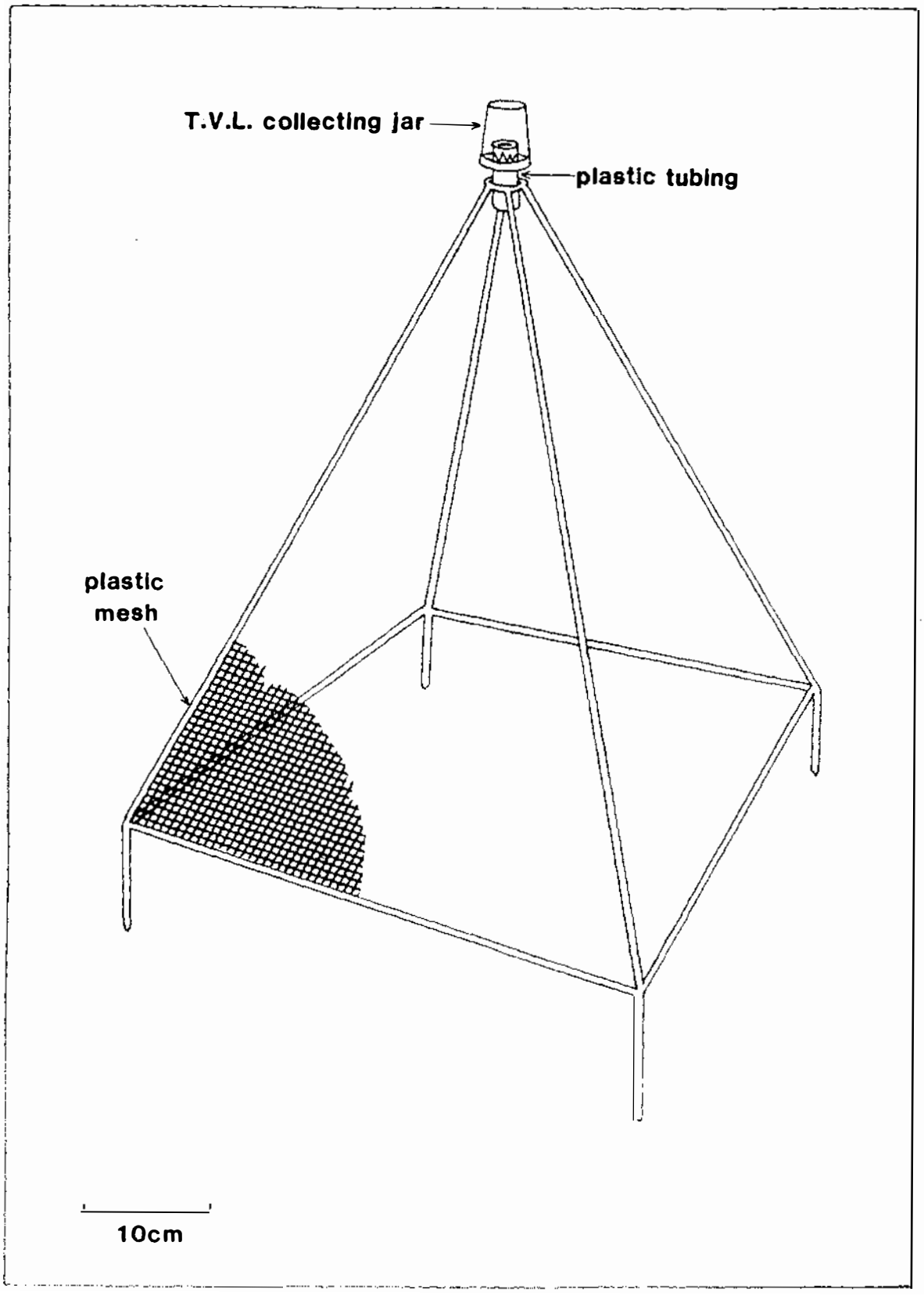


Table 2.1 Area sampled with emergence traps

	Area in m^2 (Refer to Fig 2.3 for plot locations			
	Poles Plot	Pines Plot	Road Plot	Desert Road
Spring 1982	14.2 (70 traps)	- -	- -	4.05 (20 traps)
Spring 1983	4.05 (20 traps)	7.1 (35 traps)	4.05 (20 traps)	4.05 (20 traps)

Table 2.2 Frequency distribution of stems per plant at Redwoods Forest

Stems/plant	Year when sampled 1982/83	1983/84
1	105	94
2	33	38
3	34	36
4	14	21
5	9	11
6	7	7
7	5	7
8	2	5
9	1	4
10	0	3
11	[illegible]	1
Total	210	[illegible]

2.3.5 Ragwort populations

Rosettes larger than 15cm in diameter in two 300m^2 subplots of the Poles Plot (Fig.2.3) were mapped in spring 1982 and 1983 and autumn 1983 and 1984 (Appendix 1). No distinction was made between regrowth plants and those which had developed from seedlings. The number of stems flowering in these two subplots was also recorded at each sampling date. At the end of the summer the number of stems flowering as a percentage of the total which flowered was calculated for each sampling date at the two subplots. In addition, the total number that had flowered over the entire site was determined in autumn from 9m^2 quadrats (Greig-Smith, 1964) selected at random from the mapped grids at each plot (section 2.3.2). Absolute estimates of the total number of stems flowering at each sampling date over the entire site could then be determined from the cumulative percentage curves of flowering at the two subplots. This method was preferred to collecting stems on an area basis as much larger sample sizes would have been required to allow for differing ragwort densities in the three plots.

2.3.6 Ragwort seed germination

Samples of seedheads were collected from Whakamaru and the Desert Rd in autumn 1982 and from Redwoods Forest in autumn 1983(Fig.2.1.). The seeds were removed from the seedheads and placed in petri dishes on moist filter paper at 20C with a 14 hour light and 10 hour dark photoperiod. Percentage germination was recorded after two weeks.

2.4 Results and discussion from the Redwoods Forest site

2.4.1 Emergence

Emergence trap efficiency

119 flies (54 males and 65 females) were released into traps as they became available from the laboratory population. 50±8% of the males and 20±5% of the females released were found dead in the collecting jars. Although the trapped flies often decayed over the two week period of each trial the wings always remained intact.

Emergence trap results

Flies emerged over a period of 2 months in 1982 and 4 months in 1983 (Fig.2.6a+b). Males emerged slightly before females but the sex of a proportion of flies caught (7% in 1982/82 and 37% in 1983/84) could not be determined. The female:male ratio of seedfly adults that emerged at Redwoods Forest was 3•5:1 in both years. Similar observations were recorded by Jones (1970) during studies on the wheat bulb fly, Leptohylemia coarctata Fall. (Diptera: Anthomyiidae). She also noted that males emerged before females and recorded a sex ratio which favoured females by 2:1.

Assuming that the 3•5:1 ratio occurred in the seedflies at Redwoods Forest whose presence was indicated only from wings, the total number of flies estimated to have emerged was 195,360 in 1982/83 and 1,869,000 in 1983/84 (Fig.2.7). While the flies emerged from the entire site in 1983/84 the estimate for the 1982/83 summer represented only those emerging from the "Poles

Plot" (25000 m^2). This site had been the only area infested by ragwort in the previous summer (Barry Poole pers.comm. 1982) because the rest of the site had been ploughed in preparation for pine plantation. There was little change in seedfly density at this plot during the study. An estimated 195,360 flies emerged in spring 1982 compared to 168,416 in 1983.

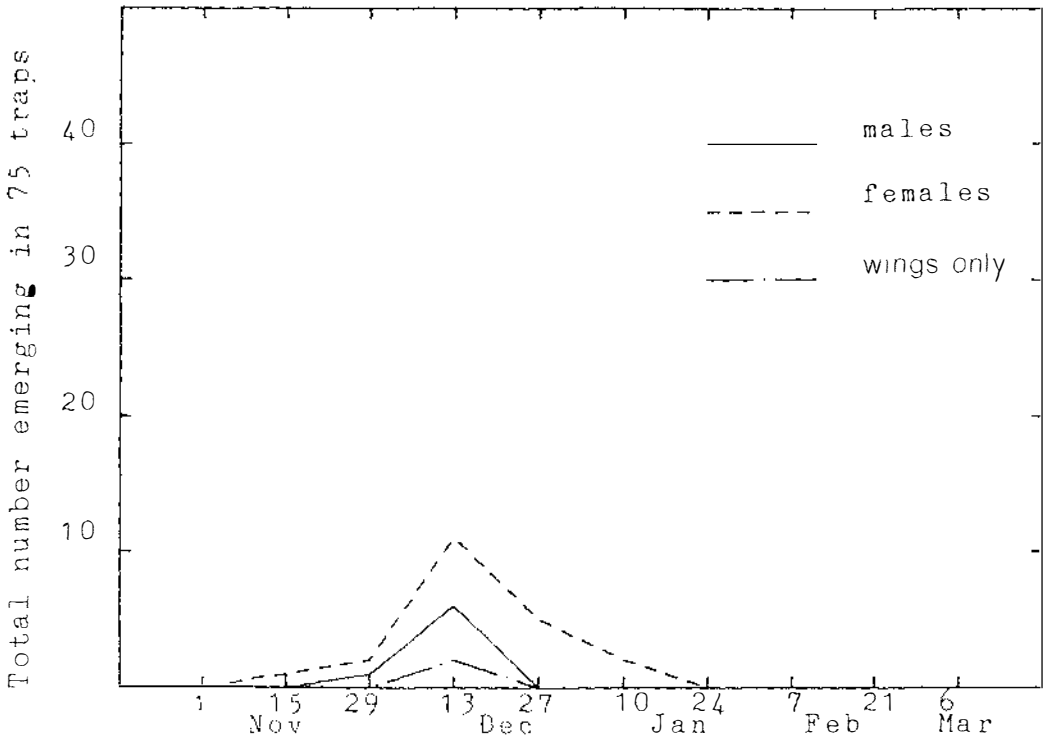
2.4.2 Sticky trap results

It appears that fewer flies were present in the area in 1982/83 although the sticky traps were not placed in the field until late Dec 1982(Fig.2.8). The male:female ratio of adults caught by the sticky trap during the 1983/84 season was 2·7:1 in November and rose to a peak of 6:1 in late December. By late February females dominated by 12:1. There was no relationship between sex of flies caught on the sticky traps and colour of the traps (Chi square -4·45, 1df, P=0·5-0·75).

The only information on host plant attractants for anthomyiids has been obtained from some of the root feeding species. Traynier (1967a), Hawkes (1975) and Hawkes et al. (1978) found that host plant odour increased activity of gravid female cabbage root flies, Delia(Erioischia) brassicae Bouche, but colour may also have been important. Coaker and Finch (1973) observed that, in an olfactometer, more cabbage root flies landed at the port emitting odour if it was green and Harris and Miller (1983) found that yellow colouration was one of the variables influencing alighting and post alighting pre-oviposition behaviour in the onion fly,

Figure 2.6 Number of Seedfly adults caught in emergence traps at Redwoods Forest

a) 1982/83



b) 1983/84

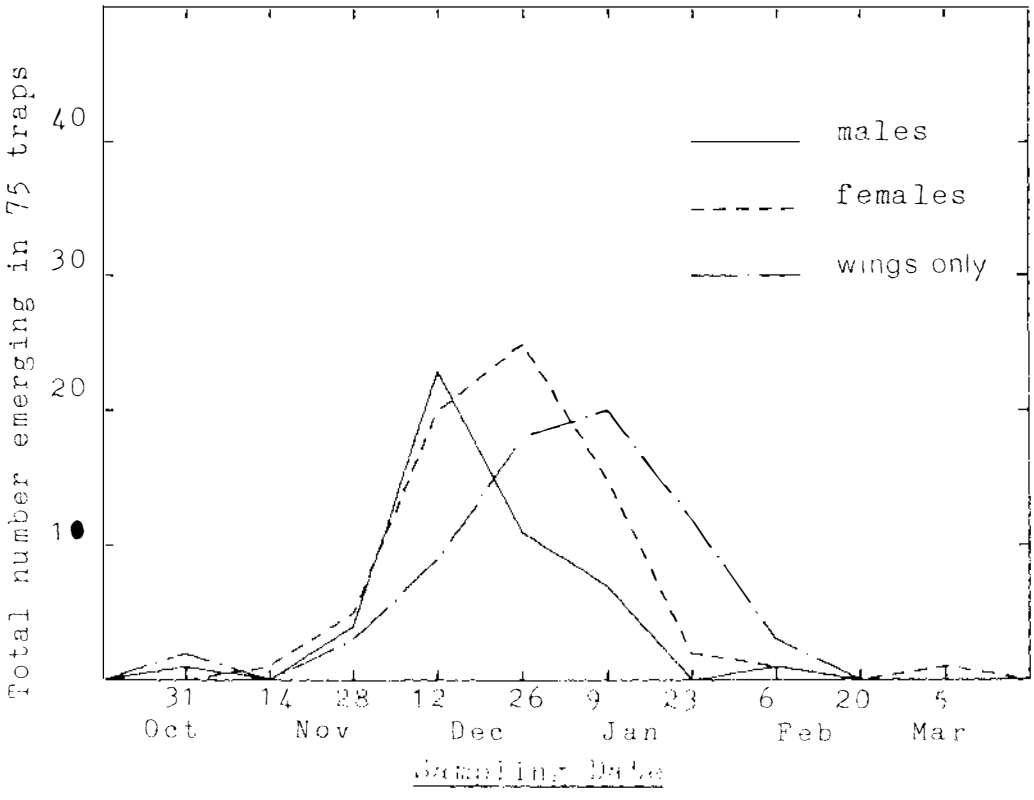


Figure 2.7 Total numbers of flies emerging at Redwoods Forest

The graphs represent the total number of flies emerging from the 6.2 hectare site after correcting for trapping efficiency

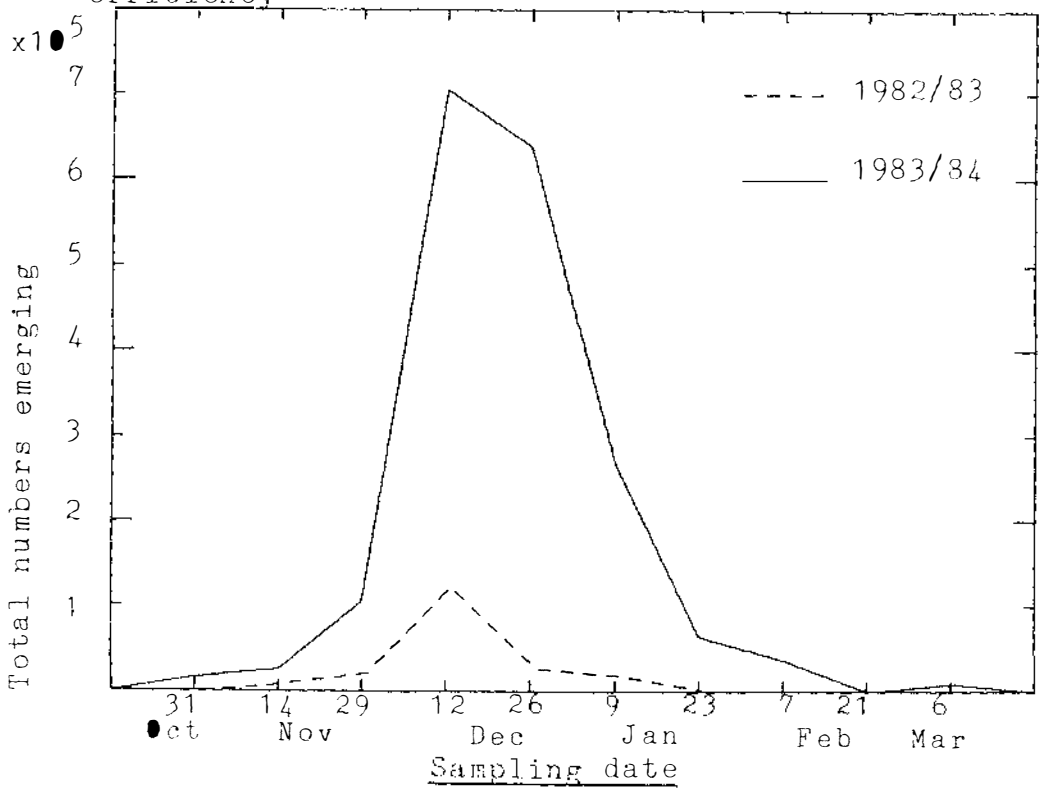
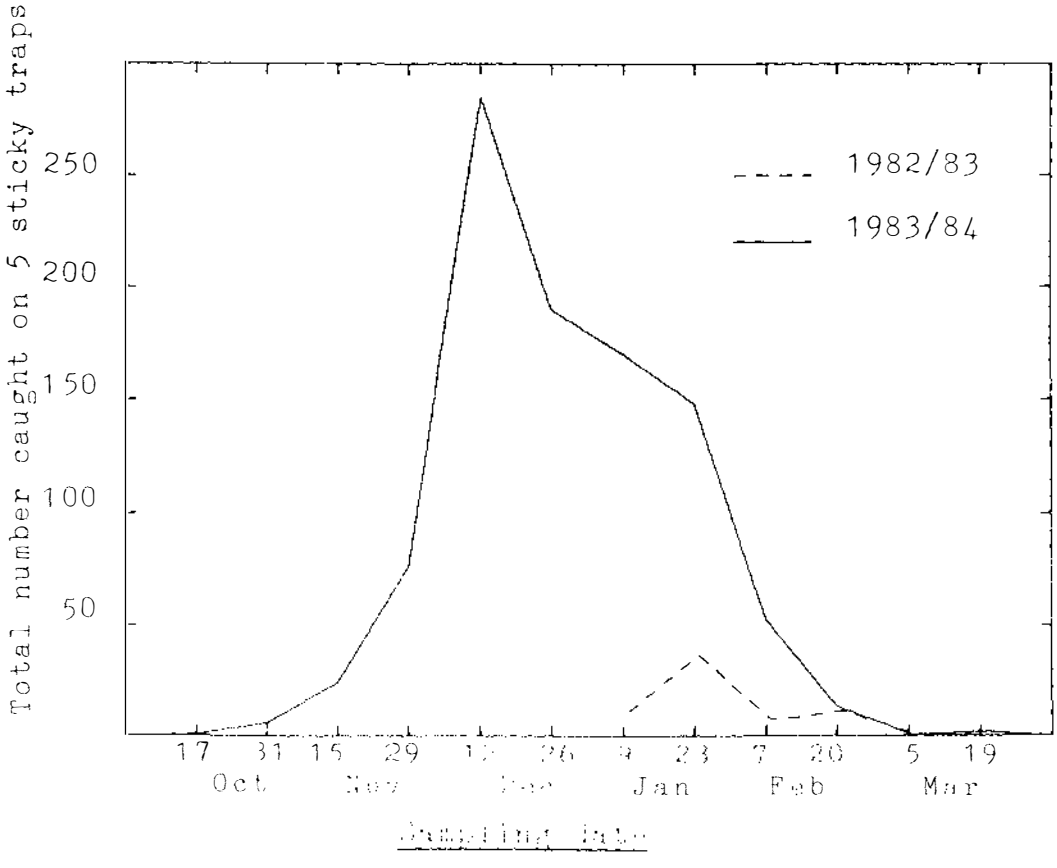


Figure 2.8 Number of Seedfly adults caught on sticky traps at RedwoodsForest



Delia antiqua Meigen. Neither of these two species are host specific.

Adult seedflies were caught on the sticky traps for a period of five months in summer 1983/84. Sticky trap catches dropped by 50% in the six weeks after they peaked in November 1983 and by a further 50% in the next 12 days (Fig.2.8). Longevity, however, was measured in the wheat bulb fly in the field. It was 55 days for males and slightly longer for females (Jones, 1970). Female beet flies, Pegomyia hyoscyami Panz. also lived longer than males (70 and 50 days respectively) but longevity decreased with increased temperature. Mated males lived longer than unmated ones but the reverse occurred in females (Hafez et al., 1970).

2.4.3 Seedfly infestation levels of ragwort

All stems were infested by seedfly at the site. Oviposition coincided with the first appearance of buds in the field in both years. Characteristics of seedheads containing eggs were measured within 24 hours of oviposition by females on potted ragwort plants placed in the field. P.jacobaeae oviposited on buds with a diameter ranging from 3•8 to 5•8 mm and a disc floret length of 2•7 to 5•6mm (Table 2.4). The number of ray florets was constant at 13. Zimmerman et al. (1984) found a positive correlation between egg deposition and inflorescence size in the seed predator Hylemya (Delia) species and Frick (1970) found bud size preferences in P.seneciella. It is likely that size is indicative of the stage of development of the bud and this is an

important consideration for the ovipositing female since first instar larvae must complete their development within unopened florets. Depth of the bud measured as the length of the disc florets was also considered as seedfly eggs which are approximately 1mm in length are laid upright. Contact chemostimulation and colour is also likely to be important in the choice of oviposition sites but was not investigated in this study. Frick (1970) found P.seneciella females preferred to oviposit on yellow and orange models but that odour was required to stimulate viposition.

The numbers of seedfly within seedheads at Redwoods Forest throughout both summers are presented in Figures 2.9a+b and Figures 2.10a+b give estimates of the number of seedheads at each sampling date. Ragwort density was 28,788 stems per hectare in 1982/83 and 30,132 in 1983/84. Table 2.5 summarizes the stem densities at the three plots in both years.

The various stages of both seedfly and ragwort life history are represented as a cumulative percentage of the total of the stage present in the season (Figs.2.11a+b). The oviposition curve is calculated from the sum of the eggs, first and second instar larvae since the sampling interval is less than the total duration of these stages. A pre-oviposition period of approximately six weeks was observed in 1982/83 and 1983/84. The timing of seedfly emergence and oviposition was similar in both seasons. Although ragwort began to flower in early December in both years ragwort

inflorescence development was faster in 1983/84. In this year the availability of oviposition sites (represented as the hatched area in Figures 2.11a+b) was increased.

No oviposition took place on buds of ragwort plants transplanted at the site from the 14th of November to 28th of November 1983. Unfortunately there were no other flowering plants available to continue this experiment. Oviposition did, however, occur on transplanted plants 12 days before the field plants flowered in 1984. When the crop contents of 30 adults collected during the pre-oviposition period in spring 1984 were examined no pollen was found but the crops of 6 of the flies contained a yellow liquid.

The number of eggs in females collected in the field in 1982 ranged from 0-29 with a mean of 7•3 (Table 2.6).

Percentage infestation declined throughout the summer from an initial peak of 19% in 1982 and 39% in 1983 (Fig.2.12). The effective levels of infestion, in late February, when third instar larvae peak and all the ragwort has flowered, was approximately 10% in 1982/83 and 20% in 1983/84.

