Frontispiece: Surroundings of the sampling area near Te Kauwhata.

THE ECOLOGY OF THE LUCERNE FLEA,

SMINTHURUS VIRIDIS, IN THE SOUTH-AUCKLAND/WAIKATO AREA

A thesis

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Voor Anny, en mijn ouders

ABSTRACT

Lucerne flea, *Sminthurus viridis* L., is an annual pest in pastures in the Auckland/Waikato area. It damages legumes, particularly white clover, from late autumn until early summer, with a peak in infestation in spring. No research into the seasonality of the lucerne flea (LF) has been done in New Zealand. It was therefore decided to study the bionomics and population dynamics of LF, and aspects related to the damage, caused by LF.

The study showed that the life cycle of LF consisted of three nymphal instars, one adult male and three adult female instars with the males being smaller and lighter in weight than the females. The population of LF built up steadily from March or April onwards to reach a peak in numbers in October or November after which the numbers declined to a low level and LF were only present as diapause eggs. Rainfall in March and April played an important role in the hatching of the diapause eggs and influenced the survival of the first instar larvae. The accumulated temperature (^{o}D) above a zero development threshold of 4 ^{o}C determined the number of generations of LF per year, with five generations in 1982 and four in 1983 in Huntly. Shutting up a paddock for hay production as well as the consecutive cutting of the hay influenced the number of LF in the field. Population dynamic studies of LF showed that LF populations had overlapping stages of development as well as overlapping generations during the study period. Examination of the data with methods, equivalent to the k-factor analysis, showed that LF populations were prone to great changes in number at the beginning of the immature stage of the life cycle of the males and the end of the life cycle of the females, but fairly stable at the time that sexual maturity was reached. The locomotory activity of LF took place during

the day and night and all growth stages were active. No statistically significant relationship could be found between the locomotory activity and temperature or rainfall. The mite, *Bdellodes lapidaria*, a predator of LF, was found in the study sites in Huntly but their numbers were so low that no control effect on LF could be established. Feeding trials showed that adult female LF ate significantly more than adult male LF, and that the feeding rate was highest at 15 and 20 ^{o}C and a photophase of 12 and 16 hours light. Other results suggested that some feeding activity would also occur at night. Severe damage by LF in the field reduced the leaf surface area of white clover plants by up to 40 % during this study, and most severe damage was observed in October and November. Observations in the field and the laboratory established that LF is a wasteful feeder.

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Abbreviations only mentioned occasionally in the text are not included.

b = regression coefficient

cm = centimetre

D = total difference value

^{o}D = degree-days

DI = paddock 1 in Huntly

DII = paddock 2 in Huntly

DM = dry matter

d_i = i^{th} difference value

d.f. = degrees of freedom

F_i = i^{th} adult female instar

g = gram

g.a.i. = gram active ingredient (pesticides)

ha = hectare

K = growth constant for Dyar's rule

KI = paddock 1 in Te Kauwhata

KII = paddock 2 in Te Kauwhata

k_i = i^{th} key-factor (Varley and Gradwell, 1970)

LF = lucerne flea

L_i = i^{th} larval instar

LSA = leaf surface area

M_i = i^{th} adult male instar

m = metre

ml = millilitre

mm = millimetre

µg = microgram

µm = micrometre

n = number of replicates

n.s. = not significant

P = level of probability

p = progression factor for Dyar's rule

r = Pearson product moment correlation coefficient

r_s = Spearman rank correlation coefficient

SEM = Standard error of the mean

s_i = i^{th} negative k_i-value (Manly, 1977a)

x = mean value

X^2 = chi square

z = statistical value to convert r_s into a test value (Freund, 1974).

CHAPTER 1. General introduction and objectives.

Lucerne flea, *Sminthurus viridis* L. (Collembola) is wide spread throughout the world. It originated from Europe and North Africa from which it has been distributed, probably as resting eggs in soil in ballast on ships, or on clover seed (Dumbleton, 1938). It is not generally looked upon as a pest in Europe, but in Australia and South Africa it causes serious damage to leguminous crops and pastures (Wallace, 1974b). Although lucerne flea (LF) has probably been present in New Zealand since the beginning of this century or earlier, it was not looked upon as a serious pest by Dumbleton (1938), even though he found in a national survey that LF was present in both the North and the South Island. An insect survey by Somerfield and Burnett (1976) of lucerne in both the North and the South Island revealed that LF was present in all areas sampled and that high numbers were collected often enough to warrant investigation of its pest status. When this study was started in 1981, the damage done by LF to pastures in spring and autumn had been the cause for farmer concern in the South Auckland/North Waikato region for more than a decade. It had been reported by Ministry of Agriculture and Fisheries advisory officers to the last three Northern North Island Regional Research Committee as the major localised insect problem in the Huntly district. Since then the problem has spread to lowland and hill country pastures on dairy farms near Kaipara Harbour, in Franklin County and in the Te Kauwhata, Huntly and Morrinsville districts (Pottinger, 1983, 1984; Pottinger *et al.*, 1983; East, 1984).

In contrast to countries such as Australia and South Africa where lucerne is one of the major host plants, in New Zealand LF does most damage on clover and is therefore often referred to by farmers as the clover flea or clover springtail. To avoid any confusion, however, the original name of LF, as listed in *Standard names for common insects of New Zealand* (D.N. Ferro *et al.*, 1977), is used in this thesis. The damage done by LF is caused by rasping off or chiselling of the green plant tissue in irregular elongate strips between the veins, leaving one cuticle intact. Although white clover and subterranean clover are preferred host plants, grasses and pasture weeds are attacked as well. The initial damage has a measle-like effect on the clover leaves but severe damage gives the leaves a whitish appearance and can affect pasture production and quality adversely (R. P. Pottinger, pers. comm.). Farmers also state that faecal fouling of the foliage by the LF makes feed less attractive to grazing animals. Due to the farm management practice, dairy farms are more susceptible to LF infestation than other farm types.

The control of this pest in Southern Hemisphere pastures has relied on the use of insecticides (Dumbleton, 1938; Cottier, 1956; MacQuillan, 1975). Although phosmet ('Imidan') and omethoate ('Folmat') are applied in Australia and South Africa respectively, maldison ('Malathion') was the only chemical, registered for control of LF in New Zealand until 1983 (Pottinger *et al.*, 1983). Repeated spraying with maldison was often required in the Waikato. Population resurgences once the maldison control programme was terminated, were frequently experienced. A possible reason for this is the elimination of *Bdellodes lapidaria*, a natural enemy of LF (Townsend *et al.*,

1979).

In New Zealand no research has been carried out on the life cycle and ecology of the LF, but detailed studies of the biology of the LF have been made in England by Maclagan (1932a, b), in Australia by Davidson (1931; 1932a, b; 1934) and in South Africa by Walters (1964). Several other aspects related to LF have been studied in Australia by Wallace (1957; 1967; 1968; 1971; 1973; 1974a, b; 1981). Since many of the studies by the above mentioned authors with reference to the biology of LF were carried out under controlled laboratory conditions, they can be used as background information for this study and need not be repeated. It was therefore decided to study the ecology and population dynamics of the LF under New Zealand conditions, to establish differences between the seasonal history of LF in New Zealand, and Australia, South Africa and Europe, to assess the damage done to clovers in the field, and to qualify some aspects related to the feeding by LF under laboratory conditions.

The following research aims were established:

- to establish the taxonomic status of the LF in New Zealand,
- to develop sampling procedures for LF,
- to establish the total number of growth stages of LF, present in the field,
- to study the bionomics and population dynamics of LF at two locations in the South-Auckland/Waikato area,
- to study the presence in the field of possible predators of LF,

- to assess the damage done by LF to white and red clover plants under field conditions, and

- to study the influence of temperature and photoperiod on the feeding activity of LF under laboratory conditions.

The biological information that was obtained would be used to complement a practical programme to control LF by Ruakura scientists (R.P. Pottinger, pers. comm.).

For the analysis of the data Minitab and BMDP programmes were used on a Digital VAX 11/780 computer. Data not presented in Tables in the respective Chapters can be found in the Appendices. Raw data are held by the author on floppy discs.

CHAPTER 2. Literature review on the biology and ecology of the lucerne flea, *Sminthurus viridis*

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CHAPTER 2. Literature review on the biology and ecology of the lucerne flea, *Sminthurus viridis*.

2.1 Introduction

Lucerne flea, *Sminthurus viridis* L., was first described as a pest by Molineux as early as 1897. After that several articles were written about it, especially in Australia (Lea, 1922; Holdaway, 1927; Newman, 1927; Davies, 1928; Nicholls, 1930; Davidson, 1931, 1932a, b, 1934; Evans, 1937; Swan, 1940; Jenkins and Forte, 1948). These publications described biological aspects of the lucerne flea (LF), the type of damage to the vegetation, host plant range, possible natural enemies and occasionally the geographical distribution. The only detailed articles on the biology of the LF were written in England by Maclagan (1932a, b), in Australia by Davidson (1934) and in South Africa by Walters (1964). Walters (1964) gave a brief description of the morphology of the reproductive organs but it was not till 1976 (Betsch-Pinot) that a proper description of the male and female sexual organs was made. However, other aspects of the LF ecology were investigated in more detail. The possible biological control of the LF has been studied by various authors (Womersley, 1933; Currie, 1934; Jenkins, 1935; Wallace, 1971, 1974a; Wallace and Mahon, 1972; Wallace and Walters, 1974; Ireson, 1982). Most research in Australia, covering the period from 1957 till 1981, has been done by M. M. C. Wallace who has described processes influencing abundance (1957, 1967), the diapause of the eggs (1968), influence of climate and land use on the local distributions (1971), as well as the taxonomy and probable world distribution of the LF (1973, 1974b). Also, as mentioned above, Wallace (1971, 1974) studied the possibility of biological control.

In New Zealand, Dumbleton (1938) described the occurrence of the LF, host plants, a short description of the life history and possible biological control. No further research on the biology has been carried out in this country.

To provide a background to this thesis, all relevant literature will be reviewed in this chapter.

2.2 Taxonomy

The Order Collembola can be subdivided into 2 Suborders: the Arthropleona, with a prognathous head, and the Symphypleona, which have a hypognathous head (Denis, 1965; Wallace and Mackerras, 1970; Richards and Davies, 1977). The lucerne flea belongs to the Suborder Symphypleona. The type species is *Podura viridis* Linnaeus 1758. In 1804 Latreille renamed the insect *Sminthurus viridis*. This has at times been written as *Smynthurus viridis* but is considered an invalid spelling (Ellis and Bellinger, 1973). Extensive keys for the Symphypleona, allowing identification of *Sminthurus viridis* are given by Salmon (1941) and Richards (1968). Scott (1961) provides a pictorial key to the genus *Sminthurus*. Gough (1977) provides a key to the families of Collembola in the British Isles.

Lawrence (1966) redescribed *Sminthurus viridis*, based on Swedish specimens and comparisons with *Sminthurus* spp examined in several countries of Europe, Morocco, South Africa and Western Australia. A comparison was made between *S. viridis* and *S. nigromaculatus* Tullberg, a closely related species. Lawrence concluded that apart from a few differences in coloration he was unable to find a clear way to separate these two forms. On the same grounds Tullberg (1872, *In* Lawrence, 1966)

considered *S. nigromaculatus* simply as a variety of *S. viridis*. Walters (1964), while rearing LF in the laboratory, found that a variety of colours could be found in LF hatched from the same egg batch. He concluded that the difference in coloration was determined more by environmental factors such as temperature, than genetically. The darker forms were found in the field during the coldest months (June and August), while the lighter coloured LF were dominant in April-May and August-September. Wallace (1973) examined collections made in Europe and was able to separate three "species populations" based on general colour pattern, absence or presence of various dark spots on the dorsum of the large and small abdomen and the nature of the pattern on the head between and behind the eyes. He was able to separate *S. nigromaculatus* from *S. viridis* and *S. marmoratus* Stach. Separation of *viridis* from *marmoratus* was less decisive. *S. nigromaculatus* feeds mainly on pollen and dead material while *S. marmoratus* has been observed feeding on green plant material like *S. viridis*.

Although there are only two *Sminthurus* spp described from New Zealand (*S. viridis* and *S. denisi* Womersley) (Salmon, 1941), I have occasionally observed darker coloured LF, closely resembling the description of *marmoratus*. Since both *S. viridis* and *S. marmoratus* have the same feeding habits, and it is difficult to distinguish them from each other, all LF caught during this study are being counted as *S. viridis*.

The taxonomic position of the LF is as follows (Salmon, 1941; Richards and Davies, 1977; Wise, 1977):

Order	Collembola
Suborder	Symphypleona
Family	Sminthuridae Lubbock, 1862
Subfamily	Sminthurinae Borner, 1906
Tribe	Sminthurini Borner, 1913
Genus	*Sminthurus* Latreille, 1804
Type species	*Podura viridis* Linneaus, 1758
Species	*Sminthurus viridis* Latreille, 1804

2.3 Geographical distribution

The Order Collembola contains more than 385 genera and 3570 species worldwide (Salmon, 1964). The first published record of any New Zealand Collembola was in 1894 (Salmon, 1941). Research done by Womersley (1936) brought the total number of described species in New Zealand to 56 and by 1941 Salmon listed 62 genera and 211 species. By 1970 more than 300 species had been described and the number is still rising (Salmon, 1970; Wise, 1970). The family Sminthuridae is worldwide and consists of about 200 described species, subspecies and colour varieties

(Richards, 1968). In New Zealand 21 nominal species are known (Salmon, 1941).

LF originates from Europe (Dumbleton, 1938). Research done by Davies (1928) and Maclagan (1932a, b) showed that LF was present all over the British Isles. The Commonwealth Institute of Entomology (Anonymous, 1956) provides an extensive list with references to the presence of the LF in most countries in Europe. LF was first reported in Australia by F.S. Crawford in 1887 (Molineux, 1897) as a "*Smynthurus*" species. Research in following years confirmed its identity as *S. viridis* and showed the insect to be established in several areas in South West Australia and Tasmania (Lea, 1922; Holdaway, 1927; Newman, 1927; Nicholls, 1930; Womersley, 1933; Davidson, 1934; Evans, 1937; Swan, 1940; Jenkins and Forte, 1948; Swan and Lower, 1951; Wallace, 1957). Wallace and Mahon (1971) assessed the influence of the climate on the distribution of the LF in Australia. The northern inland limit of its distribution agreed closely with the 250 mm isohyet for the growing season of May-October inclusive. The eastern limit in New South Wales and Victoria agreed well with a December-March isohyet of 225 mm.

More detailed research by Wallace (1973, 1974b) in Europe gave the northern limit of LF in Norway and Finland as defined by a line corresponding to localities experiencing 100 consecutive days on which the mean temperature exceeds 10 ^{o}C during the year. This is approximately 63 ^{o}N latitude at sea level, but at lower latitudes at higher altitude. Probably this time interval is necessary to ensure that at least one generation of LF can be completed before the temperature returns to lower levels. The southern limits in Spain and Morocco were defined by a winter (November-April) isohyet of 250 mm. This agrees reasonably well with that outlined by Wallace and Mahon (1971) for the northern distribution of the LF in Australia. A further

listing of references (Anonymous, 1956a; Walters, 1964; Greathead, 1971) indicate the presence of the LF in some parts of Asia, America, Africa, the USSR and both the North and the South Island of New Zealand. In South Africa LF is mainly present in the Western Cape (Walters, 1964). Wallace (1974b) mentioned that the main zones still likely to be invaded by the LF seem to be the western regions of the USA, southern Canada, and parts of Chile and Argentina.

In New Zealand *S. viridis* was recorded as being present by Davies (1928) but it was not mentioned on what information or specimen this statement was based. The first specimens of LF were collected in 1929 at Palmerston North and identified as being *S. viridis* (In Dumbleton, 1938). Dumbleton (1938) surveyed the position of LF in New Zealand. In the North Island LF was widely distributed in area including Bulls, Palmerston North, Dannevirke, Woodville and Eketahuna. Isolated occurrences of LF were recorded near Pokeno and near Maraekakaho. The insect was not found in North Auckland, Thames Valley, Bay of Plenty, Waikato, Taranaki, lower Manawatu or Wairarapa districts. In the South Island the insect was found to be present at several locations in South Canterbury and Otago.

By 1978 LF had become an annual pest in pastures in the Ruawaro and Te Kauwhata districts of the Waikato (R.P. Pottinger, pers. comm.). In the last two years LF has been reported to cause severe damage to clover on farms from the Kaipara and Manukau harbour areas as well as Te Kauwhata, Huntly and Morrinsville (East, 1984; Pottinger, 1984).

2.4 Bionomics

2.4.1 Seasonal history

The seasonality of LF has been studied in Great Britain (Davies, 1928; Maclagan, 1932a, b), South Australia (Lea, 1922; Holdaway, 1927; Davidson, 1933, 1934; Swan, 1940), Western Australia (Newman, 1927; Jenkins and Forte, 1948; Wallace, 1967), Tasmania (Nicholls, 1930; Evans, 1937), South Africa (Walters, 1964) and New Zealand (Dumbleton, 1938).

In Britain LF becomes apparent in pastures around April. The population increases in number until June. The numbers than fluctuate violently before declining in October or later. From January till March LF overwinters (hibernates) in the egg stage (Maclagan, 1932a). Obviously overwintering does not always occur since Davies (1928) found LF active all year around. As opposed to the situation in Europe, LF oversummers (aestivates) in Australia, South Africa and New Zealand. In South Australia, only aestivating eggs are found from January till March (Holdaway, 1927; Davidson, 1934). The hatching of oversummering eggs takes place in April after rainfall. LF is present in high numbers from July till September (Lea, 1922) but, depending on location, can be found as early as March to as late as November (Davidson, 1933). Usually two peaks in numbers are observed, one in May and one in September (Davidson, 1934; Swan, 1940). In Western Australia oversummering eggs start hatching from April onwards (Wallace, 1967) and LF are present in high numbers between May and October (Jenkins and Forte, 1948; Wallace, 1967). Due to a slightly warmer climate the conditions for the LF are more favourable in Western Australia than in South Australia (Davidson, 1934). In Tasmania summer diapause is broken at the end of March. The insects are present till the temperature becomes unfavourable in December and two peaks in numbers are observed, one in July and one in October (Nicholls, 1930; Swan, 1940). Due to a much moister climate in Tasmania than in South Australia the oversummering period is shorter and

may even be absent in wet summers (Nicholls, 1930). In South Africa aestivating eggs start hatching at the end of April or the beginning of May. Two peaks in numbers are observed, one at the end of May and one in October-November, although peaks in May and July have been found as well (Walters, 1964). The New Zealand situation closely resembles that in Tasmania. The first nymphs from diapause eggs hatch at the the end of March. At some locations LF are present in high numbers till November-December after which the insect is present as diapause eggs. In other areas oversummering as diapause eggs does not occur and low numbers of nymphs and adults remain active during the summer months (Dumbleton, 1938).

2.4.2 Biology and morphology

A general description of Collembola is given by Walters (1964), Denis (1965) and Wallace and Mackeras (1970). The biology of LF has been extensively studied by Lea (1922), Holdaway (1927) and Davies (1928). A description of *S. viridis* for taxonomic purposes can be found in papers by Walters (1964), Lawrence (1966), Richards (1968) and Wallace (1973).

(a) Morphology

LF are small soft-bodied insects. The adult is somewhat globular, (Fig 2.1) 2.0 to 2.5 mm long, and the general colour is greenish or greenish-yellow with irregular dark patches on the abdomen (Lea, 1922; Holdaway, 1927; Davies, 1928; Davidson, 1934; Dumbleton, 1938). The colour pattern is variable and may change during the seasons. In

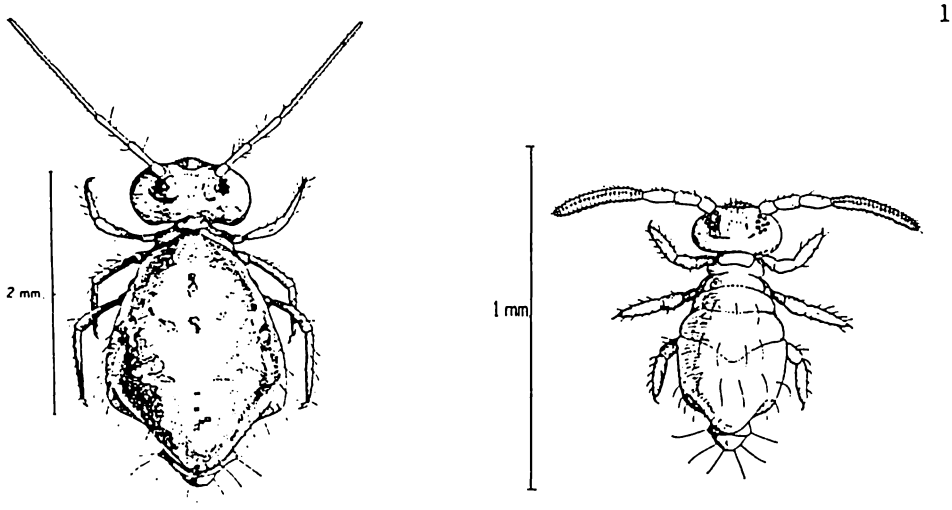

Fig 2.1.a Adult (left) and immature LF. *After* Davidson, 1934.

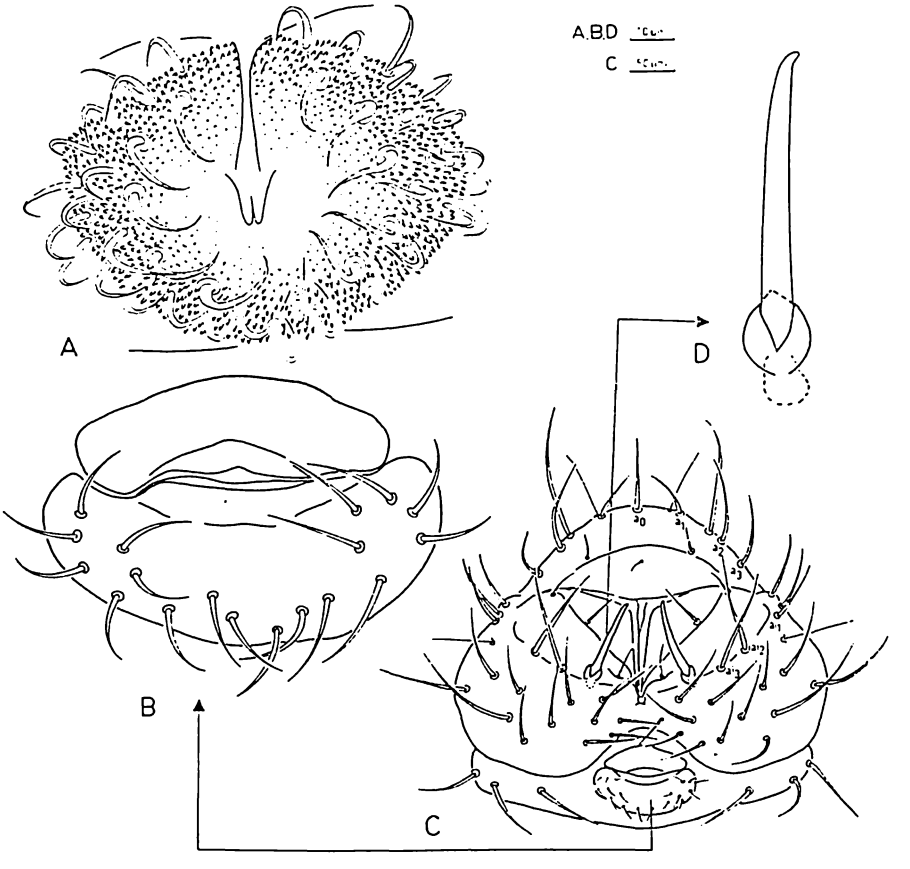

Fig 2.1.b Reproductive organ of the LF. A/ male genital plate; B/ female genital plate; C/ overview female abdominal area; D/ annal appendix. *After* Betsch-Pinot, 1976.

Australia the dark form is more common in winter, with additional black and brown markings, while in spring the yellow-green forms are most numerous (Holdaway, 1927; Swan, 1940). In Britain the greenish-yellow form is most common in spring and autumn (Davies, 1928). Temperature seems to be an important factor in determination of the pigmentation of collembolan species (Rapoport, 1969). The males are shorter than the females (Swan, 1940; Walters, 1964). Although difficult, it is possible to sex adult LF. Davidson (1932a) described the female as having a stout curved spine on each side of the anus, the appendix analis. The male has a number of short bristles surrounding the genital opening. A more detailed description of the morphology and anatomy (Fig 2.1) of the reproductive organs is given by Walters (1964) and Betsch-Pinot (1976). Like most Collembola LF is equipped with two special organs that distinguish it from any other insect Order, a/ a hinged abdominal appendix, a spring, normally carried bent forward under the insect, which, when released, enables the LF to jump up to 30 cm (Davies, 1928; Nicholls, 1930; Davidson, 1934; Swan, 1940), and b/ a collophore, or ventral tube, situated ventrally on the first segment of the abdomen (Nicholls, 1930). This consists of a projecting tube from which two long sticky threads can be shot out at will (Davies, 1928; Nicholls, 1930). Authors differ over the function of the ventral tube in Collembola. Nutman (1941) studied the use of the ventral tube of *Onychiurus armatus* Tullb and concluded that its main function was the uptake of water. Various other functions, from holding on to slippery surfaces, cleaning and the uptake of oxygen have been assumed (Davidson, 1934; Ruppel, 1952). LF is equipped with mouth parts which are adapted for both biting or chiselling and sucking (Lea, 1922; Davies, 1928).

The eggs when laid are semi-fluid, assuming a spherical shape and becoming firm on exposure to the air. The eggs are 0.27 mm in diameter and yellowish in colour (Holdaway, 1927; Davidson, 1932b). The hatching of the eggs is well described by Holdaway (1927) and Davidson (1932b). The first instars are active a few minutes after emergence. Their colour is pale yellow except for the eyes which are black and the antennae, the third and fourth segment of which are pale lavender. The width of the head is 0.21 mm. They gradually increase in size, undergoing several moults until maturity is attained. Apart from the size the larval instars show close morphological resemblance to the adults (Holdaway, 1927; Davidson, 1934; Dumbleton, 1938; Swan, 1940). Holdaway (1927) mentioned that there were at least six or seven moults until the time that the adult female started laying eggs. Maclagan (1932a) measured the head width of several nymphs and concluded that there were seven larval and one adult instar. Walters (1964) reared LF in the laboratory and measured their head width regularly. He concluded that there were four immature male instars and one adult male instar, and five immature female instars and up to five adult female instars.

An interesting anatomical aspect is that *S. viridis* is one of the few Collembola that possess a tracheal system (Davies, 1927; Denis, 1965). Southwood (1973) suggested in his discussion of insect-plant relationships the development of a tracheal system as one of the possibilities to reduce the risk of desiccation.

(b) Mating and oviposition

According to Maclagan (1932a) the nymphs become sexually mature following the sixth moult (head width 570 µm). Walters (1964) assumed sexual maturity for the males in the fifth larval stadium (head width 520 µm) and for the females in the sixth stadium (head width 660 µm). It is assumed that most, and probably all, Collembola accomplish cross insemination via the uptake of spermatophores (Christiansen, 1964). Although parthenogenesis has been observed in some Collembola (Goto, 1960b; Christiansen, 1964; Snider, 1972) this is not the case with *S. viridis*. Schaller (1971) reviewed the indirect sperm transfer by soil arthropods and concluded the following:

-spermatophore production and indirect sperm transfer are related to a low systematic position,
-indirect sperm transfer is most prevalent in species living in very humid environments. In drier habitats close contact between the sexes is necessary to avoid the sperm drying up.
-when the population density of a species increases, there is less intimate contact between the partners.

Four behavioural patterns can be distinguished among Collembola (Mayer, 1956; Bretfeld, 1969):

1. no pair forming. Sperm drops without a stalk are deposited, regardless of presence or absence of a female.
2. pair forming but only the male is active. Spermatophores are deposited, independent of female presence. But more are produced when a female is present.
3. pair forming with both partners active. Production and deposition of spermatophores more directed towards the female.
4. as in 3., but production and deposition of spermatophores only in the presence of a female. The male guides the female during sperm

uptake.

Waldorf (1974) found that *Sinella curviseta* produces sex pheromones that promote the deposition of spermatophores by the male. Betsch (1974) and Betsch-Pinot (1977) have described the sexual behaviour of some species of the Symphypleona. Betsch-Pinot (1976) gives a detailed description of the mating behaviour of LF. The mating behaviour of LF resembles pattern number 3. Although the male may deposit a spermatophore in the absence of a female, only spermatophores deposited while the female is present will be taken up. Although the spermatophores are mainly deposited on the leaves (Betsch-Pinot, 1976), oviposition takes place on the soil. Before the eggs are placed on the soil, they are coated with an anal secretion containing soil particles and glandular secretion (Davidson, 1932a; Walters, 1964). This gives the eggs a brownish colour and makes it difficult to observe them in the field (Holdaway, 1927; Maclagan, 1932a; Davidson, 1934; Dumbleton, 1938; Betsch-Pinot, 1976). Maclagan (1932a), Dumbleton (1938) and Walters (1964) described essential factors for optimum oviposition: a/ low temperature, b/ high relative humidity and c/ soil of suitable chemical and mechanical constitution.

(c) Fecundity

Studies on *Folsomia candida* have shown that crowding may reduce fecundity (Green, 1964). A similar trend was found by Walters (1964) with LF. The number of eggs per female decreased with an increase in population density of LF. This response seems to be non-specific since the same was observed when the population density was increased by adding *Halotydeus destructor* (red-legged-earth-mite). Niijima (1973) found that oviposition and fecundity of Collembola were strongly

affected by temperature. Walters (1964) gives the optimum temperature for fecundity as about 15 ^{o}C.

It is difficult to assess the number of eggs laid by female LF, because, apart from the above mentioned factors, more than one female may contribute to a batch of eggs (Swan, 1940). An average batch of eggs contains between 20 to 100 eggs (Holdaway, 1927; Nicholls, 1930; Maclagan, 1932a; Swan, 1940), but batches containing 400 to 700 eggs have been found (Davidson, 1932a; Walters, 1964). Normally a female LF will lay at least two batches of eggs, with a 10 to 14 day period in between. Often the second batch contains 50 % more eggs than the first (Maclagan, 1932a). The maximum number of eggs laid by a single female was about 120 eggs (Holdaway, 1927; Maclagan, 1932a). Hale (1965a, b) summarized estimates of fecundity in Collembola. Of the 27 mentioned species the LF showed one of the highest egg productions per female.

(d) Oversummering

Oversummering (summer diapause or aestivation) seems to be widespread among various groups of insects. Masaki (1980) showed in an in-exhaustive survey of the literature, that about 180 species belonging to 12 orders of insects and mites experienced aestivation. Harvey (1962) reviewed the metabolic aspects of insect diapause. He defined diapause as: "a state of development arrest which persists even when environmental conditions are favourable for growth". Tauber and Tauber (1976) reviewed the literature on diapause maintenance and termination. They concluded that aestivation was maintained by specific physical factors such as temperature or photoperiod conditions, or by lack of food, and that many aestivating insects require a specific stimulus to terminate diapause. Davidson (1932b) states that hatching of the

diapause eggs of the LF can be induced by giving them suitable conditions of moisture and temperature. Research done by Wallace (1968) on the diapause in the aestivating eggs of the LF yielded the following information. LF oversummers in the egg stage. The oversummering eggs have a smooth appearance opposed to the rough appearance of the non-diapause eggs. The production of diapause eggs in the female is influenced by the increasing maturity of food plants in spring. These egg batches can not only withstand dry summer conditions but must be exposed to such conditions before the eggs can hatch in autumn. After that the eggs will react to lower temperature and rainfall and the embryonic development will continue. The same tendency is found in eggs of the red-legged-earth-mite, *Halotydeus destructor* (Wallace, 1970a, b) and the predatory mite *Bdellodes lapidaria* (Wallace, 1971). Leinaas and Bleken (1983) found that the egg diapause during winter in *Lepidocyrtus lignorum* (Collembola) was initiated by low temperature. Although no literature is available on this topic, this may well be the case with the overwintering eggs of LF in Europe.

(e) Habitat preference

Although LF has a broad range of host plants, it prefers clovers, lucerne and broadleaved plants without many veins (Holdaway, 1927; Nicholls, 1930; Maclagan, 1932a; Davidson, 1934; Dumbleton, 1938; Swan, 1940; Scott, 1954), and amongst these some species are preferentially selected. Holdaway (1927) noticed that crimson clover (*Trifolium incarnatum*) was only slightly attacked, although it was standing next to subterranean clover (*Trifolium subterraneum*) which was seriously damaged. He attributed this to the hairy cover on both sides of crimson clover leaves. Davidson (1934) lists *Trifolium arvense* (hare's foot

clover) and *T. angustifolium* (narrow leaved clover) as less preferred species. Again a reference was made to the hairyness as well as to a less succulent character of the leaves. In a similar case other hairy clovers, *Medicago minima* (small hairy clover) and *M. scutellato* (snail medick) are less attacked. Both Davidson (1934) and Maclagan (1932a) mention a preference for broad leaved plants over narrow leaved plants with close set veins, such as grasses.

Oviposition is influenced by the moisture content of the soil, pH and soil texture. An average soil moisture content of 12 % is necessary for optimal oviposition. Related to the oviposition is the uptake of soil particles to cover the eggs. Coarse sand is not only unfavourable because of its particle size, but also due to a poor water holding capacity (Davidson, 1934; Jenkins and Forte, 1948; Walters, 1964). Soil containing a high silt plus clay content will increase oviposition (Walters, 1964; Wallace, 1967). A pH in the range of 5.0 to 7.0 is tolerated but a more alkaline soil will reduce oviposition (Davidson, 1932a). The optimum pH is between 5.4 and 6.4 (Holdaway, 1927; Davidson, 1932a; Maclagan, 1932a; Walters, 1964).

2.4.3 Influence of predators

Field observations and laboratory trials have revealed that Collembola have several natural enemies, including species of Diptera, Coleoptera, Arachnid a and Dermaptera (Walters, 1966; Ashraf, 1969; Christiansen, 1971), and predators such as ladybird beetles and hoverfly larvae (Lea, 1922), and spiders, beetles (Staphylinidae) and ants (Formicidae) have been suggested for the biological control of LF specifically. (Davies, 1928; Holdaway, 1927). Maclagan (1932a) studied

several possible predators, including coccinellid spp, staphilinid spp, two hemipteran spp and 13 species of arachnids. Of all the natural biotic agents of control against LF spiders exerted the greatest effect (Maclagan, 1932b).

Womersley (1933) was the first one to notice the presence of the bdellid mite *Biscirus lapidarius* Kramer in Australian pastures in 1931. He found them feeding on nymphs and adults of the LF, as well as on other Collembola, during all the stages of the mite's development. Currie (1934) and Jenkins (1935) continued the survey of this mite and found that it exercised some control of LF in certain areas. At about that time *B. lapidarius* was introduced in several areas in West Australia, South Australia, Victoria and Tasmania. Although it failed to establish in Tasmania (Evans, 1937), Jenkins and Forte (1948) found that the mite was established in the lower South West of Australia. Detailed studies on the bionomics of the bdellid mite by Wallace (1967) showed that if there were more than 20 bdellid mites per m^2 in early winter there would not be an outbreak of LF later in the season. *B. lapidarius* is well adapted to prey on LF. Although it prefers slightly moister conditions than LF (Wallace and Mahon, 1971) its area of distribution closely resembles that of LF. As in LF the eggs of the bdellid mite undergo a summer diapause and the hatching of the eggs is simultaneously with that of the LF (Wallace, 1971).

A survey for the presence of other bdellid mites in Australia was undertaken by Wallace and Mahon (1972; 1976). They found seven bdellid mite spp. feeding on collembolan species. Of these seven, three fed on Sminthuridae and two, *B. lapidarius* and *Neomolgus capillatus* Kramer, showed a preference for the LF. After it was found that *N. capillatus* was able to tolerate dry conditions in the Mediterranean area of Europe (Wallace, 1974a), Wallace (1974b) collected *N. capillatus* in Europe and

introduced them in Australia. His advice was to introduce both *B. lapidarius* and *N. capillatus* as soon as possible in vulnerable areas so that LF could not really establish. At the beginning of 1980 *N. capillatus* was established but spreading slowly (Wallace, 1981). Ireson (1982) found, that although *B. lapidarius* was introduced in 1934, it was only established in some areas of Tasmania. This predatory mite has been introduced in other areas of the world. In the Ethiopian region the introduction of *B. lapidarius* alone in 1963 was considered to be insufficient, but a more recent introduction of *N. capillatus* showed promise of permanent establishment (Greathead, 1971). Wallace and Walters (1974) indicated that *B. lapidarius* is also capable of influencing LF numbers under South African circumstances. In New Zealand the presence of *B. lapidarius* was confirmed, but the mites were found in low numbers and only in areas with high and evenly distributed rainfall (Dumbleton, 1938).

One of the factors that may have inhibited the success of predatory mites is the use of insecticides. Wilson (1960) noticed that topdressing pastures in Australia with DDT incorporated in superphosphate increased LF populations, and that this was probably due to the elimination of the two predatory species of *Biscirus*. Wallace (1954) found the same results when comparing the use of BHC and DDT incorporated in superphosphate.

2.4.4 The influence of temperature, moisture and pH

The influence of temperature and rainfall in relation to the geographical distribution of the LF has already been discussed in Paragraph 2.3. In this section attention will be paid to the influence

of moisture (or relative humidity -RH), temperature and pH on the growth and survival of the LF in different stages of development.

Christiansen (1964) reviewed the literature on the bionomics of Collembola. Most Collembola need a RH of more than 89 % to be able to survive for functional periods. Adaptations to RH conditions have been studied in depth for some collembolan species by Vannier (1972; 1973a, b; 1974; 1977). Bauer (1979) tested collembolan species for survival at low RH and found some would die within 45 minutes when exposed to 40 % RH while others survived for 22 hours. A possible protection against too much water exposure, e.g. heavy rainfall, was found by Ghiradella and Radigan (1974). They noticed that the cuticle of *Tomocerus flavescens* was covered with a wax layer, which, in combination with sculpturing, rendered the cuticle highly hydrophobic. Joosse and Groen (1970) state that the survival time of Collembola is inversely related to the saturation deficit and not simply to RH. An important reason for this is that the saturation deficit, compared to RH, is temperature independent. Due to the difficulty of measuring saturation deficit properly, however, and the fact that most authors use RH, the latter will be used in this literature review. Drought may stimulate Collembola to aggregate in more optimal humidity situations (Joosse, 1970, 1971; Joosse and Groen, 1970). Apart from the RH factor, aggregation can be caused by food (Christiansen, 1970; Barra and Christiansen, 1975; Usher and Hider, 1975; Verhoef and Nagelkerke, 1977) and steered by the presence of aggregation pheromones (Verhoef *et al.*, 1977). In all cases aggregation is a survival strategy.

Some species can survive temperatures as low as -50 ^{o}C and others temperatures as high as 55 ^{o}C, but in general Collembola function in a temperature range of 10 to 30 ^{o}C (Ashraf, 1971). Within the range of tolerable temperatures there is a direct and almost linear relationship

between temperature and speed of development (Christiansen, 1964). The thermal optimum can be defined as the temperature at which the development time is shortest and the mortality lowest (Butcher *et al.*, 1971). The growth rate of insects reared at a constant temperature regime tends to be directly proportional to the temperatures employed within the species-typical range. It is linear over much of the physiological temperature range but deviates from linearity as either minimum or maximum temperatures are approached (Beck, 1983). The influence of the temperature on the development time of the eggs of the LF is as follows (Table 2.1).

Table 2.1 The influence of the temperature on the development time of the eggs of the LF (*After* Walters, 1964).

Temperature (^{o}C)	Development time (days)	Temperature (^{o}C)	Development time (days)
7	67	18	13
10	37	21	12
12	25	26	8
14	17		

These development times, plotted against the temperature (Walters, 1964 p. 35), closely resemble the curves, presented by Davidson (1931, p. 150; 1934, p. 20). Although most eggs will hatch within 24 hours of each other, some will hatch during the following few days. This may be due to 1/ the time the eggs were laid, 2/ the variation in formation and thickness of the batches, and 3/ the variation in individual eggs (Davidson, 1932b). Also, aestivating eggs tend to hatch over a much more extended period than non-diapause eggs (Walters, 1964).

The egg development rate can be expressed in the form of a thermal

constant. When the moisture surrounding the eggs is about optimal, the development in relation to the temperature may be expressed as a hyperbola with the formula (1) :

(1) $D(T - C)=K$, with D = development time in days,
T = temperature (^{o}C),
C = zero development threshold (^{o}C), and
K = thermal constant (Davidson, 1934).

Maclagan (1932a) mentioned a lower threshold for egg development of 7.2 ^{o}C. Davidson (1934) used a lower threshold of 5.5 ^{o}C, with a corresponding K value of 161 degree-days. Hale (1965a, b) showed for 8 species of Collembola that the thermal constant K at fluctuating environment temperatures was below that calculated for constant temperatures. In general, egg development below 9 ^{o}C is very slow and below 7 ^{o}C almost inhibited (Maclagan, 1932a).

As noted in the discussion of summer diapause, the eggs of LF can sustain extreme conditions. Nymphs hatched within 12 days from re-moistened egg batches that had been kept dry for 271 days (Holdaway, 1927). Maclagan (1932a) kept newly laid eggs for 7 days at 17 to 22 ^{o}C, transferred them for ten weeks to 0 to 4 ^{o}C, and when exposed to 10 to 15 ^{o}C, he found 100 % hatched within 18 days. In all the above mentioned cases, however, it is important to know the developmental stage of the embryo. Davidson (1934) stated that the viability of the eggs is greater under adverse conditions of dryness when the embryos have attained about 50 % of their development.

The temperature and moisture of the soil are more important than of the atmosphere (Walters, 1964), although the latter plays an indirect role (Davidson, 1932b). When air humidity is the only source of moisture, 100 % RH is necessary for development and hatching (Davies,

1930 *In* Davidson, 1934). But normally free moisture from the soil can be readily absorbed by the soil excreta (adhering to the eggs), assuring the availability of moisture during short intervals between falls of rain and affording a large surface for the deposition of moisture from dew. Excessive moisture, however, is harmful to the egg development. The chorion caps may separate prematurely and the embryo becomes disintegrated (Davidson, 1934).