2.4.4 Multiple infestation of ragwort seedheads

The majority of seedfly eggs are deposited singly in ragwort capitulae. Larvae develop exclusively in the capitulae and have no ability to move from one capitulum to another. Multiple infestation does occur but only one fly per seedhead survives to

Table 2.3 Determination of seedfly larval instars by mouthpart lengths

	1st Instar larvae	2nd Instar larvae	3rd Instar larvae
$\bar{x}$	0.27mm	0.46mm	0.71mm
SE	0.0020mm	0.0023mm	0.0029mm
Range	0.22-0.31mm	0.4-0.54mm	0.64-0.80mm
n	100	100	100

Table 2.4 Characteristics of seedheads containing seedfly eggs 0-24 hours old

	Diameter of seedhead	No. of disc florets	Length of disc floret
$\bar{x}$	4.5mm	48.8	3.7mm
SE	0.04mm	0.54	0.07mm
Range	3.8-5.8mm	38-63	2.7-5.6mm
n	100	100	100

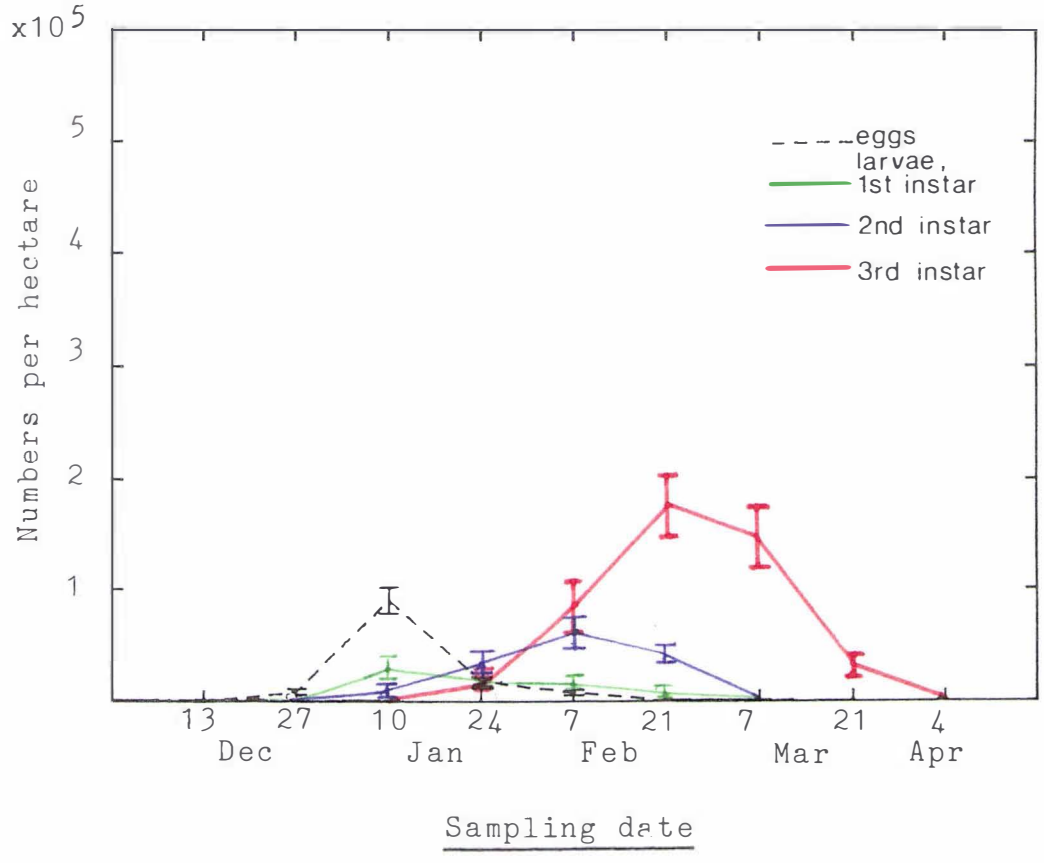
Table 2.5 Number of ragwort stems at Redwoods Forest

	Numbers per m^2 ($\bar{x}$ ± SE)		
	Polea Plot	Pines Plot	Road Plot
Autumn 1983	0.86±0.14 n = 60	3.12±0.38 n = 10	4.9±0.13 n = 10
Autumn 1984	0.65±0.09 n = 60	5.97± 0.30 n = 20	3.81±0.21 n = 20
Total area of plot	25,000m^2	13,750m^2	23,125m^2

Figure 2.9 Estimation of the numbers of seedfly eggs and larvae in ragwort seedheads (Bars indicate standard errors) at Redwoods Forest

a) Colour graph - 1982/83

b) Overlay - 1983/84



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a) Colour graph - 1982/83

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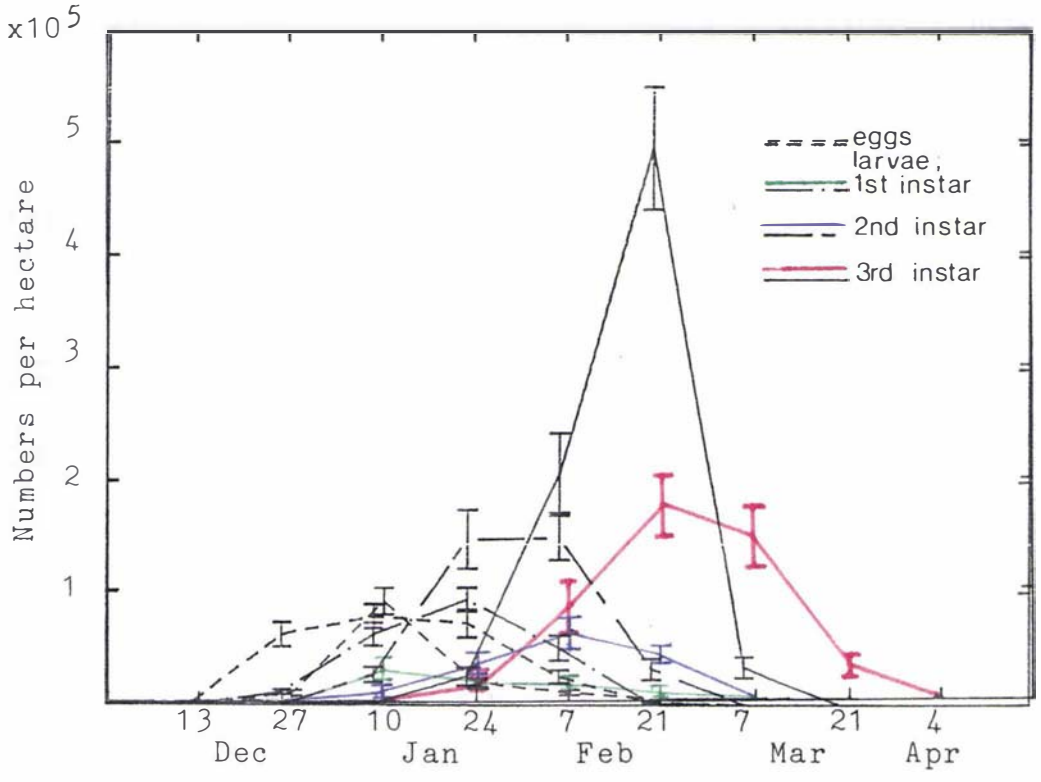
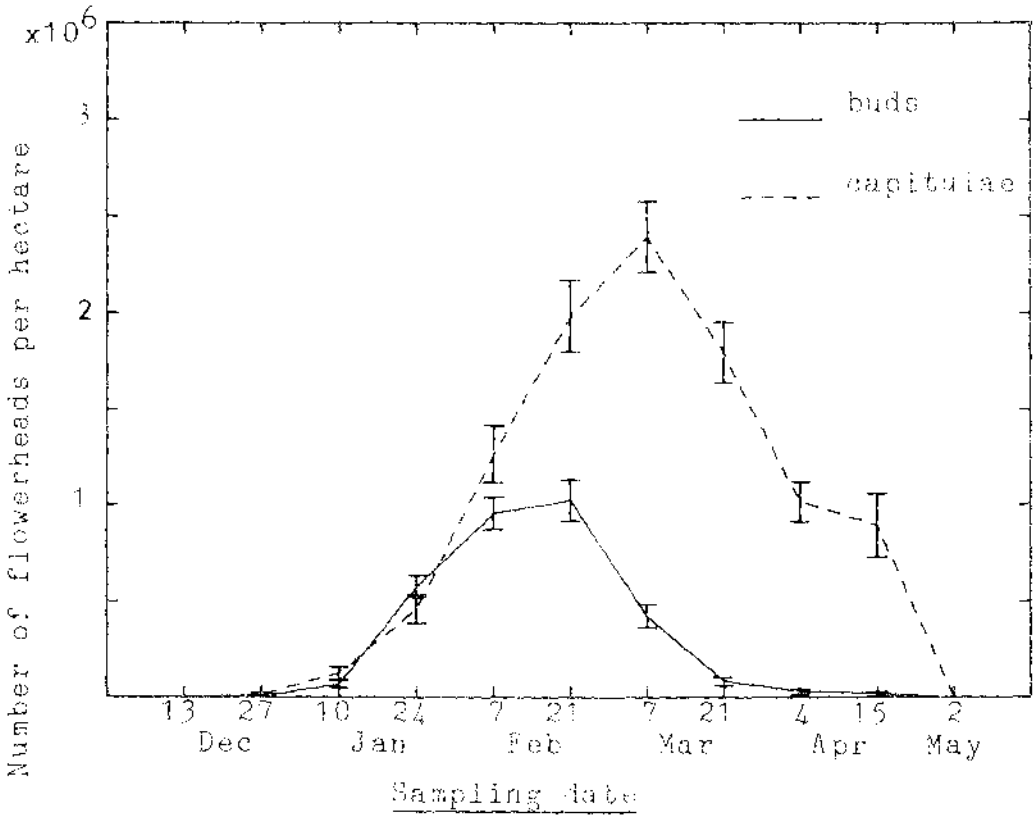


Figure 2.10 Estimation of the number of ragwort buds and capitulae (Bars indicate standard errors) at Redwoods Forest

a) 1982/83

b) overlay 1983/84

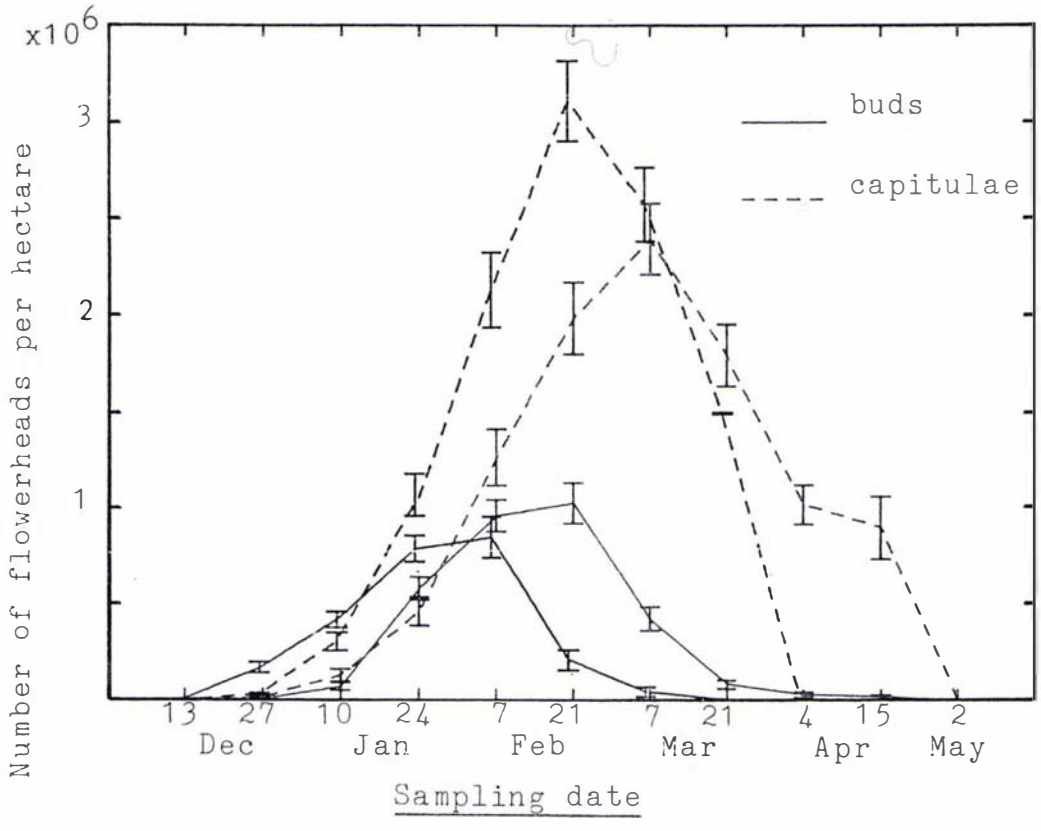


Mean no. of capitulae per stem		
Date	1982/83	1983/84
13/12	8·9	0·05
27/12	10·6	8·2
10/1	13·2	33·9
24/1	22·8	53·7
7/2	44·1	86·9
21/2	68·9	110·5
7/3	83·2	85·3

Figure 2.10 Estimation of the number of ragwort buds and capitulae (Bars indicate standard errors) at Redwoods Forest

a) 1982/83

b) overlay 1983/84



Mean no. of capitulae per stem		
Date	1982/83	1983/84
13/12	8·9	0·05
27/12	10·6	8·2
10/1	13·2	33·9
24/1	22·8	53·7
7/2	44·1	86·9
21/2	68·9	110·5
7/3	83·2	85·3

Figure 2.11 Cumulative percentage curves of seedfly and ragwort seedhead development stages of Redwoods Forest

The curves have been fitted by eye and the hatched area represents the region where seedheads are available for oviposition by seedfly

a) 1982/83

b) Overlay 1983/84

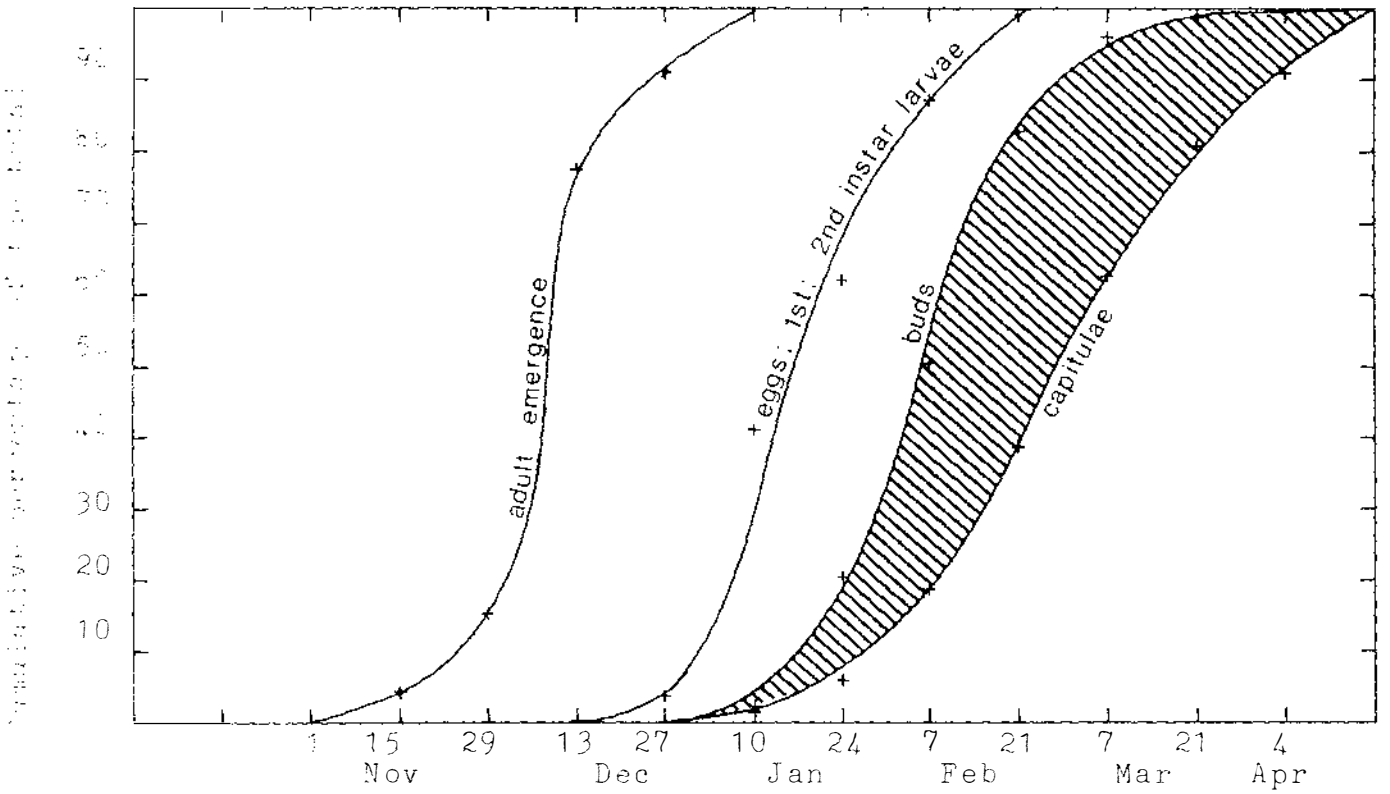


Figure 2.11 Cumulative percentage curves of seedfly and ragwort seedhead development stages of Redwoods Forest

The curves have been fitted by eye and the hatched area represents the region where seedheads are available for oviposition by seedfly

a) 1982/83

b) Overlay 1983/84

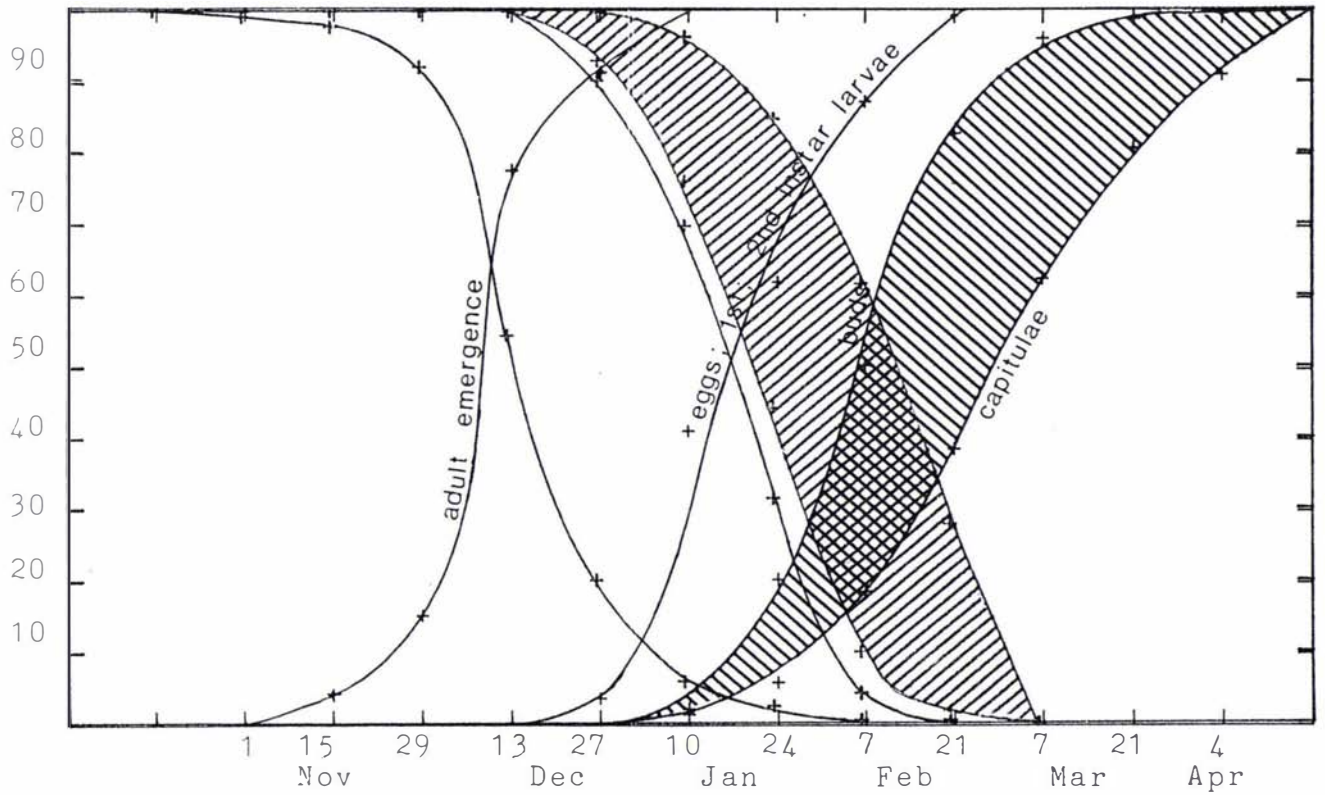
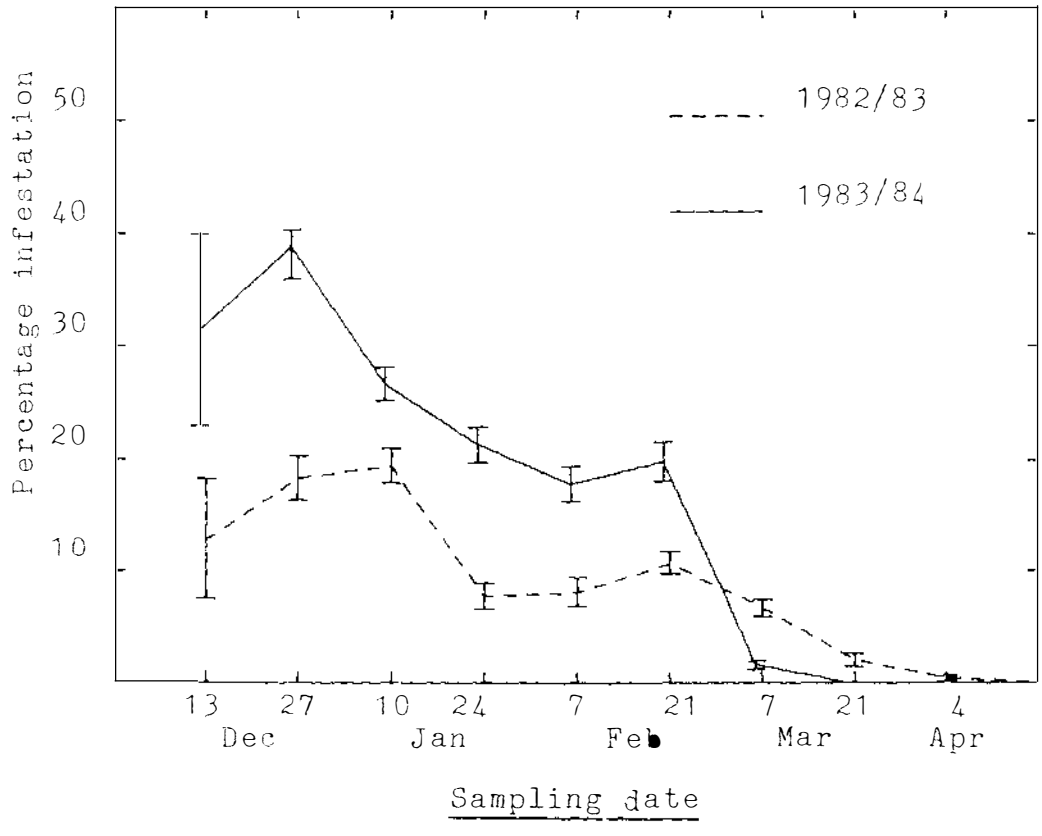


Figure 2.12 Percentage of ragwort seedheads infested by seedfly at Redwoods Forest (Bars represent standard errors)



pupate. In this study multiple infestation followed the general trend in egg laying (Figs.2.9a+b) with the lower incidence of multiple larval infestation (Figs.2.13a+b) due to the high mortality of older larvae as conditions become crowded in the seedhead. As a percentage of the total seedheads infested, multiple infestation declined from a peak of 22% at the beginning of the season in 1982/83 and 16% in 1983/84 (Fig.2.14).

Published information on other anthomyiid seed predators indicates that multiple oviposition is not unusual. Zimmerman (1979) and (1980) recorded 1.6% multiple infestation in a Hylemya species that oviposits in the seedheads of Polimonium foliossisimum Gray and 25% in a species ovipositing in Ipomopsis aggregata Pursh seedheads.

2.4.5 Distribution of seedfly eggs

The mean crowding of seedfly eggs, defined as the mean number of other individuals per sample unit per individual (Lloyd, 1967), was calculated for seedfly at each sampling date. It is not dependent on the number of buds considered as potential oviposition sites for seedfly, which was subjectively estimated in this study, and was therefore preferred to a calculation of the index of dispersion (Table 2.7) (Southwood, 1978). According to Lloyd's method the distribution of seedfly eggs was uniform (the ratio of mean crowding to mean density is less than one) in early December

and again in mid to late January (Table 2.8). Unfortunately estimates of mean density are decreased by an overestimation of buds suitable as oviposition sites for seedfly which increases this ratio of mean crowding to mean density.

Eggs of Nezara viridula L. (Heteroptera: Pentatomidae) which are found in ragwort seedheads do not appear to deter oviposition by seedfly. They were found together with seedfly eggs and larvae more often than expected if the distribution was random (Table 2.9).

2.4.6 Pupae

Table 2.10 shows that estimates of pupal density from emergence traps at the "Pines" and "Road" plots in 1983 were three times higher than those from the soil samples. Additional soil samples in autumn 1983 gave an estimate of 11·7 pupae/m^2 compared to the average pupal density for the site in spring 1983 of 11·4. Figure 2.15 gives the estimates of third instar larvae and pupae collected in the trays in autumn 1984 at each sampling date. Sampling of pupae by recording those found in the trays was cumulative and the density estimated for the site for 1984 was 670,446 per hectare. Sampling in this year coincided with or was immediately preceded by periods of rain while in 1983 a dry period in early March appeared to delay the dropping response of third instar larvae (Figs.2.16a+b).

Table 2.6 Number of eggs in females collected at Redwoods Forest

Date collected	Number of eggs
13/12/82	16,12,0,2,0,1,0,2,0,0
27/12/82	29
10/1/83	25,2,16,0,0
24/1/83	15,19,15,0,0
7/2/83	0,29,16,17
21/2/83	0,0,0,0,2

Table 2.7 Goodness of fit of seedfly egg distribution with the Poisson distribution (Southwood, 1978)

Date	$X^2 = \frac{S(n-1)}{\bar{x}}$	χ^2	$d = \sqrt{2X^2} - \sqrt{2f-1}$
13/12/82	442.1	485	-1.4
27/12/82	2094.6	2347	-3.8 *
10/1/83	2795.6	3003	-2.7 *
24/1/83	2030.1	2138	-1.7
7/2/83	1829.8	1780	0.9
12/12/83	169.3	174	-0.2
26/12/83	2090.8	2147	-0.8
9/1/84	2284.3	2322	-0.5
23/1/84	1947.1	1970	-0.3
6/2/84	1589.2	1645	-0.9

* indicates non-random distributions

Table 2.8 Distribution of seedfly eggs in ragwort seedheads

Date	Meaning crowding index* of eggs m (Lloyd, 1967)	Mean density of egg $\bar{x}$	$\frac{*}{m}$ / $\bar{x}$
13/12/82	0.20	0.30	0.67
27/12/82	0.18	0.14	1.28
10/1/83	0.09	0.16	0.56
12/12/83	0.18	0.28	0.64
26/12/83	0.43	0.35	1.23
9/1/84	0.21	0.19	1.10
23/1/84	0.06	0.09	0.67

Table 2.9 Relationship of seedfly attack to presence of Nezara viridula

Independent distributions are indicated by * (where $P \leq 0.05$)

Date	X^2 (1df)	N
13/12/82	30.7	565
27/12/82	61.9	2577
10/1/83	16.3	3662
24/1/83	19.4	3279
7/2/83	*0.134	3984
21/2/83	*2.3	4179
12/12/83	*0.50	179
26/12/83	6.25	2559
9/1/84	*4.13	4018
23/1/84	10.94	4657

Table [illegible] Estimates of fly density from soil sampling and emergence traps

[illegible] sampled by emergence traps and soil samples is [illegible]

	Soil Samples		Emergence Traps	
	Mean number pupae/m^2	Number of samples	Mean number flies/ m^2	Number of samples
[illegible] Spring [illegible]	7.5	12	7.8	70
[illegible] Spring 19[illegible]3	4.7	10	6.7	20
[illegible] Spring 1983	12	10	41.9	35
[illegible] Spring 19[illegible]3	17.5	10	48.6	20

Figure 2.13 Incidence of multiple infestations by seedfly at Redwoods Forest

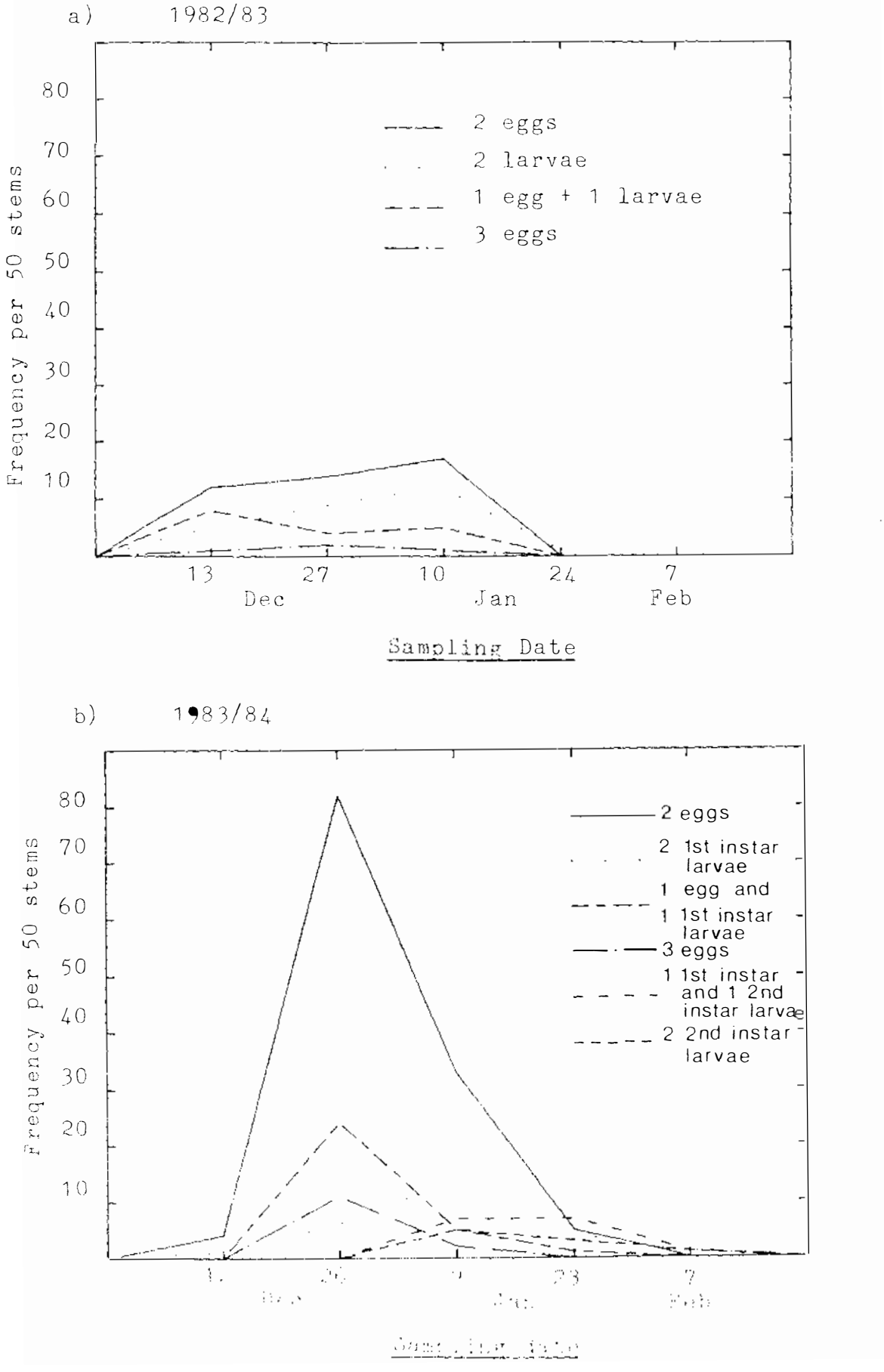


Figure 2.14 Changes in the incidence of multiple seedfly infestations with time

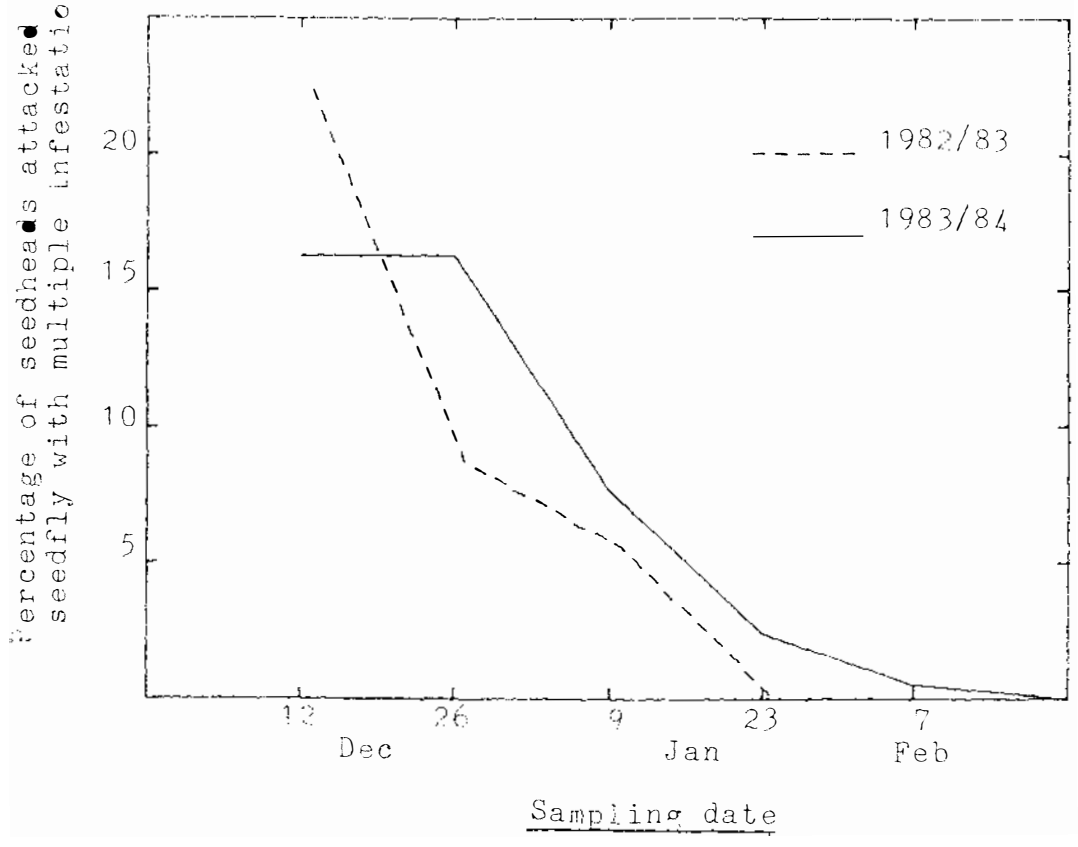


Figure 2.15 Estimates of the number of seedfly pupae and 3rd instar larvae per hectare at Redwoods Forest in 1983/84

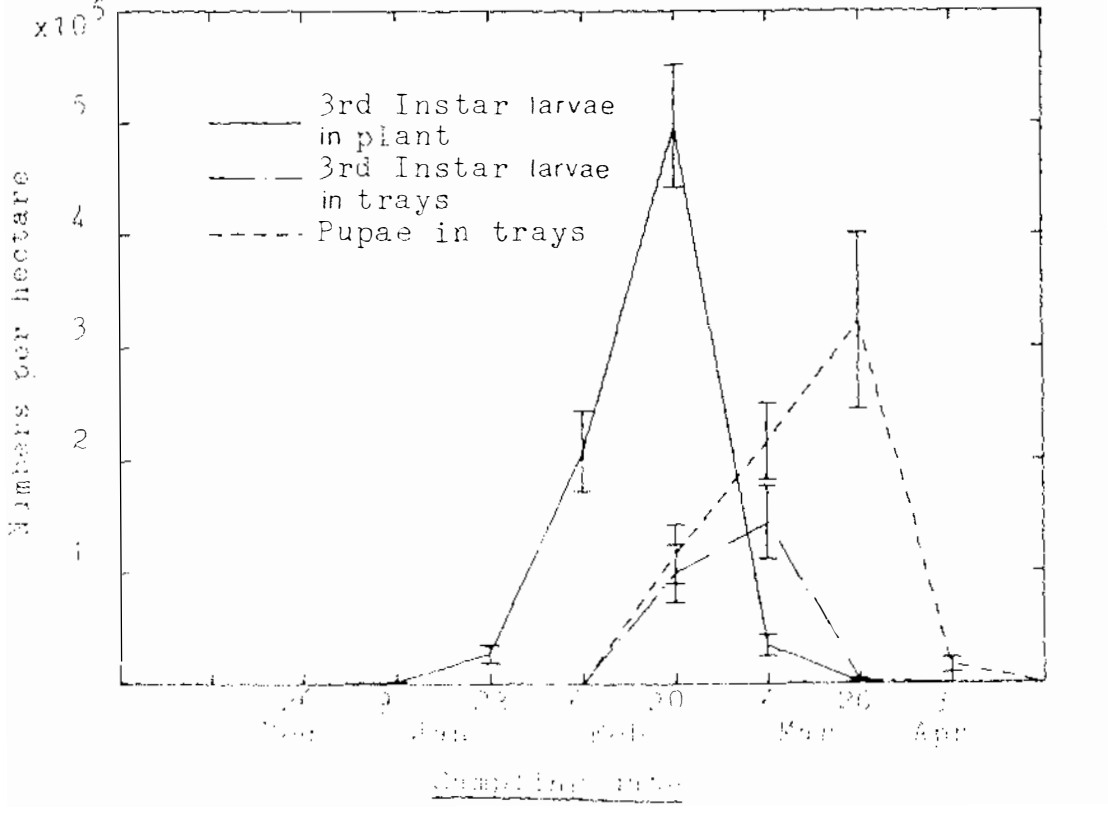
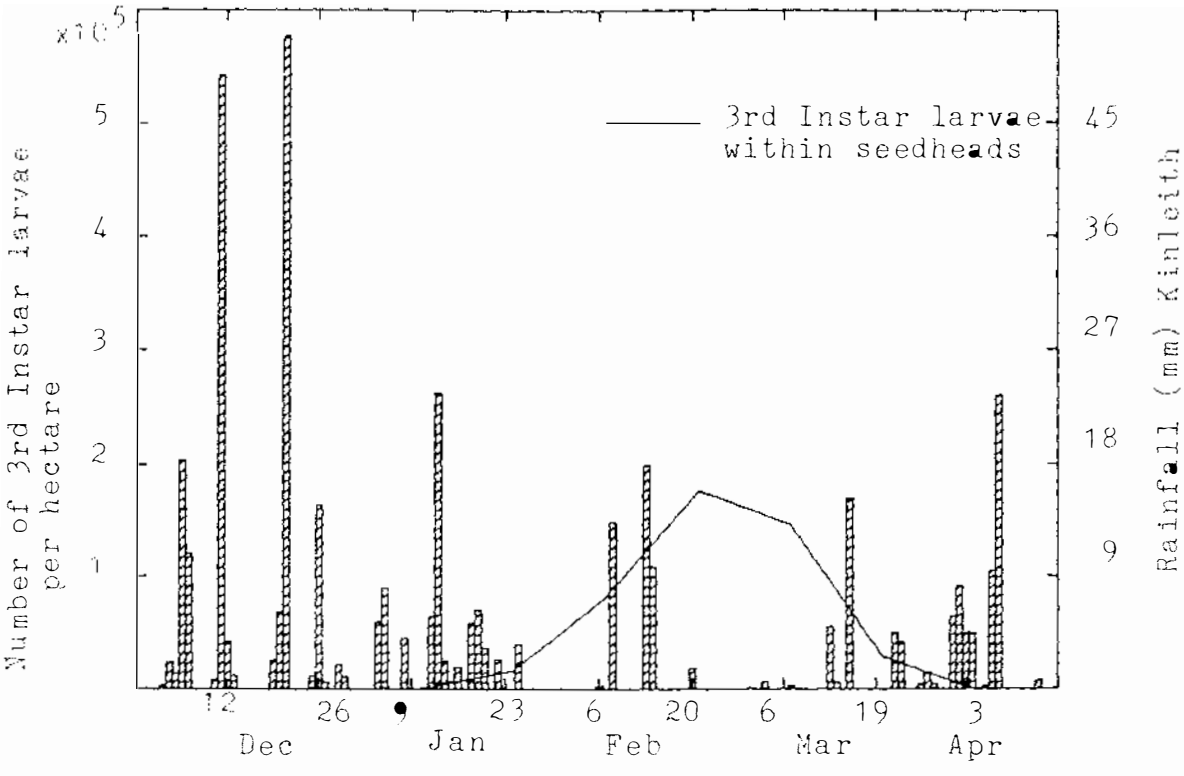
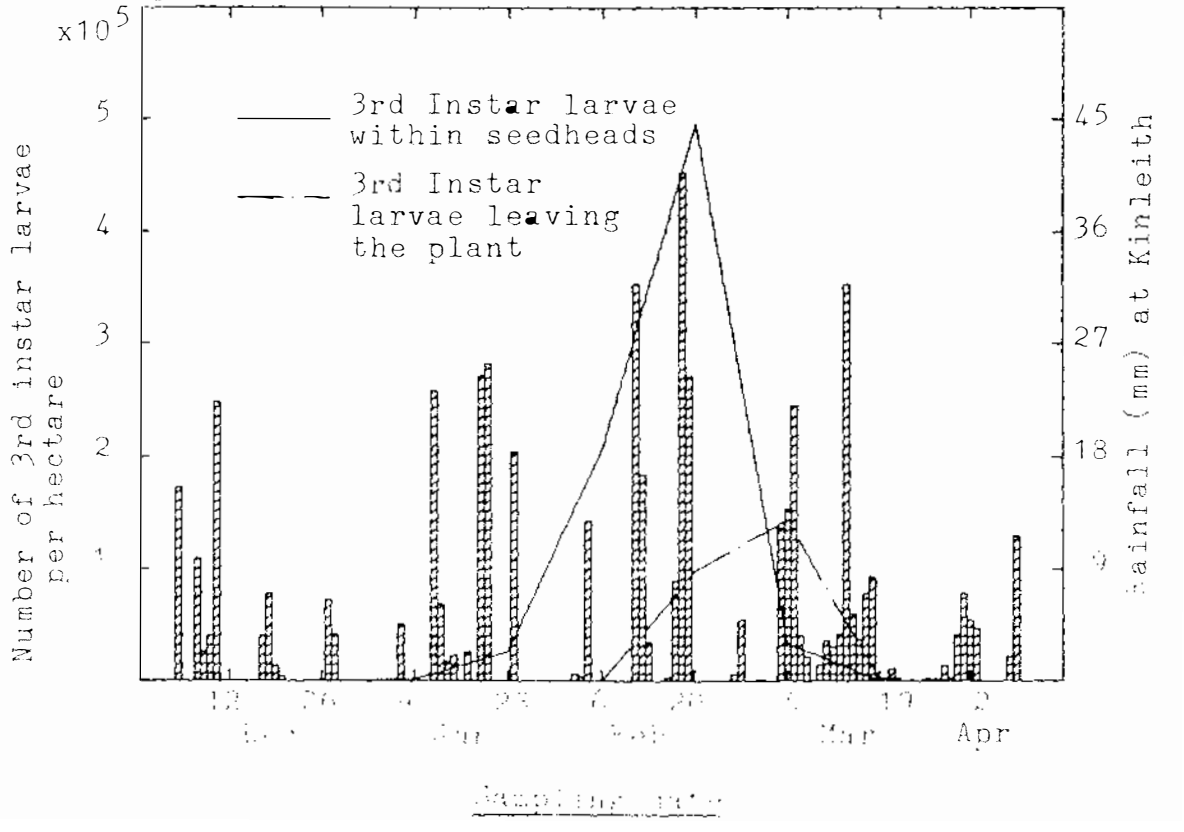


Figure 2.1c The number of seedfly 3rd instar larvae and rainfall at Redwoods Forest

a) 3rd instar larvae within seedheads in 1982/83



b) 3rd instar larvae within seedheads and leaving the plant in 1983/84



2.4.7 Germination

The number of seeds remaining in infested seedheads varied between each sampling site (Table 2.11) and the mean germination success ranged from 28-43%. In addition, the mean number of seeds (±SE) in uneaten seedheads of the same plants was 29±2·8 (n=38) and ranged from 2-58. The mean percentage germination of these seeds (±SE) was 72·7±2·8%. As all plants were infested, germination of ragwort seeds could not be compared with seeds from plants not subjected to seed predation.

2.5 Results from the Desert Rd site

Only 16 flies were caught in emergence traps in 1982/83 and 5 in 1983/84 and no flies were caught on sticky traps. Consequently little is known about the pre-oviposition period at this site. Ragwort density at the site was 0·35 stems/m^2 in 1982/83 and 0·23 stems/m^2 in 1983/84 and all plants were single stemmed. The seedfly life history and ragwort flowering was delayed in the colder conditions at the Desert Rd. A comparison of the temperatures recorded at the two sites is presented in Appendix 2. Oviposition and flowering occurred five weeks later than at the Redwoods Forest site (Figs. 2.17a+b). The overall infestation levels at the site were 1% in 1982/83 and 3% in 1983/84 (Fig.2.18) but the small sample sizes resulted in large errors. Therefore any apparent trends in the infestation levels at this site may not reflect the true situation.

Table 2.11 Number of ragwort seeds and their viability after seedfly attack

	No. of seeds remaining per seedhead	Percentage germination
Whakamaru Autumn 1982	$\bar{x}$ = 17.6 SE = 1.4 range = 0-55 n = 101	$\bar{x}$ = 43.3 SE = 2.8 n = 95
Desert Road Autumn 1982	$\bar{x}$ = 7.6 SE = 0.7 range = 0-42 n = 123	$\bar{x}$ = 28.0 SE = 3.0 n = 102
Redwoods Forest Autumn 1983	$\bar{x}$ = 13.2 SE = 0.5 range = 1-33 n = 39	$\bar{x}$ = 30.1 SE = 4.4 n = 39

Figure 2.17 Cumulative percentage curves of seedfly and ragwort seedhead development stages at the Desert Road

Curves fitted by eye; hatched area represents region of where seedheads are available for oviposition by seedfly

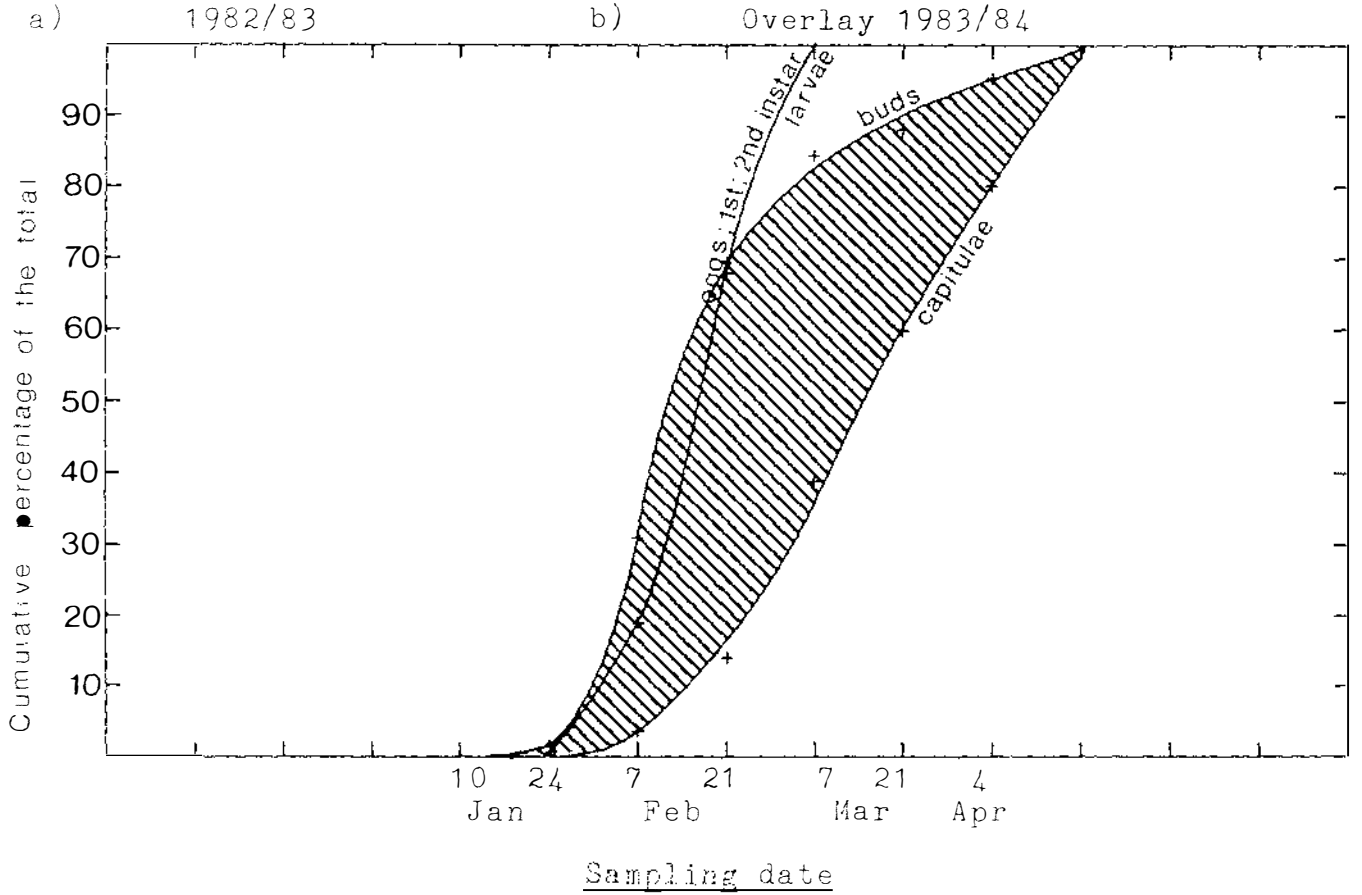


Figure 2.17 Cumulative percentage curves of seedfly and ragwort seedhead development stages at the Desert Road

Curves fitted by eye; hatched area represents region of where seedheads are available for oviposition by seedfly