Temperature and RH play an important role during the instar development. Maclagan (1932a) found that the time between egg hatching and the adult stadium was 48 days at 13 ^{o}C and 36 days at 17 ^{o}C, while the total generation time was 74 and 51 days respectively. Maclagan indicated (Fig 3, p. 127) the moment that sexual maturity is reached and oviposition commences. At 7.9 ^{o}C, 13 and 16.7 ^{o}C this was 35 (50 days for oviposition), 28 (38) and 18 (28) days respectively. This is in contradiction with his previous statement, because it would mean that sexual maturity was reached before the adult stage. Obviously Maclagan did not realise that female LF still moult after reaching the adult stage. When applying formula (1) to the above mentioned a zero development threshold of 2.6 ^{o}C is obtained. Using the results of egg hatching to adult stadium, or egg stage to adult stadium, however, a lower threshold of 1.9 and 4.8 ^{o}C respectively is found. This can be explained by one of the statements made by Beck (1983) in his review of insect photoperiodism, that development thresholds are not always identical among the larval instars. Walters (1964) reared LF in the laboratory and found the following average longevities (from first larval instar through to last mature instar) for females and males: at 14.4 ^{o}C 65.5 and 61.5 days respectively; at 16 ^{o}C 43.7 and 45.3 days; at 20 ^{o}C 43.7 and 45.3 days; and at 25 ^{o}C 30.4 and 26.5 days. The influence of temperature on the duration of the different growth stages

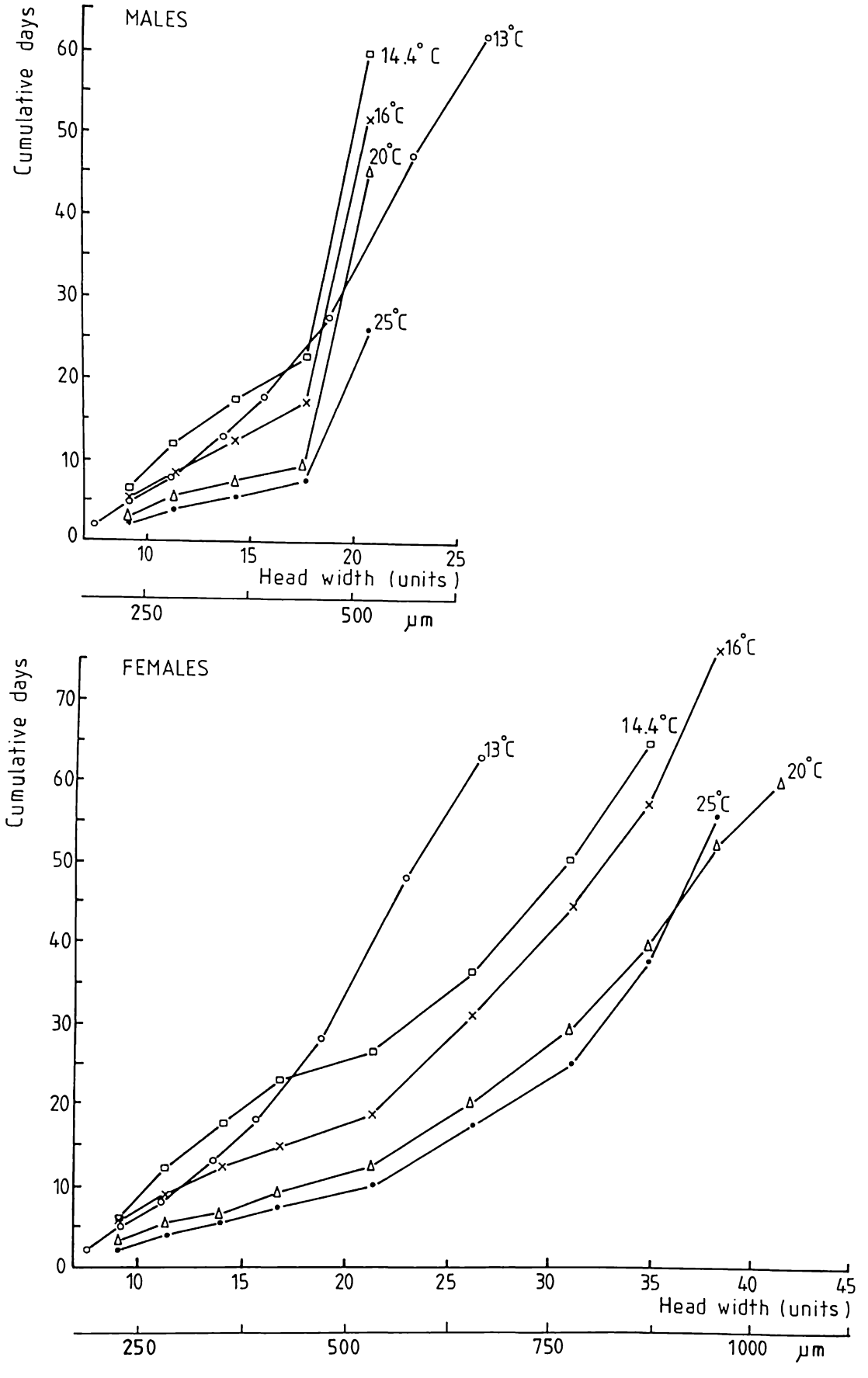

Fig 2.2 The influence of temperature on the growth and development of male (top) and female (bottom) LF. Results at 13 °C not separated into males and females. *After* Maclagan (1932a) and Walters (1964).

from Maclagan (1932a) and Walters (1964) is shown in Fig 2.2.

The nymphs of the LF reach their maximum rate of growth at 16.7 °C. Temperatures below 13 °C and above 3 °C, however, increase the total life span of the LF. For survival and reproduction 8 °C and 100 % RH is optimum. From 8 °C up to 17 °C the individuals become smaller and the time interval within which sexual maturity is reached shorter, with increasing temperatures. Twice the time is taken to reach sexual maturity at 7.9 °C as at 16.7 °C. Increases of temperature from 13 to 17 °C and from 17 to 21 °C reduce the life span of LF by 34 % and at 21 °C and 3 °C maturity is not achieved (Maclagan, 1932a). These results contradict the findings of Walters (1964), who found that no sexual maturity was reached at 35 °C, but that normal development took place at temperatures up to 25 °C. Walters states, however, that survival at this temperature in the field would only be possible under irrigated conditions.

While the differences in growth rate and maximum growth between 70 and 90 % RH must be regarded as insignificant, the differences between 100 % and 90 % RH are considerable. This can be explained by the fact that at 100 % RH both the food and the environment can make up for loss of water. Below 100 % RH only food can be used for this purpose (Maclagan, 1932a).

A soil pH range of 5.5 to 6.5 is optimal for growth. At a pH of 7.8 or 4.1 the time to reach maturity increases significantly (Maclagan, 1932a). Walters (1964) found development very retarded or non-existent at pHs below 6.3. Noticable differences in development were not found at pHs ranging from 6.3 to 12.1.

2.5 Pest status

Maclagan (1932a) states that although the agricultural importance of the Collembola in the past had been regarded with scepticism by entomologists, the activities of certain species, particularly those belonging to the genera of *Bourletiella* and *Sminthurus* had sparked renewed interest for the order. Most collembolan species are harmless and even beneficial for the structure of the soil (Rusek, 1975). Folsom (1933) lists 40 species of Collembola known to be injurious to plants, which was only 2 % of the then known 2000 species. Collembolan species damage crops such as tomatoes, beans and maize (Brown, 1954; Edwards, 1962; Given, 1973). In most cases the damage is direct but Collinge (1910) mentions Collembola as fungal spore carriers, leading to secondary damage in those plants attacked. Fink (1914) and MacNamara (1924) mention crops such as beans, beet, cabbage, carrots, cauliflower, clover, corn, cucumber, spinach, squash, tomatoes, turnips and watermelons being attacked by species of Sminthuridae. More specific details are not given but looking at the host plant range and the type of damage it is very likely that these reports refer to LF.

LF prefers the soft parts of plants. Damage is done by chiselling and biting the tissue. Nymphs make small holes through the epidermis and remove the mesophyl tissue giving leaves a speckled appearance. Older nymphs and adults attack the leaves more vigorously, enlarging the holes that are created by eating. After heavy attacks only the veins remain, giving the leaves a skeletonized appearance (Lea, 1922; Davidson, 1934). A characteristic of LF feeding is that one of the epidermal layers remains intact (Holdaway, 1927; Newman, 1927; Swan, 1940) distinguishing it from slug damage, which is also more irregular and with rougher edges. LF damage can be mistaken for the red-legged-earth-mite damage, although damage by the latter, a sap feeder, is only superficial and damaged leaves remain opaque (Swan,

1940; MacFarlane, 1970). Molineux (1897) observed LF damage on lucerne, fodder crops, vegetable and garden flower plants. In general one can say that the LF has a variety of host plants among the Urticaceae, Cruciferae, Polygonaceae, Compositae, Graminaceae and Leguminosae (Maclagan, 1932a). More specific host plants have been mentioned by Lea (1922), Holdaway (1927), Nicholls (1930), Evans (1937), Swan (1940), Jenkins and Forte (1948) and Walters (1964), but in all cases lucerne and clovers are given as the preferred host plants. Damage to clovers and lucerne not only reduces yield, but repels cattle and sheep which refuse to eat pasture fouled by LF faeces (Newman, 1927; Cottier, 1956; Walters, 1964; Pottinger, 1983). The only study on quantitative aspects of LF feeding was made by Maclagan (1932a) who measured the relative amount of food eaten in the laboratory by the LF by measurement of the damaged areas on white clover leaves with graph paper. He found that the injury caused by LF up to the fifth larval instar (18 days at 13 ^{o}C) was relatively insignificant compared with the last three stages. Although the LF is known to feed on crop plants in Europe (Davies, 1928; Maclagan, 1932a; Ulber, 1978) and some other areas of the world (Greathead, 1971), it is recognised as a pest in Australia and South Africa. Recently it has been recognised as a serious pest of white clover in some areas of the northern North Island of New Zealand (Townsend *et al.*, 1979). In 1924 the LF was declared a pest in New South Wales, Australia (In: Davies, 1928). In South Africa it infested more than 50 000 ha in 1959 (Wallace and Walters, 1974). Dumbleton (1938) considered pasture areas in New Zealand such as Hawkes Bay and the Wairarapa prone for severe LF damage. He did not expect severe damage in the high rainfall areas of the North Island. Cottier (1962) remarked that "...the LF has not so far caused sufficient damage to warrant the application of control measures". Somerfield and Burnett (1976), in a survey of lucerne insects, found that the abundance of LF

in samples varied widely, but concluded that high numbers were taken sufficiently often to warrant investigation of its pest status. Pottinger (1976) ranked the LF number eight in a list of major pasture pests. Until 1982 LF was only recognised as a pest of localised importance in the North Waikato, but since then damage on farms in the Kaipara and Manukau harbour areas, Te Kauwhata, Huntly and Morrinsville has extended the area attacked and with that its pest status (Pottinger, 1983; 1984).

2.6 Pest control

When LF was first noticed, lime sulphur was used to control outbreaks (Dumbleton, 1938; Jenkins and Forte, 1948). Swan and Lower (1951) and Wallace (1954) found BHC moderately effective, but noticed that DDT had no effect and would even increase populations. Sheals (1953), Wallace (1954), Edwards and Dennis (1960) and Menhinick (1962) noticed that after spraying with insecticides such as DDT and Dieldrin many predatory taxa were absent in the sampled areas. Walters (1964) sprayed lucerne flea infested fields with mercaptothion and recorded yield increases of 144 % for lucerne and 12.5 % for subterranean clover respectively. Martin (1975) applied the insecticides fensulfothion, fenitrothion, carbofuran and DDT to pasture as granules. All insecticides except DDT reduced the number of Sminthuridae. MacQuillan (1975) found that chlorpyrifos and phosmet both controlled LF effectively. At the start of this study only one insecticide, maldison, was registered for control of the LF in New Zealand. When spraying frequently against the pest, farmers often experience population resurgence once the insecticide programme is terminated (Townsend *et al.*, 1979). To find possible alternative for maldison, Townsend *et al.*

(1979) tested other insecticides and found that both phosmet and omethoate gave better results.

Cultural methods have been applied to eradicate LF as well. Molineux (1897) advised high intensity grazing by sheep to control LF. Grazing can reduce collembolan numbers drastically (Maclagan, 1932b; Dumbleton, 1938; King and Hutchinson, 1976; King *et al.*, 1976; Ferro, 1976; Curry and Tuohy, 1978; Purvis and Curry, 1981). Management practices such as mowing, raking or burning seem to have the same effect (Sheals, 1957; Jenkins *et al.*, 1973; Metz and Dindal, 1975; Wrenn and Pottinger, pers. comm.).

Information on the possibility of biological control has already been discussed in Paragraph 2.4.3.

CHAPTER 3. Sampling methods

CONTENTS

CHAPTER 3. Sampling methods

3.1 Sites used for the population studies

3.1.1 Introduction

When this study was started, LF was known to be a local pest in the Huntly and Te Kauwhata area (Fig 3.1). The choice of the location near Huntly at Rotongaro (hereafter referred to as Huntly) was based on the fact that research related to the LF had previously been done on this property by scientists from the Insect Control Group at Ruakura (Townsend *et al.*, 1979). The choice of the property near Te Kauwhata was based on advice from the Farm Advisory Service in Hamilton, because of the problem the insect had caused on this farm.

On both locations two paddocks were chosen next to each other. One was to be grazed and the other to be shut for hay making or silage in spring. The choice of paddocks was based on the abundance of LF and easy accessibility, while fitting in in the farm management system and causing as little disruption as possible.

3.1.2 Sampling sites

HUNTLY

The property of Mr M. Darby is located at Furniss Road, Rotongaro, near Huntly (Plates 3.1 and 3.2). The two paddocks chosen, are established pastures. On the West they border onto the main access

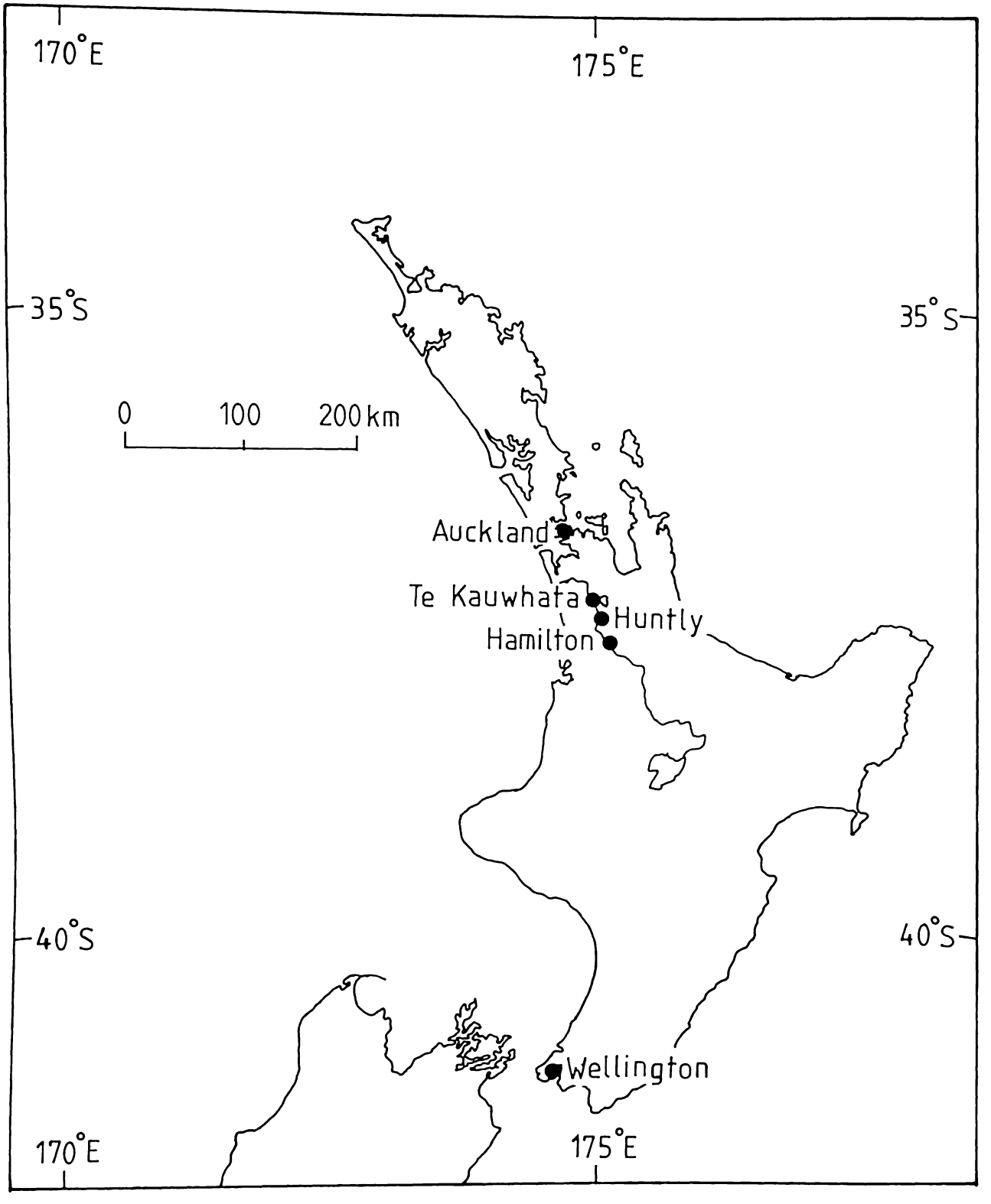

Fig 3.1 Map showing the location of the two sampling sites.

road, on the East on a farm race. On the North and South side they are bordered by other paddocks. The two paddocks are separated by barbed wire and shrubs. Paddock one (DI) is level, except for a small area in the South-East, where it slopes downhill. Paddock two (DII), North of paddock one, is completely level. The soil in the paddocks is Mahuta or Hamilton clay, with a pH ranging between 5.7 and 6.0. The LF has been known to exist on this property since the early 1970's.

Plate 3.1 Experimental plots in paddock DI in Huntly.

Plate 3.2 Experimental plots in paddock DII in Huntly.

Plate 3.3 Experimental plots in paddock KI in Te Kauwhata.

Plate 3.4 Experimental plots in paddock KII in Te Kauwhata.

TE KAUWHATA

The property of Mr M. Kenna is located at Waikere Road, Te Kauwhata (Plates 3.3 and 3.4). Both paddocks chosen are established paddocks. On the East side a farm race forms the boundary, in the South and West direction both paddocks border onto other paddocks. Paddock one (KI), North of paddock two (KII), has a boundary of pine trees on the North side. Both paddocks slope downhill in an East and South-Westerly direction, but the study sites were located on practically level ground. A barbed wire fence separates the two paddocks. The soil in the paddocks is Te Kauwhata clay loam, with a pH ranging from 5.7 to 6.0. Damage done by the LF was first noticed on this property in the spring of 1980.
The vegetation composition of both paddocks is described in Chapter 8.

3.2 Sample unit and sampling technique.

3.2.1 Sample unit

a/ Methods

To minimize the variance in the sampling method, a stratified random sampling technique was used (Southwood, 1978). In the paddock one block, consisting of nine plots or strata, each measuring 10 m by 10 m, was laid out using pegs. Care was taken to leave a buffer of land on all sides around the blocks to minimize any side effect from fences or boundaries. It was ensured that the blocks were not on a "tractor-track" or between the gate and a water trough for cattle. The size of the plot was set at 100 m^2 so that, for example, sampling with a sweepnet (diameter of the sweep 2.5 m) would not interfere with pitfall

trap sampling, positioned in the centre of each plot. In each plot one sample was taken at random. With eyes closed, four to five steps were made from the boundary of each plot and a soil sample was taken or a sweep made. With reference to the central position of the pitfall traps, Milne (1959) has shown that centric systematic area-samples can be treated statistically as if they were random samples.

b/ Discussion

The decision to divide the blocks into nine plots in each paddock was based on the following considerations:

1/ the time it takes to collect soil samples in the field and carry out other sampling methods and activities,
2/ the time necessary for the extraction of the insects from the samples,
3/ the time necessary for the analysis of these samples and other samples that are done simultaneously, and
4/ the frequency of sampling.

In Appendix 4.2 the results of the soil sampling method, expressed as mean number of LF per m^2 and a standard error of the mean (SEM) are presented. The SEM can be used as a measure of precision. Southwood (1978) mentions that for many purposes an error of 10 % of the mean is a reasonable standard. However, often this cannot be achieved. In this study, on average a SEM between 25 and 30 % was found. One can calculate the number of samples necessary to achieve a required level of accuracy with the formula

$$N = \frac{t.s}{D.x}$$, where s= standard error of the mean

D= the required level of accuracy (e.g. 0.1 = 10 %)

t= a quantity, depending on the number of samples

x= the mean number (Southwood, 1978).

When we accept a level of accuracy of 80 %, that is the SEM is 20 % of the mean, the total number of samples on all paddocks has to be increased from 36 to a number ranging from 44 to 140, depending on the date of sampling. Even when doubling the number of samples from 36 to 72 per sampling date, on more than 41 % of the sampling dates the SEM would exceed 20 % of the mean. This indicates the necessity of a compromise between the total amount of time spent on collecting the data, and the level of accuracy. Morris (1960) refers to this choice as "the law of diminishing returns".

3.2.2 Sampling techniques

Three sampling methods were used to collect information related to the different aspects of the ecology and biology of the LF. As an indication of the selectivity of each method, counts were made of all orders present in the samples during one week in the different seasons between July 1981 and July 1982. The results are presented in Appendices 3.1-3.3.

a/ Soil sampling

The method of soil sampling to estimate the population density of Collembola is practised in many studies and in all cases the size and shape of the soil corer is adjusted to the habitat of the insect (Wallace, 1956; Dhillon and Gibson, 1962; McMillan, 1969; Joosse, 1970; King and Hutchinson, 1976; Leinaas, 1978).

Methods

Due to the fact that the LF is a mobile insect and can jump a considerable distance, the soil sample has to be enclosed. A special soil corer was designed and constructed. It consists of a stainless steel tube with cutting edges, into which a PVC tube, that is closed off at the top, can be inserted (Fig 3.2.a). A long handle is attached to the outside of the tube for ease of manipulation. The soil corer is put on the ground, pressure is applied by foot on the rim of the tube, and, by giving a quick turn with the handle while pulling it towards the body, a sample is pulled free from the soil. This method is satisfactory as long as the soil is damp, but during certain periods in the summer when the soil is very dry, it was impossible to take samples in this manner. On these occasions the presence of the LF was established with the use of a sweepnet.

To study the effect of the size of the soil corer on the number of LF collected, two soil corers, covering a different surface area, were used simultaneously during seven months in Te Kauwhata (KI). One soil corer with an inner diameter of 10.2 cm covered an area of 82 cm^2 and the other soil corer, measuring 8.6 cm inner diameter, covered 58 cm^2.

Discussion of the comparison of the soil corers

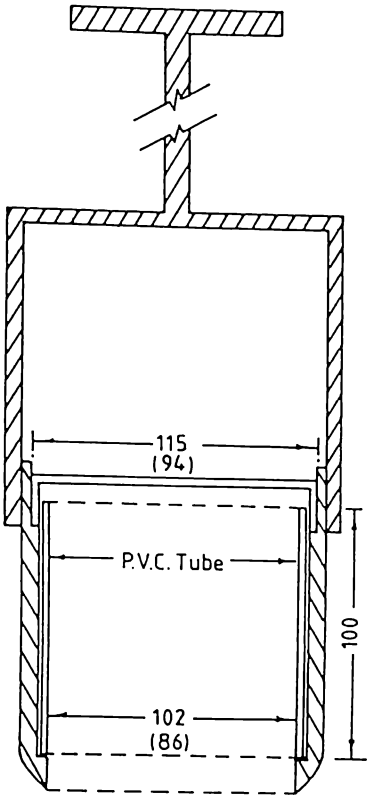

Fig 3.2.a Soil corer with PVC sampling tube and lid. Dimensions (small corer in brackets) are given in mm.

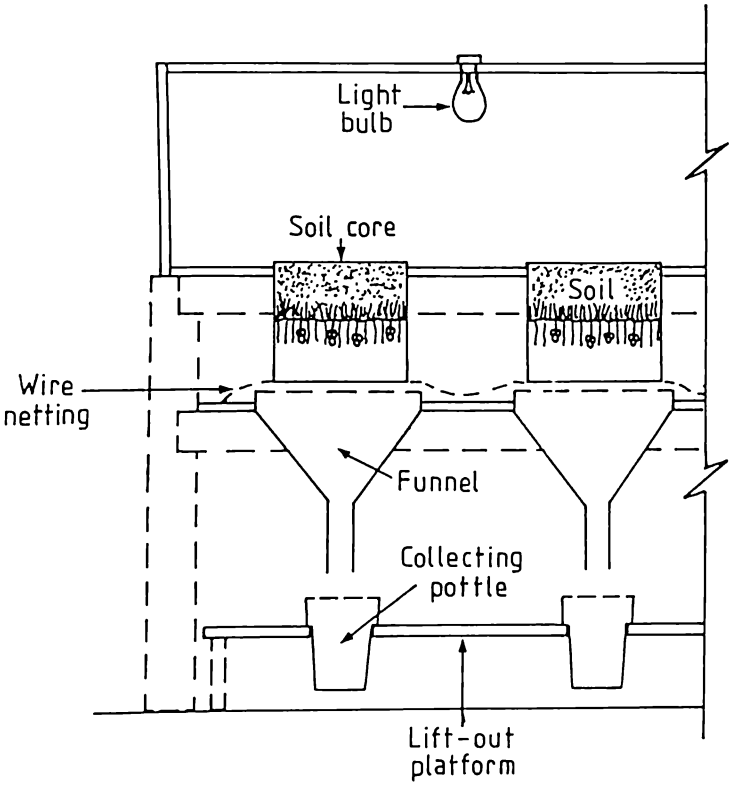

Fig 3.2.b System used to extract LF and other insects from soil samples, using a heat source. *Not to scale*

The results of the two soil corers are presented in Figs 3.4.a and 4.5. Linear regression of the LF numbers of the small and big corer on a log(x+1)-log(y+1) transformation shows a Pearson product moment correlation coefficient r= 0.906 (P= 0.001 ***). The slope of the regression line is 1.00, indicating that the difference between the number of LF, caught in each type of soil corer, is only caused by the difference in size of the corer. Wallace (1956) used a soil sampling apparatus with an inner diameter of 10.2 cm. To be able to compare the results from this study with the results from Wallace's study, the use of the soil corer with an inner diameter of 10.2 cm was continued during this study for the bionomics of the LF and other Symphypleona.

A comparison was made on the number of samples, necessary to achieve a SEM of 20 % for each core size. Application of the Spearman rank correlation coefficient test showed no significant difference (r_s= 0.469, z= 1.755, P= 0.05) between the two soil corers. This means that a reduction in the size of the soil corer will not reduce or increase the SEM.

b/ Sweepnet sampling

The sweepnet is perhaps the most widely used piece of equipment for sampling insects from vegetation. Advantages are simplicity and speed (Southwood, 1978). A disadvantage is that several factors may influence its accuracy: the collector's attitude, type of net, speed of sweeping, amount of foliar growth covered by a sweep, growth of the plants (Menhinick, 1963), temperature and humidity (Saugsted *et al.*, 1967) and the density of the insect that is studied (Parker and Drangeid, 1967). Therefore sweepnet samples are mainly used for inventory purposes in pastures or crops (Cumber, 1959; 1962) or collecting insects for

laboratory experiments (Wallace, 1968). However, Callahan *et al.* (1966) found a sweepnet to be statistically superior to a Dietrick vacuum sample system for the collection of alfalfa weevils. Saugsted *et al.* (1967) state that the use of a sweepnet is not precise enough for critical comparison, but that it can be used to determine major population trends. When keeping this in mind the method of sweepnet collecting can be used for example for comparison of the effect of insecticide applications as has been done for the LF (Townsend *et al.*, 1979; Wrenn *et al.*, 1983).

Methods

A sweepnet is thus a simple and fast method and may be incorporated in farm management as a monitoring aid for the timing of insecticides. Therefore sweepnet samples were taken and compared with soil sample counts. Between July 1981 and August 1982 the sweepnet method was used during eight week periods, with intervals of five weeks during which no sweeping took place. A sweepnet with a handle of 150 cm and a net of fine mesh fabric, with a diameter of 30 cm, was made. Standing in a plot, a 360 ^{o} sweep was made over the vegetation. The insects caught were collected from the net via a funnel that was fixed into a lid and screwed onto a pottle (modification of net emptier by Oliver, 1979). In the laboratory the insects were killed in 70 % ethyl alcohol and counted.

Discussion of the comparison of the sweepnet and soil sampling method

The number of LF caught in sweepnet was regressed against numbers caught in the big soil samples, using a log(x+1)-log(y+1) transformation. The results (Fig 3.3.a) show that in both paddocks in Huntly a positive significant relationship exists between the numbers of LF caught with the two sampling methods (DI: r=0.851***; DII:

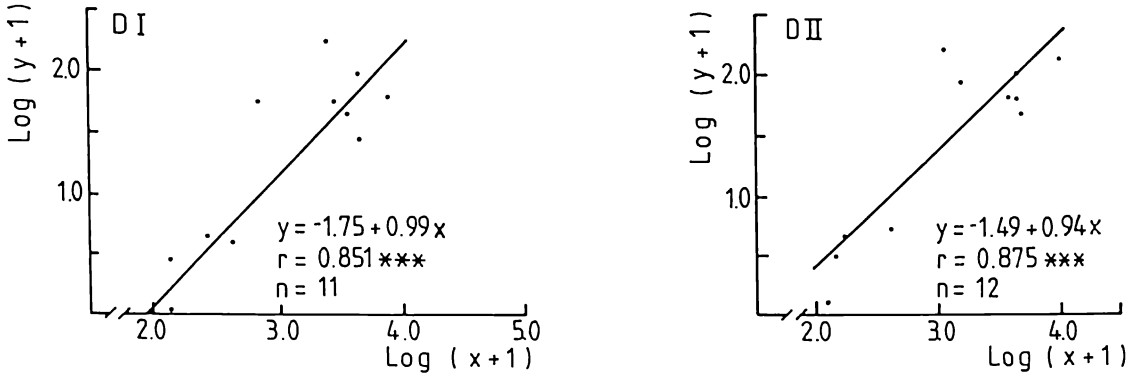

Fig 3.3.a Linear regression of the number of LF caught with the sweepnet (y-axis) and soil corer (x-axis) in two paddocks in Huntly.

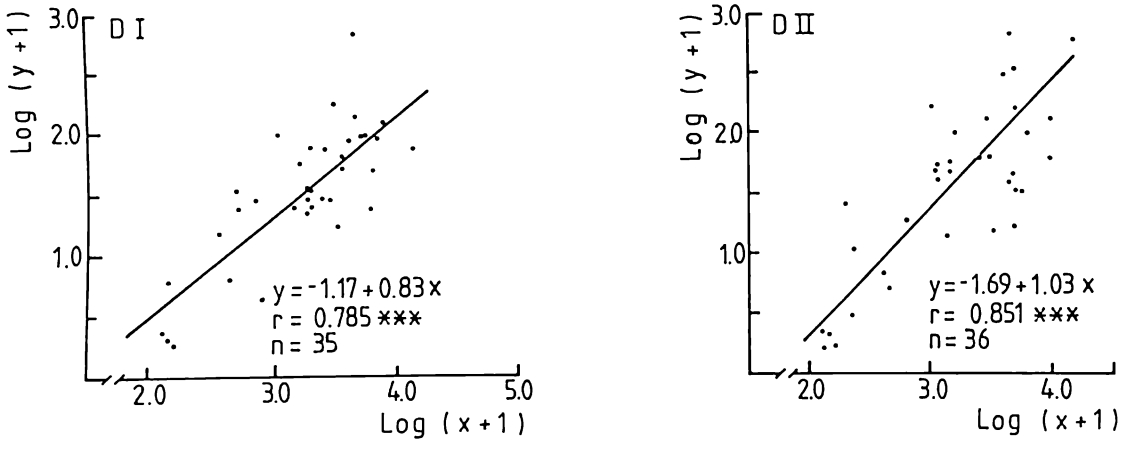

Fig 3.3.b Linear regression of the number of LF caught with pitfall traps (y-axis) and soil corer (x-axis) in the two paddocks in Huntly.

r=0.875***). In Te Kauwhata a significant relationship was found in KI (r=0.715*) but not in KII (Fig 3.4.b). A reason for this may be that the population density in KII was very low during the period of sampling.

The positive relationship between soil sampling and the sweepnet method in three of the four paddocks indicate that the use of a sweepnet may be a practical method for farmers to monitor the LF population changes and act accordingly with the timing of insecticide application.

c/ Pitfall trap sampling

Pitfall traps have been used extensively for studies on surface dwelling insects such as springtails, spiders, centipedes and beetles (Southwood, 1978). Martin (1975) used pitfall traps to study the re-invasion by springtails of areas where insecticides had been applied. Pearson and Goldson (1980) monitored the insect fauna in beet with pitfall traps. King *et al.* (1980) studied the use of pitfall traps to measure the population density of black beetle adults in spring but found them unsatisfactory. They found that the activity of the black beetle adults as determined by pitfall traps was independent of the population density and influenced by pasture management. A critical study of pitfall traps to catch Carabidae was made by Greenslade (1964). He found that the catches were determined by the size of the population and the level of locomotory activity. Species showed a differential susceptibility to trapping according to their size, behaviour and strata in which they were active in ground vegetation. Better catches of Carabidae were achieved when the ground around the traps was cleared. However, camouflaged pitfall traps were better for species feeding on plants. Greenslade concluded that "...pitfall trapping cannot properly be used for the quantitative assessment of the carabid fauna of any

habitat; nor should it be employed to compare the numbers of one species in different habitats". Greenslade and Greenslade (1971) studied the effect of baits and preservatives in pitfall traps. When comparing water and methylated spirits as liquid in the traps they found no significant difference in the number of Collembola caught, but in other experiments an alcohol-glycerol mixture was found to more effective than water. They also found that insect catches were proportional to the diameter of the trap and that the size of the pitfall traps was only important for larger sized insects. This is confirmed by Luff (1975) who found that, regardless of the shape of the trap, the perimeter length of the trap forms a basis for comparison.

Other factors may play a role in the number of insects caught in pitfall traps. Tolbert (1975) studied the insect fauna on hill sides in North Carolina. He found that when comparing the areas on a hill that were exposed differently to factors such as rainfall, temperature, wind, solar radiation and vegetation composition, the areas that were warm and dry had the highest insect activity. Joosse (1965, 1971) and Joosse and Kaptijn (1968) mention two other factors that play a role in pitfall catches of Collembola. The first factor was called "the digging-in effect". After the pitfall traps had been dug in, a high locomotory activity was noticed, which lasted for about two days. This was attributed to the release of CO_2 from the soil, due to the digging. The second factor was the influence of walking through the area where the traps were dug in. The increased activity in locomotion lasted for about one hour.

Methods

A hole was dug in the centre of each plot. A PVC tube, wide enough to contain the pitfall traps, was inserted. The tube stopped the caving-in of the hole and enabled rapid changing of the traps. The traps consisted of white plastic jars, with an outer diameter of 8.3 cm at the bottom and 6.6 cm at the top, and a volume of 550 ml. To avoid loss of insects due to the trap flowing-over after heavy rainfall, a hole with a diameter of 3.0 cm was made and covered with fine metal gauze. As soon as the trap contained more than 325 ml of liquid, the remainder would flow away through the hole. The traps were filled with 150 ml of Gault solution (E. H. A. Oliver, pers. comm.), an odourless preservative. A white plastic funnel with a diameter of 10.0 cm was placed in the pitfall trap, mouth flush with the ground surface. The traps were replaced on a weekly basis and care was taken to disturb the vegetation around the traps as little as possible. As was the case with the sweepnet sampling method, pitfall trap sampling was done on all locations between July 1981 and August 1982 on a eight week sampling-five week no sampling pattern. After that, pitfall trap sampling was continued on a weekly basis in Huntly between September 1982 and December 1983.

Discussion

In contrast to the two previously mentioned methods, the results from pitfall traps depend in part on the locomotory activity of the insects present. Therefore the number of LF caught in this manner are more a direct measure of insect activity than population density. The data from the pitfall trap method were used for a comparison with the absolute counts from the soil sampling method.

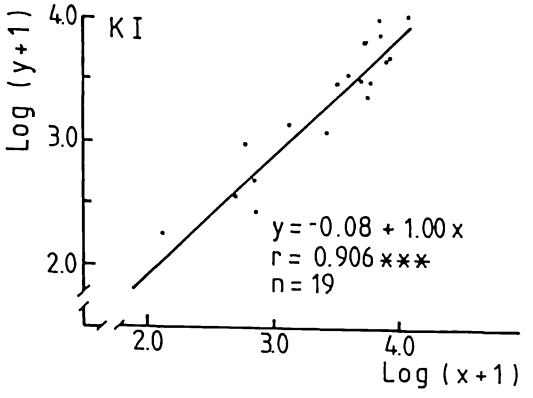

Fig 3.4.a Linear regression of the number of LF caught with the small (y-axis) and big (x-axis) soil corers in KI (Te Kauwhata).

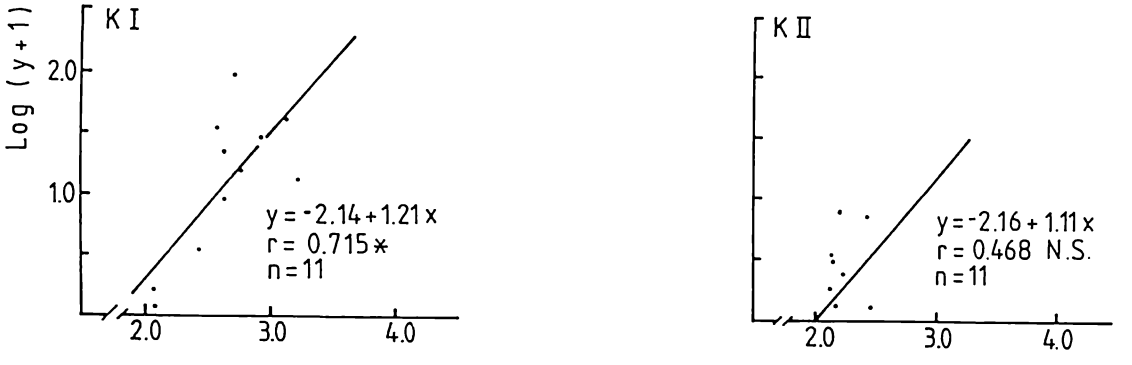

Fig 3.4.b Linear regression of the number of LF caught with the sweepnet (y-axis) and soil corer (x-axis) in two paddocks in Te Kauwhata.

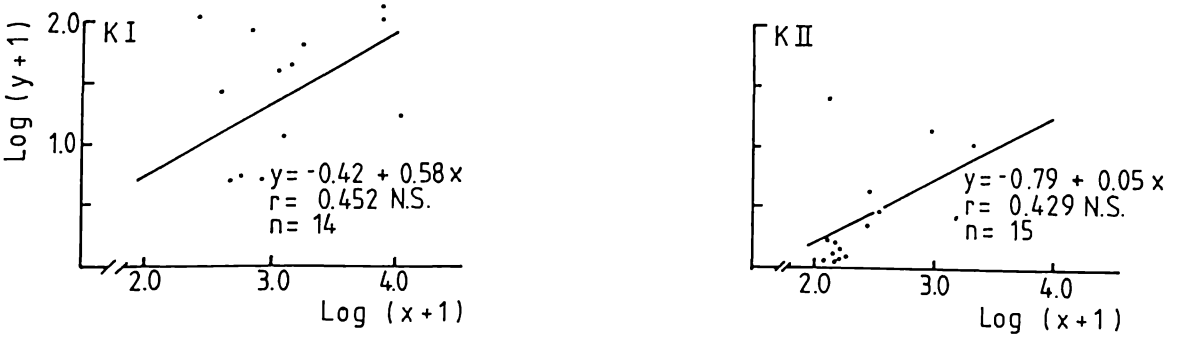

Fig 3.4.c Linear regression of the number of LF caught with pitfall traps (y-axis) and soil corer (x-axis) in the two paddocks in Te Kauwhata.

A linear regression between the number of insects caught in the pitfall traps and with the soil sampling method was made using a log(x+1)-log(y+1) transformation. The results are presented in Figs 3.3.b and 3.4.c. In both paddocks in Huntly the locomotory activity increased significantly with an increase in population numbers (DI: r=0.785***; DII: r=0.851***). In Te Kauwhata no significant relationship could be found. This is probably due to the fact that the population of the LF in Te Kauwhata was very low during the period of comparison of the sampling techniques.

The outcome of this study agrees with the conclusion of Greenslade (1964) that trap catches, as an indication of locomotory activity, are determined by the size of the population. King *et al.* (1980) compared the use of the traps with soil sampling for the black beetle and found no significant relationship. Unfortunately none of the other previously mentioned authors compared their catches with absolute methods. Only Gist and Crossley (1973) compared trapping with another method, hand sorting a known area. In their case a man-made barrier was used to stop migration of the insects and a comparison was made between the trap catches and estimates based on sorting by hand. No significant difference was found between the two methods.

3.3 Extraction unit system for soil samples

There are two basic methods to extract insects from soil samples, a mechanical and a behavioural or dynamic method. Both have their advantages and disadvantages (Southwood, 1978). For surface dwelling insects such as mites and springtails the dynamic, and especially the Tullgren funnel method (dry extraction) is most useful (Macfadyen,

1953). The earliest funnel method was developed by Berlese in 1905 and improved by Tullgren in 1918 (Edwards and Fletcher, 1971). Several modifications on this principle have followed since (Macfadyen, 1953, 1961; Dhillon and Gibson, 1962; Lasebikan, 1971, 1975). Extraction systems have even been designed for field use (Salmon, 1946; Macfadyen, 1953). The Tullgren funnel method is based on the principle that the animals are forced to leave the substrate under stimuli such as heat and lack of moisture (Lasebikan, 1975). Takeda (1979b) studied the efficiency of Macfadyen's high gradient extractor on Collembola and noticed two phases in the emergence pattern. It was difficult to determine the major factor in the first phase but in the second phase desiccation was the important stimulus for the extraction, or better expulsion. He also found that the efficiency of the system was greater for surface dwelling Collembola than for soil inhabiting springtails. Opinions differ on the steepness of the temperature gradient over the soil sample. Lasebikan (1971) advises a low temperature gradient and therefore a slow drying of the soil samples, while Macfadyen (1961) advocates a steep temperature gradient, e.g. a fast high-temperature extraction. Edwards and Fletcher (1971) made a comparison of extraction methods of terrestrial arthropods, based on the outcome of a survey. The most commonly used method of extraction was the Tullgren funnel method with heat source. Therefore the following summary applies to this method and all references are to the most common choice. The size of the funnels used was 10 to 15 cm in diameter and in most cases the soil sample was left intact (as opposed to being broken-up) on the funnel. Light bulbs of 20 to 35 Watt were used as a heat source and the average extraction time was three days. The most commonly used collecting fluid was ethyl alcohol. The survey showed that, regardless of the habitat, Sminthuridae were best extracted using the Macfadyen air conditioned funnel method.

Methods

After some initial experiments it was decided to build an extraction system that could extract up to 48 soil samples simultaneously. Based on the Tullgren funnel method, a wooden structure was built, measuring 359 by 73 by 58 cm (Fig 3.2.b). The system consists of three compartments, the outer ones containing 15 funnels each and the middle one 18 funnels. The funnels have an external diameter of 17 cm and are tightly fitted, 5 cm from each other, into a hardboard platform. Wire netting is suspended over all the funnels to prevent soil particles from clogging-up the funnels. The insects are collected in pottles (hospital specimen jars), that are positioned under the funnels in a lift-out platform and contain a 70 % ethyl alcohol-1 % glycerol-1 % Teepol mixture. The soil samples in the PVC tubes are put on the netting in inverted position, this is with the vegetation at the bottom. A loose hardboard platform with holes of 11 cm diameter is placed over the samples. For the smaller soil samples, platforms with 9 cm diameter holes were made. On top of this platform a box containing the light bulbs is placed. The box is fitted to the extraction system with hinges and can be put in an upright position to provide easy access for the exchange of soil samples. As with the base of the extraction system, there are also three light box compartments. The outer ones contain four light bulbs and the inner one six light bulbs of 40 Watt each. The electrical wiring is fitted to a light dimmer. This allows adjustment of the heat output and therefore adjustment to the moisture content of the soil samples. In normal situations an output of 20 Watt per light bulb was used. Measurements of the temperature in the light box as well as the vegetation side of the soil sample, showed an average temperature gradient of 6.5 ^{o}C. However, this will vary during the seasons, depending on the room temperature. The extraction was done

over four days. It was found that after one day an average of 80 % of the LF was extracted, and that no more LF were extracted after four days.

The extraction system was built and located at the Insect Control Group at Ruakura Agricultural Research Station (*See* Pottinger and Oliver, 1979).

3.4 Meteorological recordings and their importance

Monitoring and predicting insect population changes plays an important role in insect pest management. This is shown in a variety of studies (Blank and Olson, 1979; Watson *et al.*, 1980; Blank, 1982; East and Kain, 1982; King and Watson, 1982; Robertson and Blank, 1982). With an increased understanding of the phenology, phenological computer models have been developed, that "...dwell on the timing of key seasonal events in a pest's life cycle and in no way attempt to simulate the far more complex systems of population dynamics" (Goldson *et al.*, 1982). While these methods may be relatively simple, their value in the extension of integrated pest management has been emphasised by Welch *et al.* (1978). Recently these methods have been applied in studies on insects such as the codling moth (Riedl *et al.*, 1976), the cherry fruit fly (AliNazee, 1979), the green peach aphid (Whalon and Smilowitz, 1979), the spotted tentiform leafminer (Trimble, 1983) and the pecan nut casebearer (Ring *et al.*, 1983).