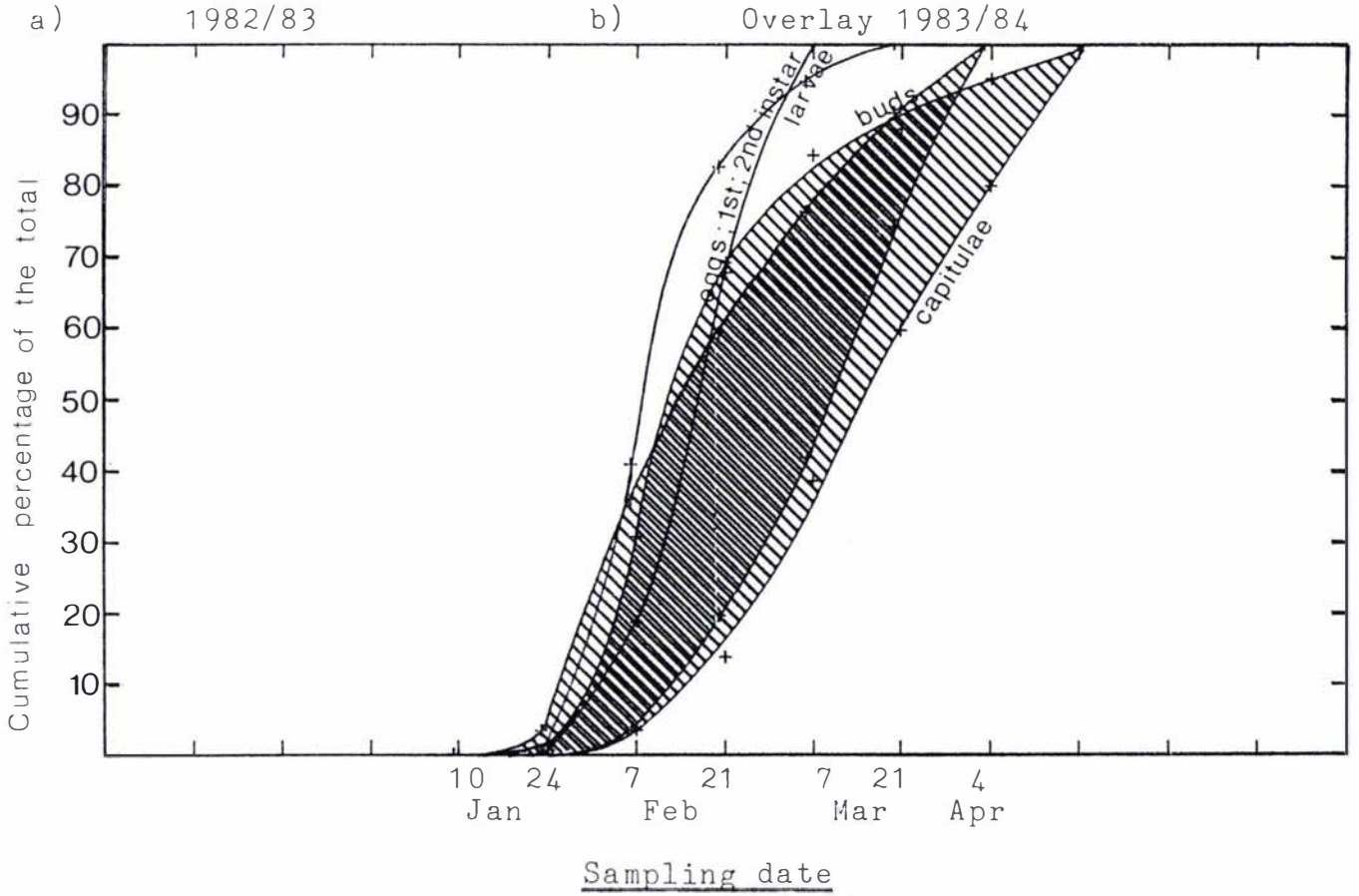
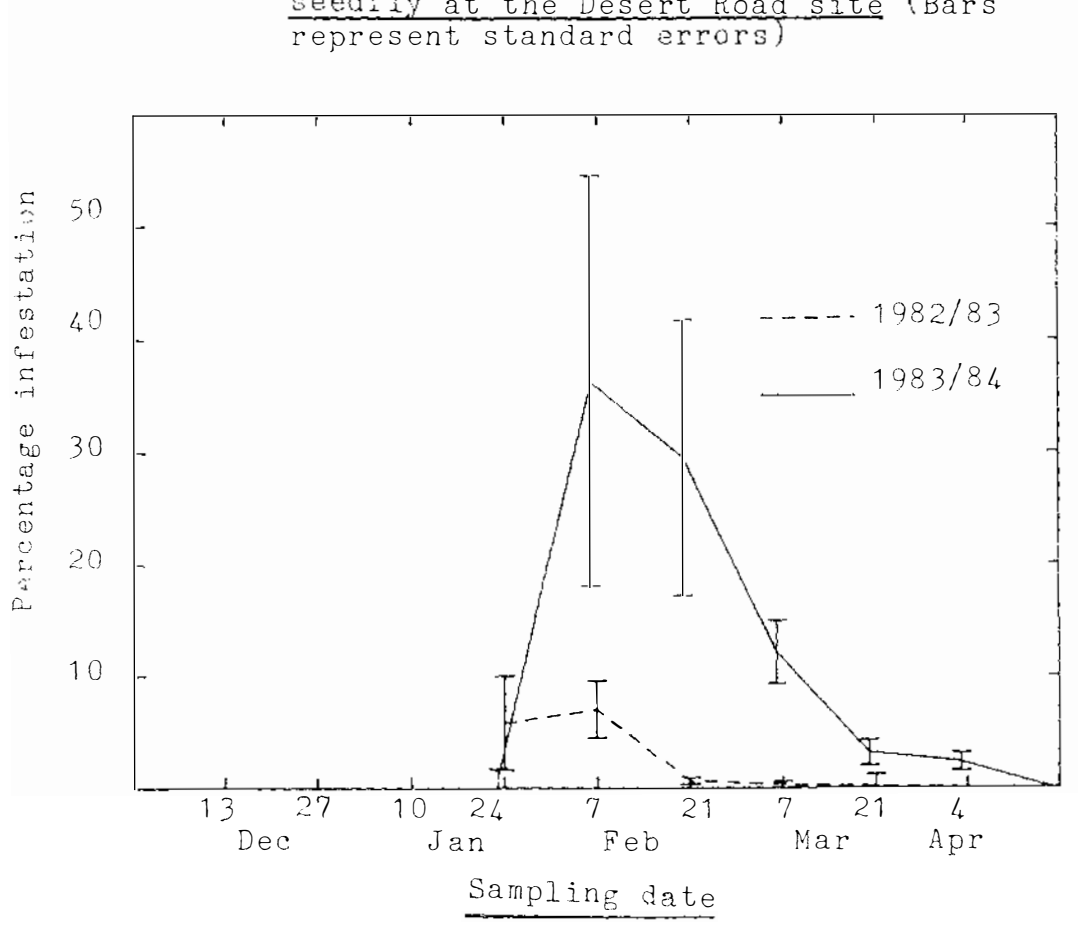


Figure 2.18 Percentage of ragwort seedheads infested by seedfly at the Desert Road site (Bars represent standard errors)



CHAPTER THREE: LABORATORY STUDIES

3.1 Introduction

Field data from spring 1982/83 and 1983/84 indicated a pre-oviposition period of approximately six weeks. However, there was an absence of ragwort flowers during this period which suggested that there was no nutritional requirement for ovary development associated with ragwort flowers and that ragwort rosettes and/or other field plants provided food for seedfly adults. There was also a possibility that ovary development could be slowed or delayed by the absence of ragwort flowers. To determine the factors affecting seedfly ovary development rates flies were reared at different temperatures in the absence and presence of various diets and stages of ragwort development.

Survivorship curves for eggs and larvae within seedheads were constructed from their development rates measured in laboratory conditions. Factors affecting the stage when third instar larvae leave the plant to pupate were also investigated in view of the variable duration of the third larval instar observed in the field. Further estimates of pupal survival over winter are presented with some information on pupal diapause.

3.2 Methods and Equipment

3.2.1 Ovary development

Flies were reared in cages in controlled conditions to determine the effect of diet and presence of the host plant on ovary development. The cages were 1m high by 70cm x 70cm and stood on

moveable trolleys 70cm above the ground (Plate 6). The frames were constructed of 6mm gauge aluminium rod fitted into $(2cm)^3$ perspex corner blocks. The frame was completely enclosed in fly proof nylon mesh and access was provided through a flap sealed with velcro. Diets were provided in 10 ml bottles which protruded through rectangular polystyrene trays positioned at one of the top corners of each cage. Cotton wicks were inserted through the screw tops of the bottles to dispense the diets.

Female flies recaptured from the cages were preserved in Carnoy's solution (Humason, 1967). When the females were dissected the lengths and widths of their ovaries were measured using an occular micrometer and the number of eggs with a chorion were recorded. These were eggs which remained intact when placed for a few minutes in a solution of 50% acetic acid. Squashes were made of the spermathecae, examined under a phase contrast microscope and the presence of sperm recorded.

I. Experiments at D.S.I.R.

Two thousand seedfly pupae were collected from Redwoods Forest in February and August, 1983 by the flotation method described in Chapter 2. The pupae were divided into lots of 50 and kept in 200ml T.V.L collecting jars in moist, sterile vermiculite. These were kept at 10C until the end of September and then transferred to 20C.

Many of the flies which emerged had wing deformities. Only 700 adults were perfectly formed and 424 of these were females. 375

of the females survived anaesthetization with CO_2 and were released into the cages with the males. They were allocated to the different treatment according to the number emerging daily and the total number expected to hatch. Because daily emergence was low, individual females were marked so that they could be aged to the nearest day. This was done by applying quick drying Modelair dope paint to the dorsal surface of the thorax with a fine needle. Marking was avoided where possible and no males were marked.

The flies were then released into the cages in the controlled environment rooms at Plant Physiology Division, D.S.I.R., Palmerston North. Temperature treatments for these experiments were maintained constant over the light and dark periods at 10, 15, 20 and 25(±0·5)C. The vapour pressure deficit was also maintained constant, at 8mb, resulting in relative humidities of 35, 53, 66 and 75(±5)% respectively. The photoperiod was 14 hours light to 10 hours dark and the irradiance (400-700nm waveband) measured at plant height was between 146 and 149 W/m^2. The lighting system used consisted of four 1000W Sylvania "Metal-arc" high-pressure discharge lamps, and four Philips tungsten iodide lamps (Warrington et al., 1978). Carbon dioxide levels measured with an infrared gas analyser during the course of the experiments were 330±20ppm.

The flies were provided with flowering ragwort potted in a soil/pumice mix with fertiliser. These plants were watered daily (200mls) via an automated microtubule system. The following diets based on the anthomyiid diets devised by Singh (1977) were

provided.

1) 70mls water, 4gms yeast, 10gms sugar, 20mls skim milk, 2mls casein peptone (4gms/l).

2) 5gms sugar, 250mls water, two egg whites.

3) Golden syrup: skim milk: water, 1:1:2 ratio by volume.

4) 30mls honey, 30mls condensed milk, 300mls water.

Plants were also lightly watered every three days to provide surface water for the flies.

Additional experiments were conducted at 20C where flies were provided with;

a) ragwort rosettes only

b) flowering ragwort only

II. Experiments at Massey University

Five hundred pupae obtained from Entomology Division, D.S.I.R. in November 1984 were used for experiments in the controlled environment rooms of the Department of Agriculture and Horticulture, Massey University. These had been obtained in autumn 1984 by inverting the seedheads over moist sand. The pupae were subsequently collected using the flotation method. They were stored in moist vermiculite at 10C and transferred to 20C in early June to initiate development. As the wings became visible through the puparium the pupae were returned to 10C. When all the pupae had reached this stage they were transferred to 20C to complete development. This ensured that large numbers of flies emerged together so these did not have to be marked. The flies were

allowed to hatch directly into the cages to further reduce handling.

Temperatures in the controlled environment rooms were maintained at 12, 15, 18C and the humidity ranged from 65 to 75%. The photoperiod was 14 hours light to 10 hours dark and the light sources consisted of 2 Philips 1000W tungsten halogen lamps, 6 Philips 375W mercury iodide lamps and 3 100W incandescent bulbs illuminating an area of $4m^2$.

A range of cut flowering field plants found at the field site during the pre-oviposition period were provided in addition to ragwort rosettes and the diets described above. These included cocksfoot, Yorkshire fog, dandelion, buttercup (Ranunculus acris L.) and paspalum (Paspalum dilatum Poir). Fifty of the 70 females that emerged in perfect condition from this consignment were reared in these conditions and the remaining 20 were used to compare the ovary size of females reared on additional diet and ragwort flowers with those reared on ragwort rosettes and diet.

3.2.2 Egg and larval development

Seedfly eggs and larvae were reared in the controlled environment rooms at the D.S.I.R. to measure their development rates at different temperatures.

Provision of host plants

Five hundred ragwort rosettes were dug from the field in spring 1983 and potted in two litre pots in a soil/pumice mix with

fertiliser. This ensured that a supply of buds suitable for oviposition by seedfly would be available when gravid females were present at the field site in December and January. The plants were kept in an open glasshouse and watered regularly. They were sprayed two months before the start of the experiments with a non-systemic insecticide, `Attack',(47•5% pirimiphos-methyl and 2•5% permethrin) and the fungicide `Manzate 500'Dupont (active ingredient 80% mancozeb). Slug killer was distributed throughout the pots. On several occasions plants were temporarily installed in the controlled environment rooms at 20 and 25C to accelerate bud development.

Conditions in the controlled environment rooms

These experiments followed those on ovary development at Plant Physiology Division, D.S.I.R, Palmerston North and the conditions described above were continued. Development was completed quickly at 25C so this room was converted to a temperature regime which fluctuated between 25C and 15C for comparison with the development rates at constant 20C. There was a six hour changeover from day/night and night/day conditions, the lights going off two hours before the completion of the changeover to night conditions (15C) and coming on two hours after the start of the changeover to day (25C) (Fig.3.1). The relative humidity was 75/53%.

Obtaining eggs for the experiments

Potted plants with buds suitable for oviposition were transported to the field site at Redwoods Forest. Several trips were made transporting 60 plants each time to minimize the number of plants

discarded when insufficient eggs were laid. The plants were left in the field for 24 hours starting at midday. They were watered in the field the following morning to prevent wilting.

Sampling procedures in the controlled environment rooms

After the six hour return trip to Palmerston North the plants were placed in the controlled environment rooms and connected to the automated watering system. They were not watered externally during the experiments. The following day a sample of buds was dissected to determine the infestation level of seedfly and the total number of eggs in the sixty plants was estimated. When infestation levels were below 3% the plants were discarded because they did not provide sufficient animals to sample destructively through to pupation. Subsequent samples were taken every 12 hours. Sampling continued each time until at least 20 animals had been found.

Flies were allocated to the controlled environment rooms as summarized in Table 3.1. One seedfly population was placed at 25C first. Although there were only sufficient numbers of flies for 12 hourly sampling at the egg and first larval instar stages this gave an estimate of the shortest duration of the life history that could be expected and reduced the numbers of flies sampled from populations developing at cooler temperatures. Flies placed at 10C were discarded when it was realised that the projected duration of the egg and larval stages was 143 days and this exceeded the time allocated for these experiments in the controlled environment rooms.

Third instar larvae that dropped to pupate were collected daily from 125ml pottles at the base of cardboard cones fitted around several stems (usually 4-5) bound together (Plate 7). Each pottle was covered in black tape and filled with moist vermiculite. It was unscrewed from the base of the cone each day so that the larvae which had dropped could be transferred to a separate container to pupate. Pupae in this container were measured and transferred daily to controlled temperature cabinets to continue development at their respective temperatures.

3.2.3 The larval dropping response

Time of day of larval dropping

Infested stems collected from the field were suspended in the laboratory over trays lined with black polythene. The temperature was maintained at constant 20C with a photoperiod of 14 hours light and 10 hours dark.

The daily dropping of larvae in response to simulated rain

Third instar larvae reared in fluctuating temperatures that remained in the seedheads after the peak in dropping were subjected to following treatments.

1) Single drench, one litre of water, using a watering can.

2) Light spray, 500mls of water, using an atomiser.

3) Light spray daily, 500mls of water, using an atomiser, followed by daily drench, one litre of water, using a watering can.

The number of third instar larvae dropping daily was recorded for each treatment.

Plate 6 Cage for rearing adults in the controlled environment room at D.S.I.R. The arrangement for dispensing the diets is at the top right-hand corner of the cage.

Plate 7 Collecting funnel for third instar larvae leaving ragwort in the controlled environment rooms at D.S.I.R.

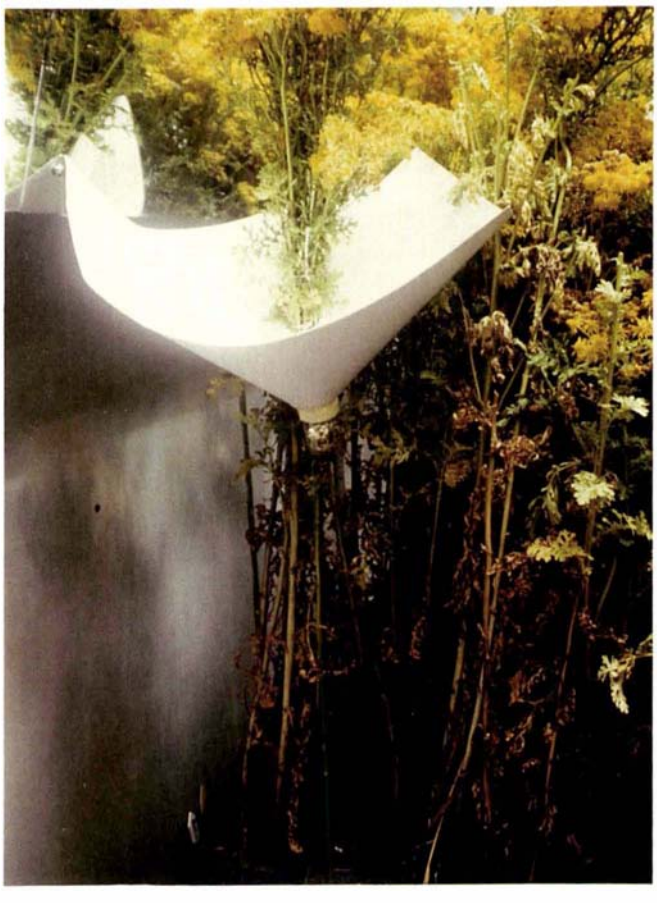


Figure 3.1 Temperature fluctuations in relation to photoperiod in the controlled environment room at Plant Physiology Division D.S.I.R.

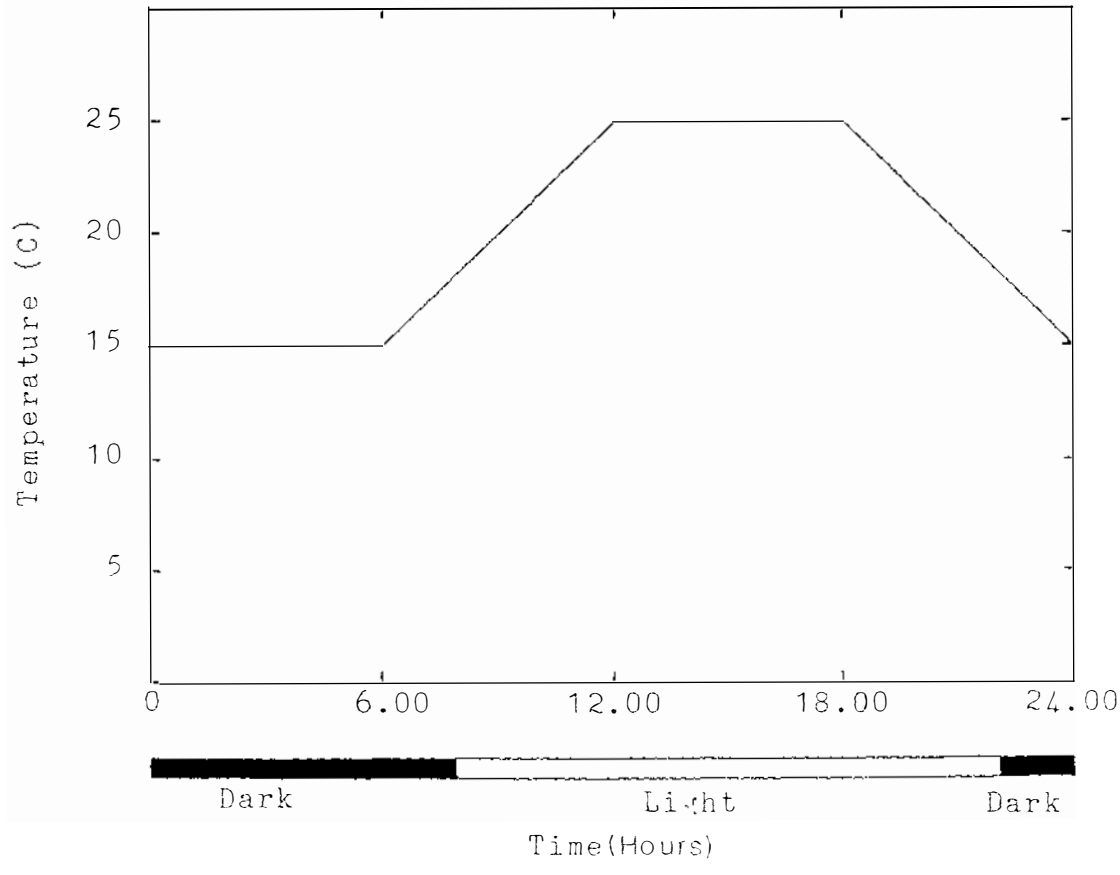


Table 3.1 Allocation of seedfly eggs to the controlled environment rooms at D.S.I.R.

Date when eggs were laid in plants placed in the field	Estimated infestation levels	Temperature of room eggs were allocated to	Numbers of seedfly destructively sampled	Number of seedfly caught by funnels
Noon 11/12/83 to noon 11/12/83	3%	25 C	66	15
Noon 17/12/83 to noon 18/12/83	< 3%	Discarded		
Noon 26/12/83 to noon 27/12/83	10%	10 C	Not completed because of time restrictions	
Noon 2/1/84 to noon 3/1/84	20%	15 C	480	45
Noon 9/1/84 to noon 10/1/84	25%	20 C	567	194
Noon 23/1/84 to noon 24/1/84	25%	15-25 C (average 20 C)	530	351 prior to dropping experiments

3.2.4 Diapause

Pupae collected from Wairakei and the Desert Rd in March 1982 (Fig.2.1) using the flotation method were kept in lots of 10 and 4 respectively in moist sand within 250ml T.V.L specimen jars. They were subjected to -15C and 5C for varying lengths of time and then placed at 20C to continue development.

3.3 Results and Discussion

3.3.1 Ovary development

Mortality of caged flies

Emergence of perfectly formed adults from the pupae collected in winter 1983 is shown in Figure 3.2. This has the same scale as Figure 2.7 to compare the spread in emergence in the laboratory and field populations and shows that males emerged slightly before females. Mortality in the cages could not be accurately determined as few of the dead flies could be found among the potted plants. It is not known whether reduced handling increased survival as no direct comparison of mortality can be made between the experiments at D.S.I.R and at Massey because of the differing ways in which the populations were sampled. Fifty of the 375 females released into the cages at D.S.I.R. were culled at various ages for dissection while 13 of the 50 flies reared at Massey University survived to maturity. Twelve of the 20 females used to determine the effects of ragwort flowers on ovary development were available for dissection after 14 days at 12C. The only published information on mortality in anthomyiids is provided by Theunissen (1974) who found a higher mortality in caged onion fly males (59% mortality at 15C after 20 days)

compared to females (25%).

Maturation of seedfly ovaries

All flies reared on ragwort rosettes without additional food died within five days. Figure 3.3 shows the effects of temperatures and diet on ovary size in the controlled temperature rooms at Plant Physiology Division, D.S.I.R. The size of ovaries from flies which had been marked were 70% that of unmarked ones and the measurements which have been adjusted to allow for marking are indicated by arrows. Females could not be reared to maturity on ragwort flowers alone and after 14 days at 20C ovary size was 40% that of those reared with additional diet. There was no significant difference in ovary size after 14 days at 12C between flies reared with flowers and diet and those reared with rosettes and diet ($t=•39$ $P=•72$ $df=10$).

The effect of diet on ovary development has been investigated for several anthomyiid species. Hafez et al.(1970) found that diet was an important determinant of the length of the pre-oviposition period in laboratory reared beet flies while additional protein was required to mature more than one batch of eggs in the cabbage root fly (Finch, 1971). In subsequent studies (Finch, 1974) found that the surfaces of pollen of Yorkshire fog and cocksfoot together with tall oat grass, Arrhenatherum elatius L., provided sufficient nutritive carbohydrates for maturation of the first batch of eggs in the cabbage root fly. Plantain, blackberry, dandelion, white clover, wild cherry, marsh marigold and stinging nettle (Urtica dioica L.) were also food sources for the cabbage

root fly but the last three were not available for the ragwort seedfly at either of the field sites, nor were the Umbellifers, Anthriscus sylvestris L.(cow parsley) and Heracleum sphondlium L.(hogweed). The latter provided the most nutritious nectar for cabbage root fly adults with 94 and 86% sugar solutions respectively (Finch, 1974).

Studies on ovary development of the cabbage root fly (Finch, 1971) and the onion fly (Theunissen, 1974) have shown that eggs are laid in batches and that all eggs in one batch ripen together. Ovary development rates for P.jacobaeae were therefore calculated as the reciprocal of the time from emergence to the first appearance of an egg in the median oviduct (Plate 8). The development rates of flies reared with additional diet both in the presence and absence of ragwort flowers are given in Figure 3.4. These results do not include marked flies. The duration of the pre-oviposition period decreased with increasing temperature and was approximately 39 days at 10C and 14 days at 20C. In comparison, the pre-oviposition period of the beet fly was 8 days at 15C and 3·5 days at 30C (Hafez et al., 1970); 7 days at room temperature for P.seneciella (Frick, 1969) and five weeks in the field for the wheat bulb fly (Jones, 1970).

The numbers of eggs in P.jacobaeae females reared in the controlled environment rooms ranged from 2-30 (Table 3.2). There were 16 ovarioles in each ovary and this was the same for the wheat bulb fly (Gough, 1946). The maximum number of eggs laid by the wheat bulb fly in the laboratory was 180 (Long, 1958b) and Raw

et al.(1968) found that females of this species laid an average of 40 eggs which represented those of the first batch and part of the second.

Females were mated one day after emergence at 25C (Table 3.3) but it is not known how often this occurs. Although examination of spermathecae squashes (Plate 9) showed if the flies had been mated during their life time their age when mated could not be determined. A female was found to have been mated within 2 days of emergence at 10C so it is unlikely that cooler temperatures extend the pre-mating period in P.jacobaeae as observed by Hafez et al.(1970) for the beet fly. They found that male beet flies were capable of mating four females and females copulated more than once. The only other relevant data published on anthomyiid mating behaviour is from Jones (1970) who reported that wheat bulb fly males each served several females and by the time ovaries were half developed the spermathecae contained spermatozoa.