Most of these models are based on physiological, rather than chronological time. Physiological time, expressed as ^{o}h (degree-hours) or ^{o}D (degree-days) (Wagner *et al.*, 1984) is the cumulative product of time and temperature above a threshold (Southwood, 1978). There are

several methods to calculate physiological time with minor differences in accuracy and ease of application (Allan, 1976; Wilson and Barnet, 1983; Worner and Penman, 1983). In an attempt to standardise methods, Pruess (1983) advocates not to demand an unattainable and unneeded degree of accuracy, to standardise thresholds at 5, 10 and 15 ^{o}C and to use air temperature for all models. The use of such physiological time models requires the accurate measurements of meteorological information.

Methods

On both locations meteorological weather stations were set up between the two paddocks. The stations consisted of Stevenson screens that were mounted on a frame work, 1.20 m above the ground. Each station contained a thermohygrograph with a seven-day recording drum, a minimum-maximum thermometer and a raingauge with an opening of 38.8 cm^2. When possible, weekly readings of the meteorological data were done. In Te Kauwhata additional temperature recordings were made with a Tasman Data Logger recorder (Solid State Equipment Ltd). Recordings were made at half-hourly intervals of the air temperature and the temperature at plant and ground level. Measurements of the air temperature closely resemble the results from the thermohygrograph and are therefore not presented. Unfortunately the recordings of the temperature at plant and ground level were, in spite of regular calibrations, not reliable.

Results

Temperature and rainfall.

The results are presented in Fig 3.5. The temperature is presented as the minimum and maximum recording during one week, the rainfall as rainfall in mm per week.

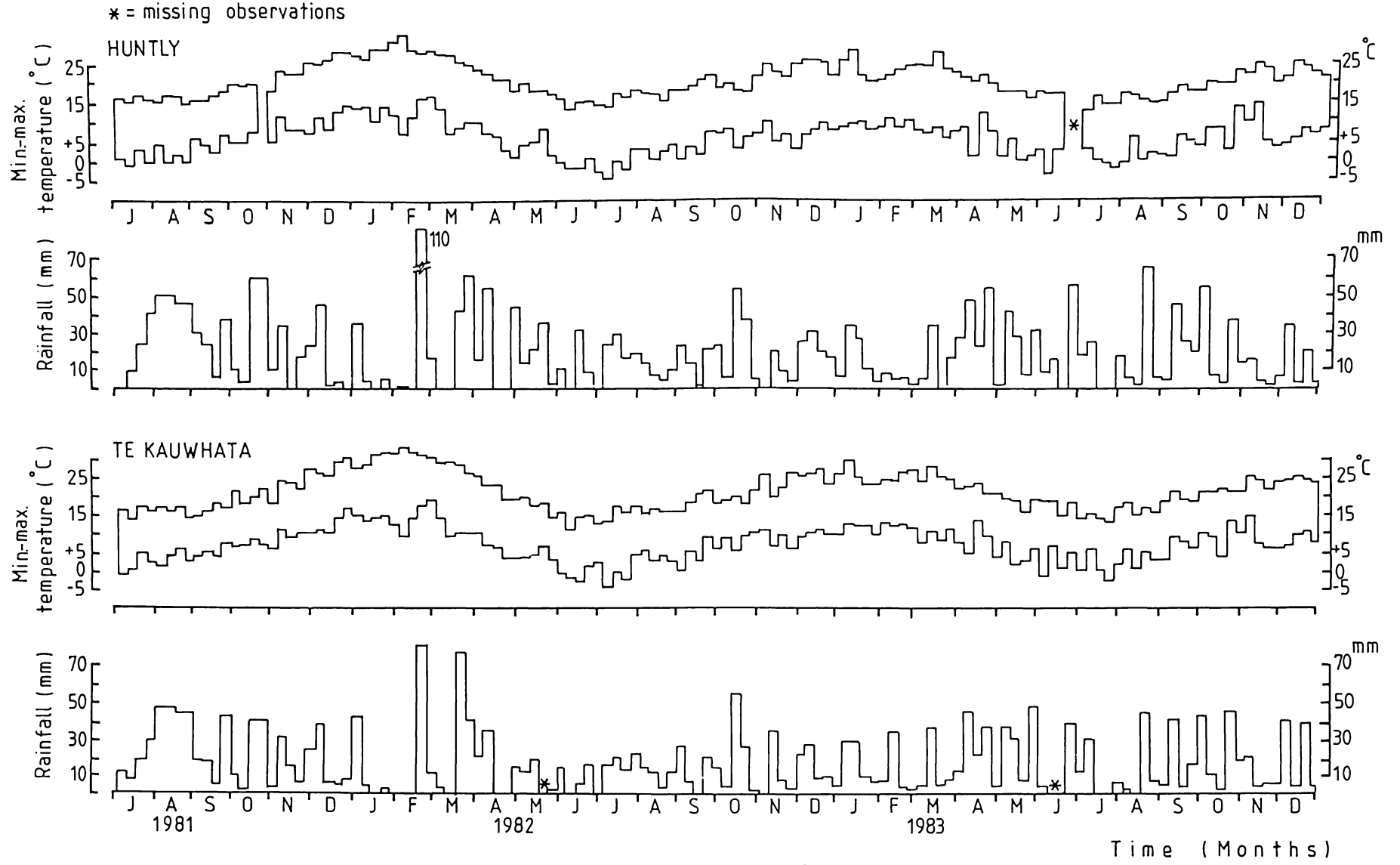

Fig 3.5 The weekly rainfall (mm) and minimum-maximum temperature (^{o}C) in Huntly and Te Kauwhata, recorded during this study.

Degree-days

The daily minimum and maximum temperature were read from the thermohygrograph charts for both locations during this study. A computer program, partly based on a study by Frazer and Gilbert (1976) and adapted by Rohitha (1979), was used to calculate the degree-days at a zero-development threshold of 7 ^{o}C (Maclagan (1932a). Due to contradicting values for the threshold, found in the different studies on the biology of the LF, calculations are also presented for a threshold of 4 and 10 ^{o}C. The results, on a weekly basis, are given in Appendices 3.4 and 3.5.

CHAPTER 4. Population studies

CONTENTS

CHAPTER 4. Population studies

4.1 Introduction

In the introduction to this chapter the literature is reviewed with reference to the methods that are used to analyse the dynamics of insect populations in general and those that apply to the LF in particular. For literature regarding other aspects discussed in this chapter the reader is referred to Chapter 2.

The analysis of insect census data and the construction of life tables is an important component in the understanding of the population dynamics of a species (Morris, 1960; Birley, 1977; Southwood, 1978). Two types of life tables can be distinguished, the age-specific (or horizontal) life table, based on the fate of a real cohort when the members of a population belong to a single generation and the population may be stationary or fluctuating, and the time-specific (or vertical) life table, based on the fate of an imaginary cohort, found by determination of the age structure at a point of time of a sample of individuals from what is assumed to be a stationary population with considerable overlap of generations (Southwood, 1978). Examples of age-specific life tables and their analysis and predictive models can be found in several articles (See Varley and Gradwell, 1960; Pottinger, 1967; Hughes and Gilbert, 1968; Ruesink, 1975; Podolor and Rodgers, 1975; Hassell *et al.*, 1976; Birley, 1977; Poole, 1978; Oster, 1981; Bellows and Birley, 1981; Hardman and Mukerji, 1982; Longstaff and Evans, 1983). However, since it is known from the literature that LF populations have overlapping generations (Walters, 1964), only the literature with reference to the time-specific life tables will be dealt with here.

The analysis of insect populations with overlapping stages and/or generations has only recently made some advance. This can be illustrated with articles written by Varley and Gradwell (1970) and Southwood (1978). Varley and Gradwell (1970) devoted 18 pages to the analysis of insect populations with distinct generations, and less than half a page to populations with overlapping generations. In that paragraph they state that "The relative simple methods of analysis which are suitable for insects which have discrete generations, are inapplicable to populations with overlapping generations which are inherently difficult to analyse and model". On the other hand, Southwood (1978) devotes two separate chapters to this.

Time-specific life tables contain data that are in essence a frequency distribution of the ages of individuals in a cross-section of the population, taken at a specific time. On the assumption that both the population size and the age structure are constant, these tables give a general picture of survivorship with age. Although they show the pattern of survival and mortality, they do not enable causes of mortality to be identified or the extent of density dependence or regulation to be quantified (Putman and Wratten, 1984).

There are several methods to analyse stage-frequency data. With reference to Collembola not much information is available. Although Niijima (1975) and Takeda (1976, 1979a) present papers on the population dynamics of some springtail species, their articles do not go beyond the level of a bionomics description. O'Neill and Styron (1970) applied compartment-modelling techniques to a collembolan population with distinct generations, and van Straalen (1982) discusses a mathematical model that handles data obtained by sampling an age-structured arthropod population, but is applicable only to the study of Collembola that have distinct generations. Takeda (1984) studied the life cycle and

population dynamics of *Folsomia octoculata* Handschin (Collembola) and calculated the birth and death rates as well as the intrinsic rate of population growth. These parameters are three of many used frequently in fresh-water ecology studies (See Edmondson, 1960; Edmondson and Winberg, 1971; Green, 1976; Burns, 1979; Hart, 1981; Cryer, 1983). They require, however, knowledge of aspects such as the egg stock and egg hatching rate. This applies also to the methods of Beaver (1966) and Berryman (1968) that are used to construct and analyse life tables for bark beetle (Coleoptera, Scolytidae) populations with overlapping stages. This problem is avoided in a stochastic model for the analysis of stage-frequency data, described by Ashford *et al.* (1970). The complexity of the calculations that are involved, however, would probably be regarded as a great disadvantage by the less mathematically inclined (Manly, 1974b).

Other methods are available to analyse stage-frequency data of insect populations in which recruitment and mortality widely overlap, and to estimate aspects such as daily (or stage-specific) survival rates and number of insects entering each growth stage. Richards *et al.* (1960) described a method of estimating mortality in successive instars in two populations, sampled at different intervals of time. In addition to the estimates of frequencies in stages at different points in time, a prerequisite for this method is a knowledge of the number of eggs laid, and the duration of the stages. Dempster (1961) presents a method that does not require knowledge of the two above mentioned parameters but in this case the rate of entry to the first stage needs to be known. A method developed by Kiritani and Nakasuji (1967) requires that samples be taken at regular intervals throughout the generation. Manly's method (1974a) assumes that the time of entry to a stage follows a normal distribution. A comparison of these methods based on a computer

simulation of the development and sampling of a number of insect populations, passing through several stages (Manly, 1974b), suggests that the method of Kiritani and Nakasuji (1967) should be used to estimate stage-specific survival rates whenever populations are sampled at equal intervals of time until almost all insects are dead, but that Manly's method (1974a) should be used when Kiritani and Nakasuji's method cannot be applied or if it is desirable to estimate the actual number of insects entering stages. A modification of Kiritani and Nakasuji's method (1967) by Manly (1976, 1977b) removes the restrictions that were incorporated in their method and allows for more population parameters to be estimated. A more detailed discussion of the above mentioned and other methods can be found in Manly (1974b), and Southwood (1978).

The previously mentioned methods have in common the assumption that the daily survival rate is constant within each stage. New techniques have been developed, however, that include variable mortality rates. Birley (1977) developed a model in which several formulations can be used for age-dependency in the mortality rate and a model was developed by Bellows and Birley (1981) in which mortality varies between the stages but is constant within a stage. A model that can be used both in analysis and prediction of insect stage-frequencies and may be applied to populations with age-dependent mortality, is described by Bellows *et al.* (1982).

4.2 The taxonomic status, the number of different instars[$] of lucerne flea, and other related aspects

4.2.1 Introduction

Since previous studies on the biology of LF did not agree on the number of different instars in its life cycle (Holdaway,1927; Maclagan, 1932a; Walters, 1964), it was necessary to determine the number of moults that LF pass through under New Zealand conditions. The number of moults may be determined by observing and counting the number of moults of the insects under laboratory conditions (a time consuming and often impractical objective) or by taking measurements such as head width, body length or other measurable parts of the insects. Two empirical laws of growth relating to such measurements are Dyar's rule and Przibram's rule (Wigglesworth, 1972). Dyar (1890) showed for lepidopterous larvae that "...the widths of the head of a larva in its successive stages follow a regular geometrical progression, and if...any deviation from the calculated progression is shown, it is evident that an error has been committed or that the larva has behaved in an abnormal manner...". This progression factor, usually about 1.4, is fairly constant for a given species. Teissier (1960) and Crosby (1973) point out that Dyar' s rule should in fact be renamed "Brooks' rule", since Brooks stated this law already in 1886 in his study on Stomatopoda. Although this argument is supported, this growth rule will be referred to as "Dyar's rule" to avoid any confusion. Przibram's rule states that the weight of each instar increases by a factor 2 or n x 2, compared with the previous instar and that the progression factor for length is 1.265 ($\sqrt[3]{2}$) or n x 1.265 (Przibram and Megusar, 1912 *In* Bodenheimer, 1933).

($) To avoid any confusion (*See* Fink, 1983; Jones, 1983), the following nomenclature will be used. The word stage will be used for expressions such as egg stage, immature stage and adult stage. Reference to immature insects will be for example to first larval/nymphal instar (or first immature instar), first instar larvae, or nymphs. References to mature insects will be for example to first adult male instar (or adult male), or mature instar. In all cases this may be replaced by abbreviations such as L_x, M, or F_x (*See* List of Abbreviations). The period between two moults will be referred to as stadium.

Measurements on several collembolan species have shown that Przibram's rule is of doubtful significance (Agrell, 1948; Milne, 1960; Hale, 1965c; Ashraf, 1969; Joosse and Veltkamp, 1970; Niijima, 1973). Studies on other groups such as Orthoptera (Richards, 1949; Clarke, 1957), Hemiptera (Harries and Henderson, 1938), Coleoptera (Hoxie and Wellso, 1974) and Plecoptera (Vaught and Stewart, 1974) came to the same conclusion. Only Bodenheimer (1933), who measured Acrididae, Phasmidae and Mantidae, supports Przibram's theory.

4.2.2 Results and discussion

The taxonomic status of LF

The identification of LF that were collected during this study was regularly checked, using the keys for the identification of Collembola mentioned in Chapter 2. LF were also sent to Dr R. T. Baker, Plant Health Diagnostic Station, MAF, Auckland, who confirmed the insects to be all lucerne flea, *Sminthurus viridis* L.

Number of different instars

The methods used for collection LF and the measurement, sexing and weighing are explained in Chapter 6. Fig 4.1 represents the frequency distribution of the different stages of development of LF found on both locations between July 1982 and December 1983, as determined by head width. Head width was chosen as the criterion because it is easy to measure and is not influenced by the intake of food as may be the case with body length. In total more than 5,200 insects were studied. The analysis of the data was made on the computer using Minitab and BMDP programs. Separation of insects into immature and adult LF was made on the possibility of the sex being able to be distinguished. The

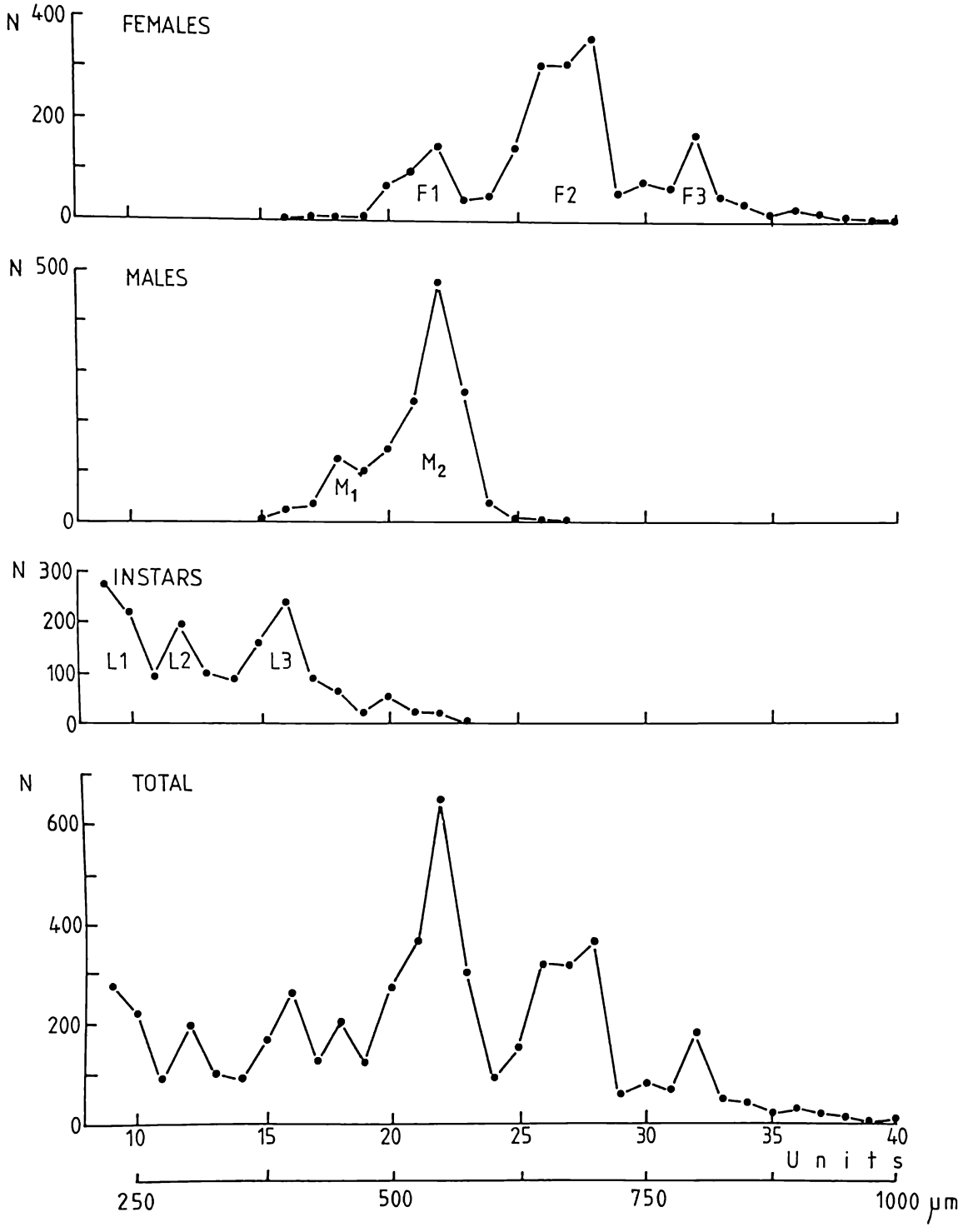

Fig 4.1 Frequency distribution of the head widths (µm) of the LF (bottom), separated into larval instars (L_1-L_3), adult male (M_1-M_2) and adult female (F_1-F_3) instars.

cutpoints between the different instars were determined by eye. In total three larval instars, two adult male and three adult female instars are recognised. Cutpoints between the first and second, and the second and third larval instar are 275 μm and 350 μm head width respectively. A cutpoint between the adult male instars was found, although not clearly, at 475 μm. Since the distinction between the two adult male instars (M_1 and M_2) was not clear (Fig 4.1), they have been grouped together (M) in later analyses. Cutpoints in the head width between the first and second, and second and third adult female instars are 575 μm and 725 μm respectively. Since the data were collected from field samples, it is impracticable to determine the average head width of the immature and mature instars. The median was therefore used (Table 4.1).

Table 4.1 Median (μm) for the head width of the different instars of the male and female LF.

Stage	Median (μm)	
	Males	Females
Immature instar		
1	240	240
2	308	308
3	400	400
Mature instar		
1	453	538
2	545	670
3	---	798

Due to the fact that it was not possible to determine the sex in the first three larval instars, the median of the head widths of the males and the females are the same. It is possible to test if instars have

been overlooked by applying Dyar's rule. This rule can be expressed by the equation: $Y = K \times p^n$, where Y is the length of any measured part of the animal after n ecdyses, and K and p are constants, p being the progression factor (Harries and Henderson, 1938; Teissier,1960; Hale, 1965c). The equation can be rewritten as log Y = log K + n x log p. If, when plotting the logarithm of the measured part against the number of ecdyses, a straight line is obtained, then Dyar's rule is upheld. This is illustrated in Fig 4.2.b for the head width of male and female LF. In both cases a straight line is obtained and the Pearson product moment correlation coefficient is significant ($r_{L1-->M2}=0.992***$; $r_{L1-->F3}=0.997***$). Although Dyar's rule may be applied to the development of LF, the progression factor p is not constant during the development. The values for the progression factor for the head width from first larval instar to adult male are p = 1.283, 1.299, 1.133 and 1.203. The values for the females are p = 1.283, 1.299, 1.345, 1.245 and 1.191. The tendency for the progression factor to increase during the immature stage and to decrease during the mature stage agrees with findings for collembolan species in general (Agrell, 1948) and the LF in particular (Maclagan, 1932a; Walters, 1964). To compare the results from this study with the results from laboratory observations by Maclagan (1932a) and Walters (1964), all relevant data are summarized in Table 4.2 and the results of a linear regression of the data presented in Figs 4.2.a and 4.2.c.

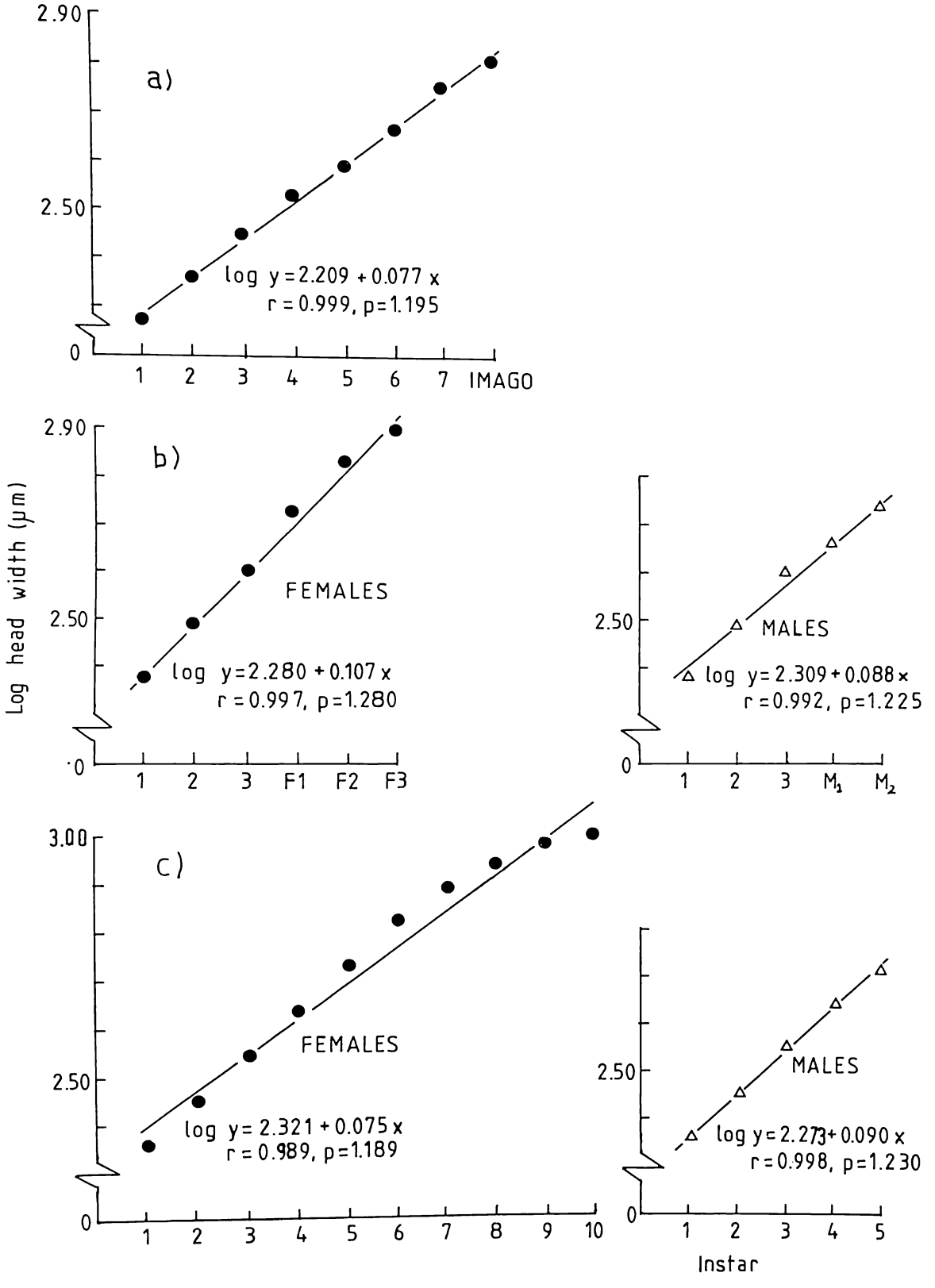

Fig 4.2 Logarithm of the head width (y-axis), plotted against the different instars (x-axis) of the LF: a/ Maclagan (1932a); b/ this study; c/ Walters (1964). In all cases r is statistically significant (P=0.001); p= progression factor for growth.

Table 4.2 The head width (μm) of the different instars as found by Walters (1964) and Maclagan (1932a).

	Instars									
Walters (1964):										
Males	1	2	3	4	$5					
Head width	229	281	355	440	516					
Female	1	2	3	4	5	6	7	8	9	10
Head width	229	284	350	422	534	656	775	872	947	1030
Maclagan (1932a):										
Combined[&]	1	2	3	4	5	6	7	Imago		
Head width	190	230	280	340	390	470	570	660		

&: no distinction between males and females; $: sexually mature

Maclagan recognised 7 nymphal instars and one adult. The head width of his first larval instar is smaller than described by Holdaway (1927: 210 μm) or Walters and this study. Measurements of newly hatched instars were found to be 225 μm (this study). Walters found four larval instars and one adult male instar. This compares favourably with what was found in this study. The LF male could already be sexed at a head width of 453 μm (M_1 and Walters' fourth larval instar). Based on laboratory observation, however, it is highly unlikely that sexual

maturity is reached before the second male stadium (M_2). Comparison of the results of development from first larval instar to last adult female instar indicates that Walters' third and fourth larval instar can be grouped together into the third larval instar in this study. As was the case with the males, it was possible to determine the sex of the females at an earlier stage than was found by Walters. The head width of the first adult female instar was 538 µm, equivalent to Walters' fifth larval instar. But again, sexual maturity is not assumed before the second female instar. Walters describes three more instars for the female than were found by Maclagan, or in this study, but they were only found at 16 and 20 ^{o}C. Under laboratory conditions an indefinite number of instars can be found in collembolan species, depending on the length of their life and the availability of food (Ashraf, 1969).

Other relationships

It was possible to clearly determine the sex of the males at a smaller size (head width 400 µm) than the females (head width 500 µm). While the maximum head width for adult males, found in the field, was 675 µm, a maximum head width of 1 000 µm was found for adult females. This indicates less growth for the males than the females and probably a shorter life span. This is found in several other collembolan species by Agrell (1948) and Christiansen (1964). The latter, however, was found not to be true for LF under optimum laboratory conditions (Walters, 1964). He found that the time spent by adult male in the last stadium approached the total time spent by females in instars five to eight.

Based on the different measurements, it was possible to determine relationships between head width, body length and weight of LF (Table 4.3). In all cases a positive linear relationship was found between

head width and body length, head width and weight, and body length and weight (P=0.001***). The mean and standard error of the mean of the body length and weight for all the different instars are presented in Appendix 4.1. The progression factor for body length (p = 1.39) is slightly higher than for the head width but the progression factor for weight is almost double the value of the other factors (p = 2.46). At both locations it was found that the average weight of the adult males was slightly higher than the average weight of the first adult female instar (F_1) but much lower than the (continued next page)

Table 4.3 Linear regression relationships between head width (H), body length (B) and weight (W) of LF at the two locations.

	Paddock		
DI	DII	KI	KII
B= -230 + 2.19 H	B= -213 + 2.16 H	B= -265 + 2.22 H	B= -255 + 2.22 H
$^{\$}$r=0.943	r=0.952	r=0.953	r=0.956
W= -646 + 1.97 H	W= -678 + 2.07 H	W= -686 + 2.01 H	W= -734 + 2.20 H
r=0.854	r=0.849	r=0.822	r=0.847
W= -429 + 0.89 B	W= -470 + 0.95 B	W= -459 + 0.92 B	W= -488 + 0.99 B
r= 0.894	r=0.889	r=0.877	r=0.893

$: in all cases the correlation coefficient is significant (P= 0.001);

B and H in μm, W in μg.

average weight of the consecutive female instars (F_2 and F_3). It is common in Collembola for the male to be much lighter in weight than the female (Niijima, 1973; Testerink, 1982).

4.3 Collembola populations in mixed ryegrass-white clover swards

The population of Symphypleona in general and LF in particular were followed for a two and a half year period at both locations. The results for the LF are presented in Appendix 4.2. Populations of Symphypleona (*not* including LF) were drawn on an overlay to make a visual comparison with LF populations possible. Both farmers in Huntly and Te Kauwhata were asked to keep a diary on farm management. While this was useful, it was not always kept up to date or quantified enough to positively state aspects such as fertiliser application or grazing pressure at each grazing. But for as far as it is known, pasture treatments such as application of fertilizer, weedkiller and insecticides, as well as shutting up and cutting for hay are presented in Appendices 4.3 and 4.4. As all grazing was done on a rotation schedule normally applied on dairy farms, specific dates are not presented. A detailed description of grazing management on dairy farms is given by Pottinger *et al.* (1985). Although every effort was made to avoid this, the experimental plots were treated once with insecticide in Huntly in 1981 and once in Te Kauwhata in 1981 and 1982. The application of insecticides against LF will be taken into account with the interpretation of the data.

Sampling started on all locations in July 1981 and therefore the hatching of the diapause eggs and the consecutive build-up of the population before this date is not known. On all paddocks the number of

LF show a strong fluctuation pattern during the period of this study. The population density was very high in 1982, very low in 1981 and in 1983 between the levels of 1981 and 1982.

4.3.1 The bionomics of lucerne flea

a/ Results and discussion

LF populations in Huntly

In DI a small peak in numbers in August was followed by a higher one in October after which the number of LF declined to a low level in December (Fig 4.3). The first LF, hatching from the diapause eggs, were found in March 1982. During the next four months the number of LF remained at a fairly low level but in August a peak in numbers was reached, followed by two more peaks at the end of September and the end of October respectively, culminating in the presence of more than 32 000 LF per m^2. Numbers then decreased rapidly and were very low in December. In 1983 the first LF were captured at the beginning of April. Numbers peaked in August (more than 6 000 LF per m^2) and again in October (reaching 14 000 per m^2) after which the population numbers declined to low levels in December.

Similar trends were obvious in DII (Fig 4.4). Although the population took longer to build up (the first peak in numbers is in September), more than 10 000 LF per m^2 were found in October, followed by a lower peak in November and a decline of the numbers in December. Again, in 1982 the build up of numbers was slower in DII than in DI, peak numbers being reached in November. In 1983 the initial LF population was higher in DII than in DI until October after which the

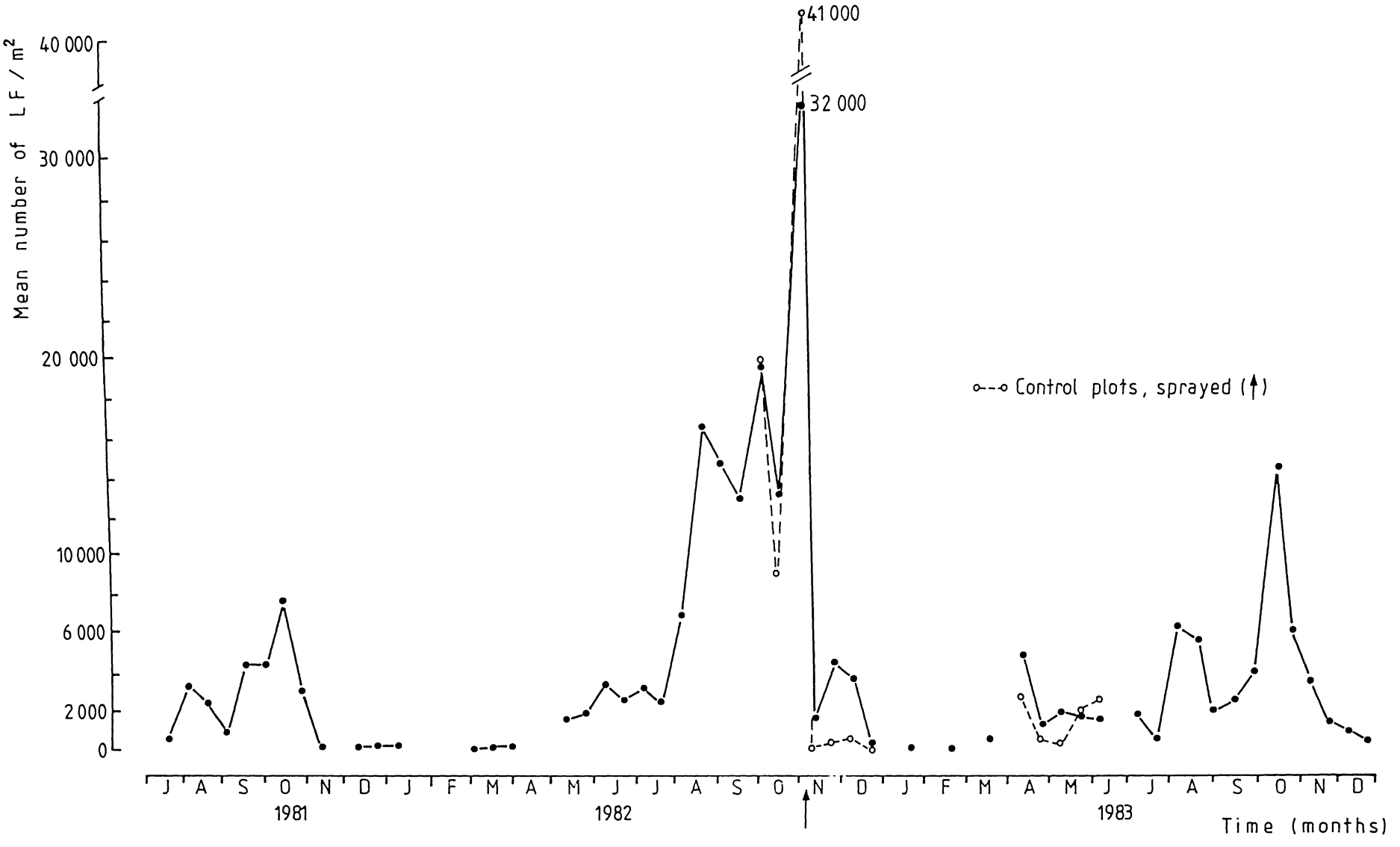

Fig 4.3 The number of LF (soil samples) per m^2 in DI, Huntly, during this study.

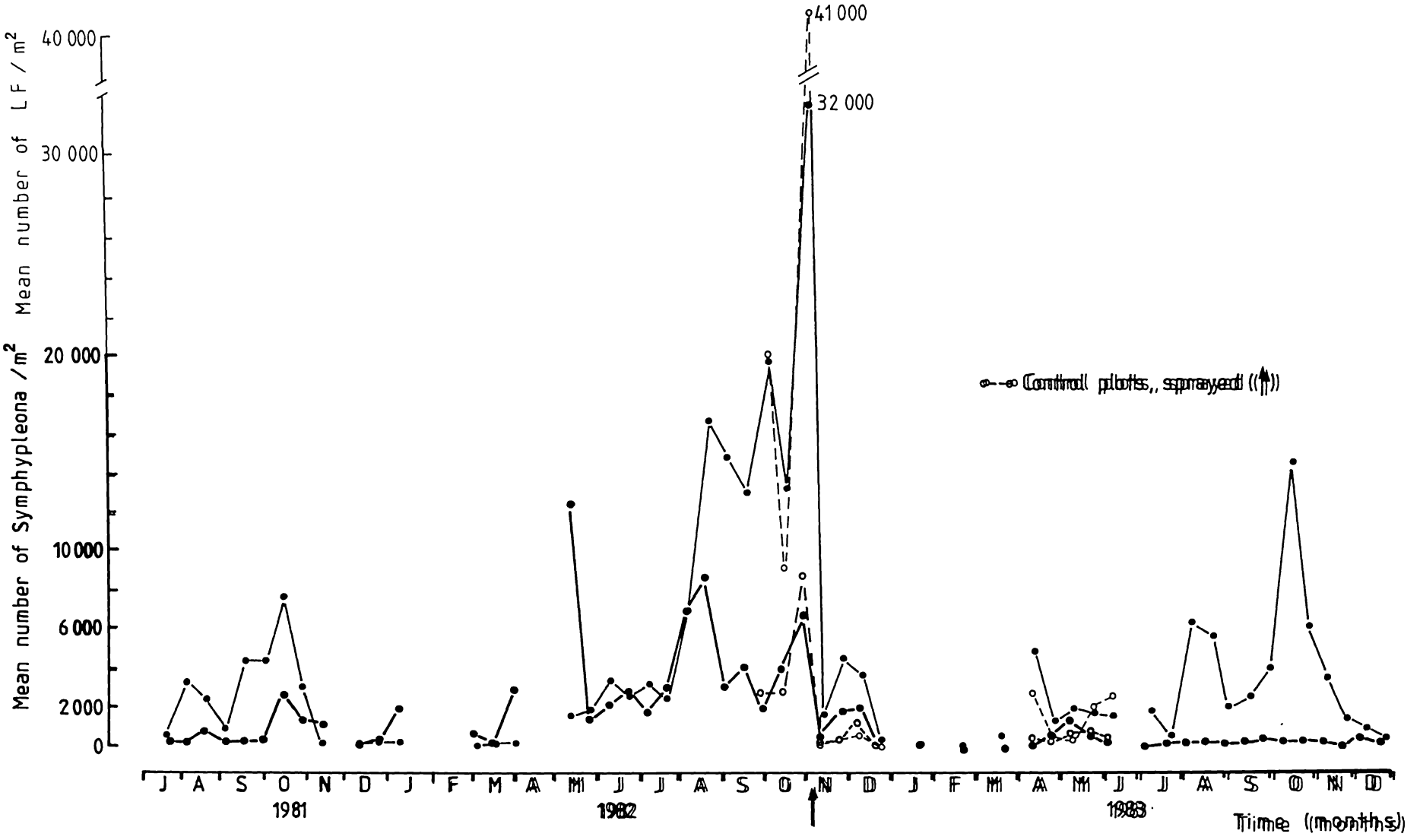

Fig 4.3.a The number of Symphypleona (soil samples) per m^2 in DI, Huntly, during this study.

Fig 4.3 The number of LF (soil samples) per m^2 in DI, Huntly, during this study.

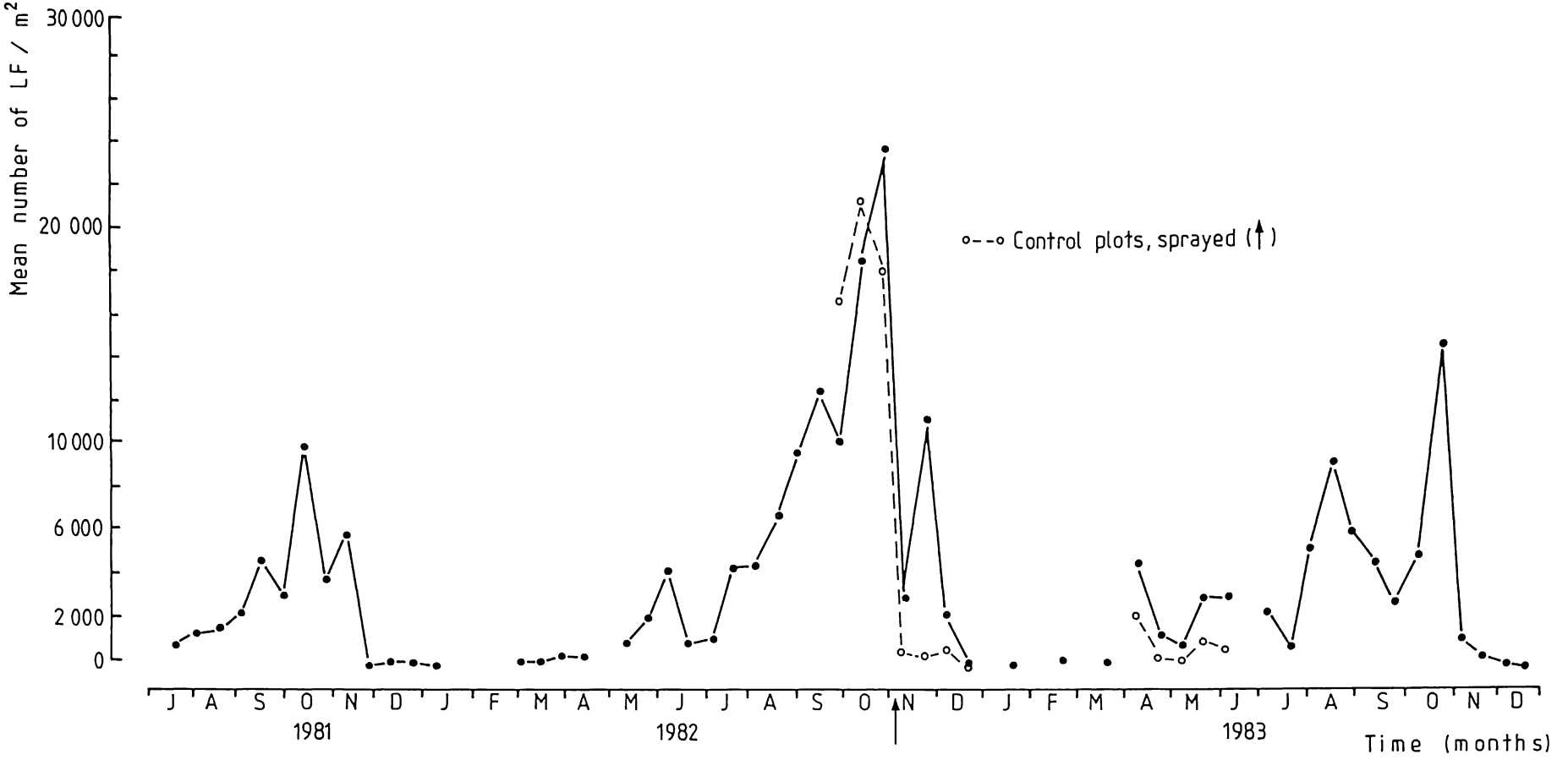

Fig 4.4 The number of LF (soil samples) per m^2 in DII, Huntly, during this study.

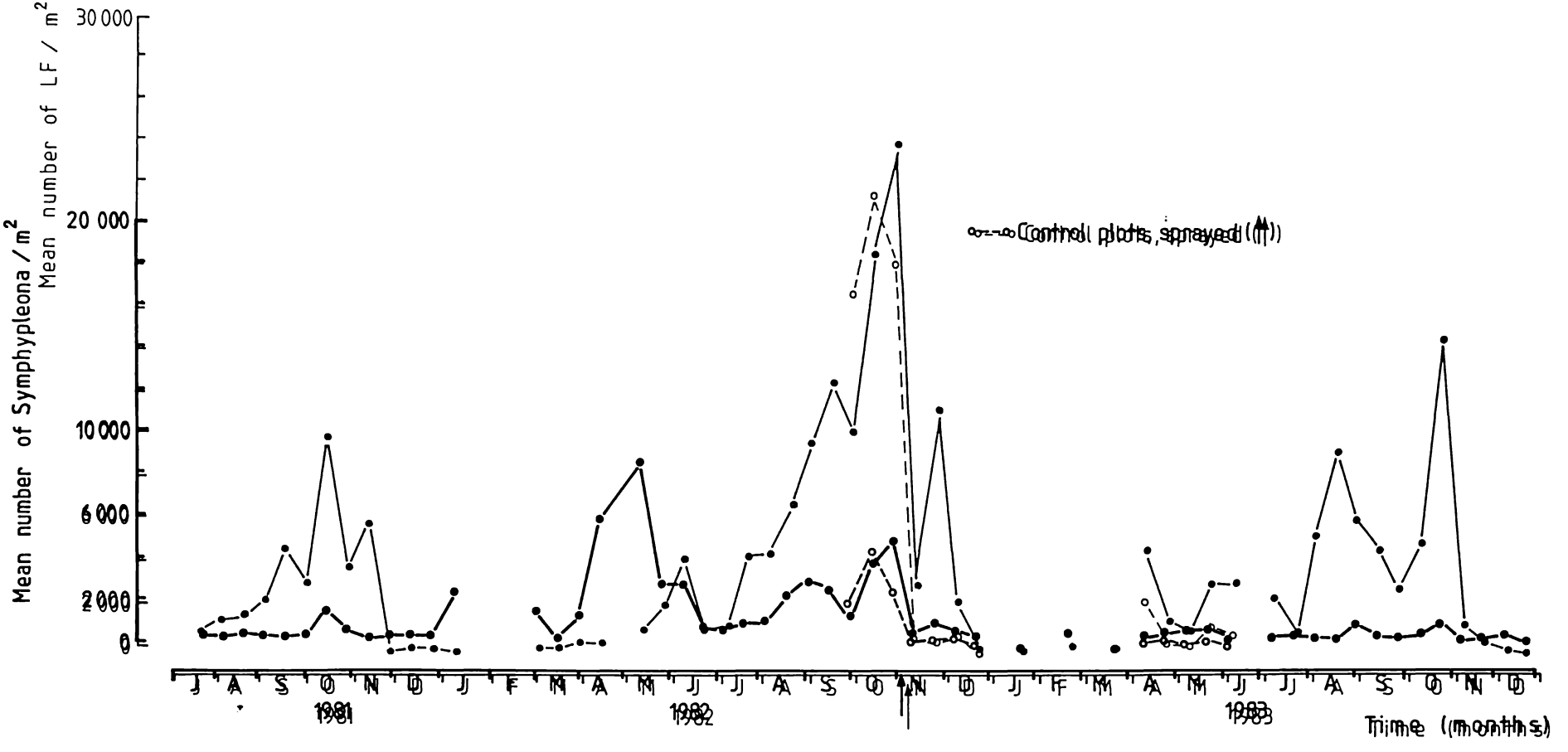

Fig 4.4.a The number of Symphypleona (soil samples) per m^2 in DII, Huntly, during this study.