3.3.2 Development of eggs and larvae within the seedhead

The duration of the egg, and first and second larval instars was taken as the time between 50% of the population entering a stage and 50% leaving the stage (Fig.3.5). At 15C the durations of the egg stage, first and second larval instars were 5•5, 7 and 8 days respectively. The duration of the third larval instar was calculated as the mean time from oviposition to larval dropping minus the mean time from oviposition to when 50% of the population had entered the third instar. This was estimated as 31•9 days at 15C and 23•5 days at 20C. Figure 3.6 shows the development rates

Figure 3.2 Emergence of seedfly adults in the laboratory

Pupae were collected in August 1983 and kept at 10 C until October 1983 when they were transferred to 20 C

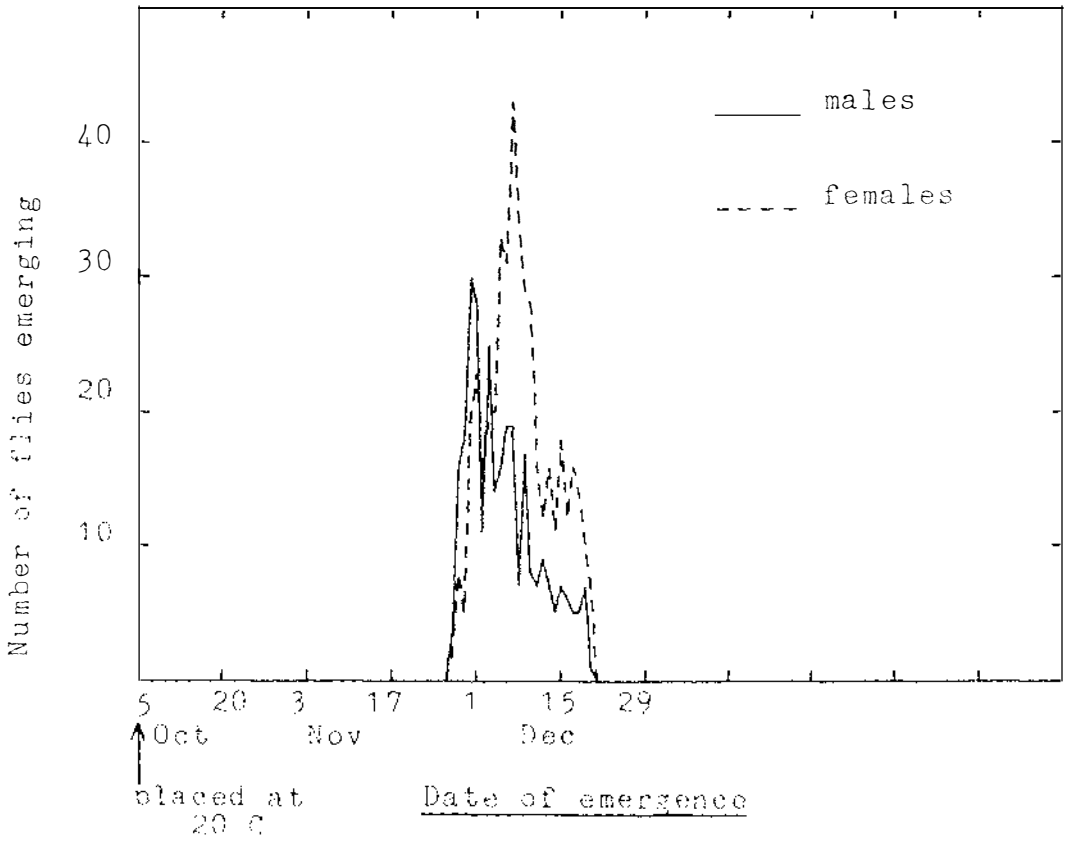


Figure 3.3 The relationship between ovary size, age and diet of seedfly females

Points indicated by arrows have been increased by 40% to correct for markings.

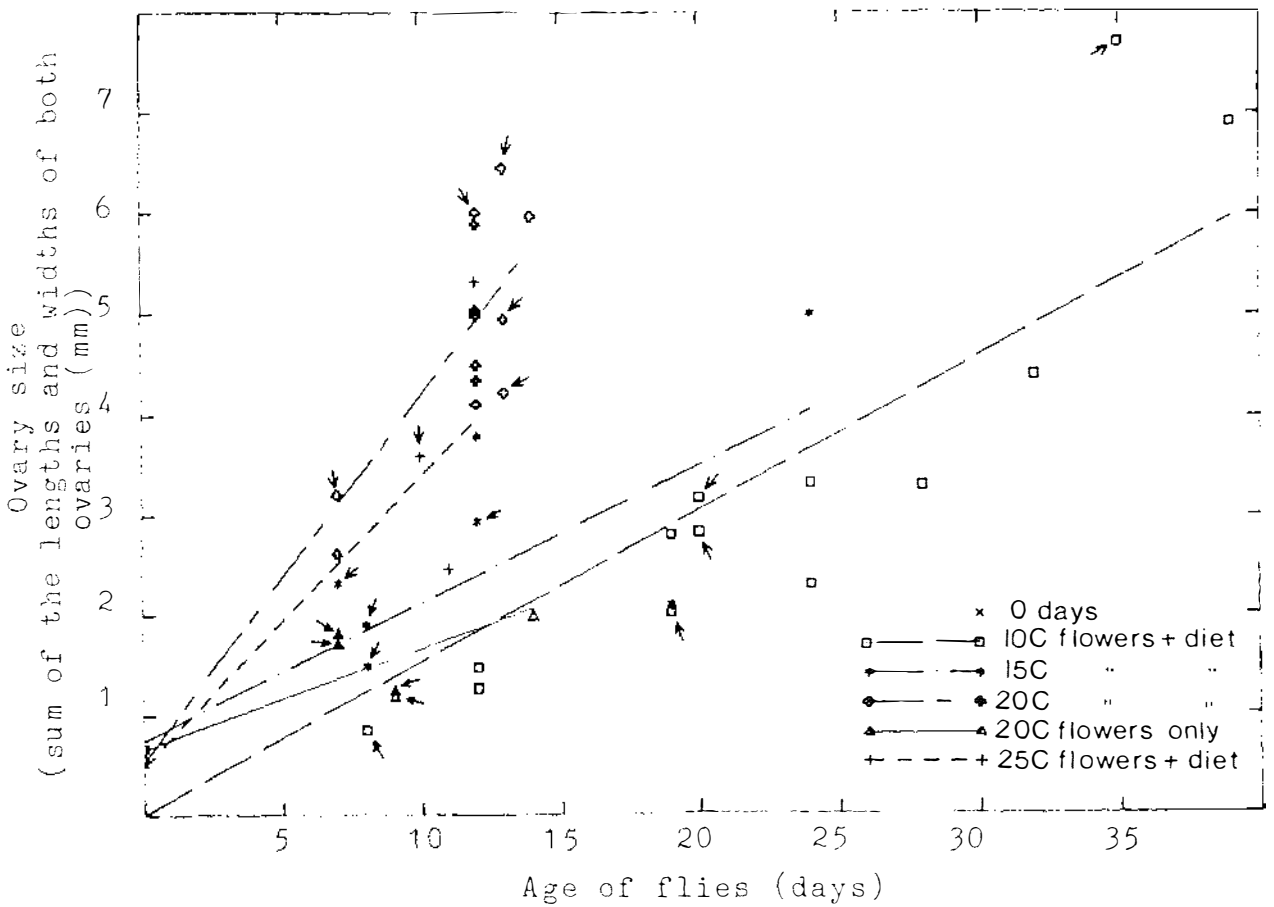


Figure 3.4 The rate of seedfly ovary development in relation to temperature

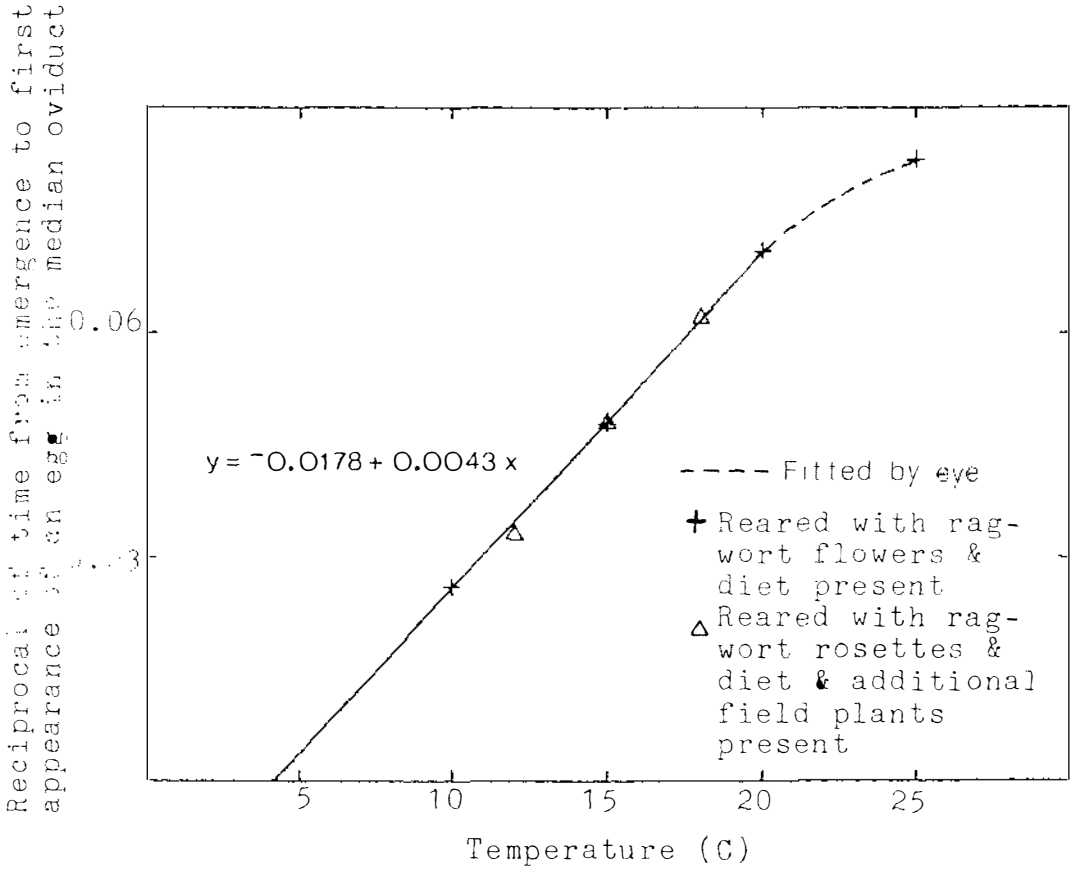
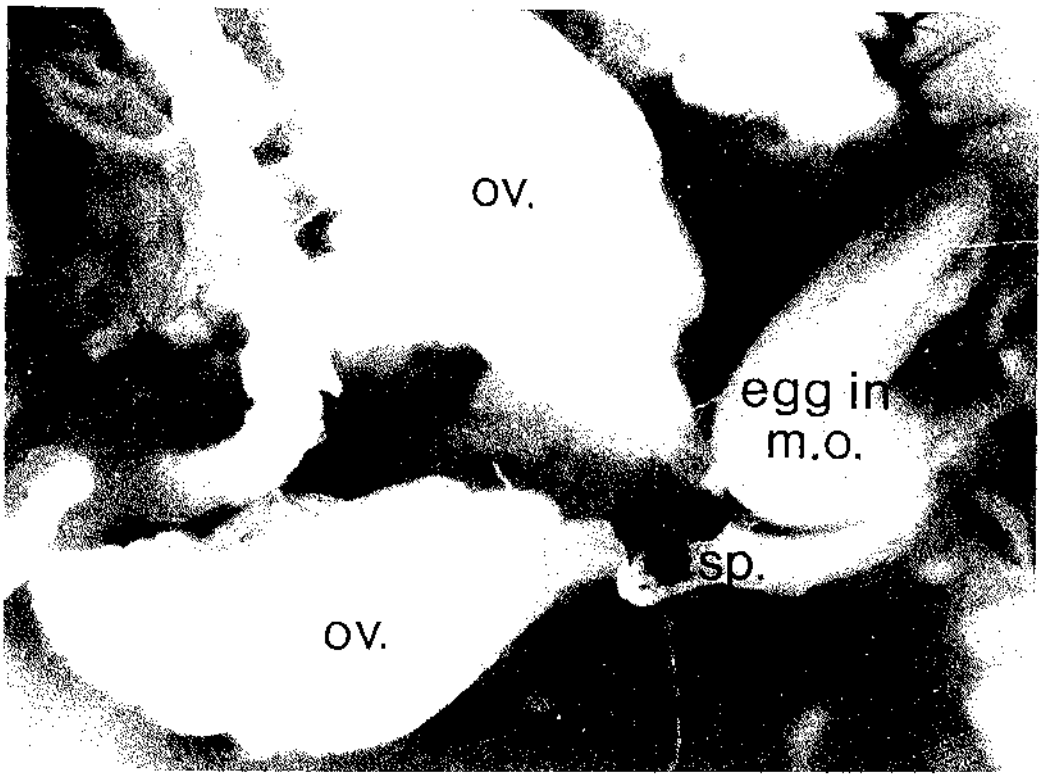


Plate 8 Reproductive organs from a 14 day old female seedfly. Reared at 20 C with ragwort flowers and additional diet.
(Magnification 40x)
ov = ovary
sp = spermatheca
m.o = median oviduct

Plate 9 Seedfly spermatheca squashed to show sperm. Dark areas indicate fragments of the spermatheca.
(Magnification 320x)


ov.
egg in
m.o.
sp.
ov.

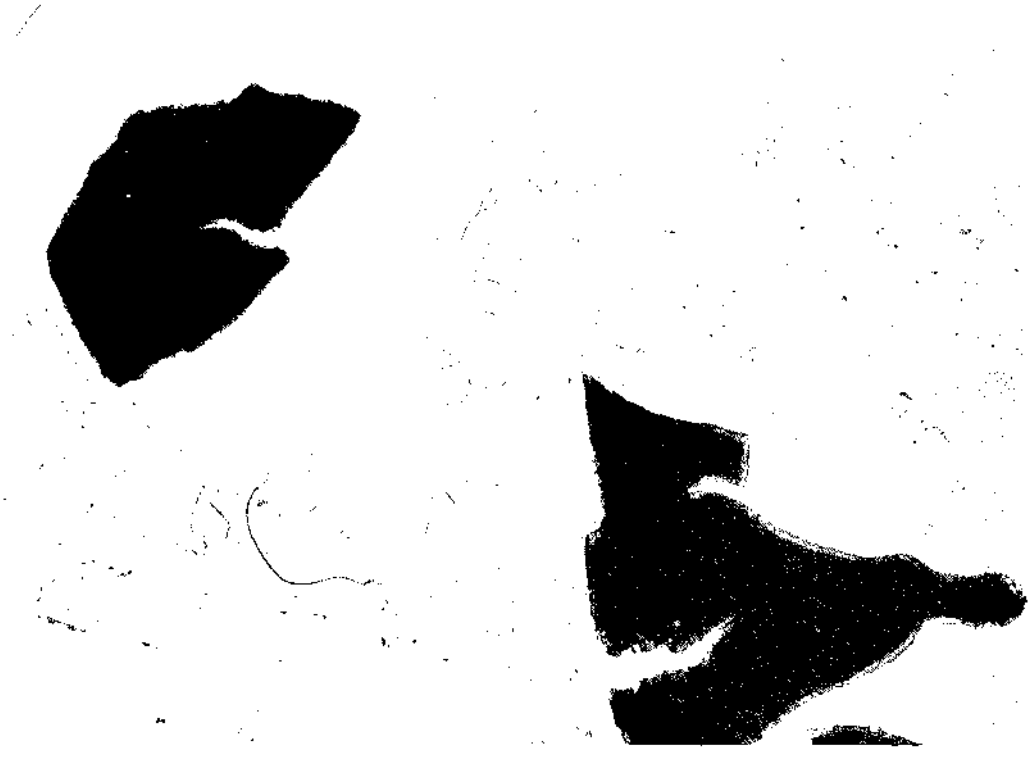


Table 3.2 Total number of seedfly eggs from seedfly females reared in the laboratory

Conditions in controlled environment rooms	Age (days) when dissected	No. eggs with a chorion
Rosettes & diet		
12°C	30	6*
15°C	16	2
	21	16*
	21	5
	21	12
	21	2
18°C	16	18
	16	3*
	16	20
	16	10
	16	6
	18	9*
	18	8
Flowers & diet		
20°C	13	2
	13	19
	13	2
	13	30
	14	19*
25°C	14	18*
	16	6*

* includes egg found in the median oviduct.

Table 3.3 Mated state of females reared in laboratory conditions at D.S.I.R.

Some females were marked with model aeroplane "dope" to indicate when they emerged.

Treatment	Age (Days)	Marked (+) Unmarked (-)	Presence of sperm
10 C Flowers & Diet	2	+	+
	3	+	-
	4	+	-
	8	+	+
	8	+	+
	35	+	-
15 C Flowers & Diet	2	-	-
	4	+	-
	8	+	-
	8	+	-
	12	-	-
	24	-	-
20 C Flowers only	2	+	+
	2	+	-
	3	+	-
	3	+	-
	4	-	+
20 C Diet only	3	+	-
	3	+	-
	3	+	-
20 C Flowers & Diet	2	-	-
	2	+	-
	2	+	-
	3	+	-
	4	+	-
	7	+	-
	8	+	-
	8	+	-
	12	-	+
	13	-	+
25 C Flowers & Diet	1	+	-
	1	+	+
	1	+	-
	1	+	+
	2	+	+
	2	+	-
	2	+	-
	2	+	-
	2	+	+
	3	+	-
	3	+	-
	3	+	-
	5	+	+
	5	+	+
	7	-	+
	7	-	-
	10	+	-
	10	+	-

of seedfly within the seedhead from oviposition to larval dropping in relation to temperature. Development rates from oviposition to pupation were also measured (Fig.3.7). The mean duration of the third larval instar after it had left the seedhead calculated from these two graphs was 3•2 days at 15C.

Development rates of seedfly at constant 20C were similar to those under fluctuating temperatures with a mean of 20C. Development rates under fluctuating and constant temperatures have been also measured for other Diptera with variable results. Wilkinson and Daugherty (1970) found that development times for eggs of Bradysia impatiens (Johannsen) (Diptera: Sciaridae) were similar under constant and fluctuating temperatures but larval development was shorter under fluctuating temperatures. Larval mortality, however, was higher under the variable temperatures. Siddiqui and Barlow (1972) found that development times of the immature stages of Drosophila melanogaster (Meigen) (Diptera: Drosophilidae) tended to be shorter at alternating temperatures than at the corresponding constant mean temperature.

Survivorship curves (Fig.3.8) were constructed by integrating the curves for each stage in Figures 2.9a+b and dividing by the duration of the stage at 15C (Southwood, 1978). This was the average temperature experienced at Redwoods Forest during the summer. It was estimated that 1,966,358 eggs survived to halfway through the egg stage at Redwoods Forest in 1982/83 and 5,761,447 in 1983/84. Therefore, assuming no mortality in the first half of the egg stage, 12•9 eggs were laid per female that emerged at the

Figure 3.5 Duration of egg and larval stages of ragwort seedfly at different temperatures

a) 25 C sampling ceased after 3½ days because of low numbers
b) 20 C
c) 15 - 25 C (average 20 C)
d) 15 C

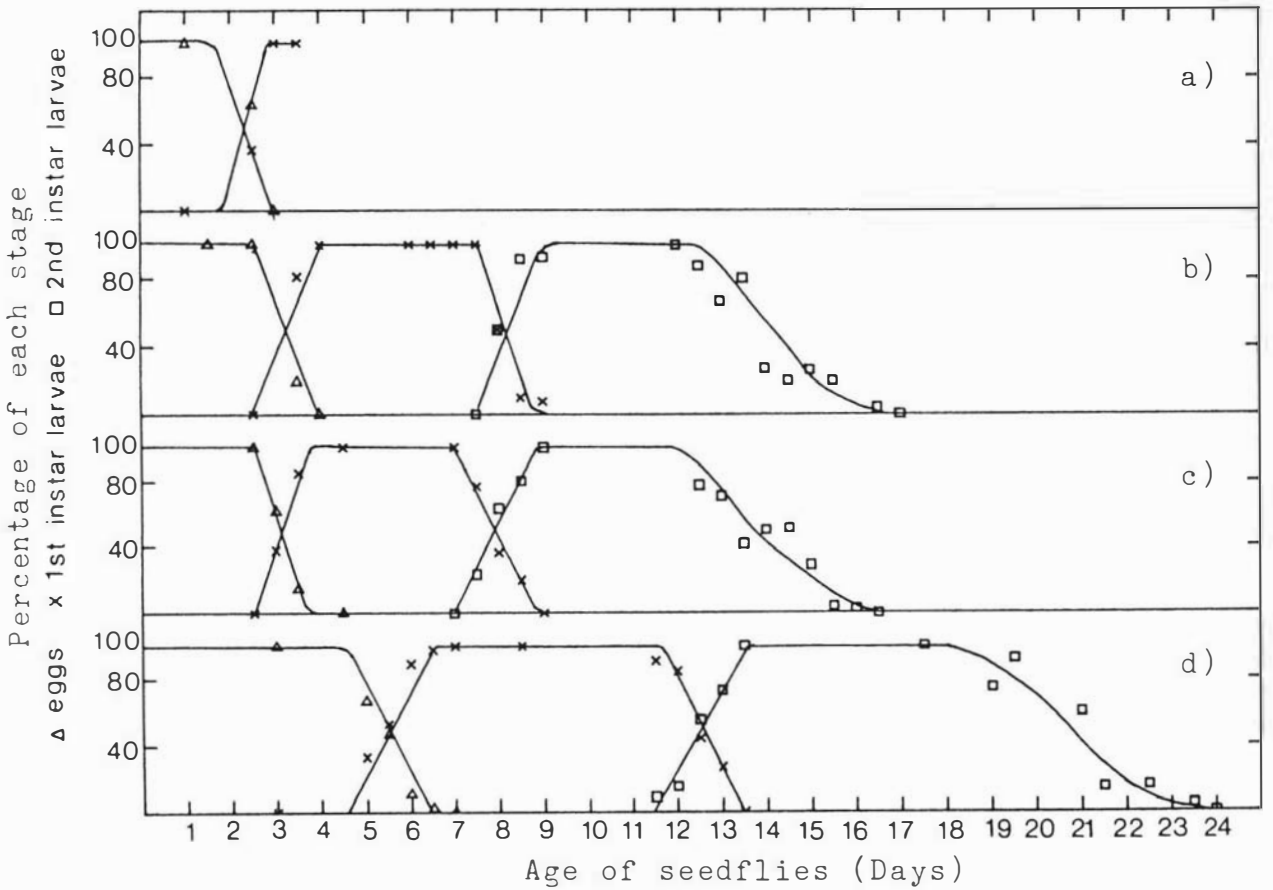


Figure 3.6 The rate of seedfly development within the seedhead in relation to temperature (Bars indicate standard errors)

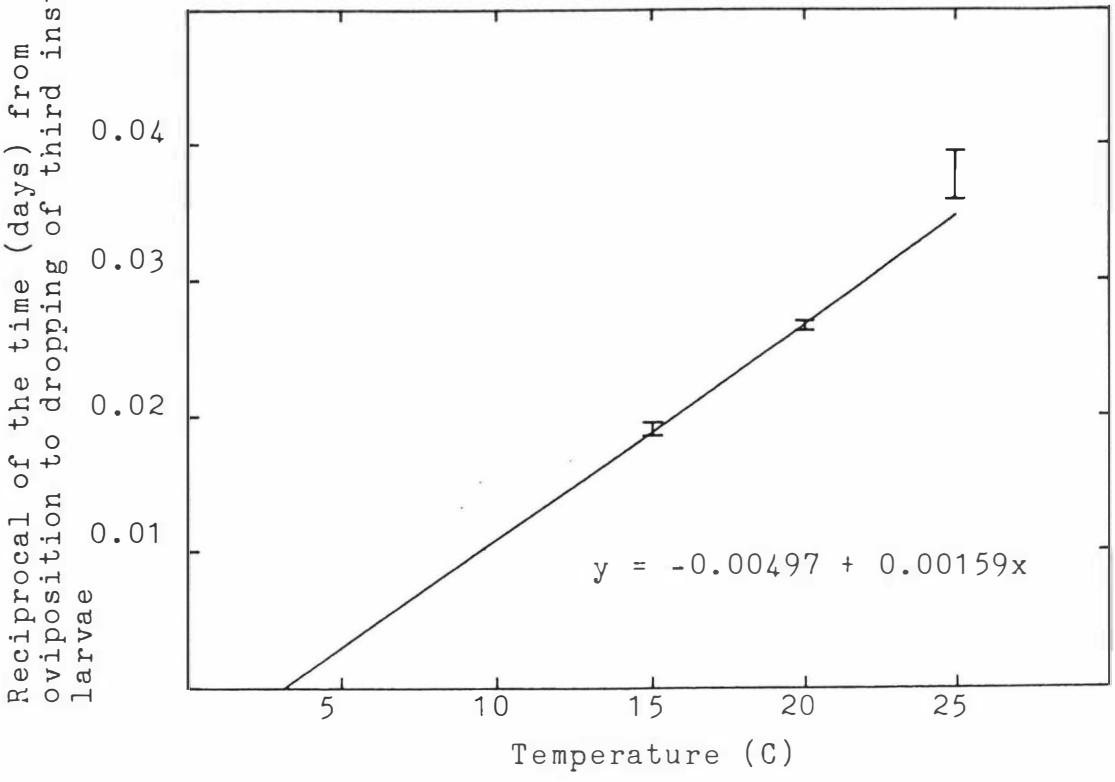


Figure 3.7 The rate of seedfly development from oviposition to pupation in relation to temperature (Bars indicate standard errors)