Fig 4.4 The number of LF (soil samples) per m^2 in DII, Huntly, during this study.

difference disappeared. In both paddocks hardly any LF were present during January and February.

LF populations in Te Kauwhata

In KI the LF population never exceeded 2 000 per m^2 in 1981 (Fig 4.5). However, a much higher population level was reached in 1982. Numbers peaked at the beginning of June, followed by a peak of more than 11 000 LF per m^2 in the beginning of July and a lower peak at the end of September (6 000 per m^2). Numbers then declined steadily to a low level in December. In 1983 the first LF were found in March but the numbers stayed at a low level until August after which one more peak in numbers was observed in October (5 500 per m^2).

The LF population in paddock KII was very small during 1981 (Fig 4.6). Although the level remained relatively constant until June 1982, a small peak in numbers occurred in July, followed by a higher one at the end of September (5 500 per m^2), after which the numbers declined to a low level in December. A similar overall pattern occurred in 1983, but here four peaks in numbers were seen, in June, August, September and November. In both paddocks hardly any LF were present during January and February.

In general terms these fluctuations in numbers show the same pattern as was found by Davidson (1934) and Wallace (1967) in Australia, Evans (1937) in Tasmania and Walters (1964) in South Africa for 1962. In his study in 1961 in South Africa, however, Walters found that the population level of the LF was at its highest in May and June. 1961 and 1962 differed in the amount and the distribution of the rainfall. In 1961 387 mm of rainfall was recorded and not enough rain fell till May to induce the hatching of the diapause eggs. In 1962 the amount of

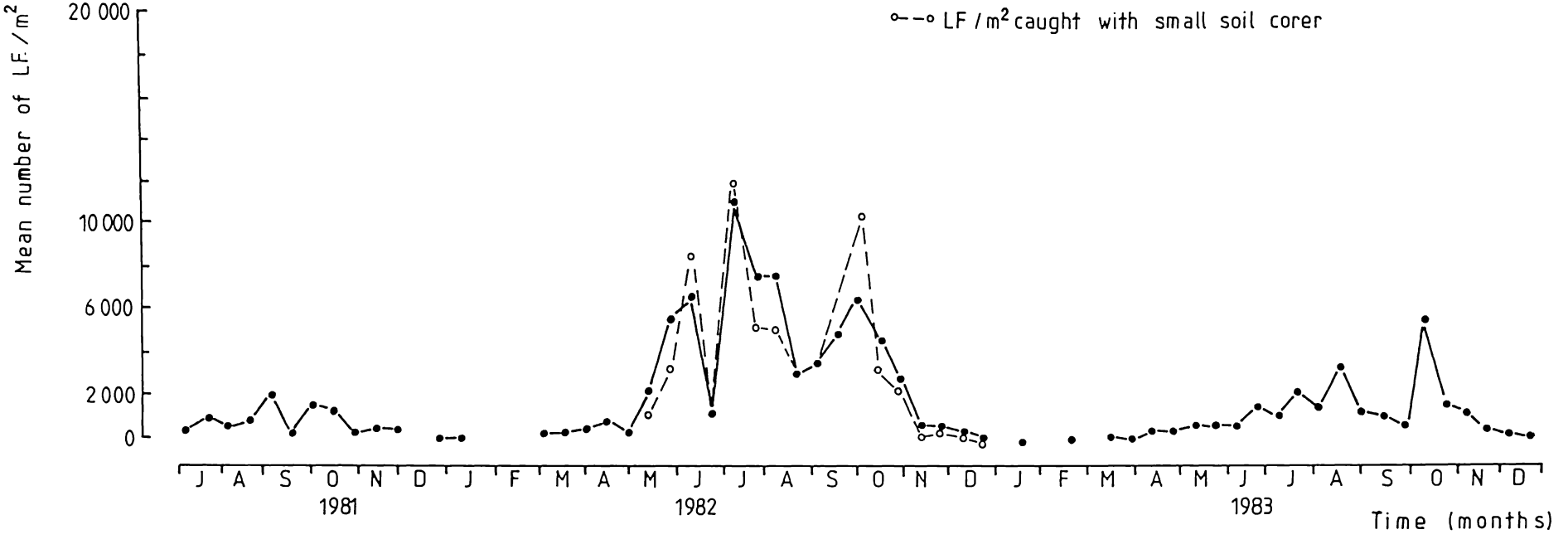

Fig 4.5 The number of LF (soil samples) per m^2 in KI, Te Kauwhata, during this study.

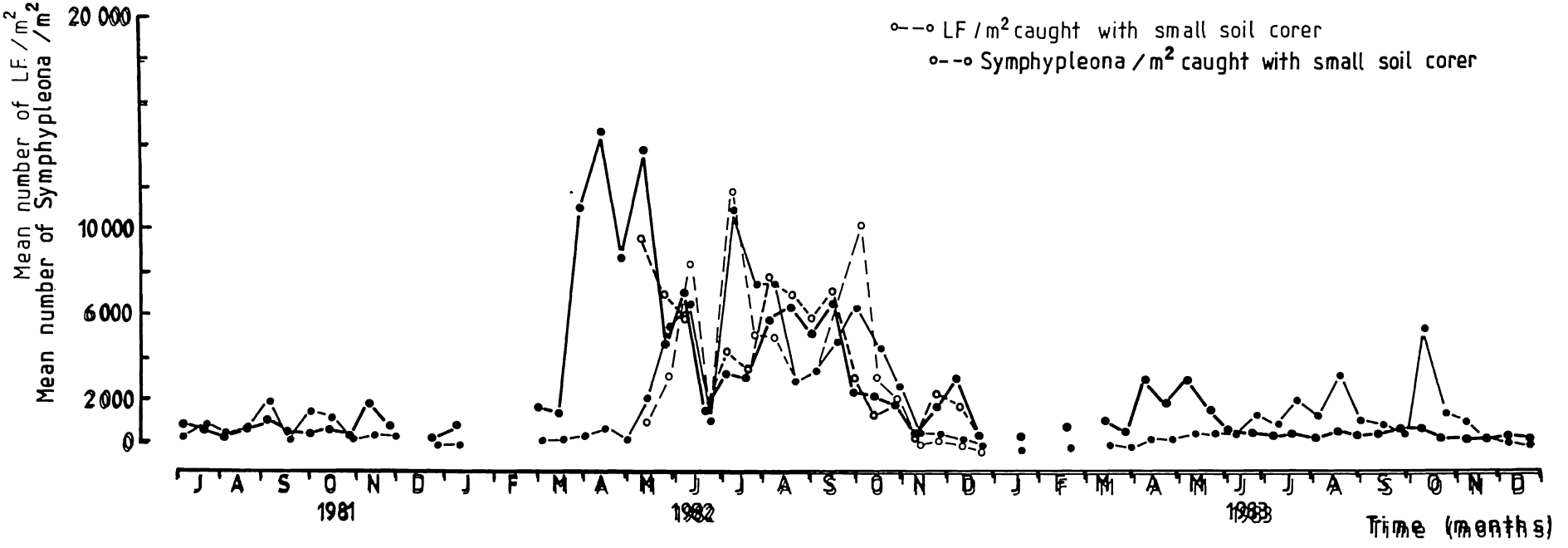

Fig 4.5.a The number of Symphypleona (soil samples) per m^2 in KI, Te Kauwhata, during this study.

Fig 4.5 The number of LF (soil samples) per m^2 in KI, Te Kauwhata, during this study.

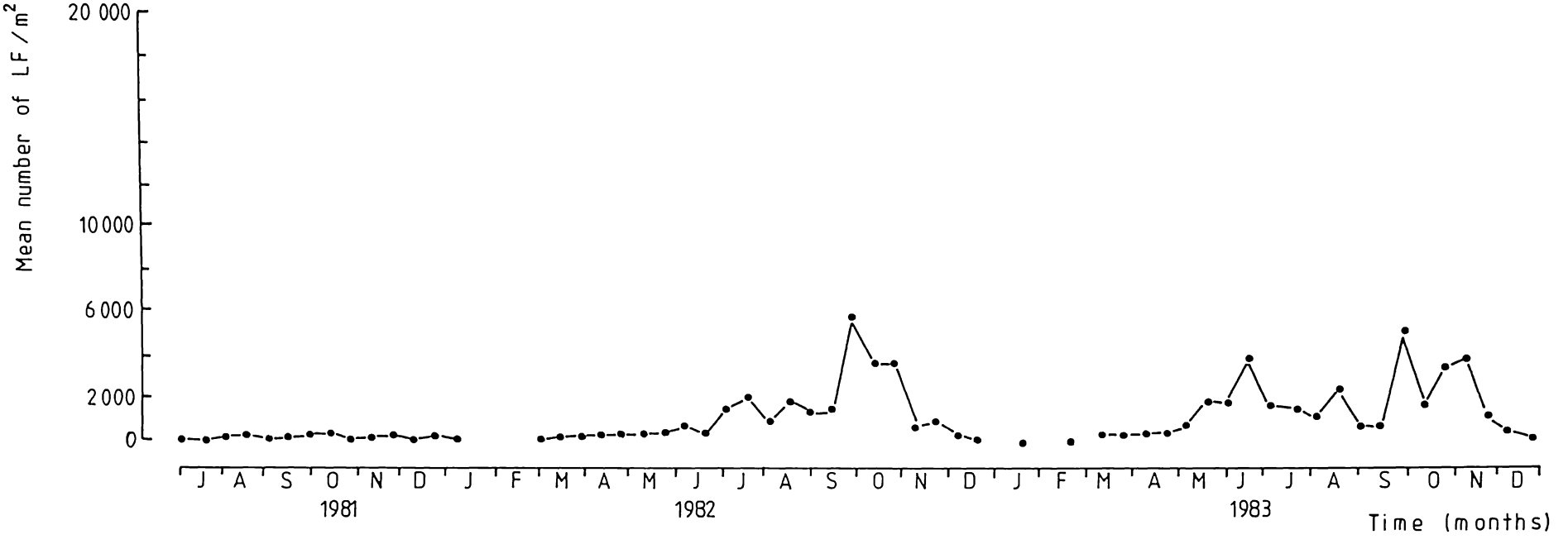

Fig 4.6 The number of LF (soil samples) per m^2 in KII, Te Kauwhata, during this study.

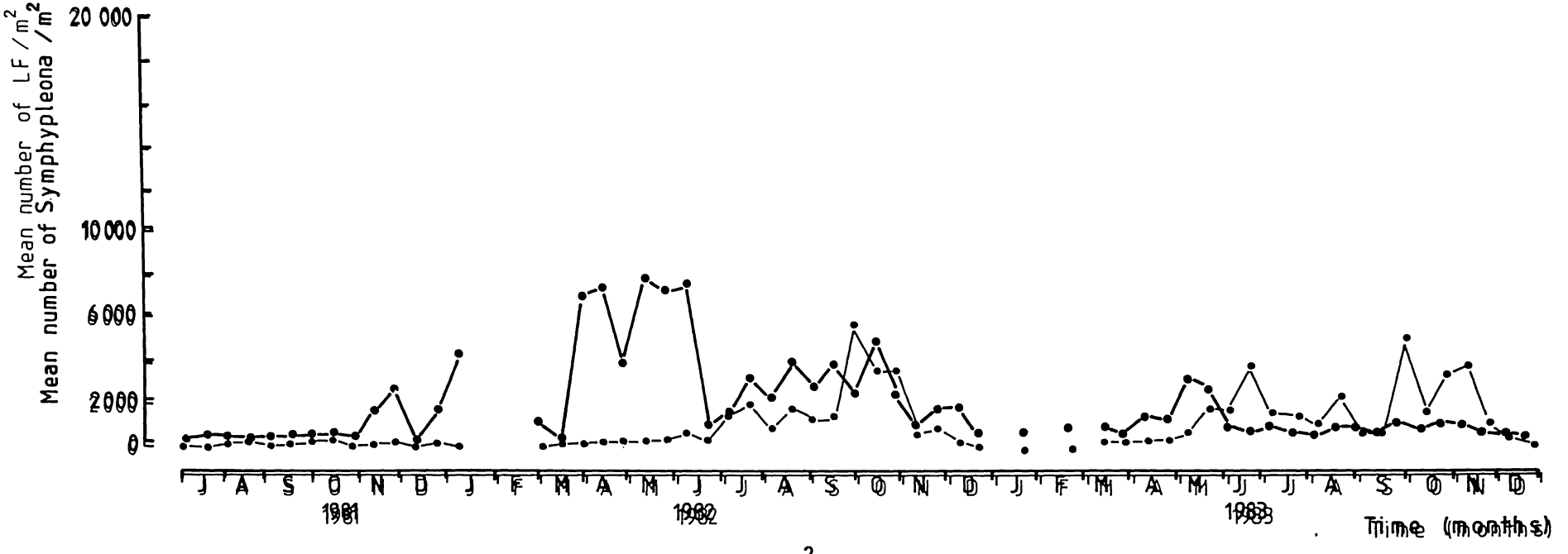

Fig 4.6.a The number of Symphypleona (soil samples) per m^2 in KII, Te Kauwhata, during this study.

Fig 4.6 The number of LF (soil samples) per m^2 in KII, Te Kauwhata, during this study.

rainfall was 622 mm and enough was recorded in the second half of April to initiate the hatching of eggs. Keeping in mind that LF hibernates in Europe (as opposed to aestivation in the Southern Hemisphere), the same comparison of bionomics applies to Maclagan's study (1932b). The main difference is that LF was present in New Zealand as late as December, while in studies in other countries aestivation (or hibernation) had already taken place, and as early as March. The explanation for this is found in the influence of climate on LF populations. According to the *Koppen System of Climates* (Koeppe and De Long, 1958) the climates in New Zealand, the eastern part of Australia, and Tasmania can be described as a humid, mesothermal warm summer (Cfb) climate, whilst the climates in a part of Victoria, the south-west of Australia, as well as the West Cape Province (South Africa) can be described as a humid, mesothermal warm *dry* summer (Csb) climate. While the mean annual temperatures are about the same in both types of climate, the mean January temperature in the south-east, south and south-west of Australia is higher than in New Zealand, Tasmania and West Cape Province. The mean precipitation in the period November-April, however, is higher in New Zealand, the east of Australia and part of Tasmania than in south Australia and West Cape Province. The combined effect of lower summer temperature and higher precipitation causes LF populations to be present in the field in New Zealand as late as December and to reappear as early as March.

4.3.2 Factors influencing the seasonal history of lucerne flea

a/ Temperature and rainfall

As long as the temperature falls within the range of favourable temperatures for the development of LF, moisture is the most important factor regulating the population fluctuations in S. Africa and Australia (Walters, 1964; Wallace, 1967). Since the temperature range, experienced in general in the Waikato (Maunder, 1974), is favourable for LF, it is most likely that rainfall plays an important role in the fluctuation of the population numbers. The weekly rainfall figures are presented in Fig 3.4. The total rainfall for the two locations was as follows (Table 4.4).

Table 4.4 The total rainfall for Huntly and Te Kauwhata for 1981$, 1982 and 1983.

	Rainfall in mm	
Year	Huntly	Te Kauwhata
1981	475	418
1982	922	828
1983	907	826

$: since 9 July 1981.

Rainfall recordings were made once a week and due to evaporation the figures may be lower than the actual rainfall figures for Huntly and Te Kauwhata. They show, however, the pattern that more rain falls in the Huntly than the Te Kauwhata area (Maunder, 1974).

The total amount of rainfall in 1982 and 1983 is approximately the same at each location. In Huntly 318 mm of rain fell between the beginning of November 1981 and the beginning of March 1982, of which 110 mm was recorded in the week before 25 February. This probably induced the hatching of diapause eggs in March (Figs 4.3 and 4.4), but no rain fell between 4 and 18 March, probably causing high mortality to the first larval instars. In the same period in 1983, 211 mm of rain was recorded and the first significant amount of rain (33 mm) fell in the week before 17 March. The following week no rain fell, but in the next two weeks 16 and 26 mm of rain were recorded. The first nymphs hatched at the beginning of April, but high rainfall (54 mm) between 21 and 28 April coincided with a drastic reduction in the number of first instar larvae (Figs 4.15 and 4.16). Apart from the fact that the respective rainfall figures were lower, the same tendency as described above, was observed at Te Kauwhata. It can be concluded from the above that rainfall is an important factor in the hatching of the diapause eggs and the survival of first instar larvae.

Walters (1964) regards moisture as the major factor affecting the seasonal activities of LF. He states that under Southern Hemisphere conditions an air saturation deficit below 5 mm Hg during April is sufficient to allow the hatching of diapause eggs. The average monthly saturation deficit figures for Te Kauwhata (Table 4.5) show, that during 1981 to 1983, the saturation deficit never exceeded 4.0 mm Hg during March and April.

Rainfall, or moisture, plays an important role in the hatching of the diapause eggs, and regulates the hatching of non-diapause eggs. The effect of rainfall on oviposition

Table 4.5 Average monthly saturation deficit figures for Te Kauwhata, as supplied by the Meteorological Service, Wellington.

Year	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1981	5.1	5.1	3.8	3.4	2.6	1.6	2.5	2.0	2.8	2.9	4.3	4.3
1982	4.7	6.6	3.3	2.9	3.0	2.5	1.6	1.9	2.3	2.6	3.7	3.5
1983	3.9	4.7	?	3.2	2.3	2.3	2.7	2.3	2.2	2.8	4.1	?

?: missing data

is much smaller since the moisture content of the soil only has to be favourable during a short period (Walters, 1964). Rainfall therefore indirectly influences the birth rate, and, due to a lack or excess of rainfall, the mortality rate.

Temperature influences the speed of development of LF, which is reflected in the duration and the number of generations per year (Walters, 1964). When the reciprocals of the development times of instars are plotted versus temperature, a shallow sigmoid ("S"-shaped) curve results. Between the lower and upper temperature limits the relationship can be represented by a straight line. This linear relationship can be written as:

$y = a + bx$ with y = 1/development time,

x = temperature (^{o}C), and derived from the equation:

$1/b$ = development time (^{o}D) above a zero threshold temperature,

$-a/b$ = zero threshold temperature t_0, below which no development can take place

(Campbell *et al.*, 1974; Wagner *et al.*, 1984).

Since no experimental data on development time are available from this study, Walters' results (1964, p. 42) were used. The application of the above mentioned formula on the cumulative days for development from egg to first larval instar, first larval instar up to and including the sixth (approximately F_2 in this study) and seventh (approximately F_3) female instar as well as the fourth and the fifth male instar (approximately M), gave the following results (Table 4.6).

To facilitate calculations, the zero development temperature will be set at 4, 7 and 10 ^{o}C respectively. As will be discussed further in Paragraph 4.4, only the data from Huntly (DI and DII) can be used here. It is obvious, however, when comparing Figs 4.11-4.14 with reference to the presence of the LF in the field, that the following comments concerning the number of generations per year applies in general to the Te Kauwhata study site as well.

Table 4.6 Linear regression equation, development time (^{o}D) and zero threshold temperature (^{o}C) for the development of some stages of the LF (*After* Walters, 1964).

Equation	^{o}D	t_0
Egg:		
$y_{egg-->L_1} = -0.024 + 0.005\ x,\ r = 0.995***$	183.5	4.4
Females:		
$\$ y_{L_1-->L_6} = -0.014 + 0.003\ x,\ r = 0.983*$	343.0	4.7
$y_{L_1-->L_7} = -0.008 + 0.002\ x,\ r = 0.982*$	508.0	4.1
Males:		
$y_{L_1-->L_4} = -0.080 + 0.009\ x,\ r = 0.990**$	115.0	9.2
$y_{L_1-->L_5} = -0.013 + 0.002\ x,\ r = 0.954*$	517.0	6.6

$: Note, development times, apart from the egg development time, include the time necessary for the completion of the last growth stage, mentioned in the equation.

The female starts to oviposit during the sixth instar stage (Walters, 1964), or F_2 in this study. This means that one full generation will take 526.5 ^{o}D (183.5 + 343 ^{o}D) above a 4 ^{o}C zero threshold temperature. In 1983 the total number of degree-days between the hatching of the first nymphs (17 March) and the last count of the F_2 (8 December) (Figs 4.15 and 4.16) was 2197 ^{o}D above 4 ^{o}C (Appendix 3.4.a). A calculation shows that, expressed in degree-days, there was time for at least four generations of LF in the field (4 x 343 + 3 x 183.5 = 1922.5 ^{o}D). Table 4.7 shows that the total number of degree-days for 1982 was higher than for 1983.

Table 4.7 The total number of degree-days in Huntly and Te Kauwhata for 1981[$], 1982 and 1983

Year	Degree-days					
	Huntly			Te Kauwhata		
	Threshold			Threshold		
	4 ^{o}C	7 ^{o}C	10 ^{o}C	4 ^{o}C	7 ^{o}C	10 ^{o}C
1981	1617	1155	740	1736	1243	802
1982	3861	2847	1929	3885	2880	1968
	[?](1601)	(1122)	(701)	(1588)	(1102)	(664)
1983	3437	2438	1557	3557	2560	1642

$: since 9 July 1981; ?: equivalent period as in 1981.

In 1982 2540 ^{o}D elapsed between the hatching of the diapause eggs (4 March) and the last appearance of the F_2 (9 December) (Figs 4.15 and 4.16), which allowed for the development of five generations (5 x 343 + 4 x 183.5= 2449 ^{o}D).

The use of degree-days in the analysis of insect populations avoids the problems that are associated with the use of a chronological time scale (Southwood, 1978). But one should not forget that other aspects, especially in an agricultural, man-handled system can reduce the rate of development, even though the climatic conditions may be favourable. However, both in 1982 and 1983 the total number of degree-days between the beginning of the first and the end of the last generation was high enough to compensate for such delays in the development of the LF. Therefore it can be assumed with some confidence that five generations occurred in 1982 and four in 1983.

A detailed discussion with reference to the development time of the male and last female instars will be made in paragraph 4.4

b/ The application of insecticides

In 1982 both paddocks in Huntly were divided into halves. One half was sprayed against the LF with diazinon (48 g.a.i./ha), while the other half, containing the experimental plots, was left unsprayed. The non-experimental area was monitored for LF numbers before and after the insecticide application, including the re-establishment phase during 1983. The timing of insecticide spraying was based on standard farmer practice for LF control on pastures shut for hay making. The dotted lines in Figs 4.3 and 4.4 represent the number of LF in the sprayed plots. The timing of spraying coincided with the natural decline in the

LF population. Although a proportion of the LF was eradicated, thus preventing short term pasture damage to some degree, it failed to prevent deposition of significant numbers of diapause eggs. Initial number of LF in 1983 was slightly lower in the sprayed plots as opposed to the experimental plots, but subsequent numbers were not greatly affected. These results imply that the other insecticide applications that took place at about the same time in 1981 (Appendices 4.3 and 4.4) and were undertaken by the farmer without making prior arrangements, did not have a major effect on the population density.

c/ Grazing and shutting up for hay making or silage

In paddocks shut for hay making or silage, grazing did not take place for at least five to six weeks prior to cutting. Shutting a paddock up has two major effects. The absence of grazing means 1/ an undisturbed fauna, and 2/ a change in vegetation height and composition. Both factors may affect LF numbers. After shutting up a paddock at both locations, population densities either remained at the same level or increased. Cutting coincided with a levelling out of the population numbers in one case, and a considerable drop in the other. Since cutting takes place at the end of the spring, at which time LF numbers usually start to decline, it is difficult to separate the effect of cutting , and the natural decline of the population. It is probable that LF populations are maintained at a higher level during the period of shutting up than would have occurred if grazing had taken place. Also, a higher sward height may protect the population from adverse weather conditions, allowing continuation of the life cycle until the pasture is cut and the soil surface exposed to hot, drier summer conditions. The combination of these factors probably results in a

higher number of diapause eggs being laid in the closed pastures. Consequently, the first generation in the following year may be expected to have a higher number of recruits than the grazed paddocks. Although one cannot statistically compare the population density of the LF between two paddocks, it is interesting to note that both at Huntly as well as Te Kauwhata the initial number of LF the following year was higher in the paddocks that had been shut for hay in the previous spring-summer, compared to the paddocks that were grazed. Purvis and Curry (1981) studied the influence of sward management on foliage arthropod communities in grassland in England and found that "...immediate, non-persistent population fluctuations accompanied management-induced changes in sward height: the abundance of most groups, particularly large insects, increased during conservation for silage...". Acarine and collembolan species richness were not increased by conservation. Cutting, however, reduced many acarine and collembolan populations to levels significantly less than in the grazed plots. The authors attributed this to a decrease in relative humidity and shade in the shorter swards. Maclagan (1932b) found a negative correlation between the yield of herbage and the population density of LF. He states that the increased amount of herbage results in more rapid drying out of the soil. This view point is supported by Walters (1964) for South African conditions. Walters mentions that a dense plant cover in winter should result in a longer persistence of moist conditions at the soil surface than would a sparse plant cover. He stated that at the end of the season, when the saturation deficit of the air is high, a dense plant cover would result in much greater loss of water from the deeper layers of the soil through transpiration, than would in an open sparse plant cover. He also found that under heavy grazing, dew and light rain were deposited directly on the soil surface and that a hard packed soil with a low porosity resulted in a concentration of soil moisture in the

upper layer of the soil which would benefit egg development at the end of the LF life cycle. This may also be one of the reasons why Purvis and Curry (1981) found that *Sminthurus* species were more abundant under continuous grazing than intermittent grazing.

There are considerable differences in habitat between the South African situation (Walters, 1964) and those at the locations of this study. Walters' study took place in paddocks where "...The stony nature of Caledon soil, its hardness during periods of dry weather....precluded the possibility of removing whole samples of soil from the paddocks". Also the amount of rain that fell during the two years of his field study was 387 and 622 mm respectively. This compares unfavourably with a clay-loam type soil as well as an average rainfall of 800 to 900 mm per year on the two locations in this study. The above is one of the reasons why in this study it was found that shutting up for hay making may have a beneficial effect on the LF population, in contrast to Walters' findings.

d/ The Symphypleona population

The Symphypleona population (*not* including *Sminthurus viridis*) was followed during this study in an attempt to determine if there was any competition between it and the LF population. Therefore, only the population counts (Figs 4.3a-4.6a) are presented and no detailed analysis of the population fluctuations has been made. Only a few species of Symphypleona were common, the dominant being *Bourletiella hortensis*, accompanied by a few other Sminthuridae species.

In both paddocks at Huntly the Symphypleona population density was very low during 1981 and 1983. In 1982, however, on some occasions numbers of up to 10 000 per m^2 were found. In Te Kauwhata the same trend was observed. Population density was low in 1981 and 1983 but high in 1982. In KI more than 14 000 Symphypleona per m^2 were present reaching peak numbers in April and May 1982. The population pattern resembles the results of similar studies on Collembola in New Zealand by McMillan (1969) and Adams (1971), and studies on Sminthuridae in England by Dhillon and Gibson (1962), but in this study the densities are much higher. The reason for this difference may be in the type of soil corer used. In this study a soil corer (*See* Fig 3.1.a) was used that prevented the escape of surface dwelling Collembola, rather than the "open type" corer used by other authors.

It is interesting to note that the overall pattern of low numbers in 1981 and 1983, and high numbers in 1982 was apparent for both LF and Symphypleona populations. It is possible that a biotic regulating factor, such as a pathogen, common to both populations, played a role. Since it was not possible within the frame work of this thesis to study possible mortality factors, more research is needed to establish the cause.

The main difference between the fluctuation of LF and Symphypleona populations is that the latter has a high population density during March, April and May after which the numbers decline to a low level and the insects disappear in December. It seems that high LF numbers coincide with low Symphypleona numbers and vice versa. The same tendency was observed by Davidson (1934). It is possible that the difference in seasonal history between LF and Symphypleona populations indicate a seasonal occupation of the same niche. All the paddocks except KII showed a significant positive correlation coefficient between

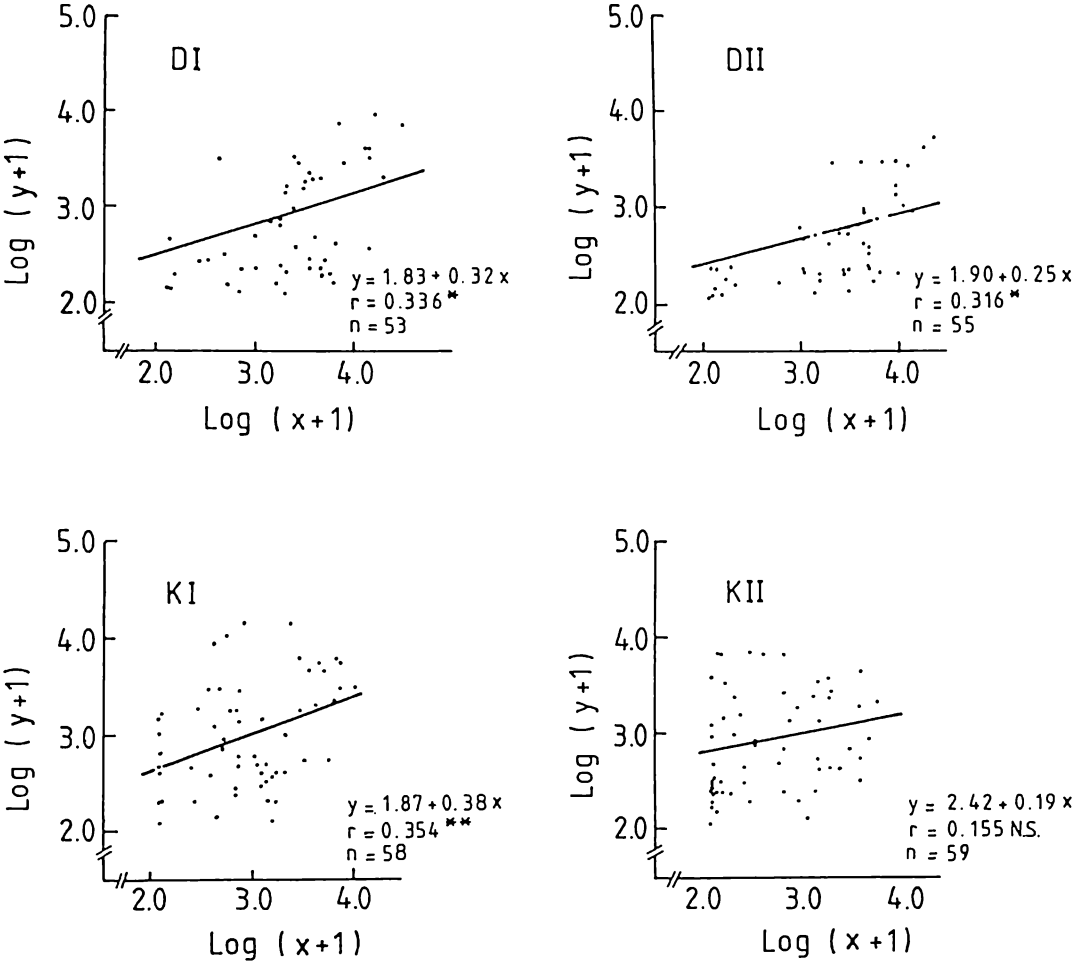

Fig 4.7 Linear regression of the number of Symphypleona (y-axis) and LF (x-axis), caught with the soil corer (Ø 10.2 cm), in the two paddocks in Huntly (top) and Te Kauwhata (bottom).

the number of LF and Symphypleona (Fig 4.7), indicating no dominance on either side. However, the spread of points makes the relationship suspect and therefore no definite conclusion can be drawn.

Christiansen (1967) found under laboratory conditions that small numbers of competitors had a stimulating effect, but that dominance could result in either preventing the reproduction of the second species or quickly eliminating it after reproduction had occurred. Davidson (1934), however, found in the field that the competition by other insects was negligible and that LF was dominant.

The influence of natural predators on LF populations will be discussed in Chapter 5.

e/ Other factors influencing the population numbers

Dempster and Pollard (1981) state that apart from the climatic conditions, fluctuations in the number of many insects are determined by the fluctuation in the carrying capacity of their habitat. However, this is probably not a main factor in determining fluctuations of the LF in the present study, where white clover is the major habitat. It will be shown in Chapter 8 that, based on the level of damage (Figs 8.6-8.13) the white clover canopy is more than sufficient to provide the LF population with a food source. One important factor in the self regulation of the population, however, may be crowding. Green (1964) found that under laboratory conditions crowding would reduce or even completely inhibit the oviposition of Collembola. Wallace (1957) noticed in the field that apart from the population fluctuations caused by changes in temperature and rainfall, local population variations, not related to these factors, could be observed. He suggested that these

differences were brought about by local differences in birth rate and survival. He also found a significant correlation between a high number of LF (more than 20 per link^2 = 405 cm^2) in May and a drastically reduced number in September, and vice versa. The density governing reaction was attributed to a reduction in fertility and an increase in mortality at a high population density. Later studies (Wallace, 1967) showed that density induced mortality, resulting from newly hatched instars eating bodies of dead LF, played a dominant role at high densities and could lead to a dramatic collapse of the population. This process operated continuously, though at decreased intensity at lower densities. It was found that LF from high density populations usually contained large quantities of uric acid in their fat-body, possibly caused by a greater metabolic activity or increased consumption of dead bodies. This may explain the dramatic reduction in numbers after a peak in population density has been reached, as can be seen in Figs 4.3-4.6.

4.3.3 The presence of diapause and non-diapause eggs

Due to the presence of diapause eggs during the summer, LF can only be found in low numbers after the middle of December and is often absent. During January and February numbers are negligible, although a few are occasionally found in sweepnet samples. LF populations start to build up again in March or April when the weather conditions become more favourable. In most cases the new population consists totally of first larval instars, hatched from diapause eggs. During wet summers with below-average temperature, however, it is possible to find adult LF that will lay eggs and contribute to the first generation. Field studies were carried out to study the main oviposition periods in the field in Te Kauwhata between July and December 1983 and to determine factors that

influence the breaking of egg diapause. Two main factors were examined, namely temperature and rainfall.

a/ Methods

Non-diapause eggs

Between July and December 1983 20 soil cores of ten cm diameter were collected in KII each fortnight. The samples were placed on fine netting over a funnel, exposed to a room temperature of 17 ± 1 ^{o}C and watered once a week with 15 ml water to avoid drying-out of the samples. Hatched LF were collected twice a week in Gault solution.

Diapause eggs

On 24 January 1983 80 soil cores were collected on a property near Huntly where LF had been abundant in the previous year. On 13 January 1984 the same number of cores were collected from paddock KII at Te Kauwhata. The soil samples were taken with a ten cm diameter soil corer (Kain and Young, 1975) and placed in a PVC tube and plastic bag to avoid drying out of the samples. In the laboratory samples were placed on fine netting over a funnel and the room temperature was used to induce hatching of the eggs. Twenty samples each were placed at 10 and 15 ^{o}C and 40 samples at 20 ^{o}C. In the event of no hatching at 20 ^{o}C, these samples would be divided between the 10 ^{o}C and 15 ^{o}C rooms. In 1983 the diapause experiment had to be stopped after 53 days due to a mechanical failure of the constant temperature rooms. In 1984, against expectation, hatching took place at 20 ^{o}C and therefore these samples were not separated and exposed to the lower temperatures. In this case the experiment was stopped after 94 days, ten days after the last insects had hatched. To avoid drying out, the samples were covered with plastic sheets and watered once a week with 15 ml of water. In order to

determine the effect of rainfall, in 1984 half of the samples at each temperature received an additional 15 ml of water per week. Insects were collected twice a week in Gault solution.

b/ Results and discussion

Non-diapause eggs

The number of LF that hatched from the eggs is presented in Fig 4.8. It should be noted, however, that the sampling does not cover the period before July 1983. Three periods with a high number of first larval instars can be distinguished: between 15 July and 18 August, 30 September and 24 October, and 3 November and 28 November. Hardly any egg hatching took place between the middle of August and the beginning of October, or after the beginning of December. The latter can be explained by the fact that a very high percentage of the eggs are in the diapause state in December (Wallace, 1968).

Approximately 183 ^{o}D above 4 ^{o}C are taken till the eggs hatch (Walters, 1964). This means (Appendix 3.5.a) that the first eggs in the above mentioned periods were deposited when the LF numbers were at a peak halfway June (Fig 4.6), the beginning of the peak in numbers in September, and halfway a build-up in numbers at the end of October. This is an indication that there is an overlap of generations during the life cycle of LF and its implication will be discussed in detail in Paragraph 4.4.

Diapause eggs

The effect of temperature

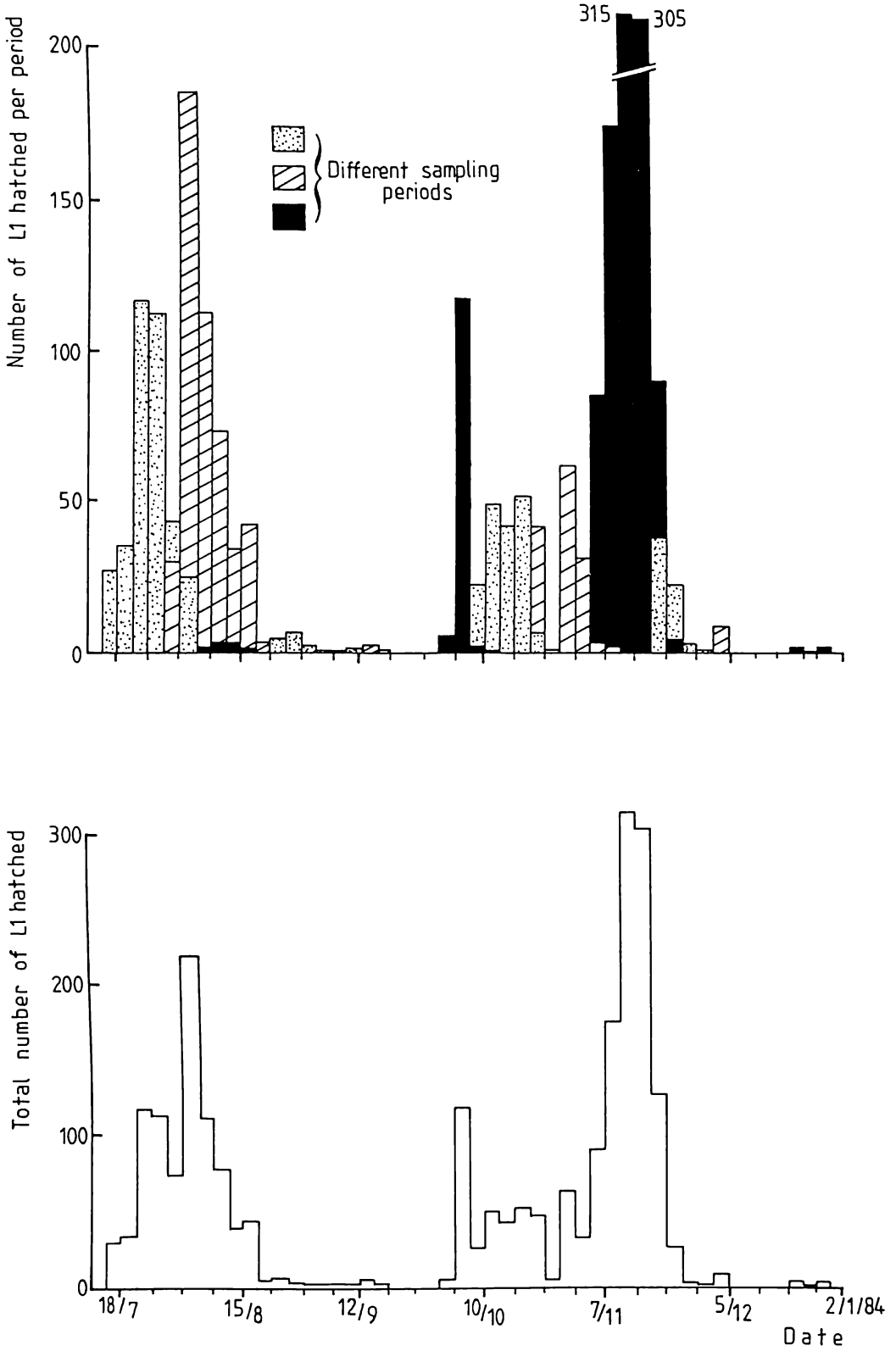

Fig 4.8 Number of first larval instar (L_1) LF hatched per period of soil sampling (top) and total number of L_1 hatched from soil samples collected in Te Kauwhata (KII) between July and December 1983. *Note* similar shaded areas, separated in time, represent different sampling periods.

1983: The results are presented as numbers of insects hatched per 20 samples at 10, 15 and 40 samples at 20 °C (Fig 4.9). The first hatching at 10 °C took place within 25 days of collection and after approximately 33 days (median = 33.1 days) 50 % of the total number of first larval instars was counted. At 15 °C the first insects were apparent on day 28 and the 50 % count of the insects was made after 41 days (median = 41.2 days). At 20 °C the occurrence of the first nymphs was within 28 days of the start of the experiment, but in total only four insects were collected. At 10 °C the 50 % hatching mark was reached 9 days earlier than at 15 °C and more insects hatched (49 opposed to 39). Although it could not be proven statistically, it seems that under the conditions of these experiments a low temperature induces hatching of the diapause eggs and that a temperature of 20 °C is unfavourable.

1984: A totally different picture is seen in 1984 (Fig 4.10). Although the first insects were found within 19 days after sampling at 10 °C, 50 % of the hatching insects were counted after 51 days (median = 50.5). The first insects at 15 °C appeared within 17 days and 50 % hatching was reached after 27 days (median = 26.5). The first insects emerged at 20 °C, as at 10 °C, within 10 days. In this case 50 % of the insects hatched after 31 days (median = 30.7). The 50 % mark was first reached at 15 °C, followed closely by 20 °C, and much later by 10 °C. A two-sample median method was used to test the statistical difference between the three temperatures. A significant difference in the speed of egg hatching was found between 10 and 15 °C (X_2=4.693, 1 d.f.), but no significant difference could be found between 10 and 20 °C or 15 and 20 °C. Although the egg hatching was faster at 15 °C, in total more first larval instars were found at 10 °C (84 per 20 samples) than at 15 °C (40 per 20 samples) or 20 °C (51.5 per 20 samples).