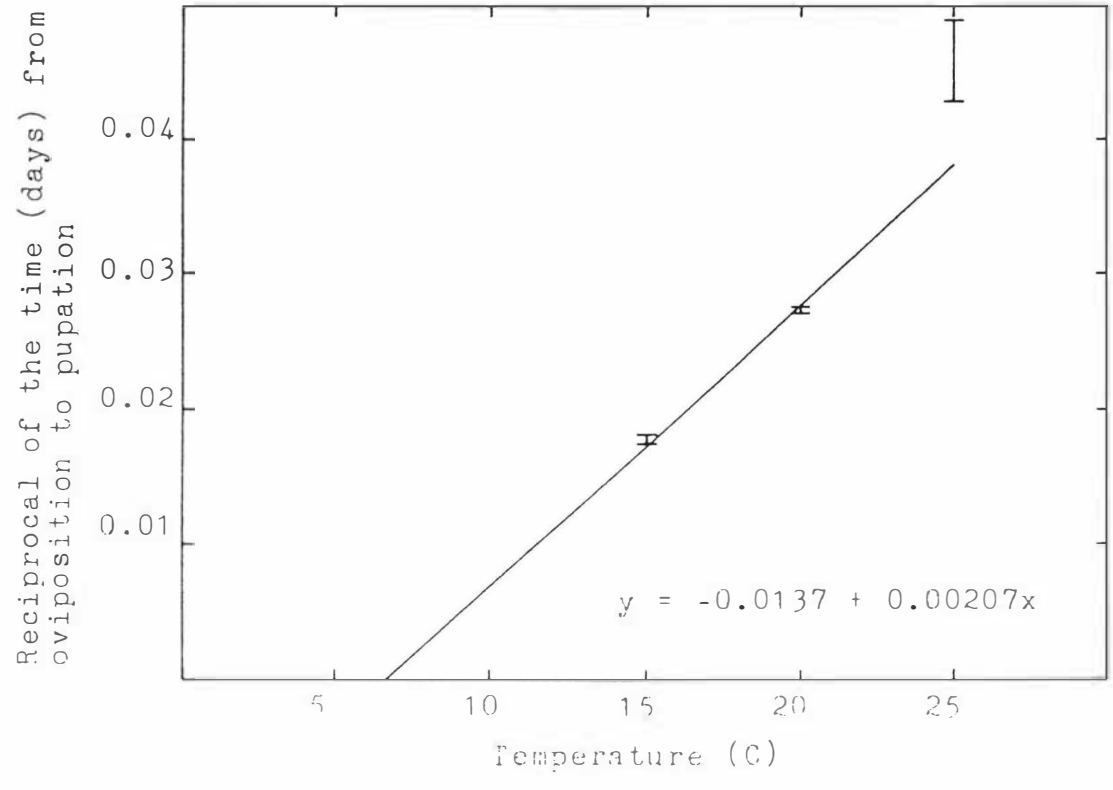
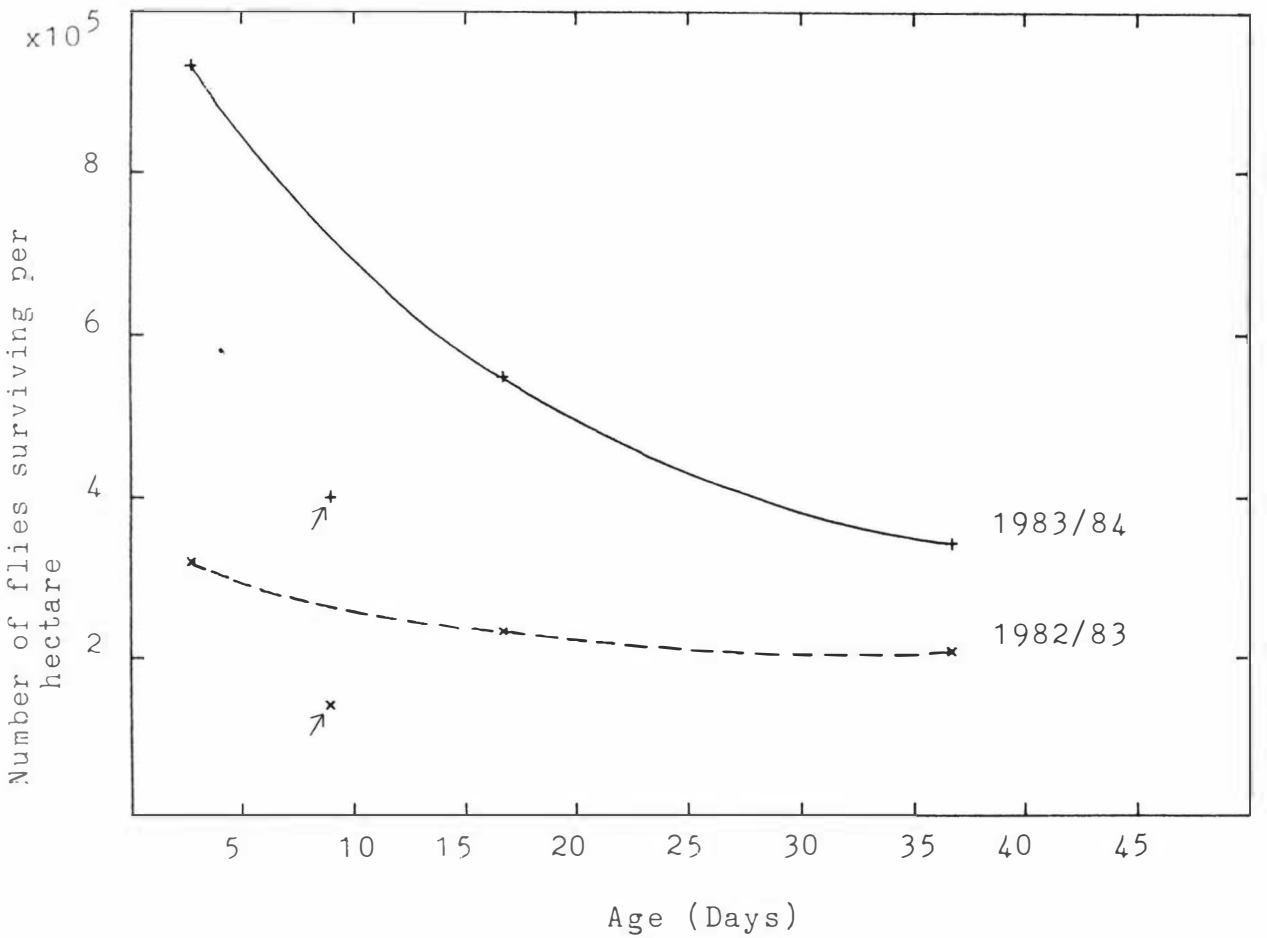


Figure 3.8 Survivorship of seedfly at Redwoods Forest

The points were calculated using the method of Southwood (1978) and the curves are fitted by eye.



Arrows indicate underestimates of 1st instar larvae

See page 80

site in 1982/83 and 3•9 in 1983/84. First instar larvae were difficult to locate in the discoloured, thawed seedhead samples and as a result they were under-estimated. The survivorship curves show that an estimated 88% of the flies surviving to halfway through the egg stage survived to halfway through the second larval instar at Redwoods Forest in 1982/83 compared to 69% in 1983/84. Mortality from halfway through the second larval instar to halfway through the third larval instar was 4% in 1982/83 and 31% in 1983/84. In autumn 1984, the number of third instar larvae within seedheads is estimated as 370,000/ha (Fig.3.8) compared to 1,580,500 third instar larvae per hectare estimated from the trays in this year. This can be compared to 670,450 pupae/ha estimated from the trays (Chapter 2, Section 2.4.6).

There was no significant difference in the size of pupae from larvae reared at constant 15C and constant 20C ($t=-1•53$ $P=0•13$ $df=51•9$) but larvae reared at constant 20C produced significantly larger pupae than those reared in fluctuating temperatures with a mean of 20C ($t=2•95$ $P=0•0036$ $df=204•7$).

3.3.3 Larval dropping

No daily rhythm associated with photoperiod was detected in the numbers of third instar larvae leaving cut stems to pupate (Appendix 3).

The possibility exists that humidity, which was closely linked to the temperature maintained in the controlled environment rooms,

influenced the larval dropping response. Figure 3.9 shows that the number of larvae dropping increased with increasing humidity and temperature in the rooms. Drenching plants with water from a watering can resulted in a marked increase in larvae dropping (Fig.3.10). Daily drenching resulted in continued high numbers dropping until all larvae had dropped. Light spraying with an atomiser increased the number dropping but not to the same extent as heavy watering.

3.3.4 Pupal survivorship and termination of diapause

Overwintering survival could be calculated for the 1983 winter using the information on survivorship of larvae within ragwort seedheads. 35.3 third instar larvae/m^2 within seedheads were estimated in autumn 1983 compared to 30 adults/m^2 estimated to have emerged in the following spring (Chapter 2).

Summer diapause in P. jacobaeae was initiated when the temperatures were between 15 and 20C. It is therefore unlikely that seedfly pupae diapause in the field as temperatures in the soil during autumn and winter drop below 15C. Adults emerged from pupae subjected to constant 15C after 209 days but did not emerge from pupae placed at constant 20C. Temperatures required to terminate diapause were one week or less at 5C and one minute at -15C. Development, however, was not arrested at 5C. When the time spent at 5C was increased the time spent at 20C until development was completed decreased but it is not clear whether this occurred in pupae placed at -15C (Fig.3.11a+b). There was no significant difference in development time at 20C between pupae collected at Wairakei and

from the Desert Rd ($t=-1{\cdot}82$ $P=0{\cdot}09$ $df=14{\cdot}8$ for pupae subjected to -15C and $t=-1{\cdot}60$ $P=0{\cdot}12$ $df=34{\cdot}5$ for those placed at 5C).

Pupal development times have been measured for other anthomyiids but all of them have more than one generation per year. For pupae of the seed corn maggot, Delia platura (Meigen) the day degrees above the threshold of 3·9C for development was 140 (Funderburk et al., 1974). This species has two generations per year compared to the cabbage root fly which has two generations in the north of England and three in the south. Collier and Finch (1983) found that a temperature of 0-6C was required for the latter to complete diapause development with a further 14 days at 20C elapsing before the adults started emerging. This is comparable to earlier studies on the cabbage root fly. Coaker and Wright (1963) found that once diapause development in the cabbage root fly has been completed by a suitable cold period an accumulation of about 205 day degrees above a threshold of 5·6C was required for pupae to complete morphogenesis.

Figure 3.9 Proportion of third instar larvae dropping at different humidities in the controlled temperature rooms at D.S.I.R.

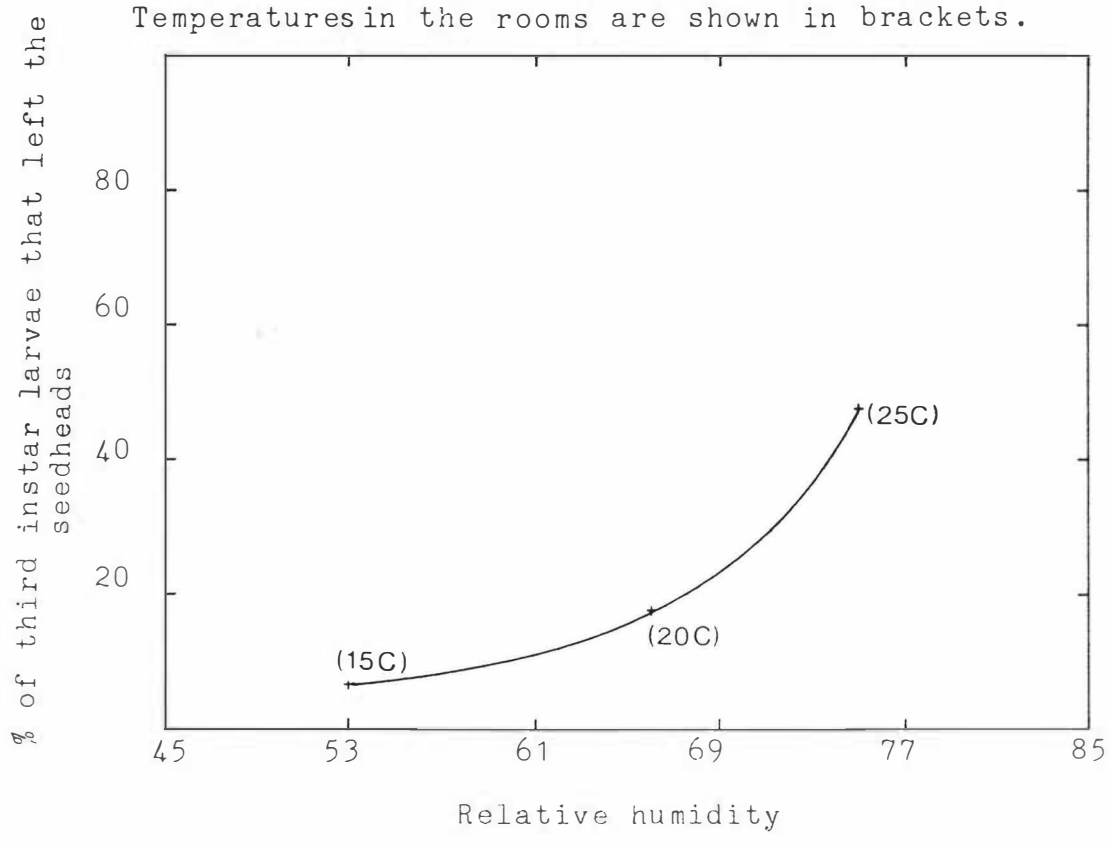


Figure 3.10 The dropping response of seedfly 3rd instar larvae in relation to watering seedheads

a) not watered
b) lightly sprayed with 500mls water daily
c) single drench with 1000mls water at the start
d) lightly sprayed with 100mls of water on days 2 and 3 then drenched daily from day 4

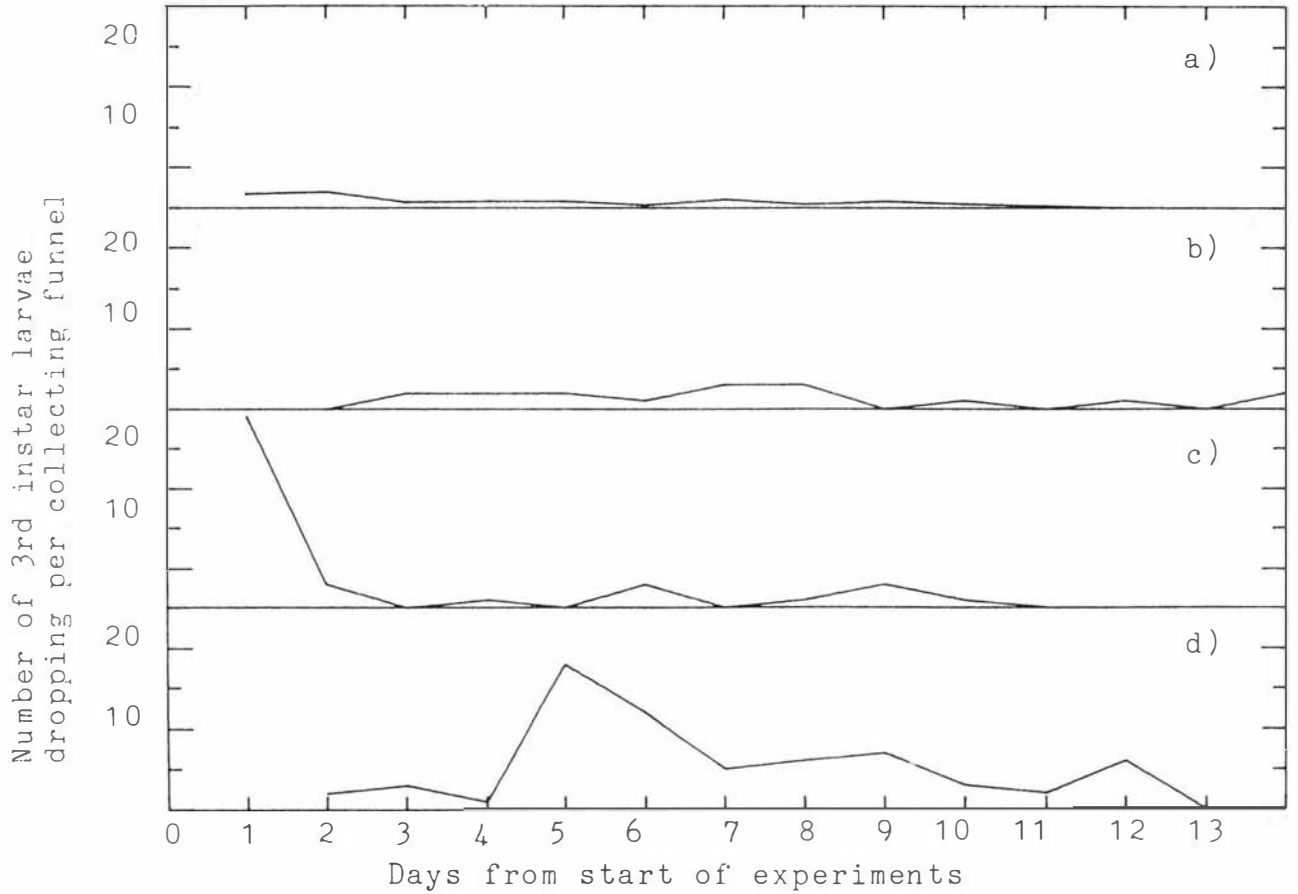
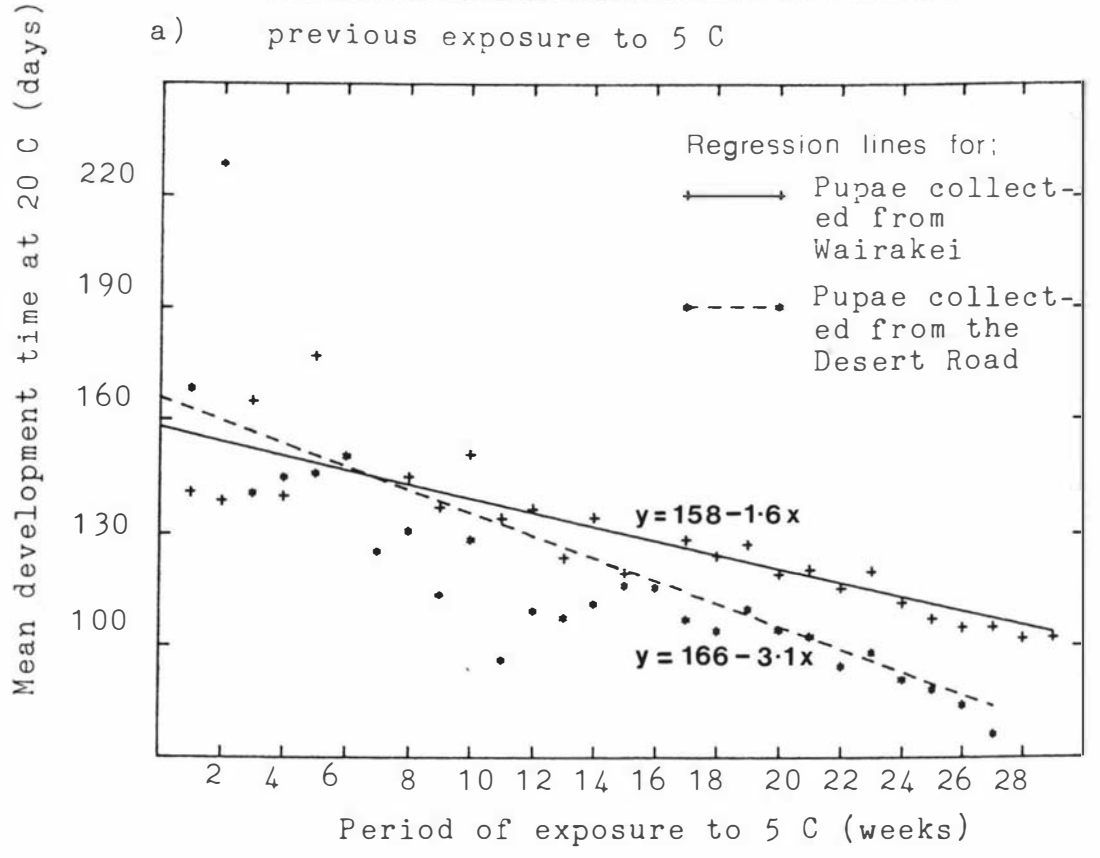
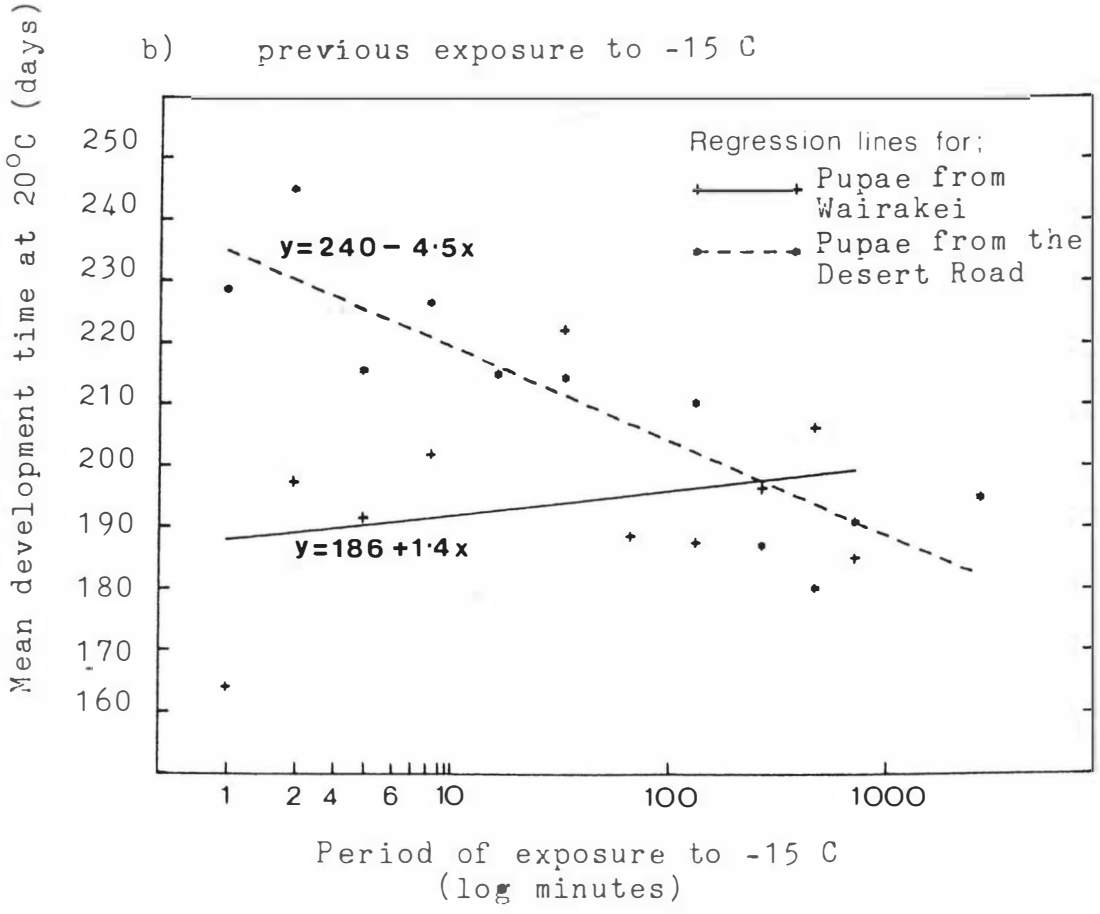


Figure 3.11 Relationship between pupal development time at 20 C and previous exposure to cold temperatures





CHAPTER FOUR: MODELLING THE SEEDFLY POPULATION

4.1 Introduction

Seedfly development rates in response to temperature obtained in laboratory conditions are used to construct a model of the pre-oviposition period and oviposition at Redwoods Forest. The models are compared with the data collected during the sampling programme at the field site during the study. The degree of synchrony between seedfly emergence and ragwort flowering which is seen as an important factor affecting seedfly infestation levels of ragwort (Fig.4.1) is also predicted.