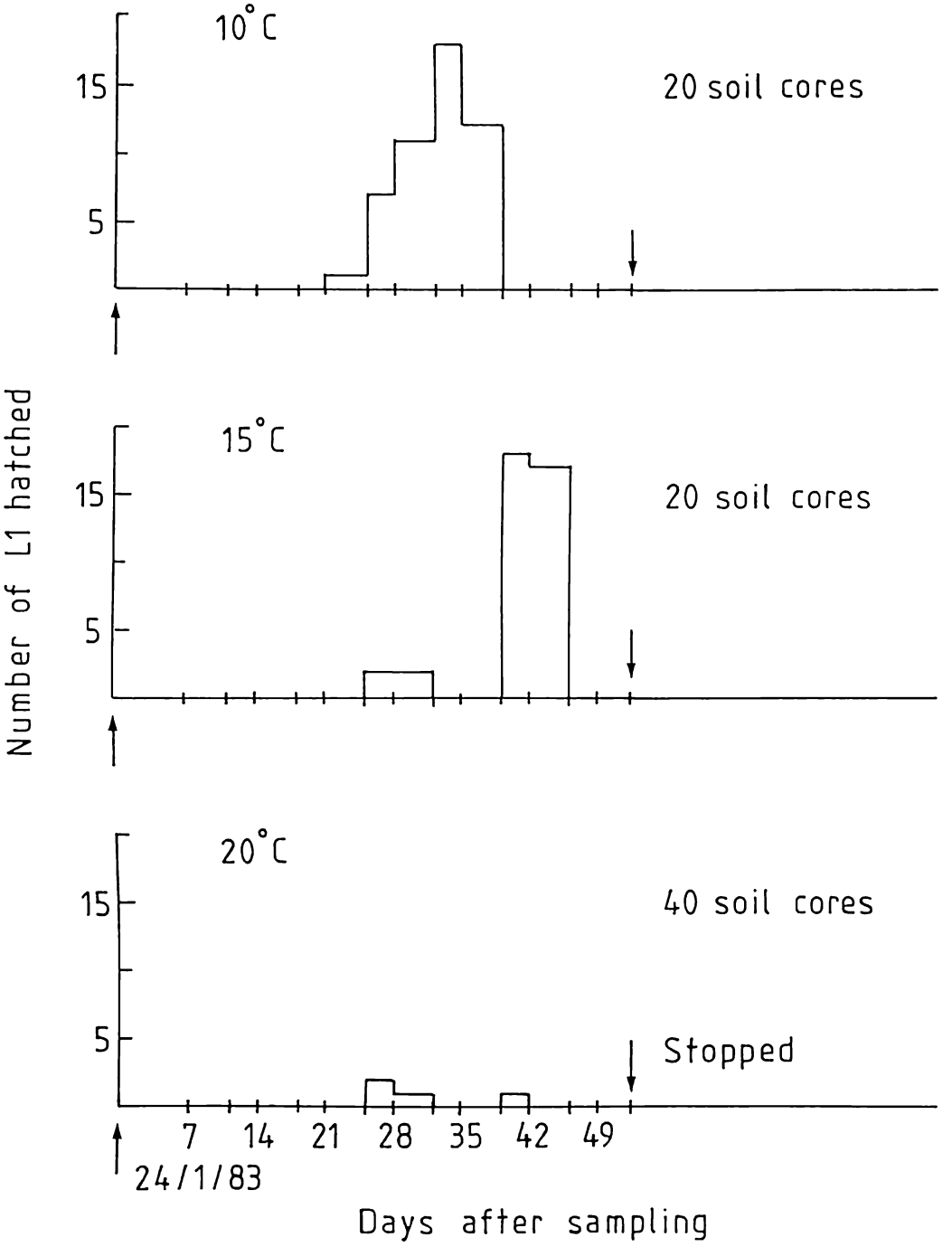

Fig 4.9 Number of first larval instar LF hatched from diapause eggs, exposed to different temperatures, in 1983.

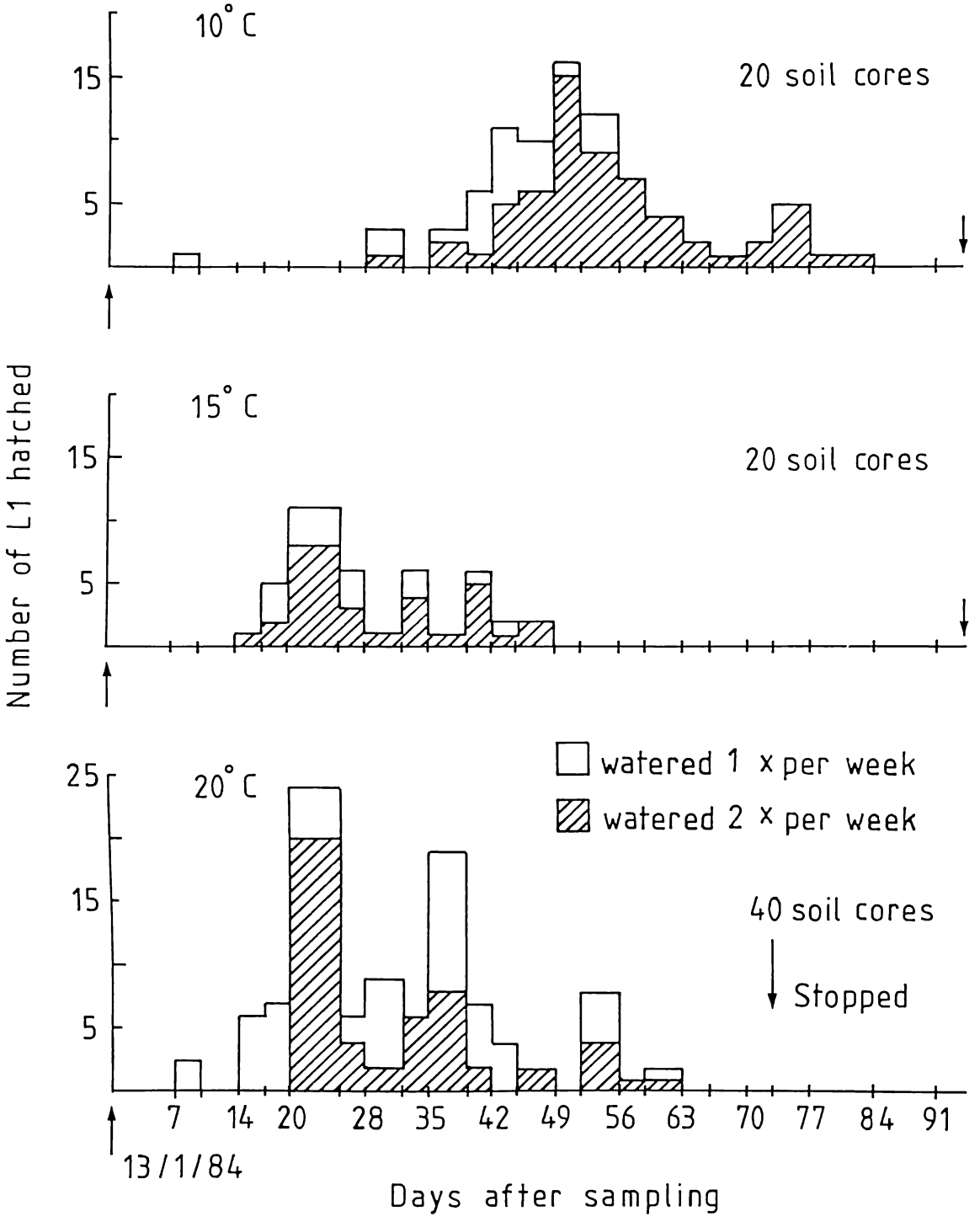

Fig 4.10 Number of first larval instar LF hatched from diapause eggs, exposed to different temperatures and two watering regimes, in 1984.

The experiment was stopped prematurely in 1983 and therefore not too much reliance can be placed on the results. The results of these trials suggest, however, that a low temperature favoured termination of diapause in eggs. The results in 1984 show a different picture. It can be clearly seen, that at all temperatures at least two peaks in the number of newly hatched insects are present. As well, hatching takes place earlier at 15 and 20 ^{o}C than at 10 ^{o}C, although, again, more eggs hatched at 10 ^{o}C than at the other temperatures. Wallace (1968) mentions that diapause eggs have to be exposed to dry summer conditions for at least two to three months before hatching can take place. It may be that all the samples that were collected for the 1984 experiment, had been sufficiently exposed to the summer conditions. This being the case, than the influence of the date of oviposition can be ruled out. Another possibility is the simultaneous presence of diapause and non-diapause eggs in the field when the samples were taken. Between November 1983 and January 14, 1984, the total rainfall figure for Te Kauwhata was 180 mm. In the same period in 1982-1983, only 137 mm of rain was recorded. The slightly wetter summer in 1984 could account for the presence of non-diapause eggs. This would explain the fact that hatching at 20 ^{o}C took place earlier than at 15 and 10 ^{o}C and agrees with the egg development times given by Davidson (1931; 10 ^{o}C: 33.9 days; 15 ^{o}C: 16.9 days; 20 ^{o}C: 11.3 days). In regard to diapause eggs it would be expected that eggs would hatch first at 10 ^{o}C, rather than at 15 ^{o}C, and if hatching took place, last at 20 ^{o}C. Although this trend is evident at 15 and 20 ^{o}C, the last insects were counted at least three weeks later than at 20 ^{o}C, when exposed to a 10 ^{o}C regime. Contrary to the outcome of this experiment, Wallace (1968) found that 80 % of the diapause eggs, collected in the field in January and kept moist at 16 ^{o}C, hatched within 30 days. It is therefore possible that the watering regime used in this study has played an important role in the

outcome of the results.

The influence of watering samples

The results of the influence of the watering regime on the hatching of the diapause eggs at the different temperatures is presented in Table 4.8.

Table 4.8 The median (days) of the hatching of diapause eggs at the three temperatures and two watering regimes in 1984.

Temperature	Watering regime (15 ml units)	
	Once per week	Twice per week
10 °C	43.3	52.8
15 °C	25.8	28.0
20 °C	31.6	30.0

A two-sample median test shows that at 10 °C the watering regime influences the speed of hatching significantly (X^2= 6.428, 1 d.f.). No influence of the watering regime on the speed of hatching was found at 15 °C and 20 °C.

A comparison of the three temperatures within each watering regime with a two-sample median test (Freund, 1974) showed no statistical difference between temperatures in the samples that were watered once a week. In the samples that were watered twice a week there was a significant difference in egg hatching between 10 and 15 °C (X^2=8.64, 1 d.f.), but there were no differences between the other temperatures.

4.4 Composition of the lucerne flea population

Regular sampling of an insect population results in a series of estimates of the number of each immature and/or adult instar on successive sampling occasions (Dempster, 1961). The analysis of these stage-frequency data is the first step in building stage-specific life-tables (Bellows *et al.*, 1982).

4.4.1 Insect stage-frequency distribution.

a/ Methods

Between July 1982 and December 1983 LF were collected on a fortnightly basis, alternatively in Huntly and Te Kauwhata. These collections were used to study the number of instar stages of LF (Paragraph 4.2) and the proportional representation of the different age groups in the field on each sampling date. A BMDP computer program was used to analyse the data.

b/ Results and discussion

The percentage representation of the different instars was multiplied by the total number of LF per m^2 on each sampling date (Figs 4.15 and 4.16). Since in Te Kauwhata there was a one week difference between the time that the absolute counts were made, and the counts for the percentage representation of the stages, only the results of the Huntly study site can be used for the stage-frequency analysis of LF. However, a comparison of the stage-frequency data in Huntly and Te

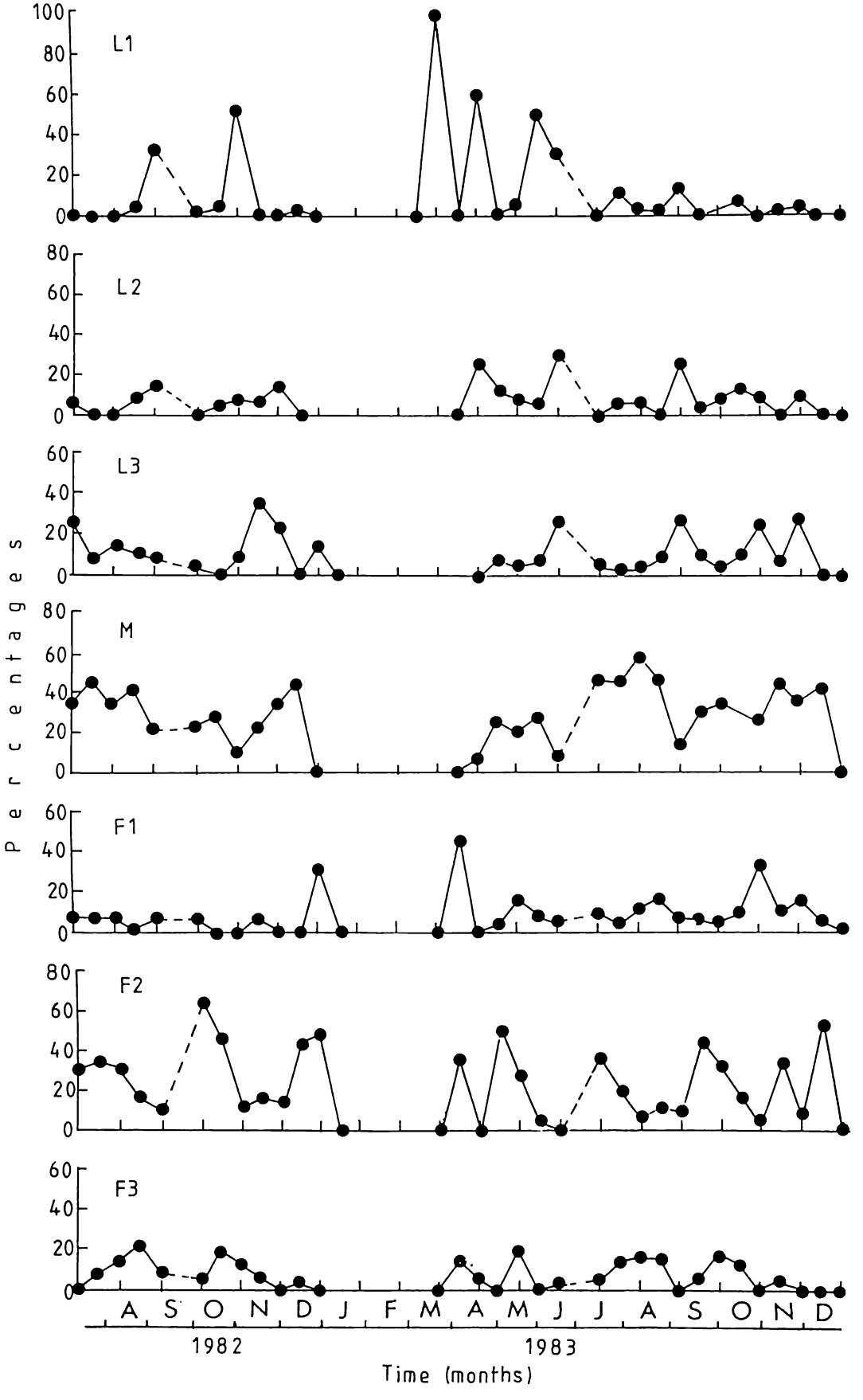

Fig 4.11 Percentage representation of the different instars in DI (Huntly) between July 1982 and December 1983.

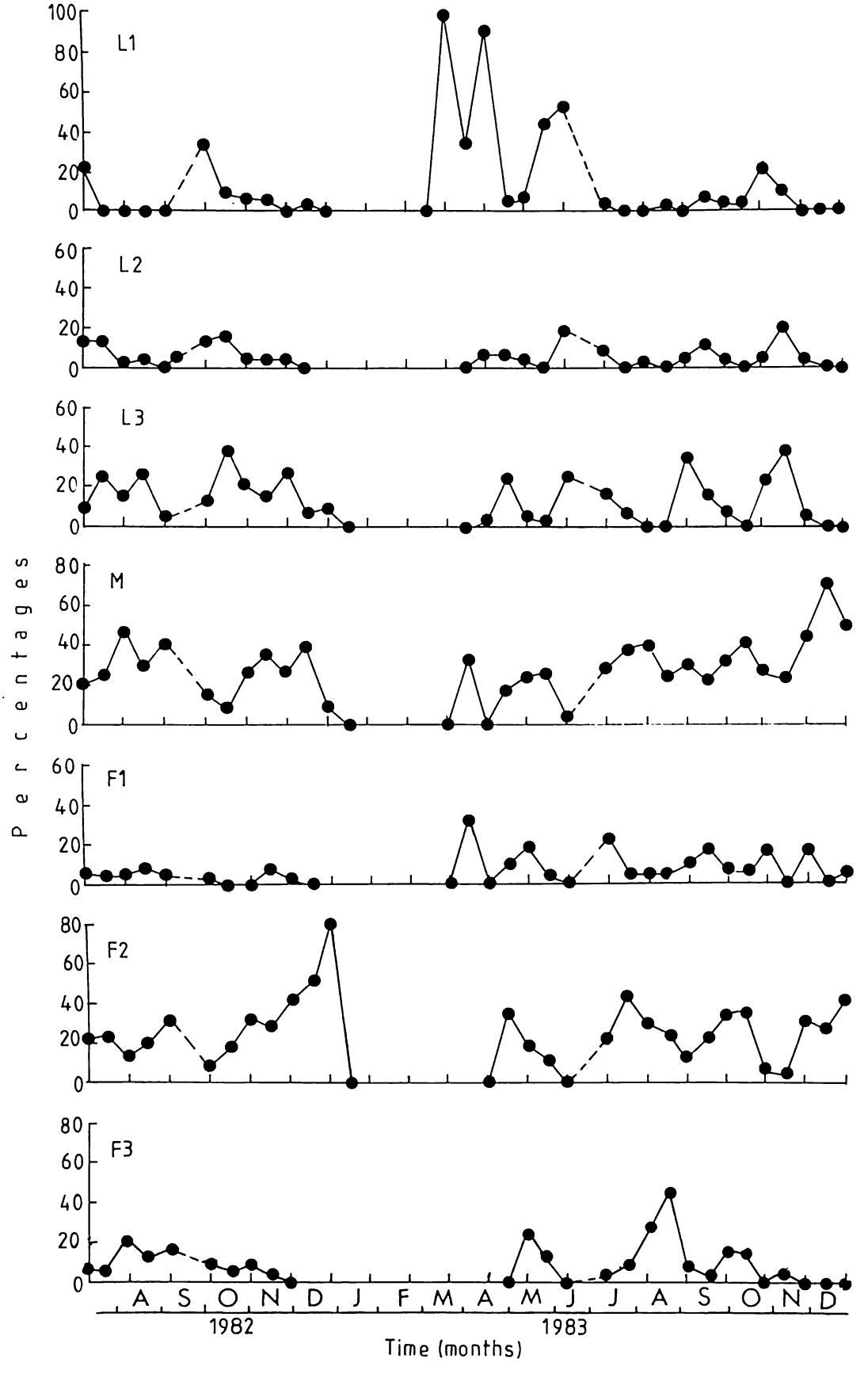

Fig 4.12 Percentage representation of the different instars in DII (Huntly) between July 1982 and December 1983.

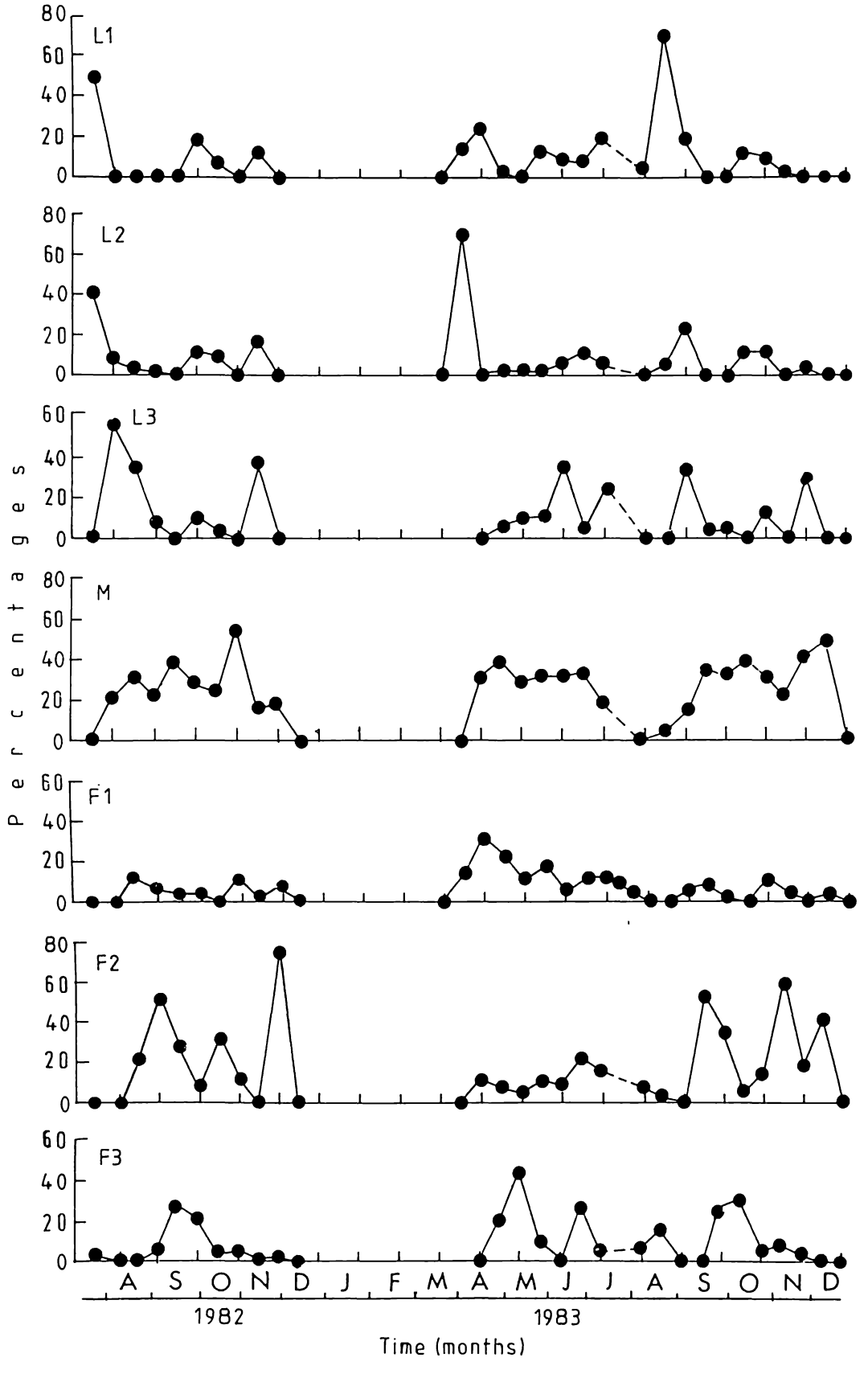

Fig 4.13 Percentage representation of the different instars in KI (Te Kauwhata) between July 1982 and December 1983.

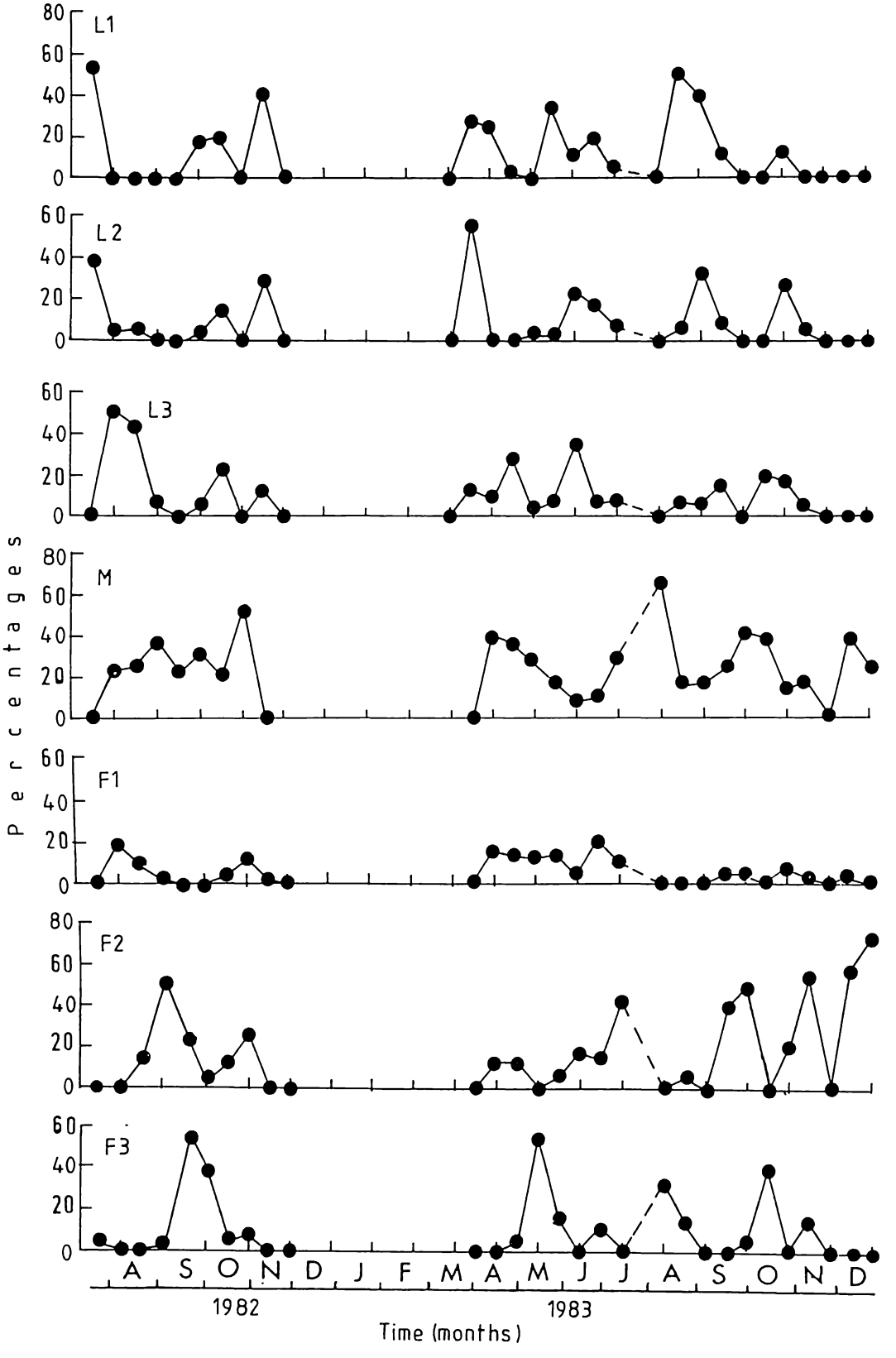

Fig 4.14 Percentage representation of the different instars in KII (Te Kauwhata) between July 1982 and December 1983.

Kauwhata (Figs 4.11-4.14) show that, in general, on both locations the same trend in stage representation occurred during 1982 and 1983.

Figs 4.15 and 4.16 show that the instar stages of LF were present in the field during most of the year and that more than one larval and/or adult instar could be found on the same sampling date. This means that LF populations had overlapping stages of development as well as generations during the study period. A method for interpretation of stage-frequency data of organisms with overlapping stages and generations is to try and distinguish cohorts and to follow their development in time. By dividing the time scale of the different stage-frequency data into periods, within which each growth stage developed during one generation, one can follow these developmental groups or cohorts (*See* footnote 1) from the early stage of development through to adulthood for each generation.

The separation of these cohorts has been done by eye, for example for Collembola (Takeda, 1984) and several-fresh water organisms (Rigler and Cooley, 1974; Green, 1976; Burns, 1979; Hart, 1981). However, it was decided in this study that a distinction of the cohorts by eye would be too arbitrary for LF. Use was made, therefore, of physiological time, although it is recognised that the use of a physiological time scale does not take into consideration management practice and other factors that can influence LF populations. The physiological time was calculated between the first and last occurrence of each instar in the field in 1983, and divided by four (the number of generations in 1983, *See* paragraph 4.3). The only exception to this is the F_3 cohort. In all cases the F_2 instar existed at least two to four weeks longer in the field than the F_3 instar. From this, and the development time,

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(1) A cohort is a recognisable group of organisms that are all at approximately the same point in their development.

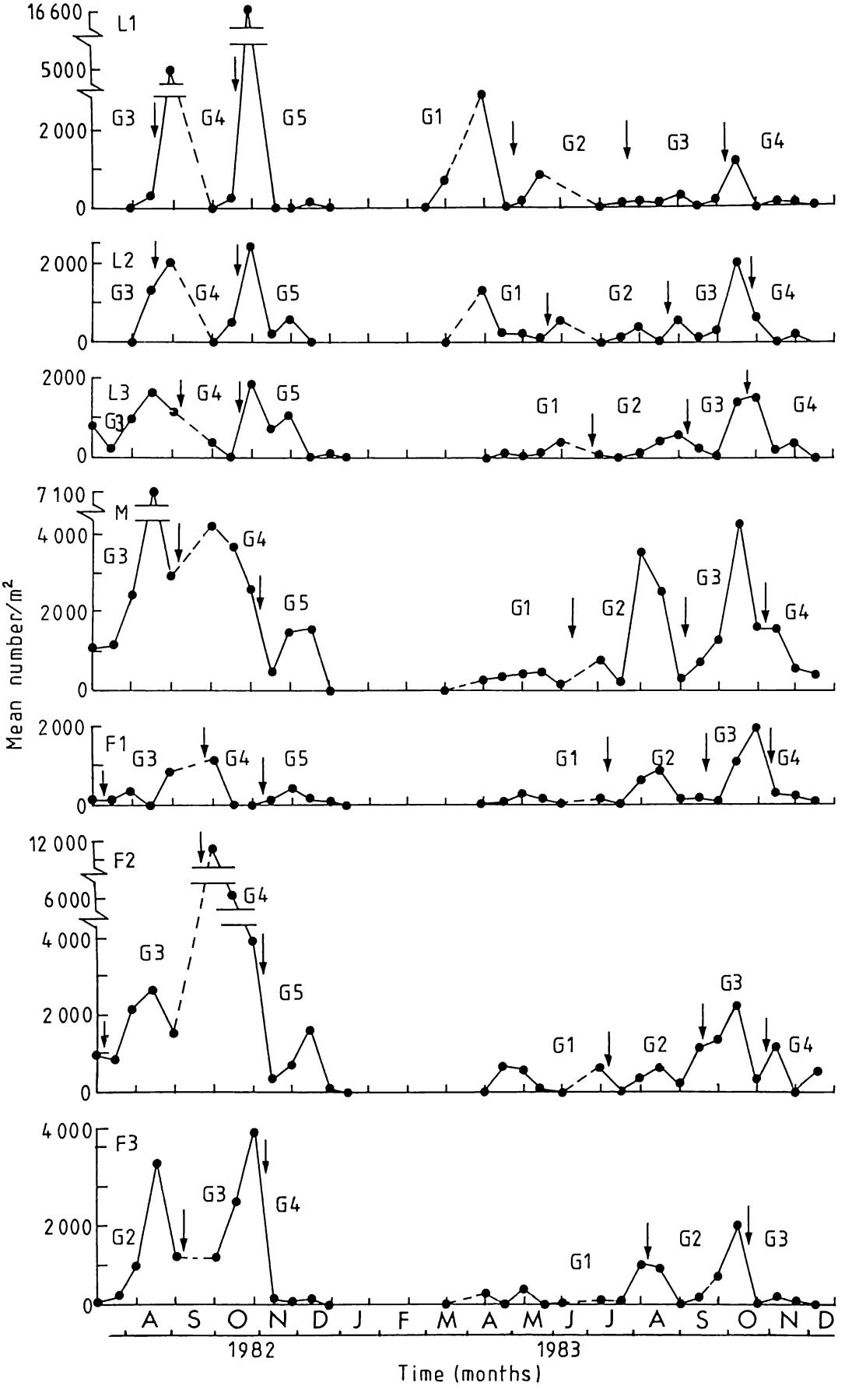


Fig 4.15 Number of different instars per m^2 in DI (Huntly) between July 1982 and December 1983. G_i = generation i; arrow= cohort).

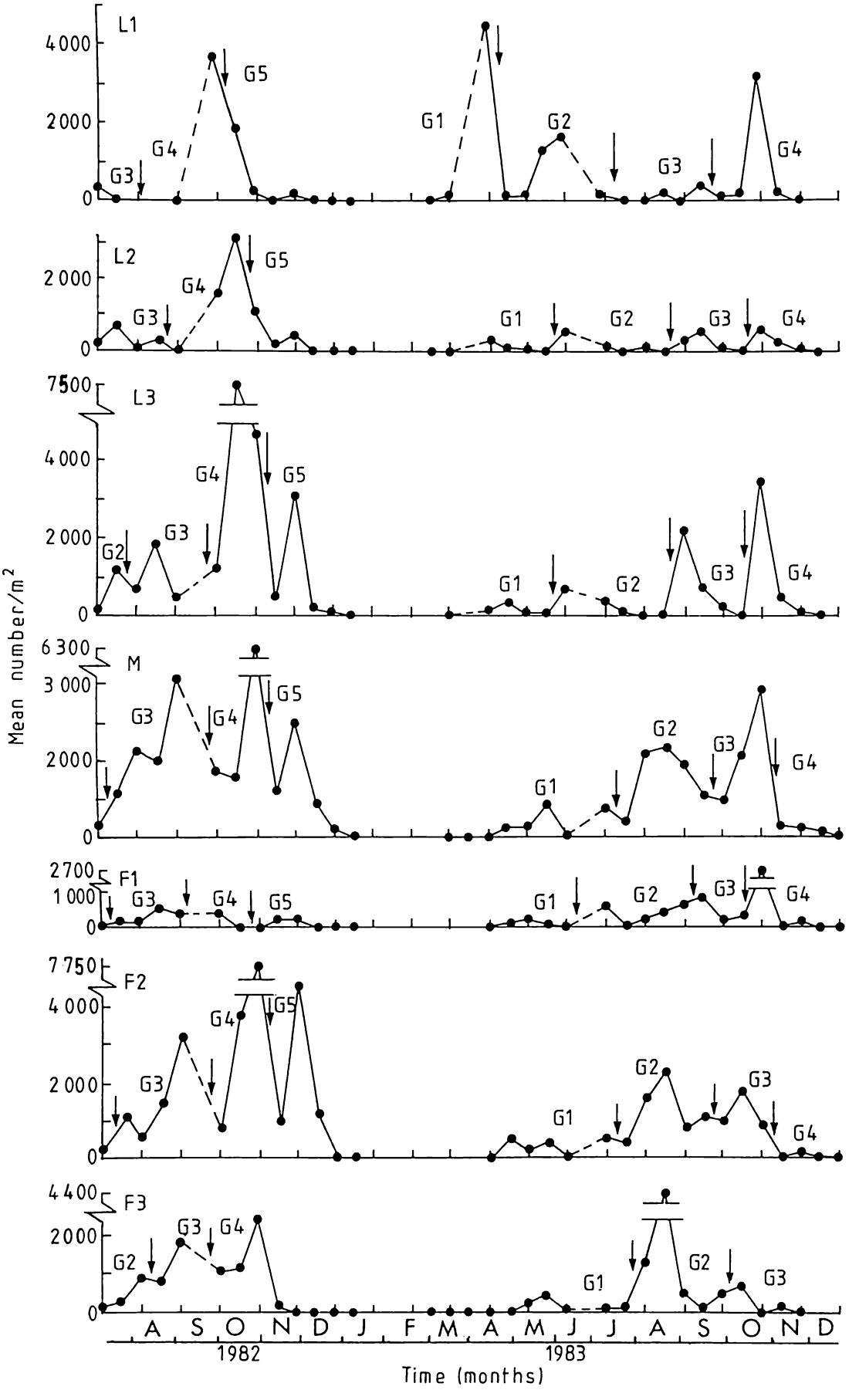


Fig 4.16 Number of different instars per m^2 in DII (Huntly) between July 1982 and December 1983. G_i = generation i; arrow= cohort).

necessary to complete the F_3 instar (Table 4.6), it was decided to separate the number of F_3 into only 3 cohorts. Although the development time necessary to complete the adult male instar (M) is greater than the development time for the F_3 instar, adult males of four cohorts are distinguished. This can be explained by the fact that the life span of the adult male is approximately the same as the life span of the F_2 and F_3 instar together, and that the adult male reaches sexual maturity at the beginning of the stadium (Walters, 1964). As well, the development time required to reach the adult male stadium (L_1-->L_4, Walters 1964) is only 115 ^oD above a zero threshold temperature of 9.2 ^oC (Table 4.6) while there are 718 ^oD (Appendix 3.4.c) between the first (14 April) and the last occurrence (8 December) of the adult male.

Since no stage-frequency data are available for the first half of 1982, the development times of the different cohorts from 1983 were used to separate the five generations (four for F_3 in 1982), and calculations were made, working backwards from the last occurrence of each instar in 1982. The cohorts are indicated by arrows. After a cohort distribution has been established for the different growth stages, a stage-frequency table can be created and analysed with the appropriate methods (paragraph 4.5).

4.4.2 Sex ratio

The sex ratio was determined by comparing the number of males and females in the total adult population sampled between July 1982 and December 1983. The total sex ratio (M : F) for the different locations was as follows:

DI	DII	KI	KII
1 : 1.34	1 : 1.44	1 : 1.44	1 : 1.57

with an overall sex ratio of 1 : 1.43, not significantly different from a 1 : 1 sex ratio (Mann-Whitney, P= 0.05).

4.5 Time table analysis

The stage-frequency data were further analysed using Kiritani and Nakasuji's method, improved by Manly (1976, 1977b) which was suitable for LF since it can be applied to populations that have been sampled at irregular intervals and requires only counts of individuals in the different stages of growth on each sampling occasion. This method was therefore used, with minor adjustments to estimate the generation survival parameter (Manly, 1985), to establish the number of LF entering the different instars. Appendices 4.5 and 4.6 and Figs 4.15 and 4.16 represent the insect stage-frequency data for 1982 and 1983 in Huntly (DI and DII). In both paddocks the samples of 23 December 1982 only represented 12 and 22 % respectively of the normal sample size (50 insects per sample) and are therefore deleted in the analysis. Since LF continues to moult even after sexual maturity has been reached, it is not justifiable to follow the population from first larval instar (L_1) to adult (M, F) only. The stage-frequency data were therefore also separated into sexes. The sex ratio was determined per generation and used to separate the third instar larvae (L_3) into future males and females. Examples of stage-frequency tables for L_1-->Adult, L_1-->M and L_1-->F_3 (DI, 1983) can be found in Tables 4.9, 4.10 and 4.11.

Table 4.9 Stage-frequency table for the development of the LF from first larval instar to adulthood in 1983.

Generation	Date	t (days)	Growth stages L_1	L_2	L_3	Adult
	17/03	1	646 (646)[$]	0 (0)	0 (0)	0
	31/03	15	no data			
	14/04	29	2884 (4521)	1349 (1637)	0 (288)	288
	28/04	43	0 (1270)	151 (1270)	102 (1119)	1017
	12/05	57	(1909)	155 (1909)	78 (1754)	1676
I	26/05	71	(838)	67 (838)	100 (771)	671
	09/06	85	(636)	(636)	468 (636)	168
	23/06	99	no data			
	07/07	113	(868)	(868)	(868)	868
	21/07	127	(56)	(56)	(56)	56
	04/08	141	(1000)	(1000)	(1000)	1000
	12/05	57	39 (39)			
	26/05	71	832 (832)			
	09/06	85	501 (1038)	537 (537)		
	23/06	99	no data			
	07/07	113	0 (863)	0 (863)	69 (863)	794
II	21/07	127	48 (347)	24 (299)	8 (275)	267
	04/08	141	(5115)	372 (5115)	123 (4743)	4620
	18/08	155	(5475)	0 (5475)	447 (5475)	5028
	01/09	169	(1150)	(1150)	603 (1150)	547
	15/09	183	(1418)	(1418)	(1418)	1418
	29/09	197	(708)	(708)	(708)	708
	13/10	211	(2042)	(2042)	(2042)	2042
	04/08	141	123 (123)			
	18/08	155	112 (112)			
	01/09	169	275 (825)	550 (550)		
	15/09	183	0 (1018)	49 (1018)	245 (969)	724
III	29/09	197	78 (3179)	309 (3101)	78 (2792)	2714
	13/10	211	(11371)	2042(11371)	1445 (9329)	7884
	27/10	225	(3867)	(3867)	(3867)	3867
	10/11	239	(138)	(138)	(138)	138
	24/11	253	(28)	(28)	(28)	28
	13/10	211	1175 (1175)			
	27/10	225	0 (2188)	603 (2188)	1585 (1585)	
IV	10/11	239	69 (3326)	0 (3257)	138 (3257)	3119
	24/11	253	28 (1389)	141 (1361)	427 (1220)	793
	08/12	267	0 (927)	0 (927)	0 (927)	927
	22/12	281	0	0	0	0

$: values between brackets are summations of stage-frequency numbers on one sampling occasion (*See* Manly, 1977b).

Table 4.10 Stage-frequency table for the development of the LF from first larval instar to adult male in 1983.

Generation	Date	t (days)	Growth stages L_1	L_2	L_3	M
	17/03	1	646 (646)[$]	0	0	0
	31/03	15		no data		
	14/04	29	2884 (4521)	1349 (1637)	0 (288)	288
	28/04	43	0 (510)	151 (510)	28 (359)	331
	12/05	57	(565)	155 (565)	21 (410)	389
I	26/05	71	(562)	67 (562)	27 (495)	468
	09/06	85	(288)	(288)	128 (228)	100
	23/06	99		no data		
	07/07	113				
	21/07	127				
	04/08	141				
	12/05	57	39 (39)			
	26/05	71	832 (832)			
	09/06	85	501 (1038)	537 (537)		
	23/06	99		no data		
	07/07	113	0 (827)	0 (827)	33 (827)	794
II	21/07	127	48 (254)	24 (206)	4 (182)	178
	04/08	141	(4062)	372 (4062)	59 (3690)	3631
	18/08	155	(2785)	0 (2785)	215 (2785)	2570
	01/09	169	(524)	(524)	290 (524)	234
	15/09	183				
	29/09	197				
	13/10	211				
	04/08	141	123 (123)			
	18/08	155	112 (112)			
	01/09	169	275 (825)	550 (550)		
	15/09	183	0 (901)	49 (901)	128 (852)	724
III	29/09	197	78 (1746)	309 (1668)	41 (1359)	1318
	13/10	211	(7159)	2042 (7159)	752 (5117)	4365
	27/10	225	(1585)	(1585)	(1585)	1585
	10/11	239				
	24/11	253				
	13/10	211	1175 (1175)			
	27/10	225	0 (1418)	603 (1418)	815 (815)	
IV	10/11	239	69 (1725)	0 (1656)	71 (1656)	1585
	24/11	253	28 (901)	141 (873)	219 (732)	513
	08/12	267	0 (389)	0 (389)	0 (389)	389
	22/12	281	0	0	0	0

$: values between brackets are summations of stage-frequency numbers on one sampling occasion (*See* Manly, 1977b).

Table 4.11 Stage-frequency table for the development of the LF from first larval instar to last female instar in 1983 (continued on next page).

Generation	date	t (days)	Growth stages L_1	L_2	L_3
	17/03	1	646 (646)[$]	0	0
	31/03	15	no data		
	14/04	29	2884 (4233)	1349 (1349)	0
	28/04	43	0 (911)	151 (911)	74 (760)
	12/05	57	(1499)	155 (1499)	57 (1344)
I	26/05	71	(343)	67 (343)	73 (276)
	09/06	85	(408)	(408)	340 (408)
	23/06	99	no data		
	07/07	113	(868)	(868)	(868)
	21/07	127	(56)	(56)	(56)
	04/08	141	(1000)	(1000)	(1000)
	12/05	57	39 (39)		
	26/05	71	832 (832)		
	09/06	85	501 (1038)	537 (537)	
	23/06	99	no data		
	07/07	113	0 (36)	0 (36)	36
II	21/07	127	48 (165)	24 (117)	4 (93)
	04/08	141	(1425)	372 (1425)	64 (1053)
	18/08	155	(2690)	0 (2690)	232 (2690)
	01/09	169	(626)	(626)	313 (626)
	15/09	183	(1418)	(1418)	(1418)
	29/09	197	(708)	(708)	(708)
	13/10	211	(2042)	(2042)	(2042)
	04/08	141	123 (123)		
	18/08	155	112 (112)		
	01/09	169	275 (825)	550 (550)	
	15/09	183	0 (166)	49 (166)	117 (117)
III	29/09	197	78 (1820)	309 (1742)	37 (1433)
	13/10	211	(6254)	2042 (6254)	693 (4212)
	27/10	225	(2282)	(2282)	(2282)
	10/11	239	(138)	(138)	(138)
	24/11	253	(28)	(28)	(28)
	13/10	211	1175 (1175)		
	27/10	225	0 (1373)	603 (1373)	770 (770)
IV	10/11	239	69 (1670)	0 (1601)	67 (1601)
	24/11	253	28 (657)	141 (629)	208 (488)
	08/12	267	0 (538)	0 (538)	0 (538)
	22/12	281	0	0	0

$: values between brackets are summations of stage-frequency numbers on one sampling occasion (*See* Manly, 1977b).

Table 4.11 Continued.

Generation	Date	t (days)	Growth stages F_1	F_2	F_3
	17/03	1	0	0	
	31/03	15	no data		
	14/04	29	0	0	
	28/04	43	25 (686)$	661 (661)	
	12/05	57	309 (1287)	589 (978)	389
I	26/05	71	135 (203)	68 (68)	0
	09/06	85	34 (68)	0 (34)	34
	23/06	99	no data		
	07/07	113	138 (868)	661 (730)	69
	21/07	127	(56)	(56)	56
	04/08	141	(1000)	(1000)	1000
	12/05	57			
	26/05	71			
	09/06	85			
	23/06	99	no data		
	07/07	113			
II	21/07	127	8 (89)	81 (81)	
	04/08	141	617 (989)	372 (372)	
	18/08	155	891 (2458)	676 (1567)	891
	01/09	169	118 (313)	195 (195)	0
	15/09	183	148 (1418)	1122 (1270)	148
	29/09	197	(708)	(708)	708
	13/10	211	(2042)	(2042)	2042
	04/08	141			
	18/08	155			
	01/09	169			
	15/09	183			
III	29/09	197	78 (1396)	1318 (1318)	
	13/10	211	1175 (3519)	2344 (2344)	
	27/10	225	2042 (2282)	240 (240)	0
	10/11	239	(138)	(138)	138
	24/11	253	(28)	(28)	28
	13/10	211			
	27/10	225			
IV	10/11	239	275 (1534)	1259 (1259)	
	24/11	253	224 (280)	56 (56)	
	08/12	267	37 (538)	501 (501)	
	22/12	281	0	0	

$: values between brackets are summations of stage-frequency numbers on one sampling occasion (*See* Manly, 1977b).

The number of insects entering the different instars for the different generations in DI and DII is presented in Table 4.12 and 4.13.

Table 4.12 Number of insects that enter the different instars in DI, presented for the group 1, 2, and 3 development (*See* text).

Growth stage	Generation						
1982:	3	4	5	1983: 1	2	3	4
L_1	33973	27751	26889	6545	6433	27479	8068
L_2	33013	23830	12187	4246	5895	26697	6929
L_3	31867	21986	9276	3206	5508	22774	6626
Adults	28194	21692	6081	2780	5094	20422	4336
L_1	20606	13270	19100	11306	4585	18826	5103
L_2	19431	9021	6499	5153	3907	17937	3946
L_3	18028	7024	4003	2368	3419	13476	3269
Males	15681	6925	2624	2057	3168	12083	2263
L_1	7694	52579	27509	6025	4368	20559	5911
L_2	7567	42884	9307	3579	3737	19530	4522
L_3	7092	38325	5702	2472	3283	14368	3710
F_1	6276	37822	3738	2142	3030	12885	2568
F_2	5641	35626	2933	1806	2357	7119	782
F_3	2977	278		739	1432	291	

Table 4.13 Number of insects that enter the different instars in DII, presented for the group 1, 2, and 3 development (*See* text).

Growth stage	Generation						
1982:	3	4	5	1983: 1	2	3	4
L_1	40101	126007	22656	5776	7068	7883	61131
L_2	39106	112900	20192	2929	6109	7573	43154
L_3	37351	100700	18423	2701	5810	7180	38841
Adults	33015	67668	14033	2445	5387	5724	18222
L_1	12430	49842	9740	4644	3434	4138	9198
L_2	11824	39154	7727	1523	2419	3902	3387
L_3	10757	29204	6282	1272	2102	3546	1992
Males	9489	19715	4785	1155	1947	2827	935
L_1	34664	416613	13142	11524	14951	18012	23493
L_2	33124	356073	10979	4432	12129	16818	15810
L_3	30411	299716	9426	3861	11250	15009	13967
F_1	26930	200892	7180	3488	10435	11967	6552
F_2	23732	194259	6690	3016	8971	9195	487
F_3	7348	56324		1003	4696	1558	

It was not possible within the frame work of this thesis to study in detail the mortality factors that influence the population numbers of the LF. A key-factor analysis is therefore not possible. It is possible, however, to determine the immature or mature instar that is most susceptible to changes in its numbers. As with key-factor analysis, the $^{10}\log$ values were determined of the numbers that enter each growth stage, and the difference between the previous and the next instar was calculated. After summation of the individual values, which are named difference- or d_i-values, a total D-value was created. By comparison of the individual d_i-values with the D-value, it is possible to determine the d-value that contributes most to changes in the D-value (Figs 4.17 and 4.19). In case a visual comparison is difficult, Podolor and Rodgers (1975) advise for the k-factor analysis to plot the individual k_i-values on the y-axis against the K-value on the x-axis. In that case the submortality which gives the greatest value for the slope (b, regression coefficient) is by definition the key-factor. Since the d-factor method, used in this study, is similar to the key-factor analysis, the method of Podolor and Rodgers was applied to the d-values (Figs 4.18 and 4.20). No data on egg stock are available, and therefore the d_1-value presents the difference between the log number of L_1 and L_2, the d_2-value between L_2 and L_3 and so on. The d-values are presented in Table 4.14 in descending order of importance. To facilitate discussion, the development from first instar larvae to adult (A) will be referred to as group 1, first instar larvae to adult male (M) as group 2, and first instar larvae to last adult female instar (F_3) as group 3 development.

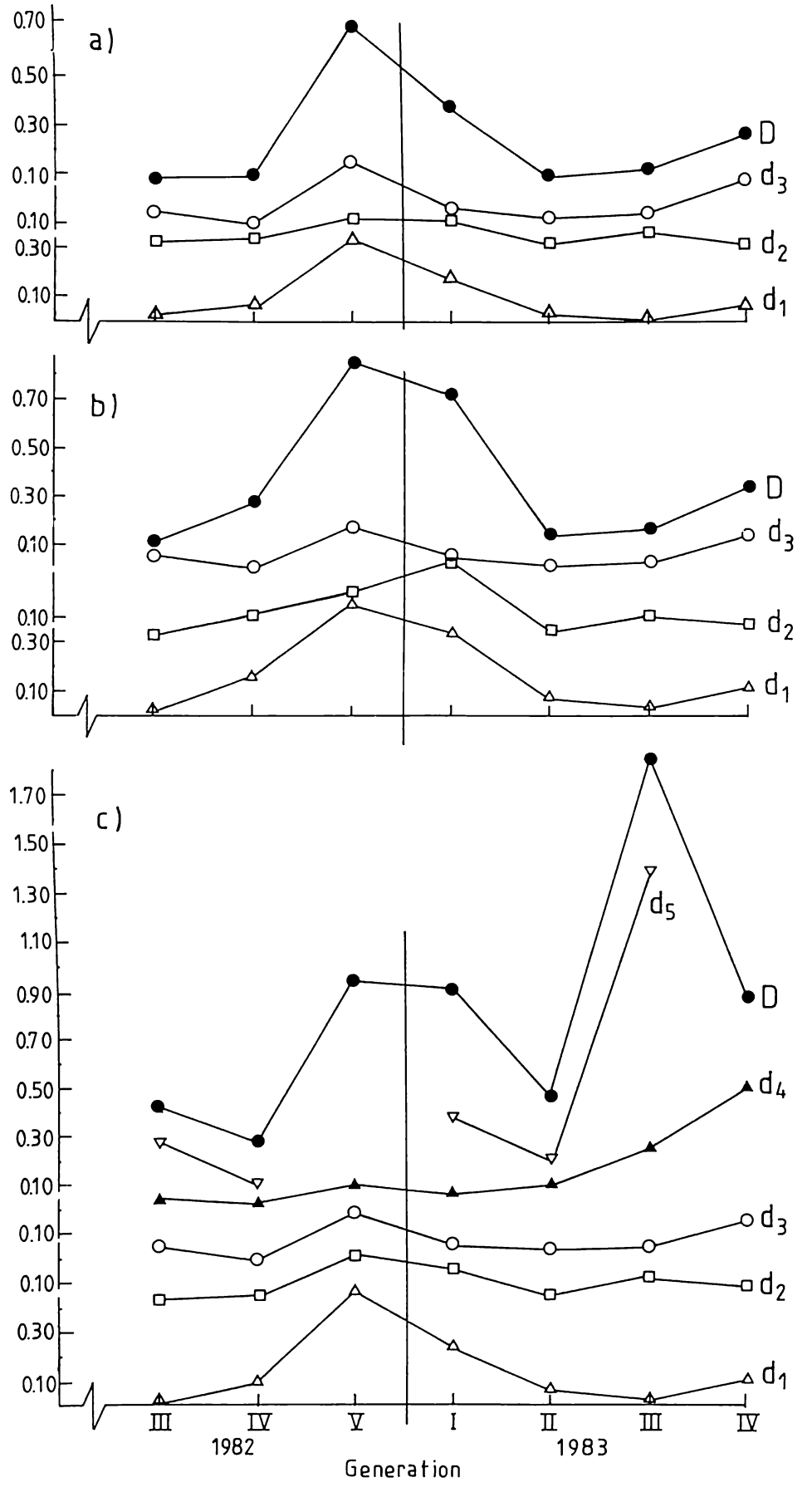


Fig 4.17 Individual d_i- and total D-values for the LF population in DI (Huntly): a/ group 1 development; b/ group 2 development; 3/ group 3 development. *For explanation* see text.

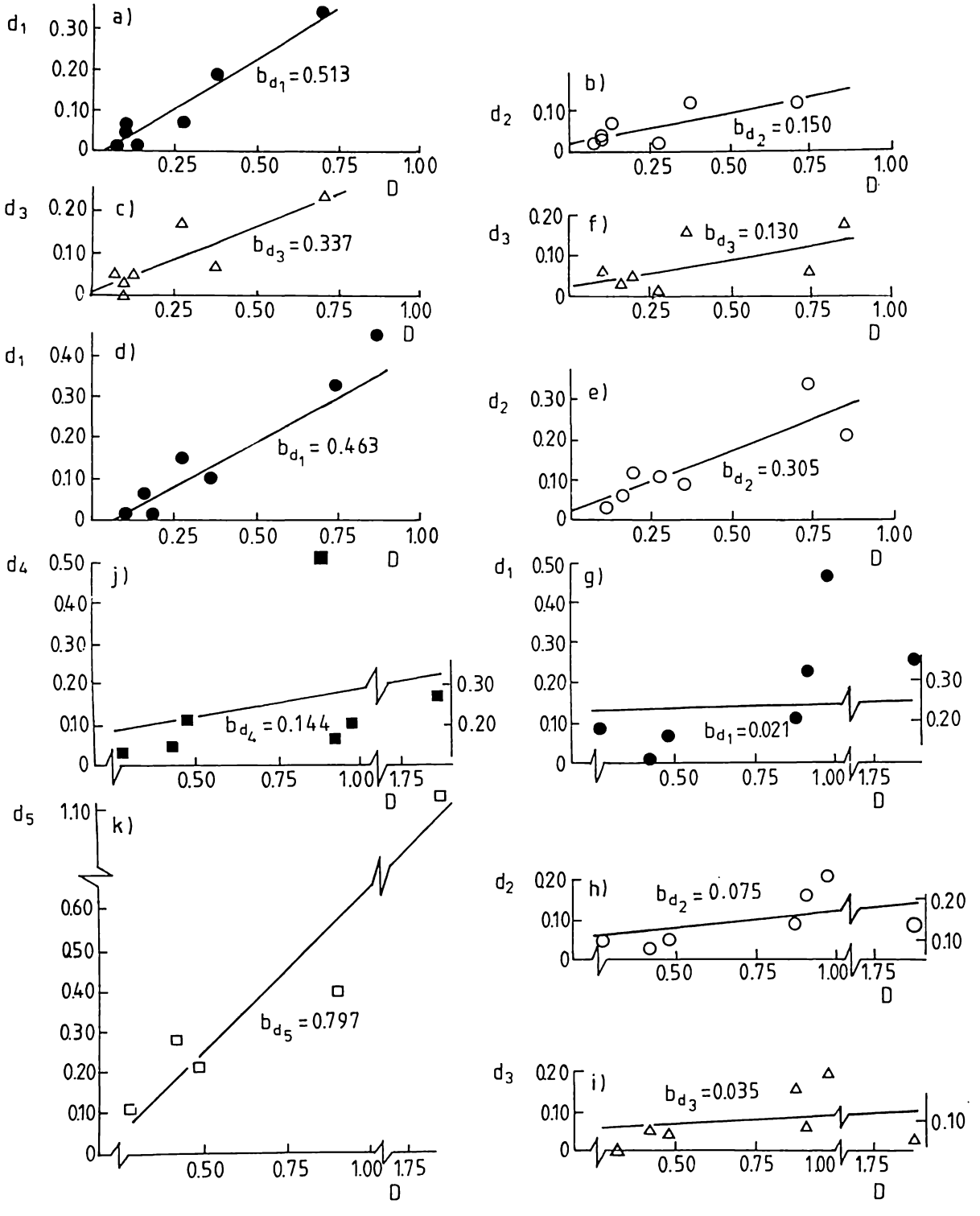


Fig 4.18 Regression of individual d_i-values against total D-value in DI (Huntly). a/ to c/: group 1 development; d/ to f/: group 2 development; g/ to k/: group 3 development. *For explanation* see text.

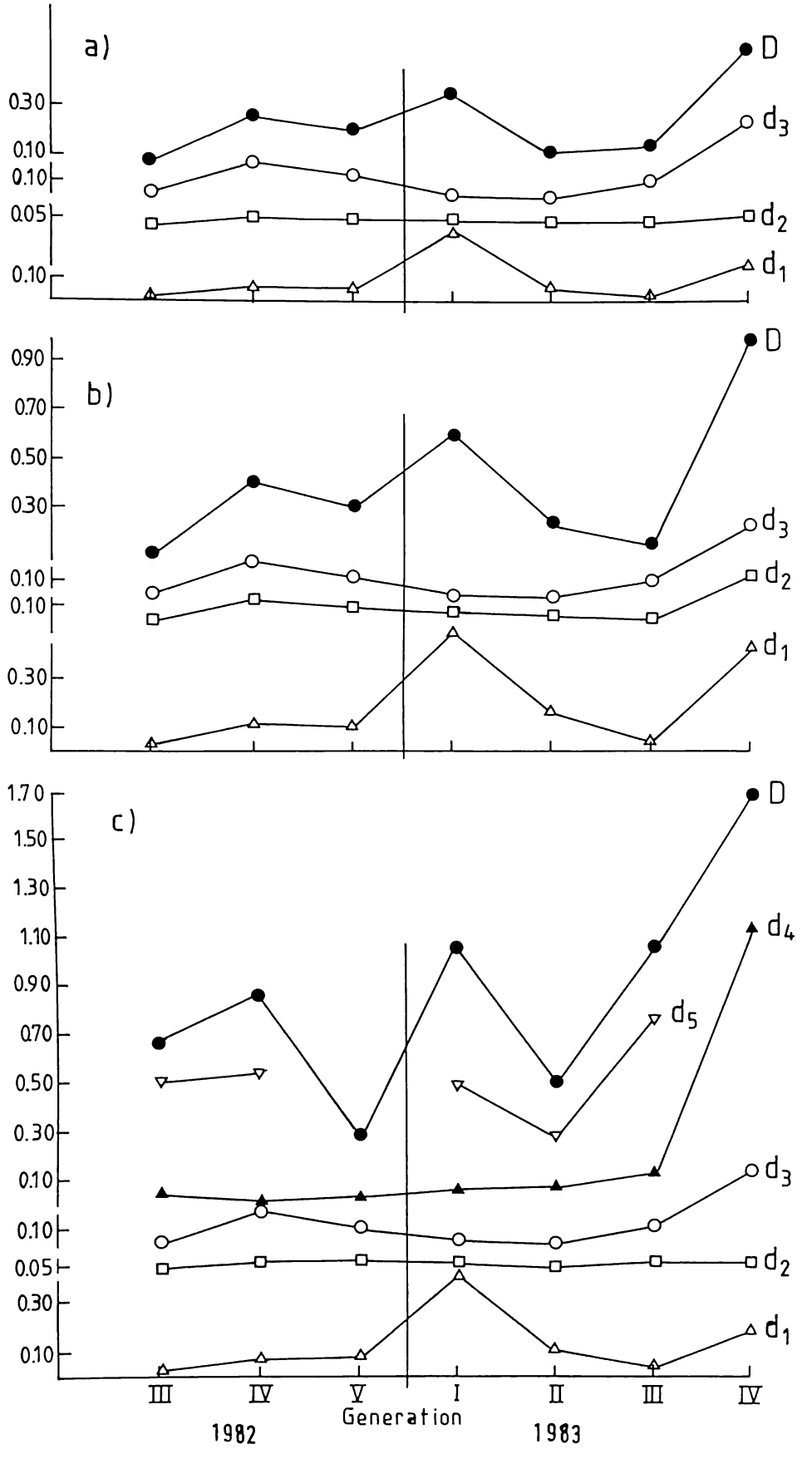


Fig 4.19 Individual d_i- and total D-values for the LF population in DII (Huntly): a/ group 1 development; b/ group 2 development; 3/ group 3 development. *For explanation* see text.

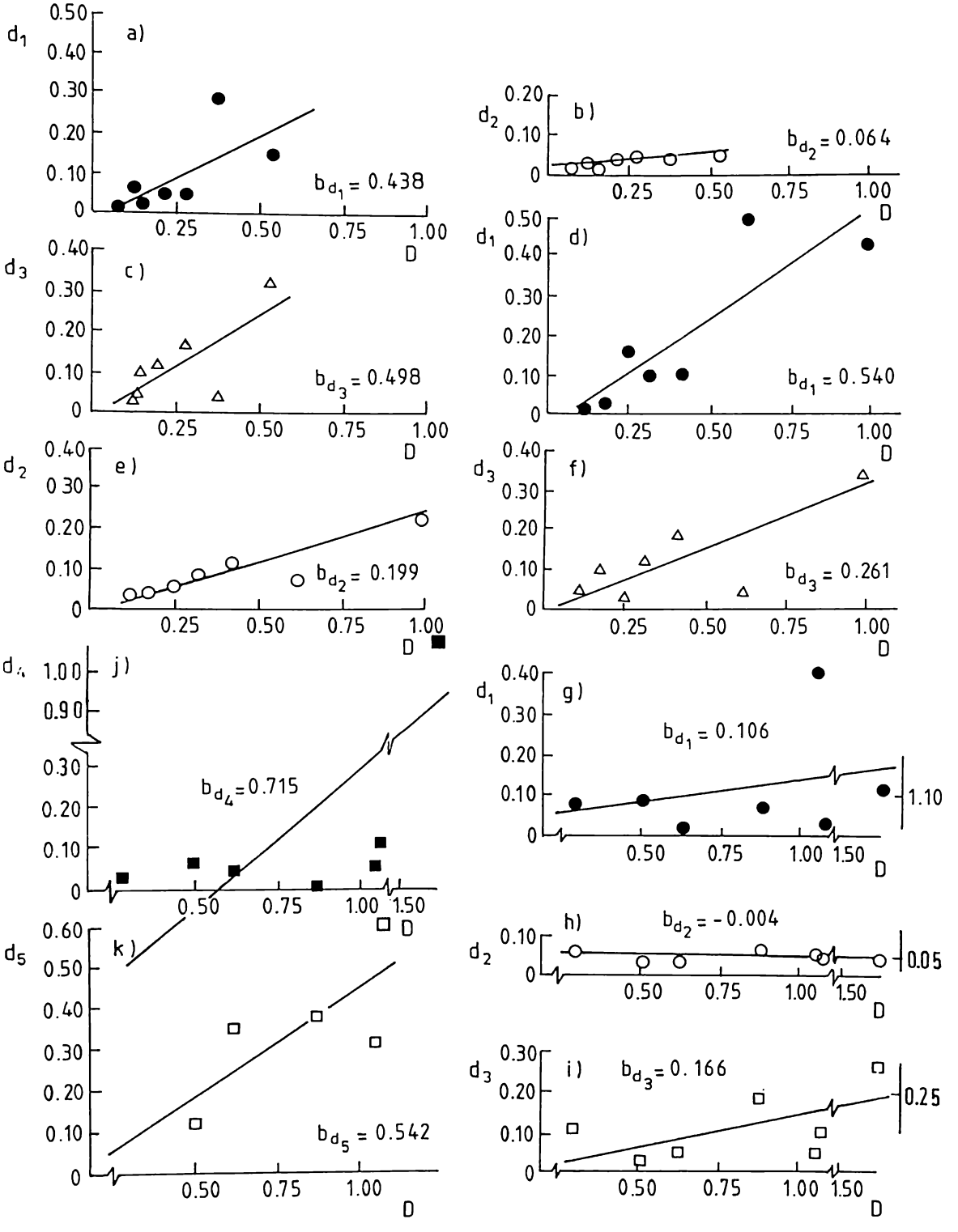


Fig 4.20 Regression of individual d_i-values against total D-value in DII (Huntly). a/ to c/: group 1 development; d/ to f/: group 2 development; g/ to k/: group 3 development. *For explanation* see text.

Table 4.14 The d_i-values (this study) and s_i-values (Manly, 1977a) for the group 1, 2, and 3 development (*See* text) of LF with reference to DI and DII, and presented in descending order of importance.

	Location			
Group	DI		DII	
	d_i-values	s_i-values	d_i-values	s_i-values
1	d_1	s_1	d_3	s_1
	d_3	s_3	d_1	s_3
	d_2	s_2	d_2	s_2
2	d_1	s_1	d_1	s_1
	d_2	s_2	d_3	s_3
	d_3	s_3	d_2	s_2
3	d_5	s_5	d_4	s_5
	d_4	s_1	d_5	s_4
	d_2	s_4	d_3	s_1
	d_3	s_2	d_1	s_3
	d_1	s_3	d_2	s_2

DI.

In the group 1 development the change in number from first to second larval instar (d_1-value) contributes most to the overall change in D-value, followed by the change in number from third larval instar to adult (d_3-value). When this is separated into male (group 2) and female (group 3) development, the change in number from first to second larval instar (d_1-value) is still the most important factor in group 2, but this is replaced in group 3 by the change in number from the second adult female to third adult female instar (d_5-value). This is an indication that the LF population in DI was prone to greatest changes in number at the beginning of the immature stage of the life cycle of the males, and at the end of the life cycle of the females, but was fairly stable at the time that sexual maturity was reached by both sexes.

DII.

In this case the change in number from the third larval instar to adulthood (d_3-value) contributed most to the overall change in the group 1 development, while the change from second to third larval instar (d_2-value) was the least important contributor. In the group 2 development the change in number from first to second larval instar (d_1-value) was the most important factor, followed by the change in number from third larval instar to adult male (d_3-value). The change in number from first to second adult female instar (d_4-value) played a major role in the total change of numbers in the group 3 development. Thus, as in DI the LF population in DII was prone to great changes in numbers at the beginning of the immature stage of the life cycle of the males, and the last stage of the life cycle of the females. It may be possible that the difference between the order of importance of the

d-values in the group 1 development in DI (d_1, d_3, d_2) and DII (d_3, d_1, d_2) was caused by the fact that DII was shut for hay making, as opposed to DI, in the two years that this part of the study was done. As has already been explained in paragraph 4.3.2.c, shutting up for hay may favour growth stages that are sensitive to extreme climatic conditions, especially the younger instars, thus changing the order of importance of the d-values.

Manly (1977a) presents another method to determine the key-factor, or in this case the most important d-value, from life table data. His method is based "...upon an equation that partitions the variance of the number alive at the end of the life cycle into components associated with variation in the number entering the first stage of the life cycle, variation in survival rates, and also density-dependent aspects of survival". The key-factor is that factor that contributes a large part to the final variance. A FORTRAN computer program (Manly, 1978) was used to carry out the fairly complicated calculations, needed for the analysis. Manly's s_i-values (Manly, 1977a), equivalent to the negative ki-values , used by Varley and Gradwell (1960, 1970), are presented in Table 4.14. A comparison with the d_i-values used in this study, show that for DI the s_i-values are equivalent to all the d_i-values for the group 1 and 2 development, and the most important d-value for group 3. For DII the s_i-values agree with the d_i-values from group 2, but the status of importance of the first two d_i-values is altered in group 1 and 3. Although there are some differences between DI and DII and between the d_i- and s_i-values the general picture is that the LF population was prone to greatest changes in number at the beginning of the immature stage of the life cycle of the males, and at the end of the life cycle of the females. Manly (1978) mentions that for about half the sets of data (13 articles in total) that he analysed, the outcome of

his method did not completely agree with that of the method used by the different authors either. The computer program also shows that the s_i-values were not density-dependent, indicating that other (a-)biotic, factors may play an important role in the regulation of the LF population.

4.6 Lucerne flea activity as indicated by pitfall trap catches

a/ Methods

Pitfall trap catches were made during 1981 and 1982 in Huntly and Te Kauwhata to compare the method with the soil sampling and Tullgren funnel extraction method. Results of this comparison have already been presented in Chapter 3. Between December 1982 and December 1983 the pitfall trap method was continued in Huntly on a weekly basis, and between July and October 1983 on a daily and day-night basis. In this paragraph the weekly, daily and day-night activity will be discussed.

b/ Results and discussion

Weekly catches

Fig 4.21 shows LF activity expressed as mean number of LF per pitfall trap in DI. Between December 1982 and December 1983 five peaks in activity can be observed, in December 1982, the beginning of April 1983, the end of August, September and October, and the beginning of December. These peaks in numbers coincide with the peaks found in Fig 4.3. This confirms what has been discussed before in this study, that a high LF activity is correlated to a high population density. The

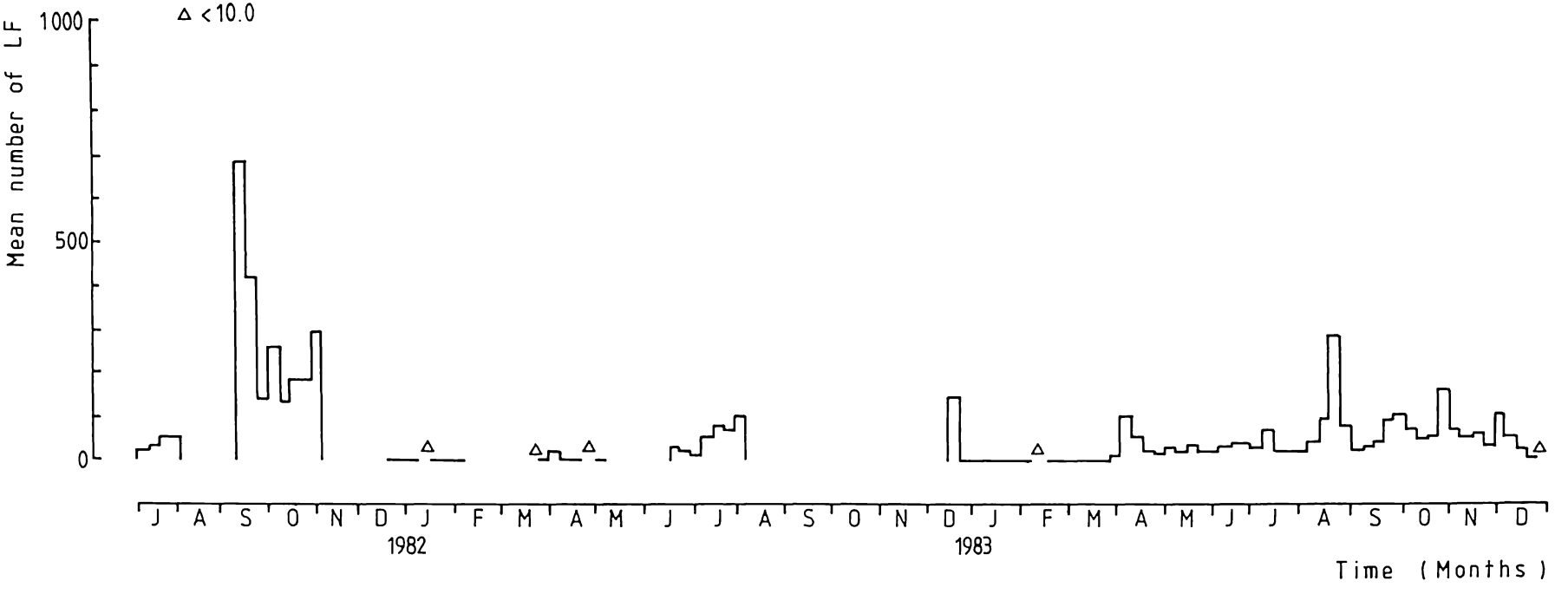


Fig 4.21 Mean number of LF in weekly pitfall trap samples during 1981, 1982 and 1983 in DI (Huntly). *Note*, during 1981 and 1982 sampling was done on a 8 week sampling-5 weeks no sampling schedule (*See text*).

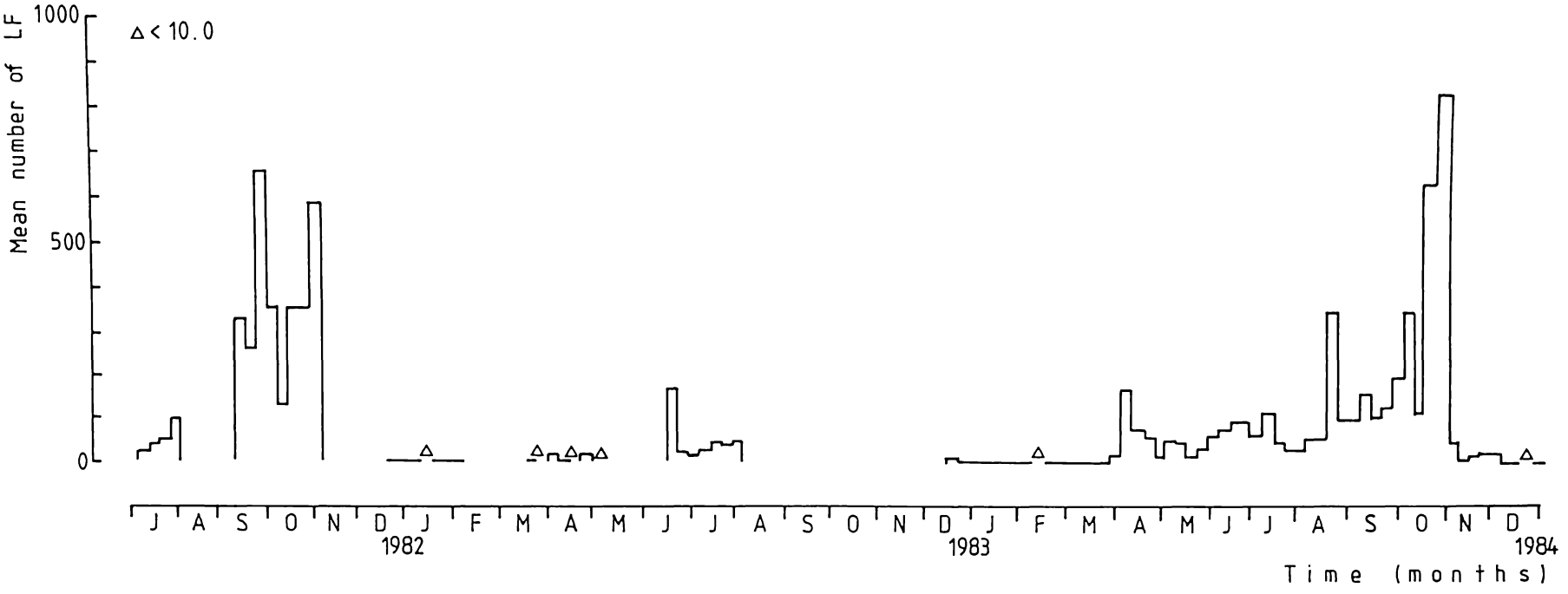


Fig 4.22 Mean number of LF in weekly pitfall trap samples during 1981, 1982 and 1983 in DII (Huntly). *Note*, during 1981 and 1982 sampling was done on a 8 week sampling-5 weeks no sampling schedule (*See text*).

results of DII show a similar pattern, but the numbers from the end of August until the end of October are much higher (Fig 4.22).

Daily activity

The daily activity of LF was followed during six weeks in DI (Fig 4.23) and twelve weeks in DII (Fig 4.24). The results of both paddocks closely resemble each other. Therefore only the results of DII will be discussed here.

LF caught were sexed, counted and measured. Fig 4.24 presents the LF activity and the percentage representation of the different growth stages. It is apparent that the LF activity differs from day to day. It is not possible to relate activity to the presence of certain growth stages in the field. The peak in activity between 18 and 25 August is dominated by first and second instar larvae. A smaller peak between 8 and 15 September is made-up of first, second and third instar larvae, whilst a peak between 22 and 29 September consisted of mainly adult males and females, and this pattern repeats itself. It seems that all the growth stages that are present in the field at a particular moment, contribute in proportion to their presence, to the total LF activity. No statistical relationships could be found between daily activity and daily temperature, expressed as heat units (^{o}D, threshold 4 and 7 ^{o}C), or between the daily activity and rainfall.

Day-night activity

LF is active both during the day and night (Fig 4.25). The night catch, covering twice the time of the day catch, is also presented per 8 hour units (overlay, Fig 4.25). A comparison of the eight hour units, using the Mann-Whitney test, shows that there is no significant difference between day and night activity (P=0.05). It is also obvious

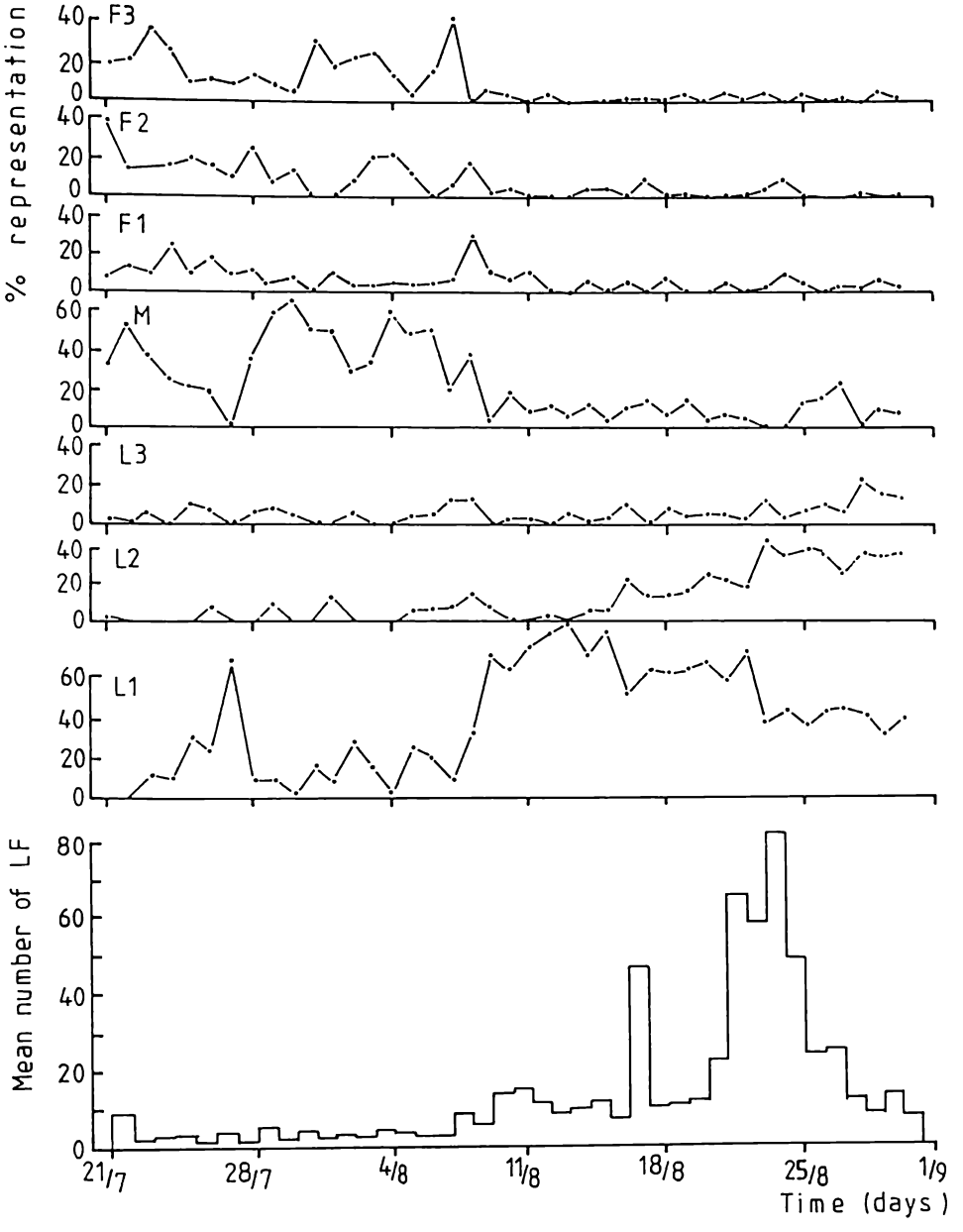


Fig 4.23 Mean number of LF (bottom) and percentage representation of the different instars in daily pitfall trap samples in DI (Huntly) in July and August 1983.

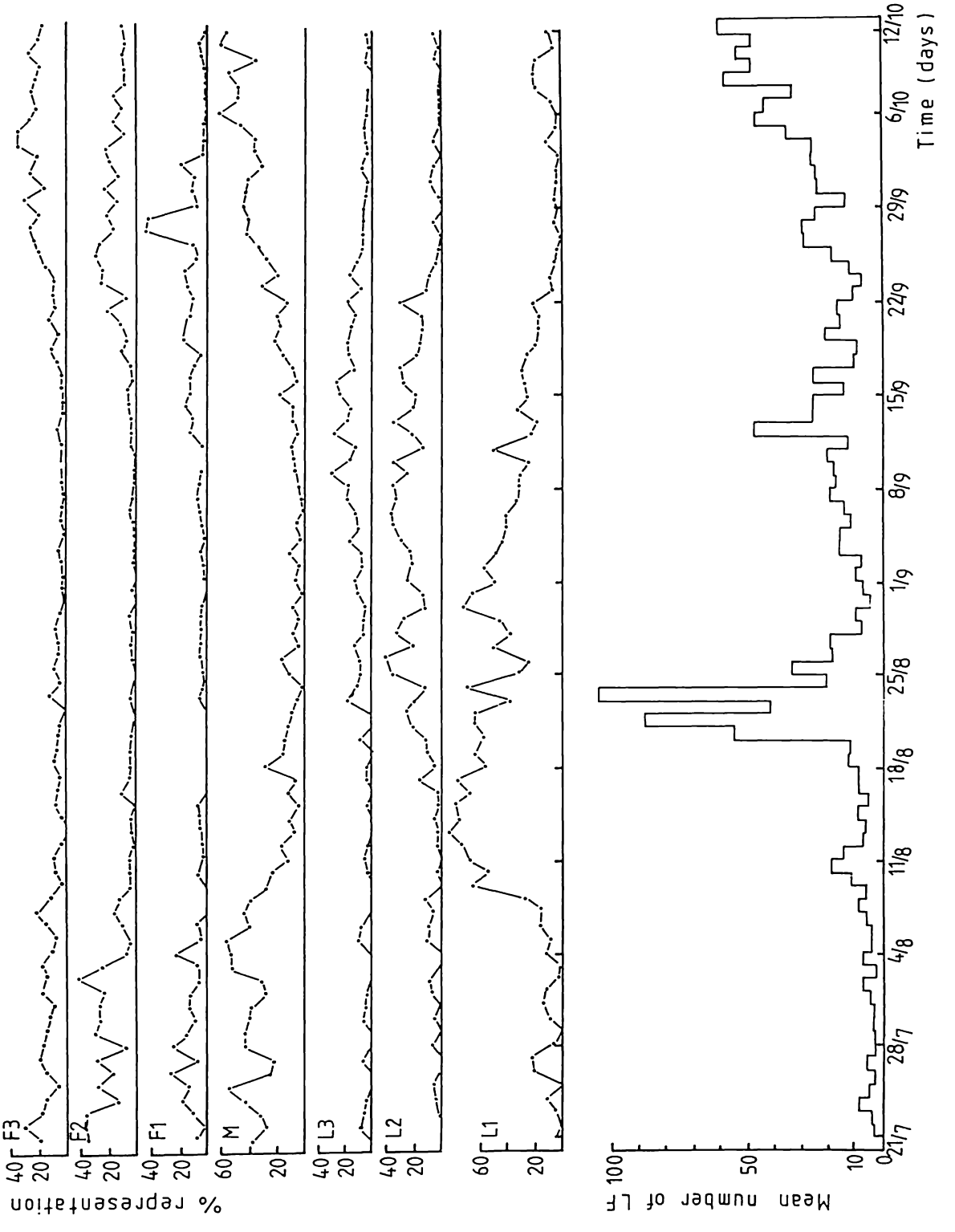


Fig 4.24 Mean number of LF (bottom) and percentage representation of the different instars in daily pitfall trap samples in DII (Huntly) between July and October 1983.

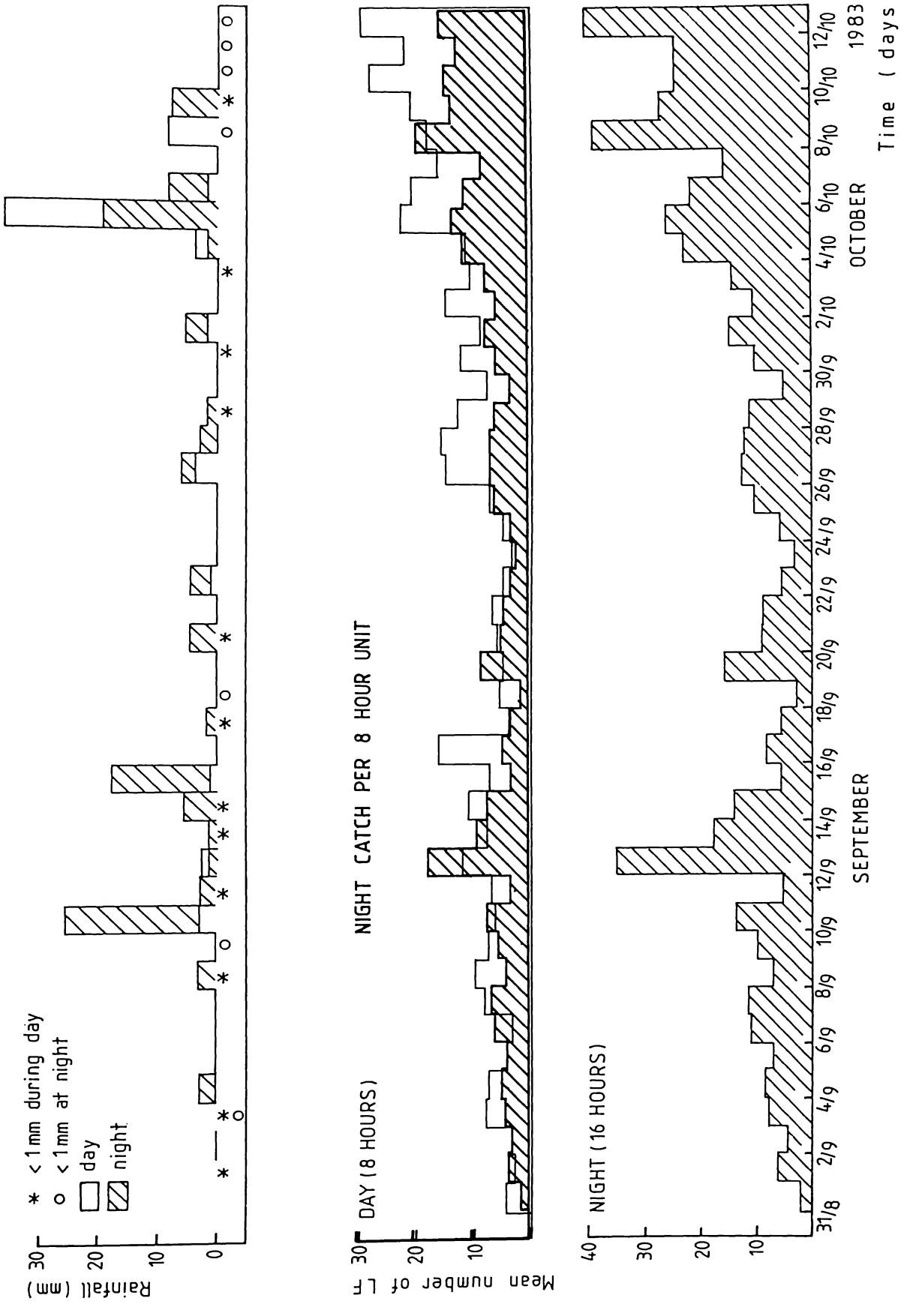


Fig 4.25 Mean number of LF in pitfall trap samples during the day (middle) and night (bottom), and corresponding rainfall figures (top) in DII (Huntly) during September and October 1983. *Overlay* shows night catch per 8 hour unit.