4.2 The pre-oviposition period

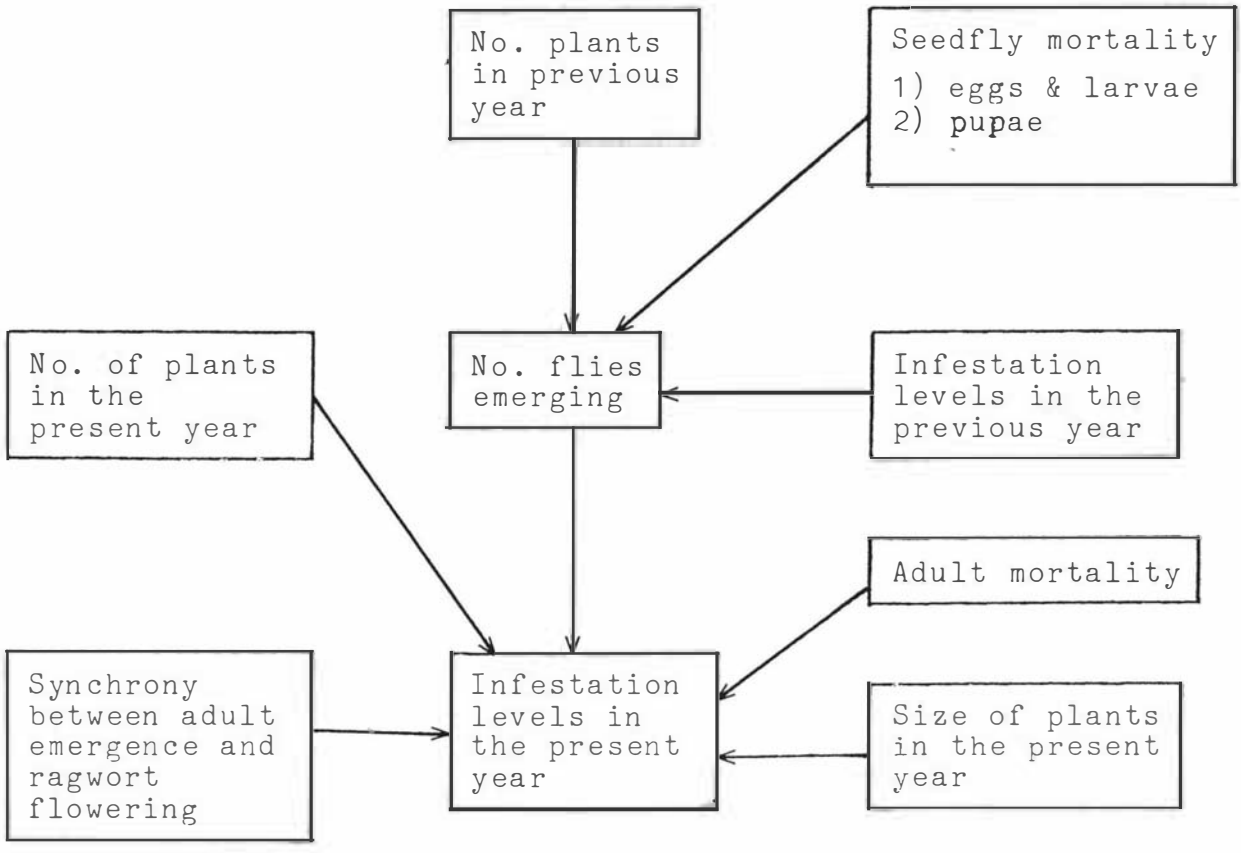
Ovary development in ragwort seedfly requires 232 day degrees above the threshold temperature for development of 4.14C. This was calculated from the regression of ovary development rate against temperature (Fig.3.4) Day degree summations were calculated from the field temperature data according to the following formula.

$$\left[\frac{\text{max temp} + \text{min temp}}{2}\right] - 4.14C$$

This method, which is valid over intermediate temperatures (Wagner et al., 1984), was considered suitable for this model since the daily minimum temperature at the field site was always above the lower threshold for development.

The emergence curves at Redwoods Forest were transformed into

Figure 4.1 Factors affecting seedfly infestation of ragwort seedheads at Redwoods Forest



curves for gravid females (Fig.4.2a+b) by summation of the day degrees from female emergence to 233. From this the number of buds per female at each sampling date could be calculated from the data collected at the field site (Table 4.1). This represents the number of buds available at the time of sampling and assumes no mortality and balanced emigration and immigration in the adult seedfly population.

4.3 Seedfly oviposition

During the field studies flies were able to pass from egg to second larval instar or first to third larval instar within the 14 day sampling interval. As the total duration of the egg and first and second larval instars is 20 days the oviposition curve was calculated from the sum of these stages obtained from each fortnightly sample. According to this method oviposition coincided with the start of ragwort flowering in both 1982 and 1983 (Fig 2.11a+b). The validity of this method can, however, be checked by summing the day degrees for development backwards from the third larval instar stage.

The day degree summation from egg to the third larval instar leaving the plant was 629. It was calculated from the regression equation for development rates against temperature (Fig.3.6). This was then reduced by the mean ratio of 0.383 (the time from oviposition to the beginning of the third larval instar divided by the time to the end of the third instar (Table 4.2)). This gave an estimate of the day degrees from oviposition to the start of the third larval instar of 241. The only other published

Figure 4.2a Cumulative percentage curves of seedfly and ragwort seedhead development stages at Redwoods Forest in 1982/83

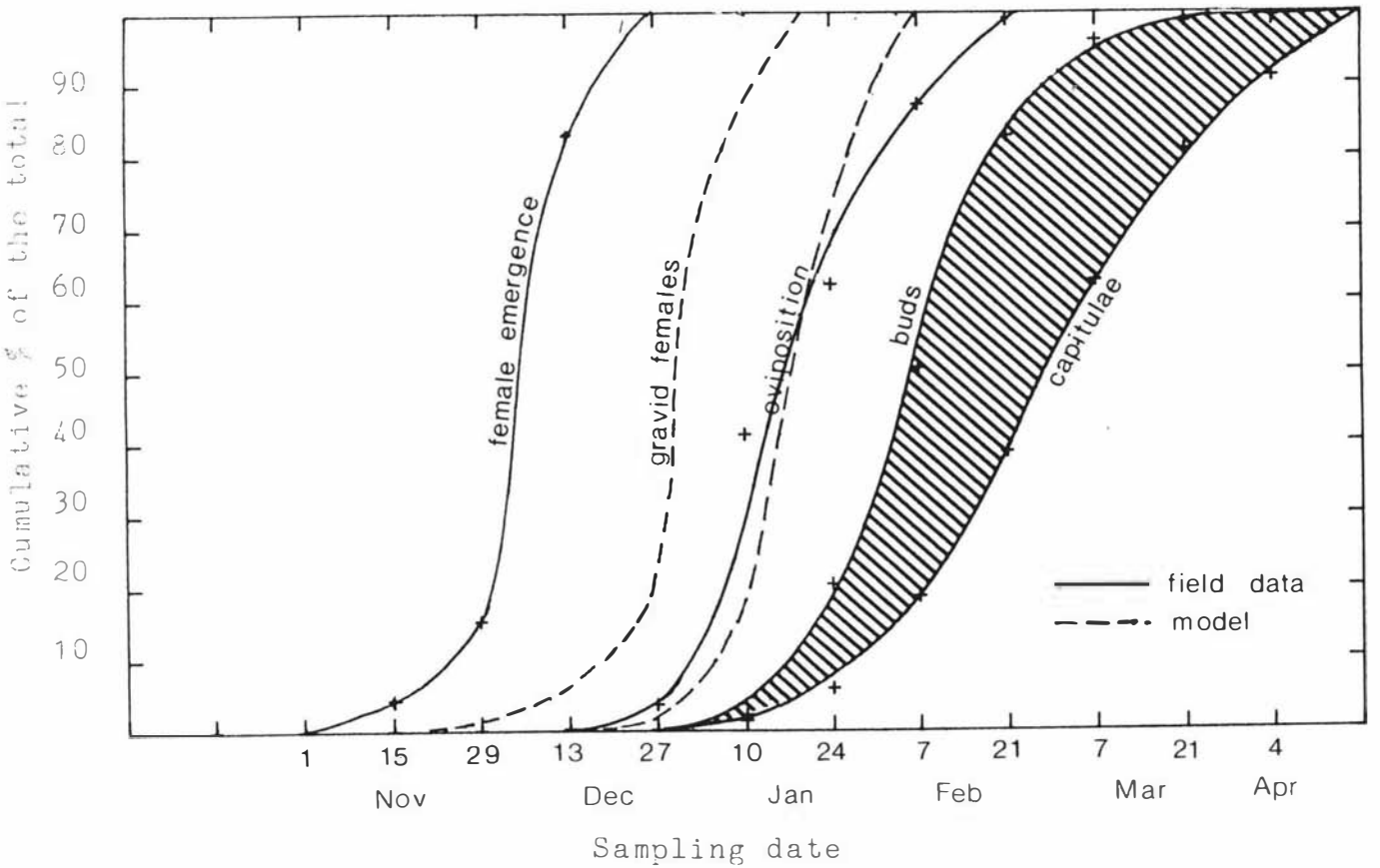


Figure 4.2b Cumulative percentage curves of seedfly and ragwort seedhead development stages at Redwoods Forest in 1983/84

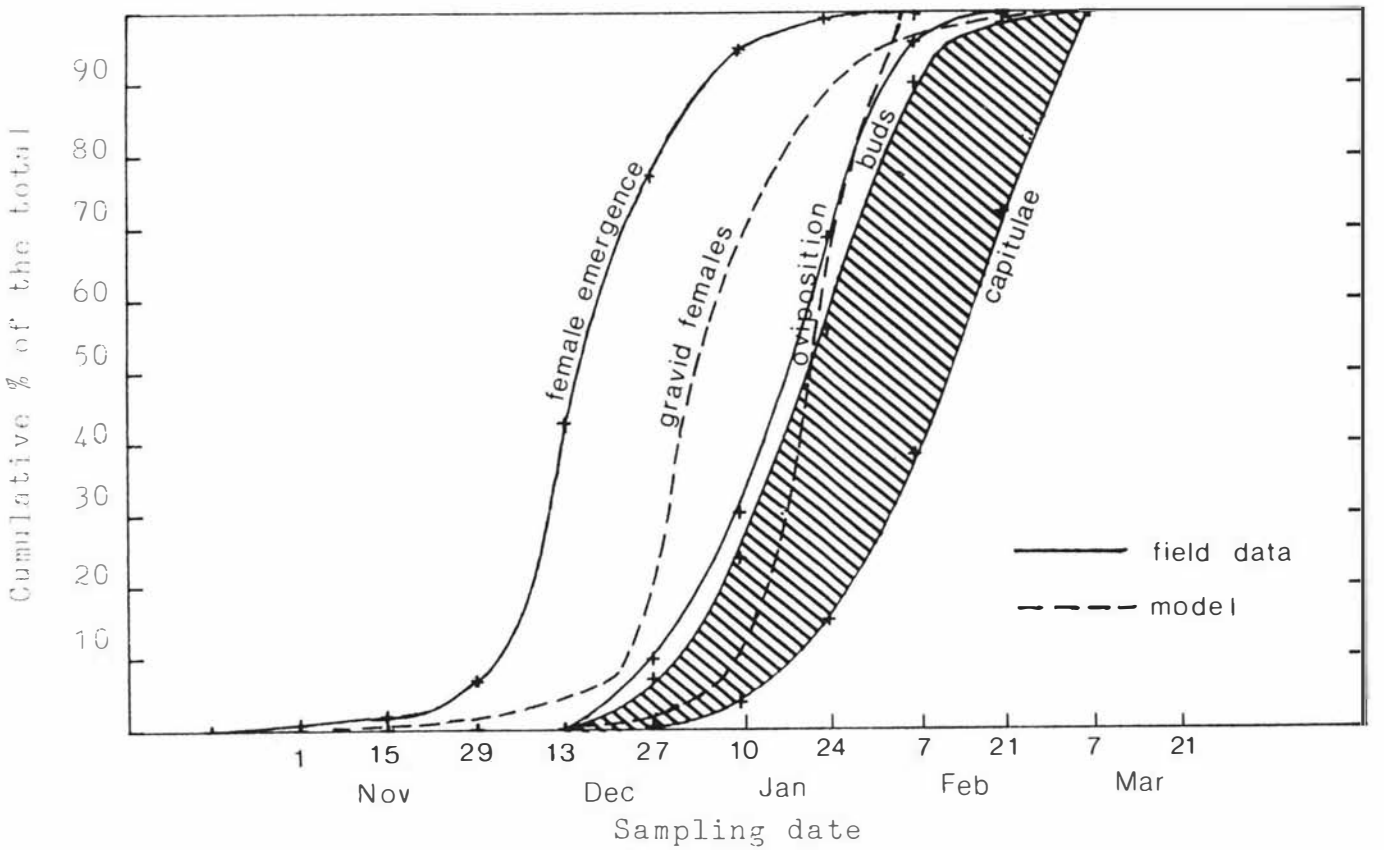


Table 4.1 Ragwort buds per ovipositing female at the Redwoods Forest field site

Date	Buds/female 1982/83	Buds/female 1983/84
12/12	0.14	0.03
26/12	0.22	0.94
9/1	2.98	2.70
23/1	26.38	6.03
6/2	65.17	9.74
20/2	106.73	10.63

Table 4.2 Development times for ragwort seedfly reared in the controlled environment rooms at Plant Physiology Division, D.S.I.R., Palmerston North

	Reared at 15 C	Reared at 20 C
Mean development time (days) from oviposition to end of the 2nd larval instar	20.5	13.9
Mean development time (days) from oviposition to 3rd instar larvae leaving the plant	50.3	37.4
Ratio of time to end of 2nd instar/time to 3rd instar leave the plant (Mean = 0.383)	0.393	0.373

information on egg and larval development rates in the Anthomyiidae is for the seed corn maggot, Delia platura Meigen, which has two generations per year. The number of day degrees above the threshold of 3.9C to complete development was 230 for eggs and larvae (Funderburk et al., 1984).

The day degrees above the threshold for the seedfly were summed to 241 from when the population at Redwoods Forest entered the third larval instar. The latter was taken as the first part of the graph of third instar larvae in Figures 2.9a+b when the number of third instar larvae was increasing and not under the influence of the larval dropping response. The calculation is therefore not affected by the extended duration of the third larval instar measured under laboratory conditions (Chapter 3). The day degrees were calculated as in Section 4.2 as the threshold temperature for development of 3.13C was always above the minimum temperatures experienced by seedfly in the field.

Figures 4.2a+b show the oviposition curves predicted by this model in 1982 and 1983. Although the model showed that in both years oviposition commenced as soon as ragwort oviposition sites became available it also predicted that the oviposition curve in early spring 1983 was not as steep as that estimated from the fortnightly samples. The oviposition period of ragwort seedfly in the field was two weeks. This was calculated as the time between the curve of gravid females and the oviposition curve obtained from the model. This can be compared with data on the oviposition period of the beet fly (Hafez at al., 1970). In this species the

egg laying period decreased with increasing temperature. It was measured in the laboratory as 42 days at 16C and 11 days at 30C.

CHAPTER FIVE: DISCUSSION

5.1 Introduction

The concept of biological control of weeds by herbivores is based on the premise that herbivorous animals affect the abundance of plant populations. Its opponents, however, argue that because there are few instances of depletion of plant populations, herbivores are rarely food limited. Hairston et al. (1960), for example, deduced from this that "producers are neither herbivore limited nor catastrophe limited and must therefore be limited by their own exhaustion of a resource." They conclude that herbivores are controlled by the depredations of natural enemies in a density dependent fashion. Andrewartha and Birch (1954), on the other hand, believe that density independent factors such as weather and other features of the physical environment control the abundance of animal populations.

Depletion of green plants is not, however, a necessary corollary of food limitation in a herbivore population. Not all plant parts are edible (Bernays, 1981) and herbivory may be reduced by the production of deterrents or escape in time and/or space. Plant populations may also persist despite high levels of herbivory because of reproductive strategies involving high seed production or vegetative propagation. While acknowledging that herbivores can be food limited but not limit their host(s) Crawley (1983) suggests that this food limitation is an essential criterion for weed management. He states that "if herbivores are not food limited, it is most unlikely that they could increase to sufficiently high densities to bring about the required dramatic

reductions in the numbers of weeds." Huffaker (1964) also states that "an (biological control) insect must be capable of decisive destruction of its host plant, thus determining the latter's abundance." However, there are many who believe that herbivores have a greater effect on plant populations than that indicated by the low level of consumption. Mattson and Addy (1975) suggest that herbivores control the function of whole ecosystems by regulating nutrient cycling and stimulating the redistribution of nutrients within the plant from stored reserves. Smiley (1985) suggests that chemical defence is only one of a number of possible elements that mediate plant-insect coevolution while Janzen (1970) argues that seed predation can be linked to the species composition of plants in tropical forests.

The more obvious ways in which ragwort reduces the impact of herbivores include alkaloid production, vegetative reproduction and the production of numerous seeds of high germinating capacity. This study, however, has focussed on the escape in time of a significant proportion of ragwort seeds from predation by the ragwort seedfly. The contribution of the ragwort seedfly to an integrated control programme for ragwort is discussed and examples of successes using this approach are given. The value of seed predators as biological control agents of weeds in general is also discussed.

5.2 Ragwort control at Redwoods Forest

The lack of synchrony between seedfly emergence and flowering of ragwort during this study is one of the major factors reducing the

impact of the seedfly on ragwort seed production. The pre-oviposition period predicted by the model was shorter than that observed in the field. However, there are two factors which may affect the validity of the model. Firstly, the number of females reared to maturity was low. Mortality was high despite efforts to reduce handling. Hoy (1960) considered pupal damage responsible for emergence of deformed flies and many flies emerged in this study with wing deformities probably as a result of the collecting methods. This may also account for mortality in the flies released into the cages. Humidity in the controlled environment rooms may have affected mortality but this was not accurately measured. Copulation was unlikely to have been an limiting factor in ovary maturation since females were mated soon after emergence and those not mated reached maturity at a similar age.

The second factor influencing the rate of ovary development in the laboratory was diet. The additional diet given to adults reared in the controlled temperature rooms could have resulted in accelerated ovary development. However, when it was not provided females failed to reach maturity and this has occurred during previous attempts to rear seedfly adults (P.Syrett, pers.comm.1983) and also Hylemyia species (Zimmerman et al., 1984). The diets provided represented a range of proteins and carbohydrates similar to that recommended for anthomyiids by Singh (1977) and those found to be necessary for development by researchers on the beet fly (Hafez et al., 1970), the cabbage root fly (Finch, 1971), the wheat bulb fly and the onion fly (Coaker

and Finch, 1973). There is no requirement for ragwort flowers for ovary development and no significant difference between development times in the presence or the absence of ragwort flowers. A pre-oviposition period in the absence of ragwort flowers is therefore not likely to affect ovary development in the field. However, in this case, the period appears to be extended in the field by the absence of oviposition sites and this is supported by the fact that females were able to lay eggs on transplanted plants which flowered before the field plants.

The pre-oviposition model predicted that competition for oviposition sites was high when ragwort first flowered and data on multiple infestation and fecundity supported this. Fecundity was low in both summers. 12•9 eggs were laid per female that emerged at the site in 1982/83 and 3•9 in 1983/84. There was a tenfold increase in the number of flies emerging from 1982/83 to 1983/84 which increased competition for oviposition sites. Density and size of ragwort was similar in both years but a combination of the increase in the number of flies and lower fecundity in 1983/84 resulted in a doubling of infestation levels from 10% in 1982/83 to 20% in 1983/84.

In 1982/83 the carrying capacity of ragwort far exceeded the egg laying potential of seedfly (32 eggs per batch) with 404 seedheads produced by ragwort per female emerged. In the following year, however, there were 39 ragwort seedheads per seedfly female that emerged at Redwoods Forest site. Oviposition behaviour may also have been affected by temperature, weather conditions and mating

activity. Hafez *et al*. (1970) found that fewer eggs were laid by beet fly females at cooler temperatures. It is also likely that the retricted number of oviposition sites may have affected egg production. Coaker and Finch (1973) found that ovary maturation in the cabbage root fly does not depend on chemostimulation from the host plant but the nearer to maturity females are when they receive a chemical stimulus the more eggs they lay.

The high percentage of multiple infestation at the beginning of spring also suggests competition for oviposition sites. A maximum of 22% of the seedheads containing seedfly were multiple infestations in 1982/83 and 16% in 1983/84. The highest recorded loss of eggs due to multiple infestation was 9•4% and 14•3% in the early December samples in 1982 and 1983 respectively.

A uniform egg distribution was recorded in *P.jacobaeae* in early December and January. This is the optimal strategy for the seedfly since only one egg per seedhead survives to pupation. Zimmerman (1979, 1980) saw the uniform egg distribution observed for *Hylemyia* in *P.foliossisimum* at least, as evidence for the existence of an oviposition deterring pheromone (ODP) associated with the egg although the pheromone has not yet been isolated. Certainly, egg recognition has been demonstrated to be facilitated by the presence of an ODP in at least 24 species of phytophagous insects (Prokopy, 1981) and usually occurs in situations where there is larval competition for resources.

The cost of pheromone production is high (Prokopy, 1981) and for

this reason Zimmerman (1982) argued that ODP production in Hylemya species was facultative. He postulated that an ODP was not deposited when the female was ovipositing on I.aggregata since high egg mortality due to dessication was reducing competition for food reserves within the seedhead. As a result, the incidence of multiple infestation was high (25%).

Although a predominantly uniform egg distribution was recorded for P.jacobaeae and females were observed wiping their abdomens on seedheads after oviposition the evidence for an ODP is equally scant. The high levels of multiple infestation recorded in this study could have resulted from lowered thresholds for oviposition so that females oviposited in spite of an ODP or the presence of another egg. Prokopy (1972) found that the physiological state of female apple maggot flies (Rhagoletis pomonella) has a strong influence on the degree of responsiveness to ODPs. Females deprived of oviposition sites for two days were more likely to oviposit in ODP-marked fruit than non-deprived females. Whether this occurs in the ragwort seedfly is, at present, largely speculative.

It is likely that the number of buds suitable as oviposition sites for seedfly was overestimated in this study. The subjectivity involved in this estimation was reduced by determining the size of buds recently infested but it was too time-consuming to measure every bud during the data collection and the chemical cues involved in the choice of oviposition sites were not investigated. Such an overestimation affects the calculation of the type of

distribution of seedfly eggs. An overestimation of buds also reduces the estimates of infestation levels in early spring which would be expected to be higher than the 18% and 36% observed in 1982 and 1983 respectively if competition for oviposition sites was high at this time.

Other factors affecting seedfly fecundity and infestation levels of ragwort are adult mortality, emigration and immigration but no information was obtained about these during this study. No direct comparison could be made between emergence and sticky trap catches since the latter does not provide an absolute estimate of adults and is biased toward males. In addition nothing is known about the dispersal capabilities of P.jacobaeae but Finch and Skinner (1975) found that the dispersal range of the cabbage root fly was within a 2-3 kilometre radius of the release site. This represented a dispersal rate of 100m per day although only 38% of the males and 15% of the females released were recaptured.

Mortality at the egg,larval and pupal stages will also contribute to the potential rate of increase of the seedfly population. The cause of death of larvae in seedheads with multiple infestations is unknown but cannibalism cannot be ruled out. Inoue (1983) found that 64% of first nymphal feedings in the assassin bug, Agriosphodrus dohrni Signoret, were cannibalistic and this was reduced to 0·04% in the third instar. Although his comments relate to a predaceous bug, Inoue believes that most cases of cannibalism are attributable to resource limitation. He suggests that it may function as a means of providing an easily accessible

nutritional source for the immature stages which have low locomotive ability. The assassin bug nymphs are similar to seedfly larvae in that they are largely confined to the sites where oviposition took place. Cannibalism was reduced in this species by modification of the female oviposition behaviour. More than half the overlapping ovipositions took place on the same day which resulted in 95% of the larvae escaping cannibalism.

Zimmerman (1980) found that single Hylemya females repeatedly oviposit in the same seedhead and believes that the first hatched larva does not destroy the others since it would be detroying its own siblings. It is not known whether P.jacobaeae females oviposit in this way but it is likely that availability of resources in the seedhead is limited. Feeding and excretory products of older larvae damage the unopened florets essential for development of first instar larvae. Larger seedheads resulting from fasciation were recorded supporting three third instar larvae.

Survivorship was calculated from the area under graph of numbers of each stage at each sampling date. The area is affected by the duration of the sampling interval. Increasing the frequency of sampling would have more accurately pinpointed the peaks of each stage. The survivorship curves presented are also steepened by the probable under-estimation of first instar larvae because of the difficulty of finding the larvae within the florets when the frozen seedhead had thawed. The disparity between estimates of pupae collected in the trays and third instar larvae within

seedheads in 1984 suggests that third instar larvae are also under-estimated. The duration of the third larval instar used to calculate the number surviving to this stage was artificially extended by the dry conditions in the controlled environment rooms.

There is certainly some evidence, both from the field studies and experimental work, that the duration of the third larval instar within the seedhead is variable. Third instar larvae were experimentally shown to leave the plant in conditions of high surface moisture and this would be an advantage to a small animal at risk from dessication. Larvae have been observed dropping from the plant and, also on one occasion when fine rain was falling, using surface moisture on the leaves and stem of the plant to slide to the ground. This behaviour was responsible for the high estimate of third instar larvae at Redwoods Forest which have left the seedhead as sampling coincided with periods of rain. It is expected that high mortality in third instar larvae similar to that observed in the controlled environment rooms could occur if there was a prolonged dry period in late summer and autumn. This is not normally the case within the seedfly's present range in New Zealand.

Information on pupal survival over winter in 1983 are contradictory. Estimates of pupal density in autumn and spring in 1983 by soil sampling were 66% lower than the corresponding estimates of third instar larvae within seedheads prior to pupation and the number of adults caught by emergence traps. The

pupal mortality calculated from the third instar larvae within seedheads to those emerging the following spring was 14.3% compared to 2•5% for the differences in soil sampling estimates of pupae in autumn and spring 1983. Unfortunately the efficiency of soil sampling was not measured. There were twice as many pupae collected in trays as third instar larvae estimated within seedheads in autumn 1984. If the number of third instar larvae within seedheads were under-estimated to the same extent in autumn 1983 the estimate of pupal mortality during the following winter would then be 57%.

Pupae are able to withstand very cold temperatures in laboratory conditions but do not survive dessication (Miller, 1970). Other factors affecting pupal survival over winter were not tested but queen ants of Cheloner antarcticus found in the sand trays did not prey on the third instar larvae or pupae when given the opportunity.

5.3 Ragwort seedfly and the biological control of ragwort

The lack of synchrony found in this study was also alluded to by Kelsey (1955) during field observations 7 years after the release of seedfly at Redwoods Forest. He noted that although the late flower crop accounted for approximately 12•5% of the total flower crop there were no adult flies to carry on infestation. A lack of synchrony was also noticed by Hoy (1958) when 4000 pupae were collected from the site for shipment to Australia. High levels of infestation were recorded soon after seedfly release but a period of adjustment to Southern Hemisphere seasons may have been

necessary as adults were originally released in autumn. Unfortunately it is not known whether a similar lag between emergence and oviposition is the norm in the fly's country of origin. Infestation levels vary throughout England and are higher in the north. Infestation levels were also low at the Desert Rd site but the degree of asynchrony at this site is unknown. It is possible that seedfly biotypes with later adult emergence may occur within the fly's native range. However, the timing of flowering was variable in this study and it is not known how climate, rainfall and soil type affect this. It is likely that ragwort biotypes also exist, further complicating the situation.