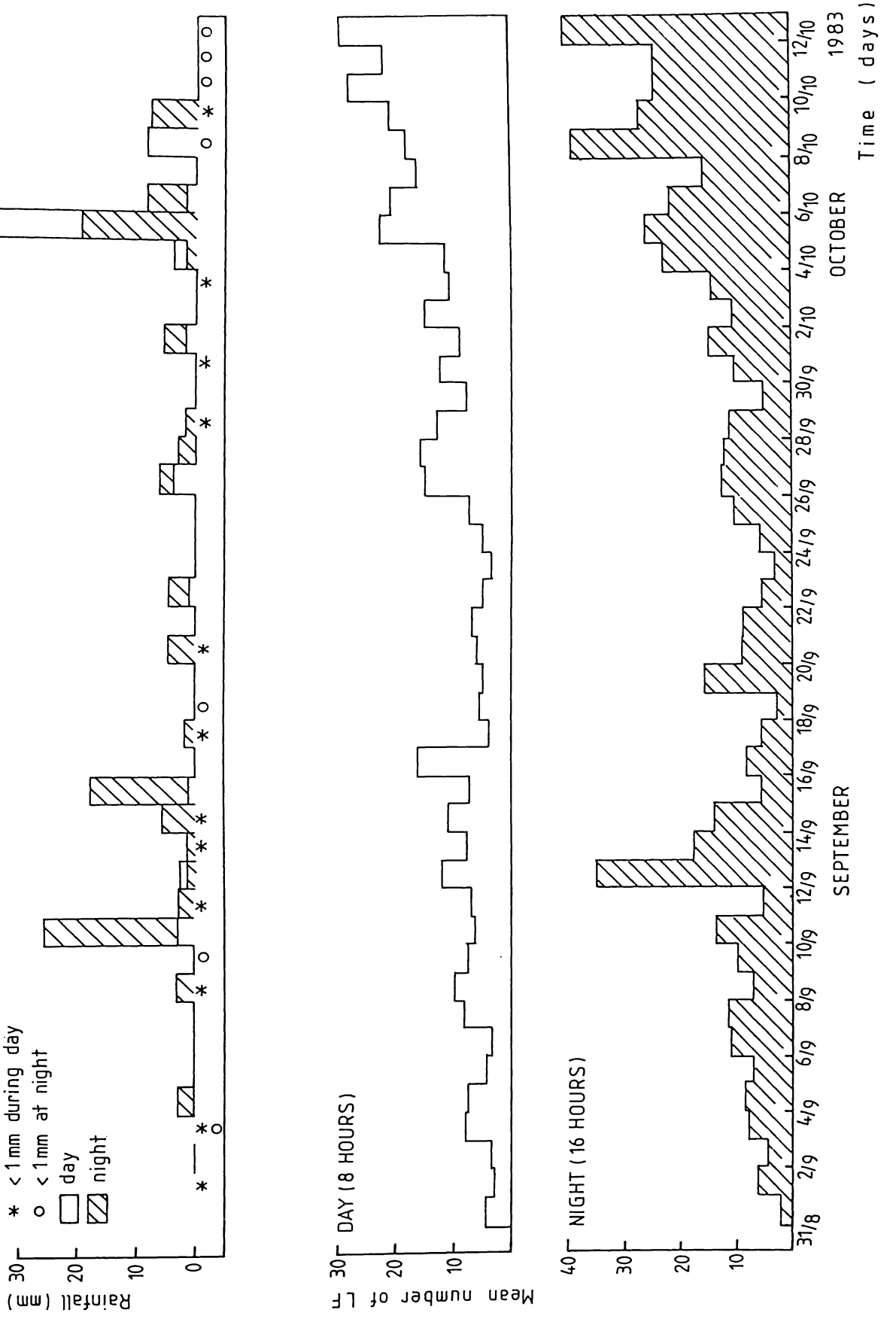


Fig 4.25 Mean number of LF in pitfall trap samples during the day (middle) and night (bottom), and corresponding rainfall figures (top) in DII (Huntly) during September and October 1983. *Overlay* shows night catch per 8 hour unit.

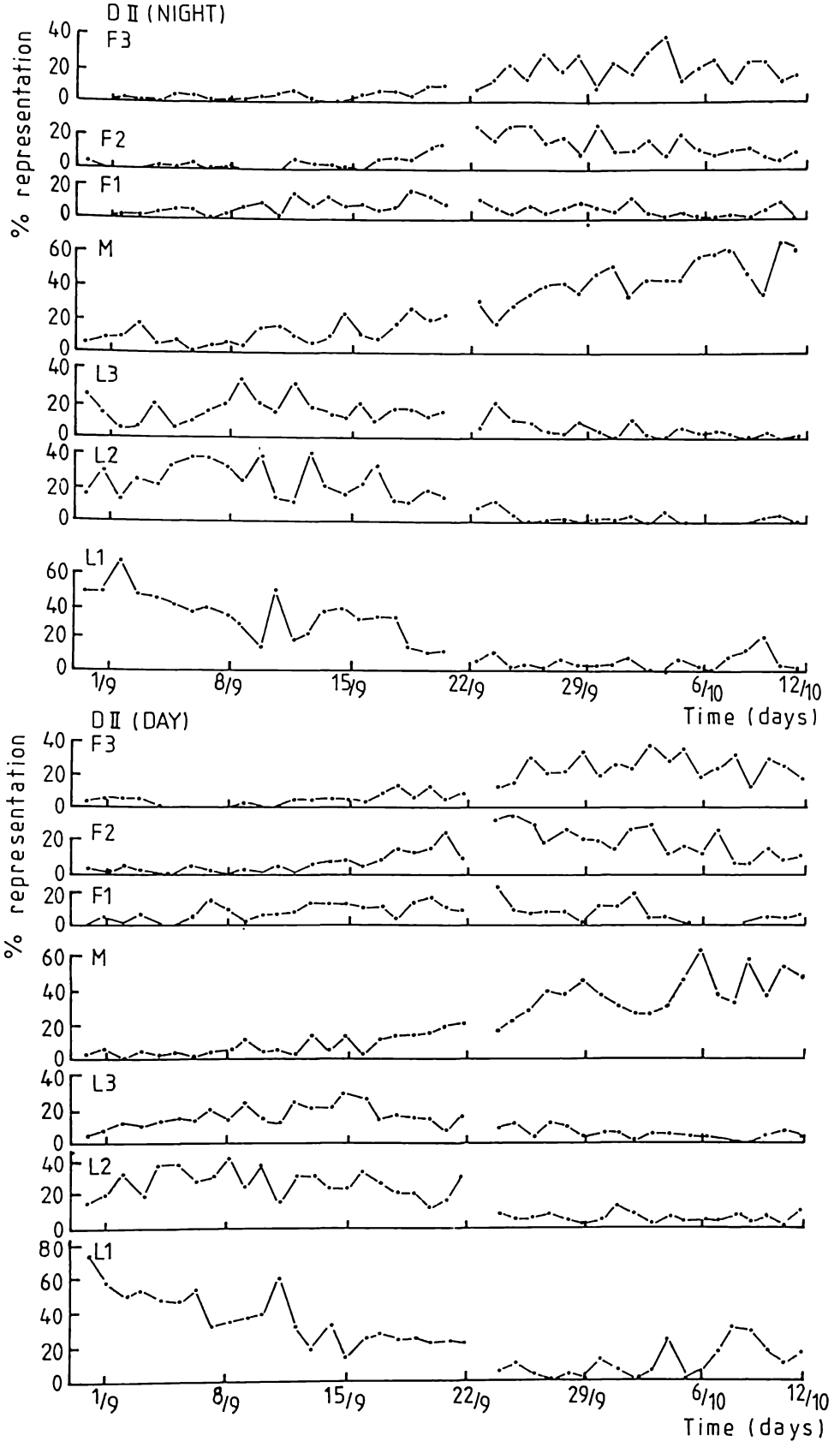


Fig 4.26 Percentage representation of different instars of the LF in daily pitfall trap samples during the day (bottom) and night (top) in DII (Huntly) in September and October 1983.

that there is no difference in the growth stages that are present during the day or night period (Fig 4.26). No statistical difference could be found between day-night activity and the corresponding rainfall figures.

These results indicate that LF activity merely depends on population density. Joosse (1965) found that some collembolan species responded to a change in temperature by either increasing or decreasing their activity and that others showed no change in activity at all. It has been established that activity is much lower during periods of ecdyses (With and Joosse, 1971) and higher during reproduction (Joosse, 1971). Joosse and Groen (1970) mention that drought stimulates Collembola to locomotory activity. LF is one of the few Collembola with a tracheal system (Davies, 1927). This reduces the risk of desiccation (Southwood, 1973) and may well be the reason why no relationship could be found between the daily activity and temperature or rainfall. The only references in the literature to the day-night activity of the LF are by Lea (1922), who found that the LF principally feeds at night, and Davies (1928) who states that feeding activity took place both during the day and night. Although the results in this chapter only refer to activity, it is highly likely that feeding is not only restricted to the day time (*See* Chapter 7).

CHAPTER 5. Presence of predators

CONTENTS

CHAPTER 5. Presence of predators

5.1 Introduction

As has already been mentioned in Chapter 2, a wide variety of insects prey on the LF. Bdellid mites are considered the most important group of predators (Wallace, 1967; 1974b). Although the potential of mites as biological control agents of mite and insect pests is recognised, their use is fairly new (Gerson and van de Vrie, 1974). Snetsinger (1956) noticed that *Bdella depressa* was predaceous on mites such as clover mite and two-spotted spider mite, as well as on Collembola, including *Bourletiellla hortensis*. He concluded that *Bdella depressa* was an important predator of the clover mite in grassy areas. Harris and Usher (1978) described research on the grassland mite *Pergamasus lingicornis* and the possible implications for the population dynamics of Collembola. Most research, however, has concentrated on the use of predatory mites against pests such as spider mites in glasshouses (Strickler and Croft, 1982) or on fruits such as apple and pear (Wearing and Profitt, 1982; Hoy *et al.*, 1983). Reasonable control of LF by the bdellid mites *Bdellodes lapidaria* and *Neomolgus capillatus* has been achieved in Australia (Wallace, 1981) and South Africa (Wallace and Walters, 1974).

There are 22 bdellid mites known in New Zealand (Atyeo, 1963). The presence of *Bdellodes lapidaria* was confirmed by Dumbleton (1938), but only low numbers of mites were found. *B. lapidaria* is a prostigmatic mite (Baker and Balock, 1944), also called predatory snout mite or red snout mite (Ramsey, 1980) and belongs to the family Bdellidae, subfamily Odontoscirinae, genus *Bdellodes* (Atyeo, 1963;

Wallace and Mahon, 1976). A general description of mites and their biology can be found in André (1968). No previous research has been done in New Zealand on the biology of the bdellid mites or their influence on LF populations. McMillan (1969), however, has described in general population changes of prostigmatic mites in New Zealand pastures. Although slight differences occurred from year to year, the main peaks were observed in the May-June period and in October. Wallace (1967) provided data (fig 8, p. 1186) on the number of *Bdellodes lapidaria* between 1953 and 1961 in Australia, but since his observations include experiments on the use of DDT, only part of the data can be utilised validly to obtain information on the bionomics of the mite. In general in Australia mites occur in April and numbers build up until they peak in July-August or August-September, after which they decline and enter an aestivating egg stage in December. Wallace and Walters (1974) showed in South Africa that bdellid mites first appear in samples during January after which the numbers increase to peak in March-April, followed by a decline in numbers. This pattern is repeated later in the season with a peak in December.

Although *B. lapidaria* prefers LF, it has been observed to feed on other springtails in the field (Currie, 1934; Wallace, 1967; Wallace and Walters, 1974; Ireson, 1982). A non-selective predator such as the bdellid mite is ideal as a biological control agent since it is able to maintain itself on other prey species during adverse periods, whilst still maintaining a useful control of the main prey species (Wallace and Mahon, 1974). Wallace (1967) studied the relationship between the number of LF and *B. lapidaria* in Australia and found a highly significant regression of LF numbers on *B. lapidaria* numbers recorded 8 to 9 weeks earlier in the season. He concluded that a predator density early in the season of more than 20

mites/m^2 would prevent any outbreaks of LF later in the season. Predator densities less than 10 per m^2, however, could not prevent LF numbers to outbreak proportion. The analysis also revealed a significant positive regression of the number of bdellid mites on the number of LF recorded 8 to 9 weeks previously, indicating a response by the predator to its increased food supply. In South Africa, due to low numbers of LF, bdellid mites preyed on the more abundant springtail *Bourletiellla arvalis* (Wallace and Walters, 1974). A significant negative regression of *B. arvalis* numbers on the number of *B. lapidaria* was found. Low prey density followed high bdellid mite numbers and vice versa.

To investigate the presence and possible influence of the bdellid mite *B. lapidaria* on the LF, soil samples and pitfall trap catches from both sampling sites were examined during the year.

5.2 Presence of *Bdellodes lapidaria* in the field

Soil samples and pitfall trap catches were examined for the presence of the bdellid mites between September 1982 and January 1984. No mites were ever found in the two paddocks at Te Kauwhata. The following results were obtained from Huntly soil samples: In DI a total of 25 bdellid mites were collected on seven sampling occasions while in DII 19 mites were collected on nine sampling days. The dates and the absolute numbers of bdellid mites/m^2 are presented in Table 5.1. Most bdellid mites were found in April 1983 and January 1984. Due to very low numbers and frequency of catches no further conclusions can be drawn from these data.

Table 5.1 Absolute number of *B. lapidaria* per m^2 in Huntly during 1983 and January 1984.

Date	Paddock		Date	Paddock		Date	Paddock	
	DI	DII		DI	DII		DI	DII
17/02	14	14	21/07	0	14	24/11	0	14
14/04	81	14	29/09	0	14	21/12	14	0
28/04	81	27	13/10	27	0	1984		
12/05	27	14	27/10	0	41	05/01	95	108

The pitfall trap catches show a different picture. In both paddocks bdellid mites were found during most of the year. Fig 5.1 shows the fluctuation of bdellid mite numbers between September 1982 and January 1984. Pitfall trap catches are a measure of the activity of the animal and so do not give an absolute measure of density. However, since there was a positive relationship between the number of LF in pitfall traps and soil samples (Chapter 3), it is likely that pitfall trap catches give a good relative estimate of mite density also. In DI mite activity occurred from January onwards, with peak activity during autumn and little activity during winter and spring. In DII mite activity became apparent in March, increasing to a peak level in May, followed by a decline before peaking again in August and November. The difference in mite activity could be explained by pasture management. Shutting up for hay making eliminates grazing disturbances which may increase mortality. It also creates a favourable microclimate and may thus slow down the moment of diapause. This does not only apply to the bdellid mites but also to LF. Shutting up for hay making therefore favours the bdellid mite in more than one way. DI was shut up for hay in October 1982, possibly giving an earlier start to mite activity in DI than in DII. The opposite occurred when DII was shut up for hay making in October 1983, causing

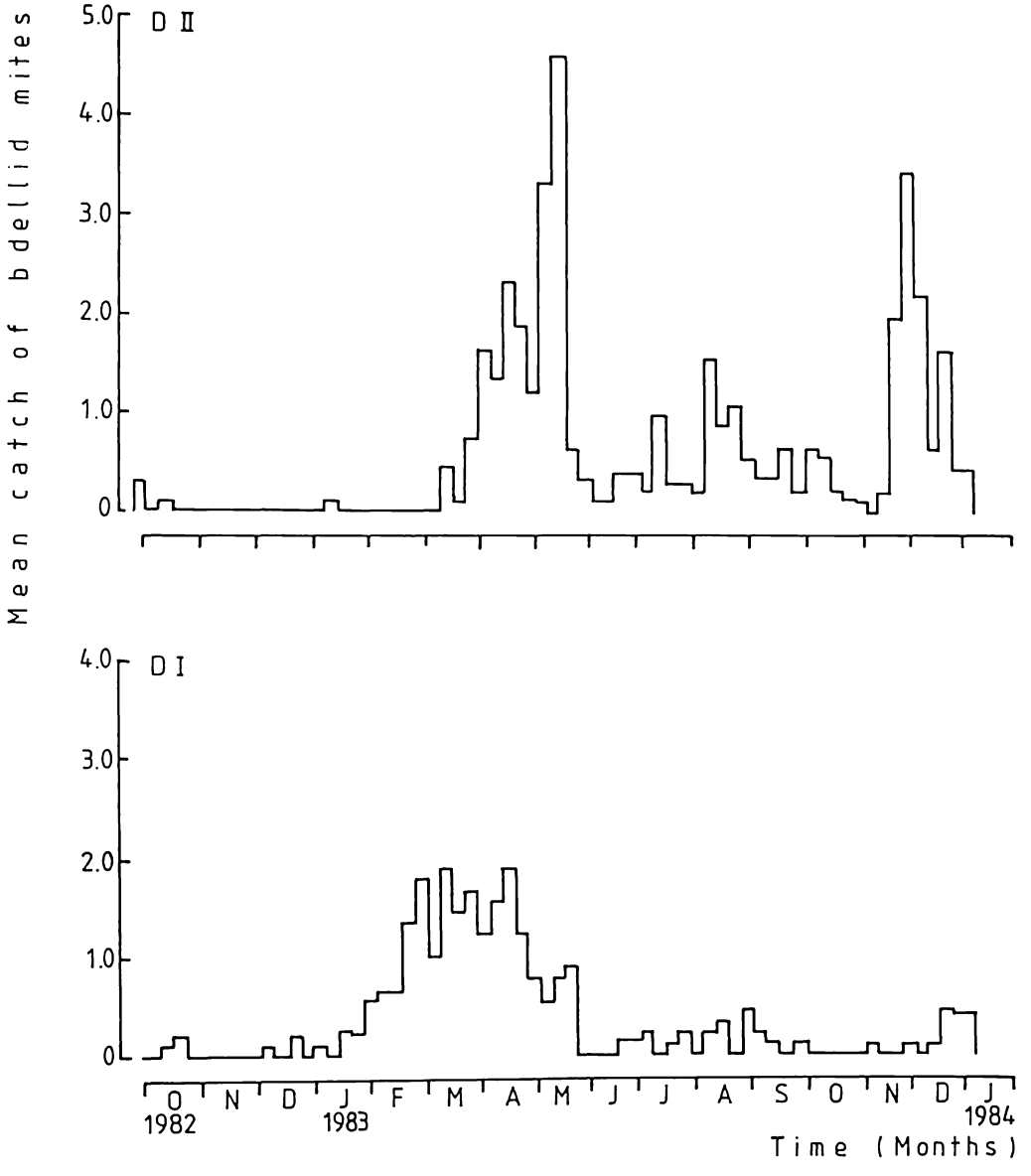


Fig 5.1 Mean number of the bdellid mite, *Bdellodes lapidaria*, in weekly pitfall trap samples in two paddocks in Huntly between October 1982 and December 1983.

the activity in DII to be much higher than in DI. In both paddocks, however, the number of bdellid mites was very low. In DI bdellid mite activity never exceeded two mites per pitfall trap. The same applies to DII, except for the two observed peaks in activity in May (x=4.67) and November (x=3.44).

During the day- and night-pitfall trap sampling in September and October 1983 (Paragraph 4.6) a total of 11 bdellid mites was found between between 5 PM and 9 AM on 10 separate days, while 14 bdellid mites were found from 9 AM to 5 PM on 12 separate days. When it is taken into account that the sampling period during the night is twice as long as the sampling period during the day, these data show that in the observed period the mites were more active during the day than at night.

The average number of bdellid mites are plotted against the average number of LF and other Symphypleona (Collembola)(Fig 5.2). Low numbers of LF coincide with high numbers of bdellid mites and vice versa. This is even more obvious when the number of mites are plotted against the number of Symphypleona. An attempt was made to fit a line, based on a log-log transformation, through the points. Although the Pearson product moment correlation coefficient (r) is significant in DI for the relationship mites-LF and mites-Symphypleona (r=0.391*** and r=0.527*** respectively), the line is not a good fit due to the spread of the points. Therefore no predictive value can be extracted from these results. The relationship between mites-LF and mites-Symphypleona in DII was examined with a non-parametric test, based on Spearman's rank correlation coefficient (r_s).

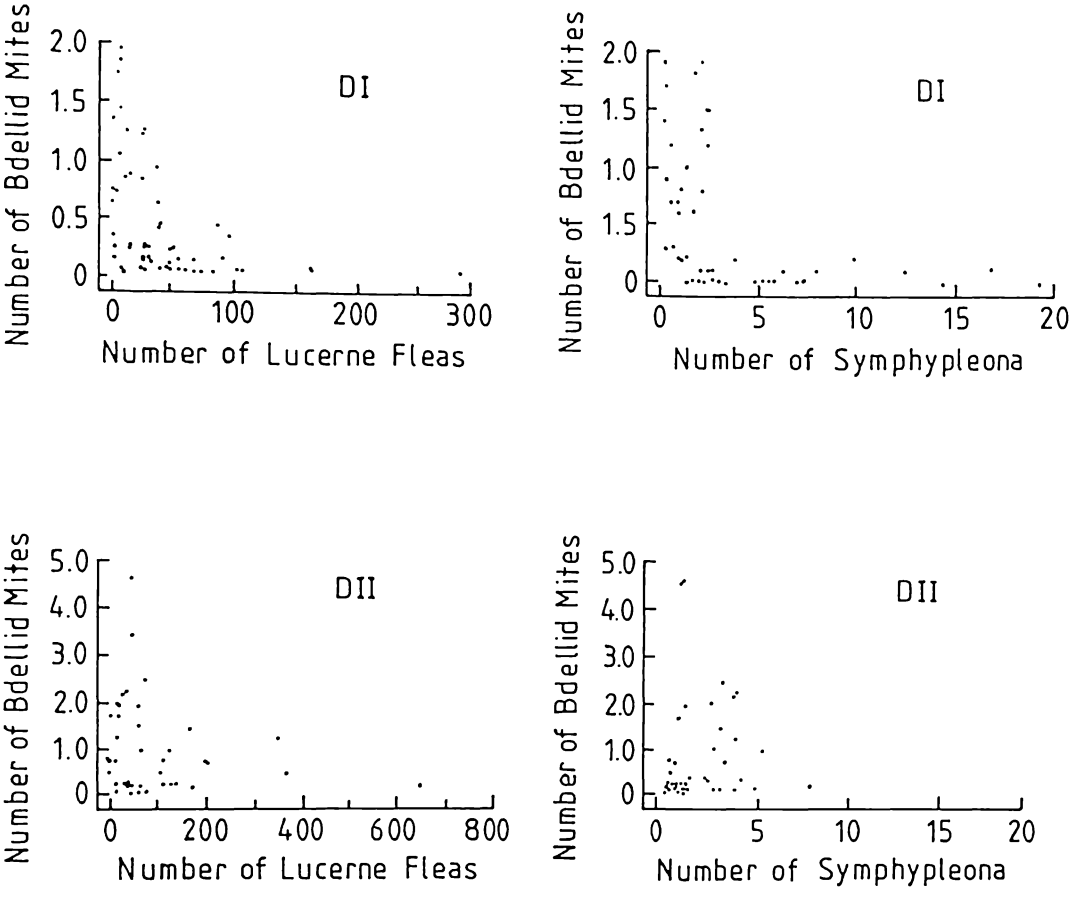


Fig 5.2 Mean number of *Bdellodes lapidaria* plotted against the number of LF (left) and other Symphypleona (right) in pitfall trap samples in DI (top) and DII (bottom) in Huntly.

Spearman's r_s can be converted into the test statistic z using the formula : $z = R\sqrt{n-1}$, which has approximately the standard normal distribution (Freund, 1974). Table 5.2 gives the r and z values for both paddocks.

Table 5.2 R- and z-values as well as statistical significance for the relationship of the mite with the LF and Symphypleona.

Relationship	test statistic r	test statistic z	significance
DI			
Mites-LF	-0.412	2.97	**
Mites-Symph.	-0.553	3.99	***
DII			
Mites-LF	0.340	2.45	*
Mites-Symph.	0.383	2.76	**

LF: lucerne flea; Symph.: Symphypleona; *: P=0.05; **: P=0.01; ***: P=0.001

These results are comparable with the results obtained by Wallace (1967) and Wallace and Walters (1974) who assumed a numerical response from the predator on the prey density. Hence Wallace (1967) plotted the number of bdellid mites against the number of LF recorded in the field eight to nine weeks previously, assuming a lifespan of the mite of eight to nine weeks. Wallace and Walters (1974) found that a high density of *Bourletiella arvalis* in March was followed four weeks later by a peak in bdellid mite numbers. A similar response, but delayed for up to 12 weeks, was found in October. The more rapid response in March was attributed to higher temperatures experienced in the

March-April period than in late spring. Wallace and Walters (1974), however, fail to mention other factors that may influence the predatory activity of the mite and therefore a possible numerical response. First of all the bdellid mite is not a specific predator, which means that the presence of other Sminthuridae, or springtails in general, may have contributed to the response. Secondly, both predator and prey are influenced by seasonal conditions and react to temperature and humidity changes with changing development times. Plotting numbers of prey and predator that have been collected on different dates, therefore introduces other unknown parameters. This means that care must be exercised when placing a predictive value on information that is gathered in this way.

More detailed research into the mite-springtail relationship is necessary to gain insight into the regulatory role of the mite on the LF in New Zealand pastures. At the moment it is possible to state that high mite numbers coincide with low LF numbers and numbers of Symphypleona, and vice versa.

5.3 Presence of other predators

To test for possible predators, other than *B. lapidaria*, several paddocks at the Ruakura Agricultural Research Station in Hamilton were sampled with a sweepnet and a vacuum-suction sampling machine. Coleoptera, Diptera, Hymenoptera and Arachnida were collected. In the laboratory the insects were sorted and each possible predator was put in a petri dish with LF of different growth stages. Regular observations were made to determine the feeding on LF. Except for spiders, no other predators preyed on LF. The main spiders that

preyed on LF were males and females, belonging to the family Gnaphosidae (B. Moyle, pers. comm.). In the field, LF were regularly found caught in spider webs. However, although spiders eat LF, the latter does not seem to be a primary food source for spiders. Spiders are general insect predators (Riechert and Lockley, 1984) and eat most insects that are trapped in their webs. Placement of spiders and LF together in an enclosure creates a non-choice situation, which results in predation, a situation not so common in the field.

CHAPTER 6. Rearing and handling of lucerne flea

CONTENTS

CHAPTER 6. Rearing and handling of lucerne flea

6.1 Introduction

(a) Food source

While in natural situations Collembola may only select one or two items from the available food sources (Christiansen, 1964), in culture they will accept various diets, both artificial and natural, different from their natural selection (Butcher *et al.*, 1971). As a consequence considerable research has been done to find the optimal diet for culturing Collembola. One of the most used techniques is gut content analysis (McMillan and Healey, 1971; Anderson and Healey, 1972; Massoud and Najt, 1976). Gut content analysis, however, can be misleading (Butcher *et al.*, 1971) and the use of different techniques may give contradicting information (Massoud and Najt, 1976). Gut content analysis tends to overemphasize the relative importance of durable non-digestible material and underestimate the importance of quickly digested materials, also ignoring liquids and transparent or minute substances (McMillan and Healey, 1971). It is therefore advisable to simultaneously observe types of food ingested under natural conditions. This has led many researchers to use such food as fungi and bacteria (Singh, 1969), algae (Joosse and Testerink, 1977; Testerink, 1982), bracken spores (Milne, 1960) and, in the case of LF, soil (Holdaway, 1927), or clover leaves for the purpose of culturing springtails. (Davidson, 1932a; Maclagan, 1932a; Wallace, 1968). Sometimes an artificial food source such as Tetramin fish food (Zettel, 1982) is used, but in most cases, however, baker's or brewer's yeast in dried or moistened form is used (Goto, 1960a; Green,

1964; Hale, 1965a; Christiansen, 1967; Snider, 1971; Niijama, 1973). Yeast is the most universal and successful diet for the widest variety of Collembolan species (Butcher *et al.*, 1971).

(b) Cages and substrate

A wide variety of glass containers, varying from crystallizing dishes to petri dishes (Maclagan, 1932a; Milne, 1960; Hale, 1965a; Niijima, 1973; Zettel, 1982) as well as plastic containers have been used (Wallace, 1968; Snider, 1971; Testerink, 1982). The advantage of heat resistant glass containers is that they may easily be sterilised (Goto, 1960a). In some cases the containers are of such a size that examination under the stereo microscope is possible (Rohde, 1956).

Most researchers use a mixture of plaster of Paris and charcoal (9 : 1 down to 1 : 1 ratio) as a substrate due to its good water holding capacity (Rohde, 1956; Goto, 1960; Green, 1964; Snider, 1971; Zettel, 1982), although moist filterpaper (Singh, 1960) and soil (Davidson, 1932a; Maclagan, 1932a) have been used. Goto (1960a) mentions that charcoal not only provides a good background but also absorbs vapours potentially toxic for Collembola. Nipagin-M was used by Goto (1960) as a fungicide in the food.

(c) Handling, anaesthetizing and killing.

Ireson (1982) kept field samples stored at 4 and 8 ^{o}C and found that after three days most of the fauna was still alive. For sorting and transfer of Collembola an aspirator and fine brush are the best tools (Davidson, 1932a; McMillan and Healey, 1971; Niijima, 1973).

For easier handling it is advisable to use insects straight from the refrigerator or to use a refrigerated table (Birkenmeyer and Greenwell, 1982). A refrigerated table was built for this research but the condensation build-up at room temperature made its application for microscopic study of LF impossible. Other ways of improving handling of Collembola is to use such anaesthetics as narcose ether (Joosse *et al.*, 1973) or carbon dioxide. The latter, however, prolongs the recovery period when the period of application is extended within the sublethal limits. It also seems to be less effective for mites and Collembola living in or on highly nutritive media than for those in less nutritive environments (Moursi, 1975). Also, Tanaka (1982) found that carbon dioxide used as an anaesthetic for the German cockroach during larval development increased the number of moults and prolonged the larval duration. McMillan and Healey (1971) used chloroform for the killing of Collembola, but more often 70 % to 100 % ethyl alcohol is used for killing and storage (Anderson and Healey, 1972; Wallace, 1973). Gisin (1970), who also gives various recipes for fixing, studying, mounting and preserving Collembola, points out that 70 % ethyl alcohol is not totally satisfactory due to slow penetration, hardening and degreasing qualities.

6.2 Methods

(a) Handling of LF

Insects were collected in the field and kept in plastic hospital specimen pottles (130 ml) with gauze covered lids to stop build-up of

condensation. The insects were kept at 4 ^{o}C for 3 to 4 days after which they were taken into the laboratory, sorted and sexed, and used for experimentation. This exposure to a low temperature slowed down their activity and feeding, synchronising them for feeding trials. LF were first sorted from the pasture fauna, using a fine brush and an aspirator, connected to a regulated low-vacuum system (Fig 6.1.a) consisting of a water-jet-vacuum-pump and a membrane-actuated relief valve, connected to a reservoir. The membrane used was a 'Therma-Brand' rubber membrane. This low-vacuum system allowed collection of LF in all stages of development, without damage. The insects were collected in the Pyrex glass reagent tube (180 ml) of the aspirator or, when closed of by fine gauze, in the plastic tube inside the aspirator. In the latter case the insects could be easily deposited into specific vials by applying pressure on the vacuum hose (*see* arrow in drawing). After possible males and females had been sorted by eye, sexing was done with assistance of a binocular microscope, at 10 to 40 times magnification. Morphological features of the genital area, described by Betsch-Pinot (1976) were used to determine the sex. Originally carbon dioxide was used as an anaesthetic to slow down LF during sexing. But it was found that the effect wore off quickly after a relatively short exposure period and was lethal after a slightly longer exposure time. Therefore a new method was designed. A small round mirror was connected under the glass base plate of the binocular microscope in such a way that, by focussing onto the mirror, in which the ventral side of the insect was reflected, sexing could be done quickly and the insect sucked up with the aspirator. Up to 100 insects could be sexed in one hour with this method.

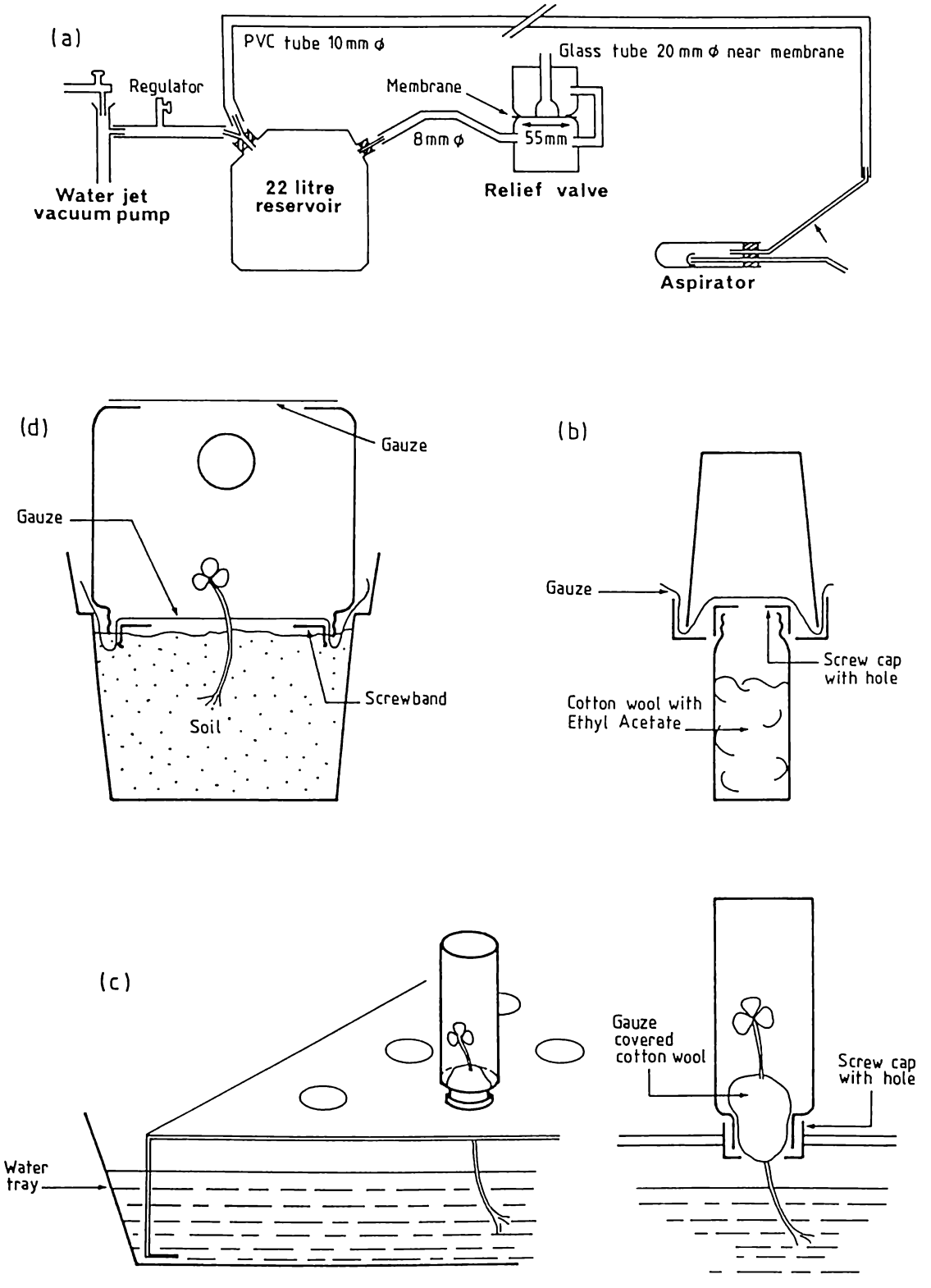


Fig 6.1 a/ low-vacuum suction system to collect insects. Pressure on hose (arrow) releases insects from aspirator; b/ killing chamber for LF; c/ set-up used to grow individual LF on clover leaves and to observe feeding; d/ caged plant for feeding experiment. *For explanation* see text.

Insects required for counting were preserved in 70 % ethyl alcohol, which was found to be a fast and convenient method. Insects that were used for measurement and weighing were kept for 18 to 20 hours at 4 ^{o}C after which they were killed by exposure to ethyl acetate for 20 minutes. A special killing chamber was designed for this purpose (Fig 6.1.b). LF were measured at 40 times magnification with the use of a micrometer eyepiece (40 divisions to 1 mm) and a stereo binocular microscope, and weighed to ± 1 µg on a Mettler microbalance. All head measurements were taken at the greatest width, visible from the dorsum. Due to the fact that morphological features such as the head and the anal appendix can point in several directions and therefore induce considerable variation in the measurements, it was decided to define the body length as the distance between the prothorax and the point where the anal appendix joins the abdomen, as seen from a lateral viewpoint.

(b) Cages

Several types of cages were used for different experiments. Pyrex crystallizing dishes, 90 mm diameter and 45 mm high, lined with a plaster of Paris and charcoal mixture (9 : 1 ratio) were used for observation, egg laying and feeding trials. The dishes were closed with "Glad Wrap" brand clear plastic sheet and a 100 mm diameter petri dish lid. 100 % humidity was achieved by regularly adding distilled water. For one-day feeding trials standard plastic petri dishes, 85 mm diameter, with "Whatman" filterpaper (grade 1) and distilled water were used, with "Glad Wrap" under the lid. For longer feeding trials with individual LF, 30 ml glass vials with metal screw tops, were used. Aluminium tables, 430 x 230 x 40 mm and with 24 holes of 23 mm diameter, were made to hold the vials. A stem of a clover leaf was

inserted through the hole in the screw top so that the lamina was suspended in the vial. The hole was closed with gauze and cotton wool, and the vial was placed upside down in the aluminium table (Fig 6.1.c). The table was placed in a tray filled with water and nutrients into which the stems were suspended. In this way leaves were kept fresh for several weeks.

Different cages were designed for feeding trials on plants. A screw band (B2, "Perfit Seal"), covered with mesh, was pressed into the soil. Small holes were made in the mesh and pre-germinated seeds of clover or ryegrass planted in the soil. A clear plastic jar, 90 and 105 mm diameter at the top and bottom respectively and 100 mm high, was used to construct the chamber. With the bottom covered with fine mesh and a hole of 23 mm diameter cut in the side to give access for the introduction of the LF, the jar was placed upside down over the screw band to create a miniature cage (Fig 6.1.d). Although the system allowed normal plant growth and reasonably natural conditions in an artificial environment, the low recovery rate of insects after a week of trials made it impossible to assess density dependent damage.

The feeding experiments with the cages were carried out at 10, 15 and 20 ^{o}C in growth rooms (fluctuation ± 1 ^{o}C at 10 and 15 C, ± 2 ^{o}C at 20 ^{o}C). The experiments with the crystallizing dishes, petri dishes and vials were carried out in refrigerated incubators at 10, 15 and 20 ^{o}C (± 1 ^{o}C at all temperatures) and, depending on the experiments, at a photophase of 0, 8, 12, 16 or 24 hrs light. Light was supplied by one 8 Watt Bilsun fluorescent light. Egg production was done at laboratory temperature of 18 ^{o}C ± 5 ^{o}C with no additional light. Depending on the experiment white clover (*Trifolium repens* cv 'Huia'), red clover (*T. pratense* cv 'Turoa') or perennial ryegrass (*Lolium perenne* cv 'Ruanui') were used. In some of the biological

observations first larval instar LF were fed initially on moistened baker's yeast after which they were fed on white clover leaves.

After the experiments were finished the cages were first washed in a cleansing agent (Decon 90), rinsed properly and sterilized with 3 % hydrogen peroxide or 10 % sodium hypochloride (Janola). However, better results were obtained using 0.3 % Halamid (sodium-para-toluol-sulfone-chloaramide) (van der Schaaf and Jaartsveld, 1956). Its advantages are that it is very stable in powder form, does not effect or stain clothing or irritate the skin. Brushes were dipped in Halamid before eggs were transferred from the crystallizing dishes to petri dishes. This prevented early fungal growth and bacterial contamination. Additional information on techniques or methods, differing from the above, will be dealt with in the respective chapters.

CHAPTER 7. The influence of temperature and photoperiod on the consumption of white clover by lucerne flea in the laboratory.

CONTENTS

CHAPTER 7. The influence of temperature and photoperiod on the consumption of white clover by lucerne flea in the laboratory.

7.1 Introduction

From April onwards, when LF eggs hatch, populations of LF build up to a peak about October, after which numbers decline and almost disappear by December. The same trend is noticeable in the damage done by LF to pasture plants. It is important therefore to determine if the amount of damage is dependent on population density or whether temperature and photoperiod play an important role as well by affecting timing of feeding and rates of consumption. To determine the role of temperature and photoperiod on the activity of LF feeding, trials were conducted under laboratory conditions. White clover was chosen as the food source because it is the preferred host plant in the Waikato region of New Zealand, it is important to New Zealand pastoral farming and it is easy to grow. Maclagan (1932a) showed that the consumption by larval instars is not equivalent to that of the adults, but since it was too difficult to do experiments with the first two larval instars of LF due to a very low survival rate, it was decided to follow a group of third instar larvae till they became adults or died. Because of size differences and the fact that the females spend part of their time ovipositing, it was assumed that the sex of the insect could influence feeding. Therefore, separate feeding trials were conducted with males, females and the immature stage. Third instar larvae were selected on head width. Males and females were sexed and in both cases representatives of all age groups were chosen. Data not presented in tables, can be found in Appendices

7.1-7.5.

7.2 Feeding by adult male and female LF

(a) Methods

Ten individuals of each sex were selected and left in a glass vial for one to three hours before the experiment was begun. Two white clover leaves, each with three leaflets, were placed on moistened filter paper in a petri dish, and LF introduced. The insects were exposed to 10, 15 or 20 ^{o}C and a photophase of 0, 8, 12, 16 or 24 hours light. The experiments were of 24 hours duration. After each experiment the number of live insects was counted and new leaf material provided. Depending on the needs of the experiment insects were put at another temperature or photophase for 24 hours. The leaflets were separated from the stem and the extent of the damage was determined by placing the leaflet over graph paper (held down with a glass slide) and counting the number of mm squares, visible through the damaged area. The total surface area of each leaflet was measured on a portable area meter (Licor, LI 3000). Feeding is expressed as mm^2 consumption per individual per day. If less than 10 individuals were alive after an experiment, the total consumption was divided by (S + F)/2, were S is the number of LF at the start of the experiment and F the number at the finish.

(b) Results and discussion

Experiments were conducted from August until December 1983. To attain sufficient replicates within each experiment, replicates done at different dates were grouped together when there was no significant difference (Mann-Whitney, P=0.05) between the results at the different dates. The one exception to this, the experiments done at 20 ^{o}C and with 24 hrs dark, will be discussed later. Throughout this chapter the Mann-Whitney test, a non-parametric test (Zar, 1974) will be used to detect significant differences between treatments (P=0.05, unless specified otherwise). A two-sample t-test, although stronger, cannot be used because normality cannot be assumed.

Survival rate of the insects

A percentage survival of insects was calculated for all the feeding experiments. The survival rate ranged from 80 % to 100 %. There was no significant difference between females and males used for the first time in experiments ("new") and females and males used at a different temperature or photophase 24 hrs later ("old"). Only at 10 ^{o}C and 24 hrs light was the survival rate of the females significantly (P=0.0142) higher than the survival rate of the males. And at 20 ^{o}C the survival rate of the females was significantly (P=0.05) higher at 12 hrs light than at 24 hrs dark. These results indicate that neither the handling of the insects nor the experimental conditions were sufficiently stressful to result in a high mortality rate.