The ragwort seedfly's potential as a biocontrol agent of ragwort would be greatly enhanced if two generations per year were possible as it would enable the fly to infest some of the later developing flowers. The spread of ragwort flowering extends over 3-4 months but seedfly is not able to complete its life cycle in less than 9 months at constant 15C which represents the average summer temperatures in the field. Even if seedfly were able to infest every seedhead, uneaten seeds from seedheads infested by seedfly will germinate and it is not known if ragwort compensates for seed predation by reducing its allocation of resources to this form of reproduction.

The contribution of P.jacobaeae to the integrated control of ragwort will depend on competition with other species for seedhead resources. In particular, competition with the closely related P.seneciella may be intense. These two species coexist in

their country of origin but it is not known in what proportions and to what extent the infestation levels are affected by the competition. Frick (1969) states that the pre-oviposition period in P.seneciella is 7 to 10 days but does not elaborate under what conditions this was measured. If this is an estimate at average spring temperatures then the population may be expected to be even further out of synchrony with the ragwort population if released into New Zealand and may explain why it failed to establish here. However, in England the shorter pre-oviposition period of P.seneciella may serve to reduce the overlap of the oviposition period of the two species. Seedfly may also be in direct competition with cinnabar moth larvae which prefer to feed on the developing ragwort buds (Dempster, 1982).

Most biological control programmes at present follow the innoculative approach, that is, herbivore populations are released and left to increase to effective levels on their own. The alternative is the inundative approach where relatively short term control is achieved by releasing a biocontrol agent in heavy concentrations (Tisdell et al., 1984). This is not self perpetuating and may be costly. It certainly would not be considered worthwhile for the ragwort seedfly. Although easy to collect and transport seedfly pupae can easily be damaged or dessicated. A high proportion of the initial releases, both in New Zealand and overseas, were unsuccessful and rearing adults has proved to be difficult. Further research in this area would be required before large scale releases could be considered feasible.

There is evidence that biological control of ragwort may more effectively be accomplished by a cinnabar moth/flea beetle combination. The ragwort flea beetle Longitarsus jacobaeae which feeds on the roots over winter is expected to give good control in conjunction with either grazing or cinnabar moth defoliation (Hawkes and Johnson, 1976). Ragwort's regenerative capacity is dependent on it root carbohydrate reserves so that root damage is likely to seriously weaken the plant.

Climatic stress may enhance the effect of the cinnabar moth Tyria jacobaeae as a biological control agent of ragwort. On the east coast of the USA defoliation by the cinnabar moth led to a decline in plant numbers because regenerating rosettes were killed by frost at the critical stage of recovery (Harris et al., 1976). Autumn frosts damaged regrowth flowers after defoliation by Tyria in a population studied by Islam (1981) in England. Cox and McEvoy (1983) state that the full potential of the cinnabar moth as a biocontrol agent will be apparent in years with below average summer rainfall as this decreases the capacity for ragwort to compensate for defoliation.

Farming practices may also work against the spread of ragwort. Smith (1982) states that there are many farms where ragwort is kept in check with relatively little annual effort in time or cost. Provided that a vigorous and competitive pasture sward can be developed and maintained, ragwort can be kept in check. He cites lack of finance as a major factor leading to neglect of persistent control of ragwort.

5.4 Theories and practice of biological control of weeds

The insects that have been highly effective in the biological control of weeds include a stem borer (*Cactoblastis* species, Lepidoptera: Pyralidae, on *Opuntia*); plant suckers (3 species of *Dactylopius*, Hemiptera: Dactylopiidae, on *Opuntia* species); leaf feeders (*Chrysolina quadrigemina* Suffrian, Coleoptera: Chrysomelidae, on St John's Wort, *Hypericum perforatum* L. and *Metrogaleruca obscura* DeGeer. (Coleoptera: Chrysomelidae) on black sage, *Cordia macrostachya* (Jacquin)). A gall insect, *Procecidochares utilis* Stone (Diptera: Tephritidae) was effective against crofton weed, *Eupatorium adenophorum* Sprenge and *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae) a stem and leaf feeder has substantially reduced alligator weed, *Alternanthera philoxeroides* (Martius) (Julien, 1982). However, 60-75% of introductions recorded by Julien (1982) have been unsuccessful and DeBach (1974) cites that 75% of the 41 projects for which there was published information achieved a measurable degree of success. Eight had been rated as a complete success, 9 as substantial successes and 14 as partial successes.

Insect seed predators are often favoured biological agents because of their host specificity but their success as biological control agents of weeds is generally low. Table 5.1 shows the type of control obtained by seed predators as presented in the world catalogue of weed biocontrol programmes (Julien, 1982). In addition, 20% of the 120 weed species (representing 34 families) which have been the targets of biological control programmes (Julien, 1982) belong to the family Asteraceae (=Compositae).

Table 5.1 Effectiveness of seed predators as biological control agents of weeds (from Julien (1982))

Weed and its origin	Control Agent	Status and degree of control
Compositae Carduus acanthoides L. (plumeless thistle) Eurasia, N. Africa, W. Asia	Rhinocyllus conicus Froelich (Coleoptera; Curculionidae)	Canada: thistle stands are reportedly less dense. USA: destroys some of the seeds but does not reduce thistle density.
Carduus nutans L. (nodding thistle) Europe, Asia	"	Canada: reduced thistle to less than 10% of its former density. Less effect when thistle is growing without competition. USA: thistle reduced 90-99% at some release sites.
Carduus pycnocephalus L. (slender winged thistle) Europe, Asia	"	NZ: expect good control USA: high rates of flowerhead infest-ation and seed destruction but little effect on overall weed density where weevils have been long established
Carduus tenuiflorus Curtis (winged thistle) W. Europe	"	NZ: expect good control
Silybum marianum L. (milk thistle) Mediterranean, S.W. Europe	Rhinocyllus conicus Froelich (Coleoptera: Curculionidae)	USA: 90% or more of flowerheads attacked in some sites but little direct seed destruction or effect on plant density

Table cont...2

Weed and its origin	Control Agent	Status and degree of control
Xanthium spinosum L. (Bathurst burr) Cosmopolitan	Euaresta bullans Wiedemann (Diplera: Tephritidae)	S. Africa: infests up to 20% of burrs
Xanthium strumarium L. (noogoora burr) Cosmopolitan	Euaresta aequalis Loew. (Diptera: Tephritidae)	Australia: giving no control of the weed
Leguminoceae Ulex europaeus L. (gorse, furze) W. Europe	Exapion ulicis (Forster) (known also as Apion)	Hawaii: effect negligible USA: no detectable impact except at one interior site Australia: has not affected spread of gorse in Tasmania or Victoria
Verbenaceae Lantana camara L. tropical America	Epinotia lantana Busck (Lepidoptera: Tortricidae)	Australia: minimal seed reduction
	Ophiomyia lantanae Frogatt (Diptera: Agromyzidae)	S. Africa: contribute. little to seed destruction
Boraginaceae Cordia macrostachya (black sage)	Eurytoma ativa Burks (Hymenoptera: Eurytomidae)	Mauritius: high percentage of seeds are affected but part played is unclear
Linstis dalmatia L. Linaria vulgaris L. (toad flax) Europe	Brachypterolus pulicarius (Coleoptera: Nitidulidae) and Gymnaetron antirrhini (Coleoptera: Curculionidae)	In combination give 80-90% seed reduction. Apparently the reason for the decline in seriousness of the weed
Orobanchaceae Orobanche cumana Walter Eurasia	Phytomyza orobanchia Kaltenbach (Diptera: Agromyzidae)	Yugoslavia: can achieve considerable control by destroying up to 96% of seeds
Orobanche ramosa L.	"	USSR: good control achieved but problems with synchronising P.orobanchia development of the weed

Table cont...3

Weed and its origin	Control Agent	Status and degree of control
Orobanche ramosa L.	"	Yugoslavia: can achieve considerable control by destroying up to 96% of seeds
Protaceae Hakea servicea Shrader (silky hakea) Australia	Erytenna consputa (Pascoe) (Coleoptera: Curculionidae)	S, Africa: significant seed destruction

These characteristically produce numerous small seeds which are easily dispersed so that the potential for predators which feed on the seeds once they have left the plant to reduce plant populations is therefore also limited. Burdon and Marshall (1981) have also recorded that asexual reproduction occurred in 60% of the 40 target species they surveyed.

Poor synchronization of damage has also been recorded in a number of biological control programmes involving seed predators. Waterhouse (1967) suggested that lack of synchrony between the seedfly Euaresta aqualis Loew. and the occurrence of seeds of the Noogoora burr (Xanthium pungens Wallr.) at the right stage of development is responsible for the low level of infestation of this weed. Forster (1977) found that pod infestation of gorse, Ulex europaeus L. by the seed weevil Exapion ulicus Forster (formerly Apion) over twelve months was 19•5%. The weed flowered throughout the year but infestation declined from a maximum of 44% in spring. Popay et al. (1984) found that maximum egg laying of the nodding thistle receptacle weevil (Rhinocyllus conicus) did not coincide with maximum flower production in its host Carduus nutans. This resulted in almost 100% infestation of the first flowers but declined to approximately 5% in February 1983 and 20% in February 1984. The few weevils remaining ($0•2/m^2$) in March 1984 were able to infest a high proportion of the low number ($0•05/m^2$) of flowerheads available. The highest overall infestation recorded was 75•9%, which allowed 2000 seeds per m^2 to escape predation.

Successes in biological control of weeds have often resulted from a combination of physical and biological factors as has already been described for ragwort. Variations in soil, water, disturbance of the habitat and cropping practices all influence abundance of weeds (Andres et al., 1976) and the level of control is not always similar throughout the range of the weed. For example, the tingid Teleonomia scrupulosa causes death of Lantana only if heavy attack is coupled with severe stress, i.e. prolonged drought (Schroeder, 1983). Diseases associated with the cactus feeding moth Cactoblastis cactorum assisted in the successful control of prickly pear in Australia (Wilson, 1964). Defoliation of Hypericum rosettes in the autumn and winter by the larvae of Chrysolina quadrigemina contribute to the death of the plant during the dry summer season in California. The defoliated plants did not have time to redevelop an adequate root system before the summer drought (Huffaker, 1957). Exploitation of stress factors involving interactions between climate, soil, competing plants and natural enemies is seen as an important strategy in the biological control of weeds (Harris, 1980). Stress, however, acted against prickly pear control in parts of Queensland, Australia as it reduced plant succulence and hence insect attack (Schroeder, 1983).

Determination of weed status is a factor often neglected prior to the initiation of a control programme. Often estimates of the severity of a weed problem come from the costs of control measures employed against the weed and these sometimes do not reflect the real incidence of infestations. Studies on weed cover in New

Zealand include a survey of scrubweed cover of South Island agricultural and pastoral land from 1972-1976 by Bascard and Jowett (1981). Measurements of incidence and cover of 12 herbaceous weed species at improved pasture sites (1/1000 hectares) chosen randomly from four areas in both the North and South Islands also began last summer (Ian Popay and Dave Kelly, pers.comm.1985). This will give some long overdue quantitative data on the weed status of many species including ragwort.

The loss in animal production as a result of weed infestations is often difficult to determine. For ragwort, in particular, alkaloid poisoning of domestic stock is an important factor. Only 287 cases were diagnosed in Animal Health Laboratories in New Zealand from 1973-1984 (Peter Watson, pers.com.1985) which represents 0.05% of the cases investigated. However, this is not likely to represent the true situation as many cases are not reported by farmers or veterinarians. Sub-lethal effects of ragwort poisoning in stock such as poor growth, lowered milk production and quality are also difficult to quantify. Assessment of the weed status of the target species is more complicated where a conflict of interests arises. Commercial blackberry production in Australia is threatened by the apparently illegal introduction of the blackberry rust, Phragmidium violaceum, and Australian graziers and beekeepers have also opposed the C.S.I.R.O. biological control programme for Echium planatagineum L. (Salvation Jane/Paterson's Curse) (P.Syrett, pers.comm.1984).

Quantitative reviews of insect releases are also important. The level of reduction of the target species, more readily precisely obtained for seed predators (Table 5.1), rarely determine the overall effect on the weed population since little is known of the ecology of the plant. For ragwort, in particular, nothing is known about the level of seed reduction required to ensure a significant reduction in the the population, the factors which govern flowering or compensatory growth in response to seed predation.

5.5 Conclusions

This study has shown that assessment of insect releases is important for planning further research in the field of biological control. In addition to determining the potential of P.jacobaeae as a biological control agent of ragwort it also highlights the need for assessing the weed status of the target plant and research into the ecology of the weed with respect to maintenance of the weed population and responses of the plant to herbivore attack.

The prospects for biological control of weeds using insects must also be considered in relation to current theories of how herbivores affect plant populations as outlined at the beginning of this chapter. The aims of weed control and consequently the ways in which control programmes are conducted depends on the expectations of the interested parties. There are those who believe that "control" of the weed population is feasible. That is, plant numbers or biomass can be restrained or reduced to an

acceptably low level. "Depletion" or eradication of the weed may even be considered a realistic aim of such projects despite the rarity of such events (Hairston et al., 1960). Herbicide application, mechanical removal and augmentation of herbivore populations are examples of control measures employed to this end and generally require regular input of labour and money. The alternative is the establishment of a herbivore population that regulates or continually adapts and adjusts the weed population resulting in "long term stabilisation of weed density at a sub-economic level" (Schroeder, 1983). The research input into this approach is higher since the more subtle ways that herbivores and their hosts interact with each other and the physical environment must be investigated. Often the weed population may be regulated at a level that does not justify the cost of a biological control programme. Herbivore releases must therefore be continually reviewed and the "sub-economic level" of the weed appropriate for climate and land use should be determined as soon as possible.

SUMMARY

Populations of ragwort seedfly were sampled fortnightly at two climatically different field sites from October to April in 1982/83 and 1983/84 to determine the potential of the seedfly as a biological control agent of ragwort. Data collection was more intense at the warmer Redwoods Forest site than at the higher altitude Desert Rd site.

Seedfly adults emerged six weeks before ragwort flowered in both years at Redwoods Forest and oviposition coincided with the first appearance of ragwort flowers. The absence of ragwort flowers did not affect ovary development in flies reared in the laboratory but the necessary nutrients must be obtained from sources other than ragwort rosettes. A model based on the ovary development rates of flies provided with artificial diets and a range of flowering field plants showed that the preoviposition period in the field was extended because of the absence of oviposition sites. Females also laid eggs on flowering ragwort transplanted at the field site prior to the onset of flowering in the field population. This lack of synchrony between seedfly emergence and ragwort flowering resulted in competition for oviposition sites when ragwort first flowered. The number of buds available for oviposition per seedfly ranged from 0•14 to 106•7 in 1982/83 and 0•03 to 10•6 in 1983/84. Multiple infestations occurred in 22% and 16% of the seedheads in 1982/83 and 1983/84 respectively. Fecundity was also low in both years. The number of eggs laid per female emerged at Redwoods Forest was 12•9 in 1982/83 and 3•9 in 1983/84.

Overall infestation levels were 10% and 1% at Redwoods Forest and the Desert Rd respectively in 1982/83, and 20% and 3% in 1983/84. Ragwort density was constant at Redwoods Forest throughout the study period with an estimate of 28,788 stems per hectare in 1982/83 and 30,132 in 1983/84. The increase in infestation levels in the second year can be attributed partly to the increase in the number of flies that emerged at this site. Approximately 1,869,000 flies emerged in 1982/83 compared with 195,360 in 1983/84. The number of ragwort seedheads exceeded the egg laying capacity of the seedfly population in 1982/83 with 404 seedheads produced by ragwort during the summer per female that emerged at the site compared to 39 seedheads per female in 1983/84.

Seedfly females oviposited in seedheads with a diameter ranging from 3•8 to 5•8 mm and a disc floret length ranging from 2•7 to 5•6 mm. The distribution of seedfly eggs within seedheads was uniform in early December and January in both years. The mean number of seeds remaining in seedfly infested seedheads ranged from 7•6 to 17•6 and the percentage germination ranged from 28% to 43%.

Seedfly mortality from halfway through the egg stage to halfway through the third larval instar was estimated as 33% in 1982/83 and 60% in 1983/84. Third instar larvae about to pupate leave the seedheads in conditions of high surface moisture so that the duration of the third larval instar may have been extended in the dry conditions of the controlled environment rooms. The number of third instar larvae within seedheads may have been under estimated as a result. High estimates of third instar larvae which had left ragwort to pupate were obtained because sampling coincided with conditions favourable for larval dropping. Temperatures as low as -15C for short periods do not harm

seedfly pupae and temperatures must reach 15-20C to initiate diapause. Estimates of pupal mortality over winter ranged from 14•3% to 57%.

In view of the high numbers of seeds escaping predation, the high germinating capacity and longevity of ragwort seed and ragwort's ability to reproduce vegetatively, seedfly's impact on ragwort populations is considered negligible.

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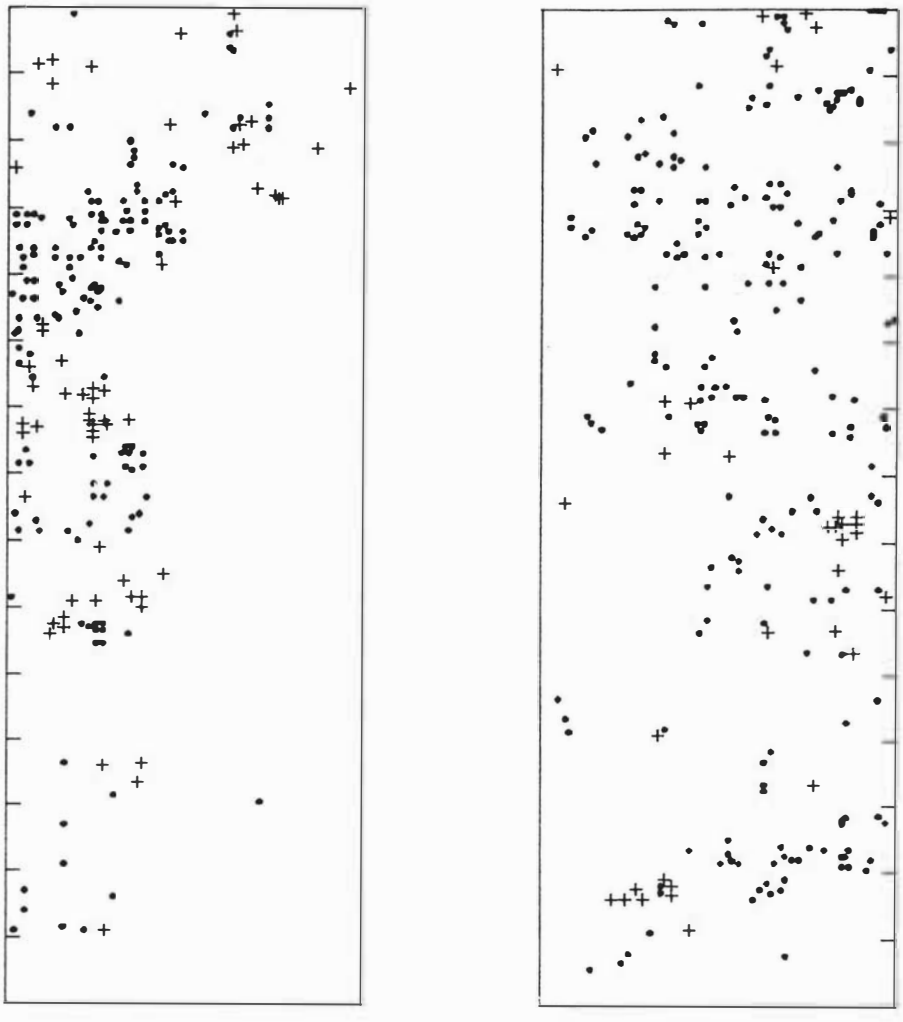
Appendix 1. Distribution map of ragwort rosettes in two $300m^2$ subplots of the Poles Plot

a) 1982/83



Key

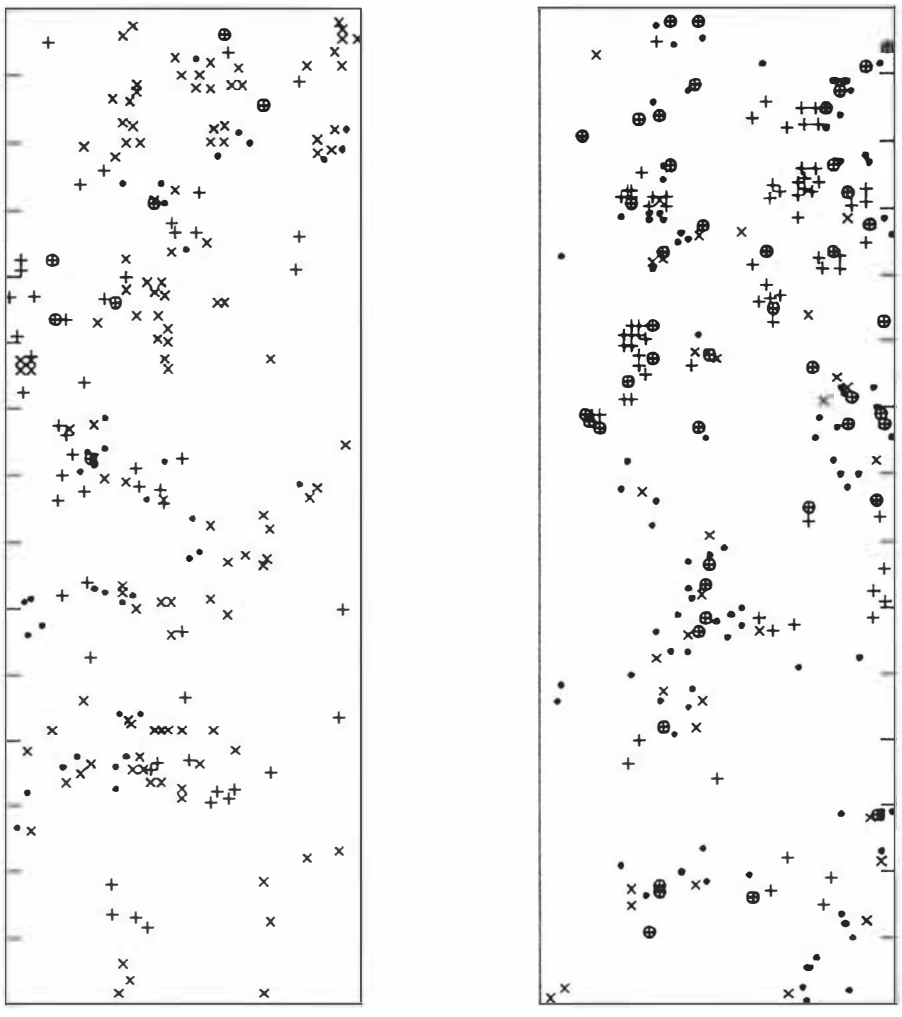
Scale ⌊——⌋ = 2 metres

+ rosettes present in Spring 1982 which failed to flower

• rosettes which flowered over Summer

The map on the left represents the most northern sub plot (see Fig. 2 3)

b) 1983/84



Key

Scale ⌊——⌋ = 2 metres

\+ rosettes present in Spring 1983 which failed to flower
• rosettes which flowered over Summer
⊕ dead stems from 1982/83
x rosettes present in Autumn 1984

Appendix 2. Fortnightly means of daily maximum and minimum temperatures at the Redwoods Forest and Desert Rd field sites

		Redwoods Forest		Desert Rd	
	Sampling interval	Mean daily maximum	Mean daily minimum	Mean daily maximum	Mean daily minimum
	19/10-1/11	15.1	5.5	10.9	2.2
	2/11-15/11	20.1	10.0	20.6	5.4
	16/11-29/11	18.9	11.2	16.4	3.5
	30/11-13/12	18.4	8.3	17.4	1.9
	14/12-27/12	20.0	10.1	20.6	7.9
1982/83	28/12-10/1	22.9	5.6	not available	
	11/1-24/1	21.2	6.4	16.9	2.0
	25/1-7/2	22.2	7.0	20.3	4.1
	8/2-21/2	22.8	8.7	19.0	5.3
	22/2-7/3	24.8	6.0	20.8	5.5
	8/3-21/3	23.0	9.4	19.3	5.6
	19/10-1/11	17.4	10.6	not available	
	2/11-15/11	18.9	9.4	"	"
	16/11-29/11	22.8	3.8	18.0	7.1
	30/11-13/12	20.8	10.3	15.5	3.1
	14/12-27/12	19.7	7.9	18.4	6.5
1983/84	28/12-10/1	20.9	9.9	14.1	4.0
	11/1-24/1	19.9	11.7		
	25/1-7/2	21.8	10.7		
	8/2-21/2	21.7	12.6	not available	
	22/2-6/3	20.5	11.6		
	7/3-20/3	19.6	12.3		

Appendix 3. Numbers of third instar seedfly larvae dropping from cut stems in the laboratory. The period of dark was from 8pm to 6am.

Sampling Time	Number dropping
0900 hours	0
1000	1
1100	6
1200	2
1300	2
1400	3
1500	0
1600	0
1700	0
1800	1
1900	0
2000	0
2100	1
2200	0
2300	2
2400	1
0100	0
0200	0
0300	0
0400	0
0500	1
0600	0
0700	0
0800	0