FEMALES

Influence of photoperiod on feeding

Feeding rates for the females are presented in fig 7.1. When increasing the photophase from 8 hrs light to 12 hrs light there is a significant increase in feeding at 10 ^{o}C (P=0.0001), 15 ^{o}C (P=0.0055) and 20 ^{o}C (P=0.0023). The same is observed when increasing the

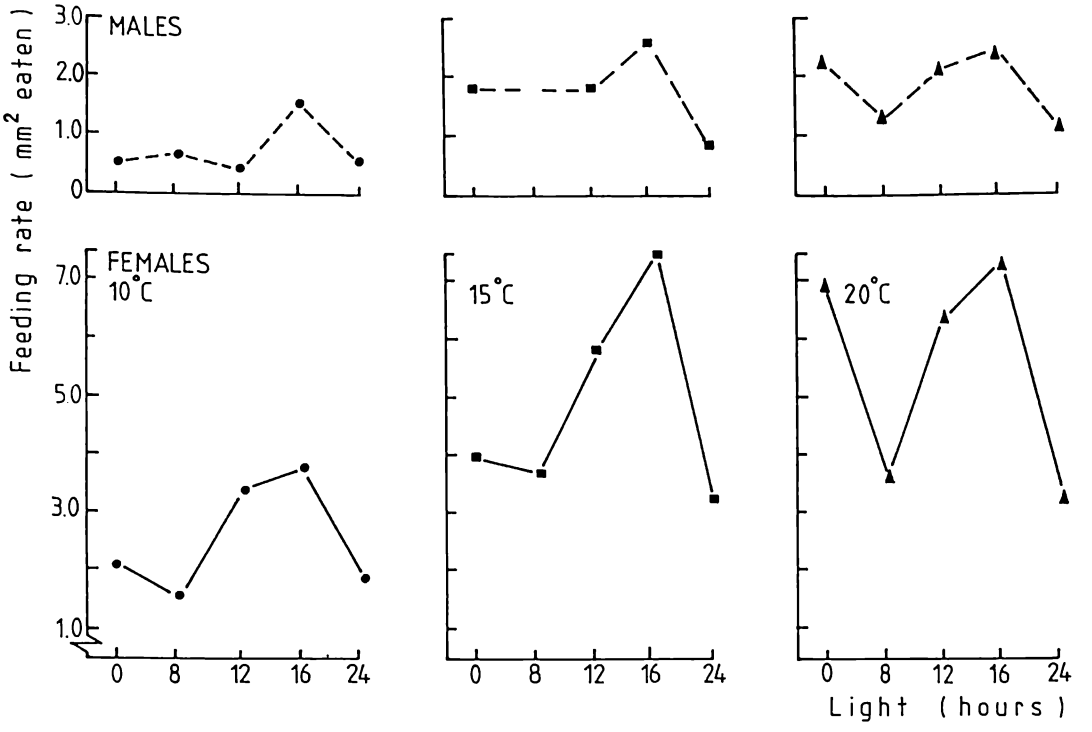


Fig 7.1 The influence of the photoperiod on the feeding rate of adult male and female LF. Feeding rate expressed as average mm^2 eaten per individual per day.

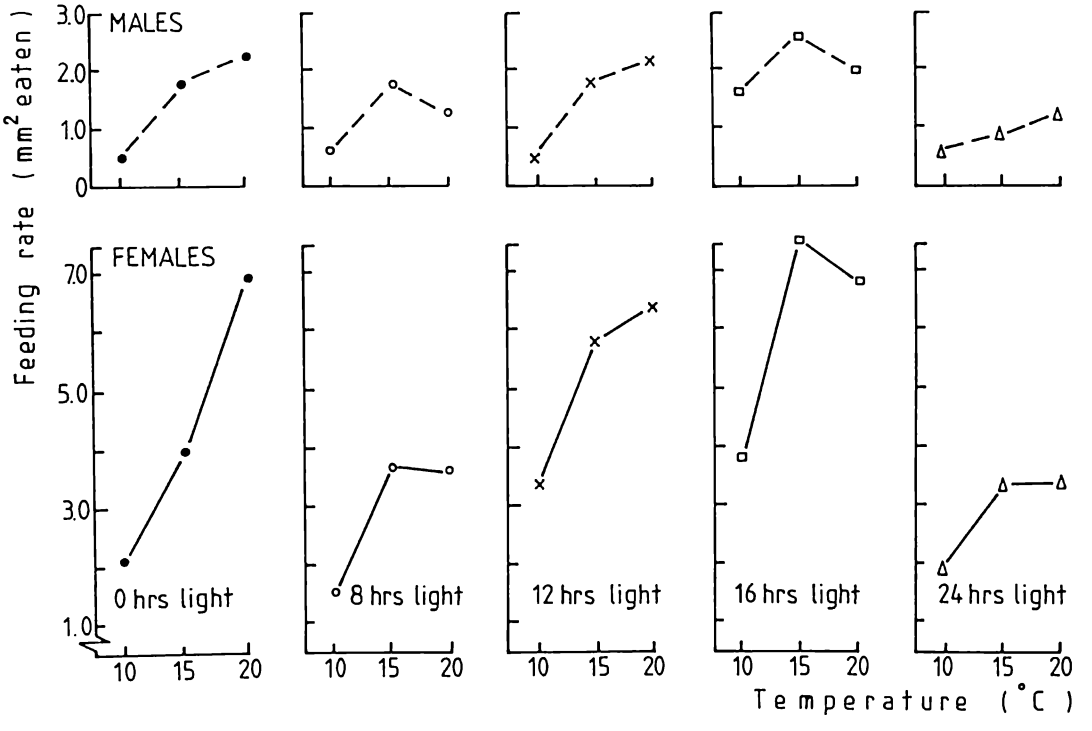


Fig 7.2 The influence of the temperature on the feeding rate of adult male and female LF. Feeding rate expressed as average mm^2 eaten per individual per day.

photophase from 8 hrs light to 16 hrs light (10 °C: P=0.0000; 15 °C: P=0.0002; 20 °C: P=0.0076). However, an increase from 12 hrs light to 16 hrs light did not significantly change feeding activity. Increasing the photophase from 8 hrs light to 24 hrs light did not significantly change the feeding pattern either. But insects at 24 hrs light eat significantly less than insects at 12 hrs light (10 °C : P=0.008; 15 °C : P=0.008; 20 °C : P=0.0066). The same trend was observed when the feeding activity at 16 hrs light and 24 hrs light was compared (10 °C : P=0.008; 15 °C : P=0.0005; 20 °C : P=0.0082). At 10 and 15 °C a change from 8 hrs light to 24 hrs dark was not significantly different but a change from 12 hrs light to 24 hrs dark (P=0.002 and P=0.0035 respectively) and 16 hrs light to 24 hrs dark (P=0.0006 and P=0.0001 resp.) significantly decreased the feeding rate. At 10 and 15 °C there was no significant difference between 24 hrs light and 24 hrs dark. There was a significant increase, however, in feeding at 20 °C between insects exposed to 24 hrs light and 24 hrs dark (P=0.023). The same applied at 20 °C when feeding was compared at 8 hrs light and 24 hrs dark (P=0.0168), while there was no significant difference between 12 hrs light and 24 hrs dark or 16 hrs light and 24 hrs dark. This deviation from the patterns at 10 and 15 °C may be explained as follows. When grouping replicates from the different dates in the 20 °C , 24 hrs dark experiments, two groups were significantly (P=0.0122) different from each other. Although the insects were thoroughly mixed and other experiments conducted during that day showed no significant difference, it may be that this group of insects deviated enough in behaviour from the others to cause the difference.

Influence of temperature on feeding activity

The results are given in Fig 7.2. When exposed to 8 hrs light, female LF ate significantly more at 15 °C (P=0.001) and 20 °C (P=0.002) than at 10 °C. The same tendency was observed in experiments conducted at 12 hrs light (P=0.004 and P=0.000 respectively) and 16 hrs light (P=0.002 and P=0.0042 respectively). In all cases an increase in temperature from 15 to 20 °C did not significantly alter the feeding activity. At 24 hrs dark the difference between 10 and 15 °C and 10 and 20 °C was significant (in both cases: P=0.0000), while the difference between 15 and 20 °C resulted in a significant increase in feeding at 20 °C (P=0.0165). The reason for the last result has already been explained above. When exposing insects to 24 hrs light there was no significant difference between feeding at 10 and 15 °C or 15 and 20 °C, but females ate significantly (P=0.034) more at 20 °C than at 10 °C.

When it was found that insect feeding was significantly different between 10 and 15 °C but not between 15 and 20 °C, more experiments were carried out to confirm the importance of a temperature rise or fall. At three photophases (8 hrs, 12 hrs and 16 hrs light) both females and males were exposed to 10 °C for 24 hrs after which they were transferred for 24 hrs to 15 °C, and vice versa. In all cases (Tables 7.1 and 7.2), when transferred from 10 to 15 °C, females ate significantly more at 15 °C than at 10 °C (8 hrs light: P=0.008; 12 hrs light: P=0.005; 16 hrs light: P=0.005) and significantly less when transferred from 15 to 10 °C (8 hrs light: P=0.045; 16 hrs light: P=0.013). At a photophase of 12 hrs light the difference was not significant but the same tendency in reduction of feeding was observed.

Table 7.1 The influence of a change in temperature from 10 to 15 °C on the feeding rate of male and female LF. Feeding rate expressed as mm^2 eaten per individual per day (mean ± SEM). For level of significance between treatments, see text.

Photoperiod (hours light)	Females	Males
	10 °C ---> 15 °C	10 °C ---> 15 °C
8	1.78 ± 0.35 4.48 ± 0.09 (n=6)	0.71 ± 0.09 2.25 ± 0.15 (n=3)
12	3.17 ± 0.45 6.30 ± 0.34 (n=6)	0.62 ± 0.17 1.95 ± 0.23 (n=3)
16	3.45 ± 0.32 6.94 ± 1.55 (n=6)	2.18 ± 1.23 2.89 ± 1.11 (n=2)

Table 7.2 The influence of a change in temperature from 15 to 10 °C on the feeding rate of male and female LF. Feeding rate expressed as mm^2 eaten per individual per day (mean ± SEM). For level of significance between treatments, see text.

Photoperiod (hours light)	Females	Males
	15 °C ---> 10 °C	15 °C ---> 10 °C
8	3.85 ± 0.98 1.39 ± 0.31 (n=6)	1.88 ± 0.23 0.97 ± 0.32 (n=3)
12	5.73 ± 1.07 4.24 ± 0.87 (n=6)	
16	6.02 ± 0.68 2.00 ± 0.69 (n=6)	1.10 ± 0.30 0.94 ± 0.07 (n=2)

Thus female LF achieve a maximum rate of feeding at a photophase of 12 hrs light and 16 hrs light. It is also obvious that absence of light during a certain period of time is essential. An interesting point is that female LF ate as much in the dark as they did at a photophase of 8 hrs light, suggesting that some feeding activity may occur at night under field conditions. The latter has been confirmed by Pottinger and Wrenn (pers. comm.). It can also be concluded that within the range of temperatures tested, maximum feeding was achieved at 15 and 20 ^{o}C .

MALES

Influence of photoperiod on feeding

Results are presented in Fig 7.1. Although the same tendencies found for the females (Fig 7.1) are also present in the feeding activity of the males, statistically significant differences between photophases only occurred in a few cases. At 10 and 20 ^{o}C male LF ate significantly more at 16 hrs light than at 8 hrs light (P=0.008 and P=0.0295 respectively). At 15 ^{o}C there was a significant (P=0.0168) decrease in feeding at 24 hrs light, opposed to 8 hrs light, 12 hrs light (P=0.03) and 24 hrs dark (P=0.0338). At 10 ^{o}C the insects consumed significantly more at 16 hrs light than at 12 hrs light (P=0.033) or 24 hrs light (P=0.014) and significantly more at 16 hrs light than at 24 hrs dark (P=0.007).

Influence of temperature on feeding

Results are presented in Fig 7.2. As with the photoperiod, the influence of temperature on the feeding activity of the male LF resembles that of the females. When exposed to a photoperiod of 8 hrs light there was a significant increase in feeding at 15 ^{o}C (P=0.0015)

and at 20 °C (P=0.0128), as opposed to 10 °C. No significance could be found between 15 and 20 °C. At a 12 hrs light photophase the increases at 15 °C (P=0.0304) and at 20 °C (P=0.0085), as opposed to 10 °C, were significant. No difference was found between 15 and 20 °C. The same was found when the insects were exposed to 24 hrs dark. The results were as follows: a significant increase at 15 °C (P=0.0011) and 20 °C (P=0.0003) but no significant difference between 15 and 20 °C. When exposed to 16 hrs light and 24 hrs light no significant difference between any of the temperatures was found.

The difference in feeding activity, when transferred from 10 to 15 °C and 15 to 10 °C was also tested for the males (Tables 7.1 and 7.2). In all cases an increase was found when the insects were transferred from 10 to 15 °C and a decrease when transferred from 15 to 10 °C. But none of the differences were statistically significant. While it is obvious from the results (Appendices 7.3 and 7.4) that the average *seasonal* temperature influences the feeding rate of LF, the results of this experiment (Tables 7.1 and 7.2) indicate that the increase in feeding rate, when rasing the temperature from 10 to 15 °C is possibly related to an optimum *diurnal* range that occurs when LF are feeding in the field.

As already mentioned, both the influence of the photoperiod and the temperature on the feeding of the females and the males resemble each other, but in the case of the latter this could not always be proven statistically. This may be because the number of males present in the samples on the day of collection was always less than that of the females. This resulted in fewer replicates for the males than the females and reduced the numbers of degrees of freedom in the statistical analysis. One other factor may have played an important role as well. In all cases where valid comparisons could be made,

Table 7.3 Probability levels for statistical difference in feeding activity between female and male LF in all feeding experiments.

Photoperiod (hours light)	Temperature 10 °C		15 °C		20 °C	
0		N.S.		N.S.	**	P=0.0057
8	**	P=0.0022	*	P=0.0348	***	P=0.0008
12	**	P=0.0044		?	**	P=0.0044
16	*	P=0.0157	**	P=0.0074		N.S.
24	*	P=0.0107	*	P=0.0107	*	P=0.0142

*: P=0.05; **: P=0.01; ***: P=0.001; N.S.=not significant at P=0.05;
?= not enough observations.

female LF ate significantly more than male LF (Table 7.3). This much lower feeding activity by the male LF, reflected in smaller differences between photophase and temperature treatments than found for the females, and combined with high relative variability, made any real differences difficult to detect statistically.

7.3 Feeding by third instar larvae

(a) Methods

Feeding of third instar larvae was assessed as for adults, but the experiments were only conducted at a photophase of 12 hrs light and the leaves were replaced every 3 to 4 days. Humidity was checked regularly and distilled water was added when necessary.

(b) Results and discussion

Since the feeding activity of the insects was determined at different time intervals (3 days, 3.2 days and 3.8 days) the results are expressed as feeding per individual per period as well as feeding per individual per day (Fig 7.3). Due to the non-uniformity of the sampling periods only the feeding per day was used for analysis. At all temperatures there was an increase in feeding activity with increasing time. The feeding at the end of the experiment was significantly higher than at the beginning (10 ^{o}C : P=0.0162; 15 ^{o}C : P=0.0109; 20 ^{o}C : P=0.0034). At 15 ^{o}C there was a drop in feeding noticeable after 20 days, but this result was not significantly different from the previous period or the following one (P=0.05).

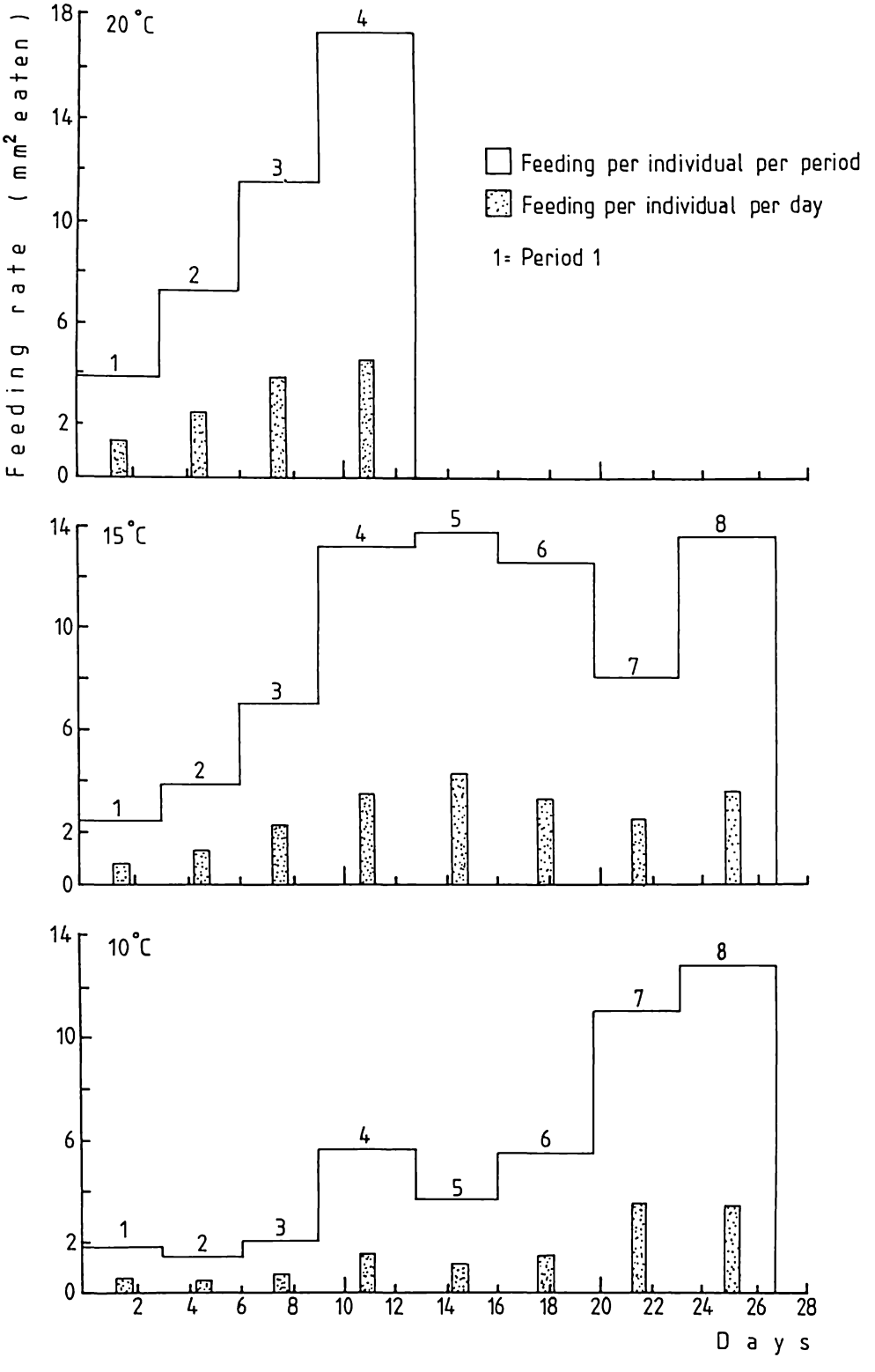


Fig 7.3 The influence of the temperature on the feeding rate of third instar LF at a photophase of 12 hrs light. Feeding rate expressed as average mm^2 eaten per individual per period and per day.

At 10 °C feeding per day in period 1, 2 and 3 each differed significantly (P=0.0015; P=0.0015; P=0.003) from feeding in period 4. Further, only feeding in period 6 was significantly lower from period 7 and 8 (P=0.0367; P=0.0369).

At 15 °C there was a significant increase in feeding between period 2 and 1 (P=0.0104), period 3 and 2 (P=0.020) and period 4 and 3 (P=0.0341). No further significant differences between following periods could be found.

At 20 °C the increase in feeding between period 2 and 1 (P=0.0036) and between period 4 and 2 (P=0.005) was significant, but the other periods did not significantly differ from each other.

Summing up the above results: at 10 °C significant increases after days 9 and 20, at 15 °C significant increases up to day 13, whilst at 20 °C a significant increase up to day 6 occurred. Extrapolation of the results of Maclagan (1932a) and Walters (1964) on the effect of temperature on the development of LF (Fig 2.2) clearly shows the influence of the different growth stages on the feeding activity. At 15 °C the insects reached the first adult stadium around day 6, which lasted till day 14 to 16. This explains the significant increase in feeding activity up to the end of period 4. A drop in feeding, although not significant, may indicate moulting and a change into the second adult instar. The same occurs at 20 °C where the adult stadium is reached during period 1. When comparing feeding at 15 and 20 °C it is obvious that the development is about three to four days faster at the latter temperature. Since neither Maclagan (1932a) nor Walters (1964) mention the influence of temperature on development at 10 °C, the feeding activity at this temperature needs to be compared with 15 and 20 °C. It appears that the adult stadium is

reached about day 8 or 9 after which feeding increases significantly. The second adult stadium is reached between day 18 and 20, and is also followed by a significant increase in feeding.

Since it is obvious that over a period of four weeks temperature will not only influence feeding activity but also insect development, it is not possible to compare feeding in the three temperature regimes.

It can be concluded from this experiment that in third instar larvae, and first and second adult instars of the LF there is a significant increase in feeding activity with an increase in age.

7.4 Other feeding trials

Other feeding trials were conducted using the glass vials and plastic cages with screw bands as described in Chapter 6. However, several problems were encountered using these methods. The glass vials were used for observation on growth and feeding at different temperatures. Although it was possible to rear LF from the egg stage to adulthood, the survival rate was very low. In general, when using glass vials or crystallizing dishes with plaster of Paris as medium, after two to three weeks a survival rate of only 10 to 20 % was found, making this an unsatisfactory method to follow feeding patterns during the different growth stages. Feeding trials utilising white clover, red clover and ryegrass in pots, covered with the above mentioned plastic cages, resulted in survival rates of 5 to 50 % after one week of experiments. One other aspect which made pot plant trials unsuitable was the time involved to recover dead or alive LF and assessment of the damage. An experiment involving 7 pots took more

than 5 hours to assess. The outcome of these experiments indicated that, although more artificial, it was better to do short term experiments (24 hrs) in a well controlled environment (petri dishes with damp filter paper, plus leaves), using refrigerated incubators, as opposed to growth rooms.

CHAPTER 8. Pasture sampling and damage on white and red clover plants

CONTENTS

CHAPTER 8. Pasture sampling and damage on white and red clover plants

8.1 Introduction

Given (1968) based the decision on what constitutes a major pasture insect pest on the following points: a/ an assessment on the ability to reduce the natural production potential, and b/ an assessment on the immediate threat to the agricultural economy. While the herbage production of pastures can be estimated from vegetation samples taken at regular intervals, the assessment of the damage caused by insects to pasture plants is more difficult. The major problem associated with detailed pasture insect pest assessment studies is the translation of losses in pasture quality and quantity into losses in animal production. This conversion is desirable if the economics of insect damage are to be meaningfully assessed (Kain and Atkinson, 1975; Pottinger, 1976). Roberts (1979a), in his review of insect damage assessment and survey techniques, compiled a list of factors that have bearing on evaluations of pasture damage caused by insects and other invertebrates. The complexity of pest assessment in pastures led to the conclusion that at the moment it is probably best to settle for a lesser goal, the prediction of pest abundance and damage to pasture.

Three types of damage can be distinguished: damage where plant cover is partially or completely destroyed, leaving bare ground into which weed species establish; damage were pasture production is impared without an associated change in botanical composition; damage causing an insidious change in botanical composition unaccompanied by any abrupt change in composition (Kain and Atkinson, 1975).

Plate 8.1 Damage caused by the lucerne flea to white clover in the field.

Damage done by LF falls in the first category (Plate 8.1), and an attempt was made to:

1/ determine the pasture composition during the different seasons,

2/ assess the damage done by LF on white and red clovers periodically, and

3/ try to express the damage quantitatively in lost white clover leaf surface area per pasture area unit.

White clover was chosen since it was a preferred host plant for LF in New Zealand pastures and it was easier to more accurately measure leaf surface area than on grasses. From the pasture system view point white clover plays a very important role in nitrogen fixation and as quality food source for grazing animals. The type of damage caused by the LF on plants has been described in Chapter 2. Damage in this context is defined as the amount of surface area lost due to LF feeding on the leaves, and expressed as a percentage of the total surface area of the leaflet.

Ideally, total pasture production should have been measured on each site for the duration of the trials, but 1/ equipment to do this was not available, 2/ cutting of vegetation before each grazing was not always possible, and 3/ the time factor involved did not allow this aspect, combined with the population dynamics study. Since measurements of pasture production were undertaken by Ruakura scientists (Wrenn and Pottinger, pers. comm.), it was decided to complement their research and study LF damage at the plant level.

Data not presented in tables can be found in Appendices 8.1-8.13

8.2 Collection and analysis of vegetation samples taken in the field

8.2.1 Methods

Pasture composition

A preliminary series of vegetation samples were taken on 19 November 1981, 4 March 1982, and 27 May 1982, and examined for pasture composition and damage. After that date vegetation cuts were made at four- to six-weekly intervals in the nine plots in each block at all locations. One sample was taken from each plot by a quadrat of 30 x 30 cm, thrown into the plot at random. All the vegetation within the frame was cut with motorised handshears to a height 2 cm above the ground. The vegetation samples were stored at 4 ^{o}C for one to four days until they could be sorted into the following components: grasses, white clover, red clover, weeds, and, depending on the season, into dead grasses and dead clovers. The samples were then dried to constant weight for 48 hours at 95 ^{o}C, after which the samples were weighed. Botanical composition was expressed as species components on a dry weight basis.

Assessment of damage and leaflet surface area measurements

A second sample taken in each plot close to the first sample was stored at 4 ^{o}C for one to two days until examination. Each sample was mixed thoroughly and 100 leaflets were taken at random and examined for damage. Damage was scored on a scale of zero to nine (0 to 90 % of the leaflet surface area damaged). The area of the leaflets, minus the stem, were then measured with a portable area meter (LICOR, LI 3000), before being dried to constant weight together with their stems at 95 ^{o}C for 48 hours and weighed.

8.2.2 Results and discussion

a/ Pasture composition

The pastures in Huntly and Te Kauwhata consist of a typical dairy farm ryegrass-clover sward. The main plant species in Huntly were perennial ryegrass (*Lolium perenne*), *Poa trivialis*, prairy grass (*Bromus unioloides*), white clover (*Trifolium repens*) and red clover (*T. pratense*) (DII). Apart from the absence of red clover the situation was the same in Te Kauwhata. The grasses were dominant, representing 60 to 90 % by weight of all the vegetation.

HUNTLY

In DI the level of grasses fluctuated between 75 and 90 % (Fig 8.1). Grasses were most abundant during November and December 1982 and June-July 1983. Between October 1982 and April 1983 up to 40 % of the total sample consisted of dead grasses. With a reduction in grasses in July and August 1982 and March and April 1983 increases in white clover occurred. The percentage representation for white clover fluctuated between 6 and 26 %. The percentage dead white clover was minimal (1 %). Weeds made up less than 8 % of the total vegetation sample. The dry matter weight of the total sample fluctuated during the year and was highest between October and February.

The same trend was observed in DII (Fig 8.2). The difference with DI was a more extreme fluctuation in percentage grasses (60 to 90 %) and white clover (10 to 39 %) in the vegetation. Dead grasses were found during a shorter period. DII was the only paddock where red clover was found, although the level was very low (less than 3 % during most of the year).

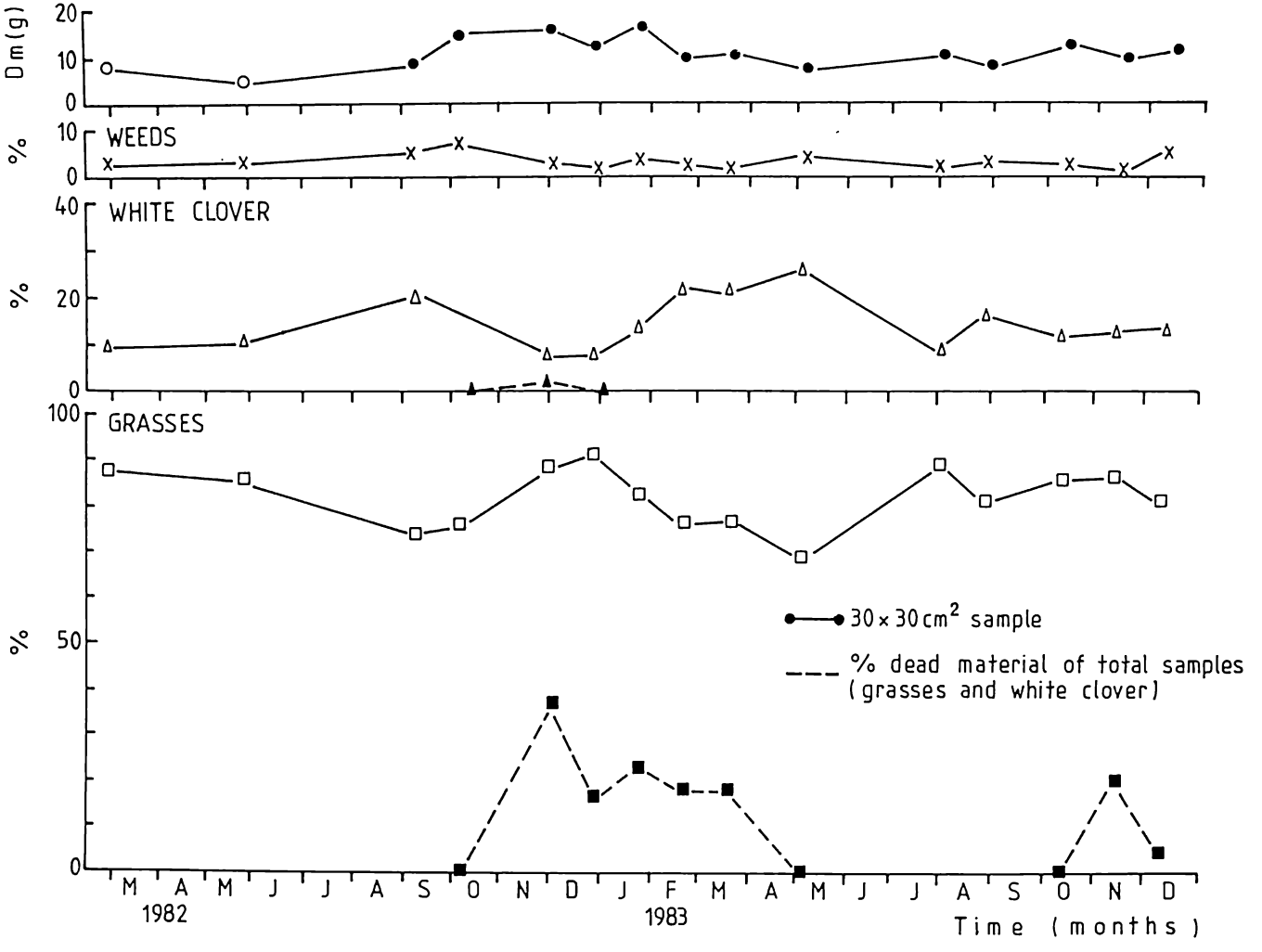


Fig 8.1 Dry matter weight (top) and percentage representation of three pasture vegetation components in DI (Huntly).

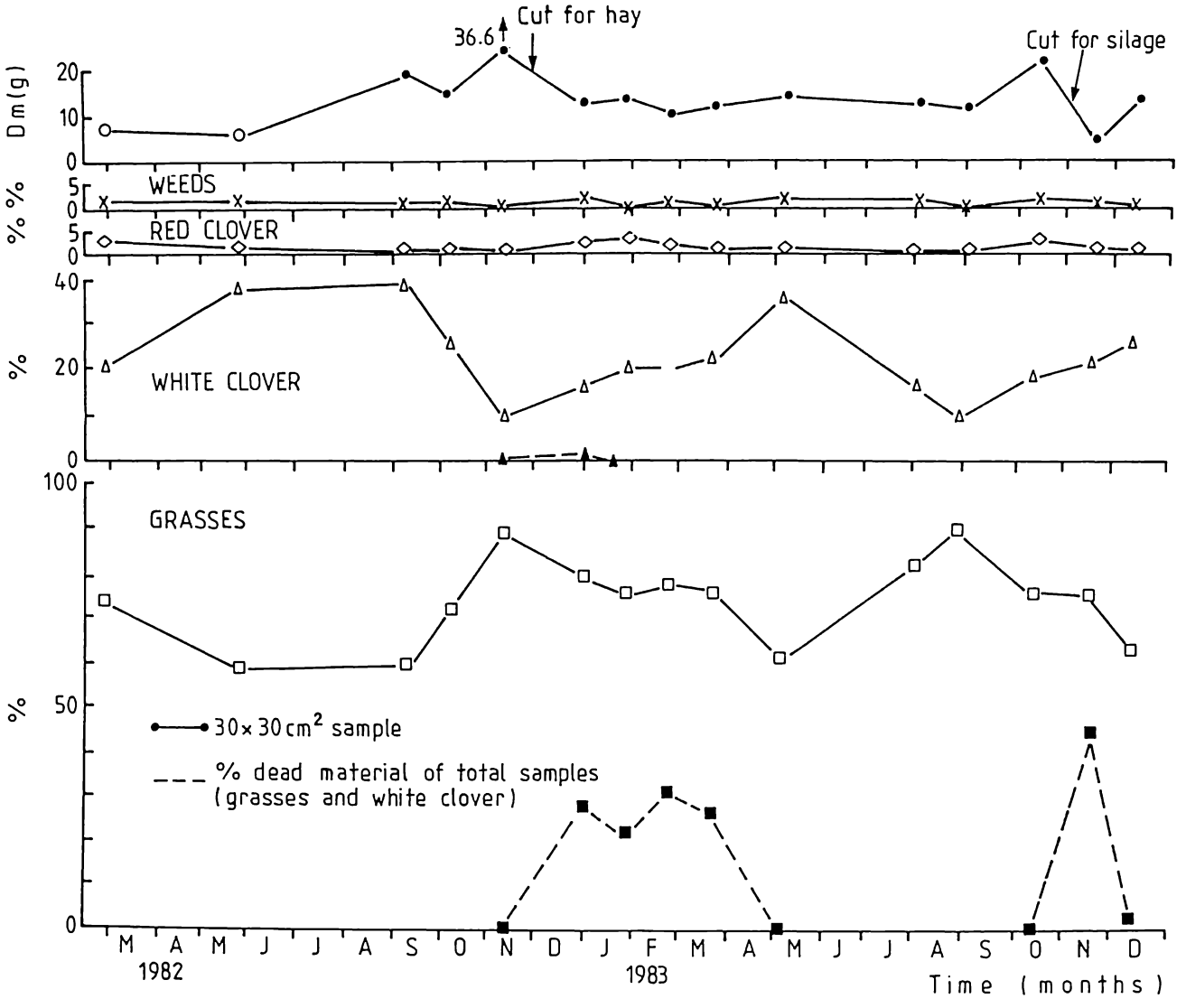


Fig 8.2 Dry matter weight (top) and percentage representation of three pasture vegetation components in DII (Huntly).

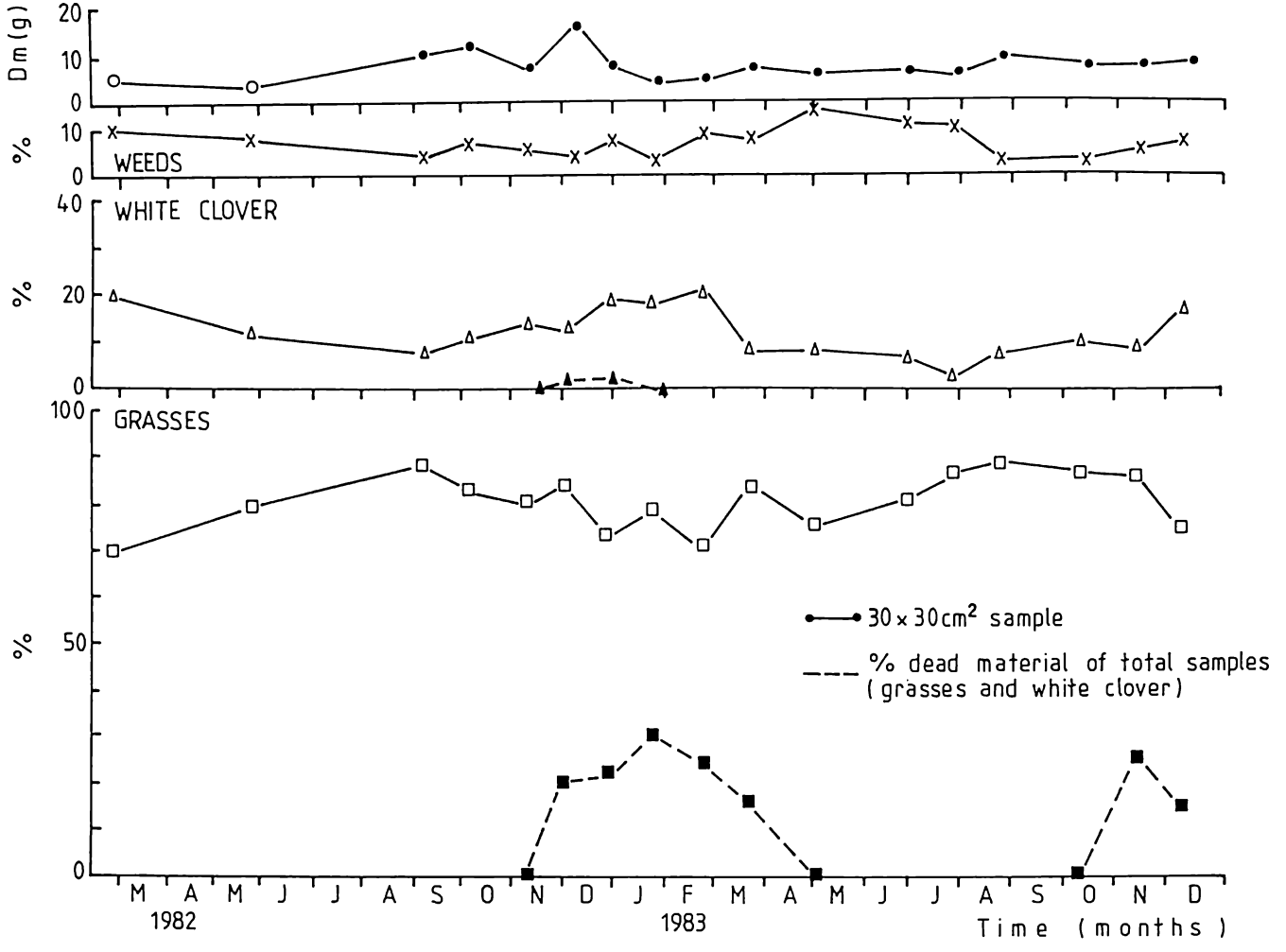


Fig 8.3 Dry matter weight (top) and percentage representation of three pasture vegetation components in KI (Te Kauwhata).

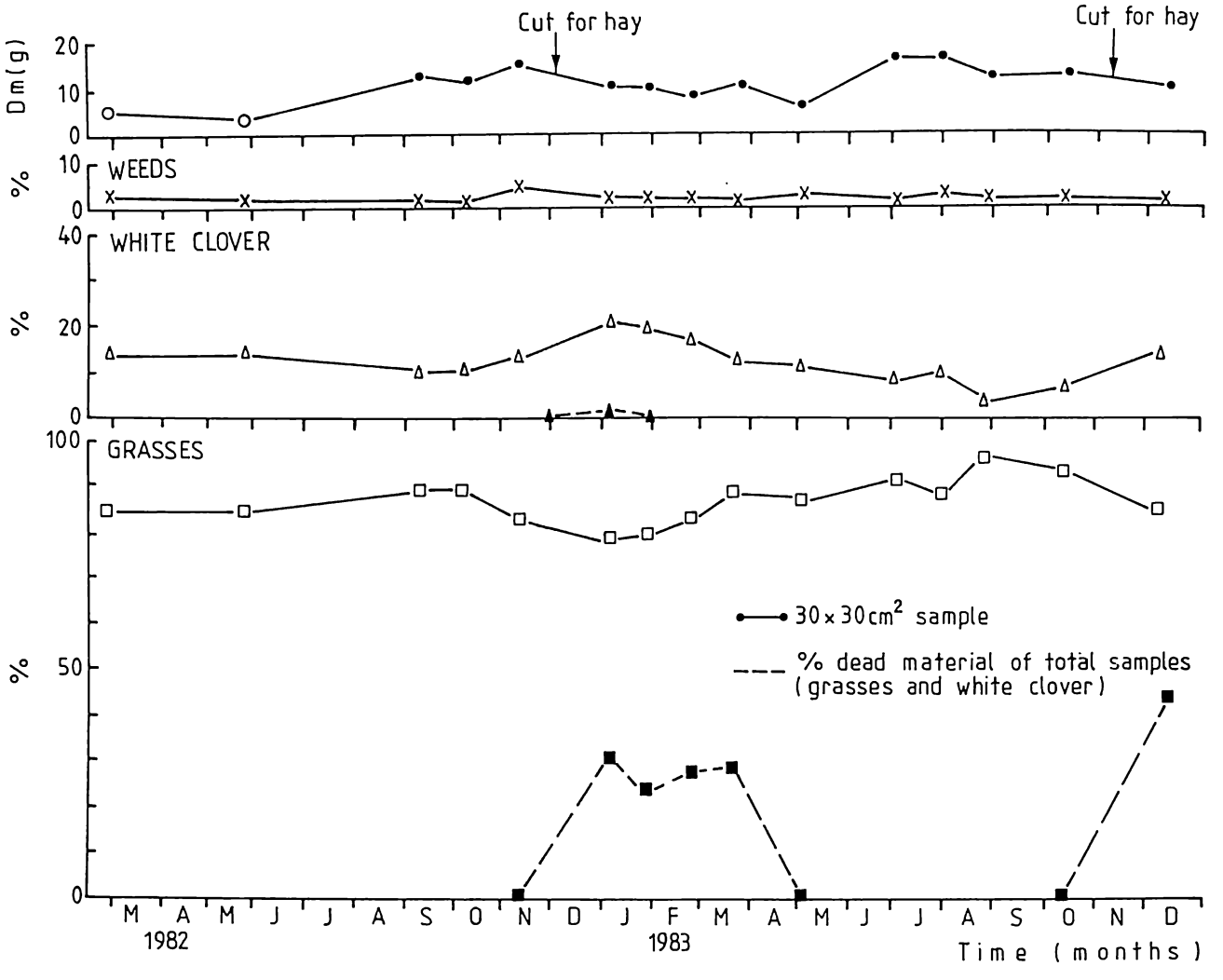


Fig 8.4 Dry matter weight (top) and percentage representation of three pasture vegetation components in KII (Te Kauwhata).

TE KAUWHATA

The percentage representation of grasses (Figs 8.3 and 8.4) in both KI (70 to 89 %) and KII (78 to 96 %) was much higher than in the paddocks in Huntly. Consequently the level of white clover was much lower (KI and KII: 3 to 21 %). KI had a higher level of weeds than any of the other paddocks (3 to 17 %). As in Huntly dead grasses were found between November and April, consisting of up to 40 % of the total sample. Dead white clover was mainly found in KI (10 %).

Very high percentages of grasses (90 % or more of the total sample) that were found on some occasions during this study, were preceeded in most cases by high numbers of LF (Figs 4.3-4.6). This suggests that LF populations had a significant effect on pasture composition which resulted, in combination with the level of damage and the percentage dead grasses and clovers, in poor pasture quality in spring.

b/ Leaflet surface area measurements

The results of leaflet surface area (LSA) measurements per 100 leaflets of white clover as well as dry matter weight are given in Fig 8.5. The change in LSA in both paddocks in Te Kauwhata during the year was very smooth. There was a steady decline from November onwards which continues till March after which there was an increase, with a peak in October. In Huntly there were more fluctuations than in Te Kauwhata. An extra peak, although smaller than the other ones, occurred in May. In all cases the dry matter weight follows the curves of the LSA results. The results from the percentage representation of the vegetation samples and the previous mentioned

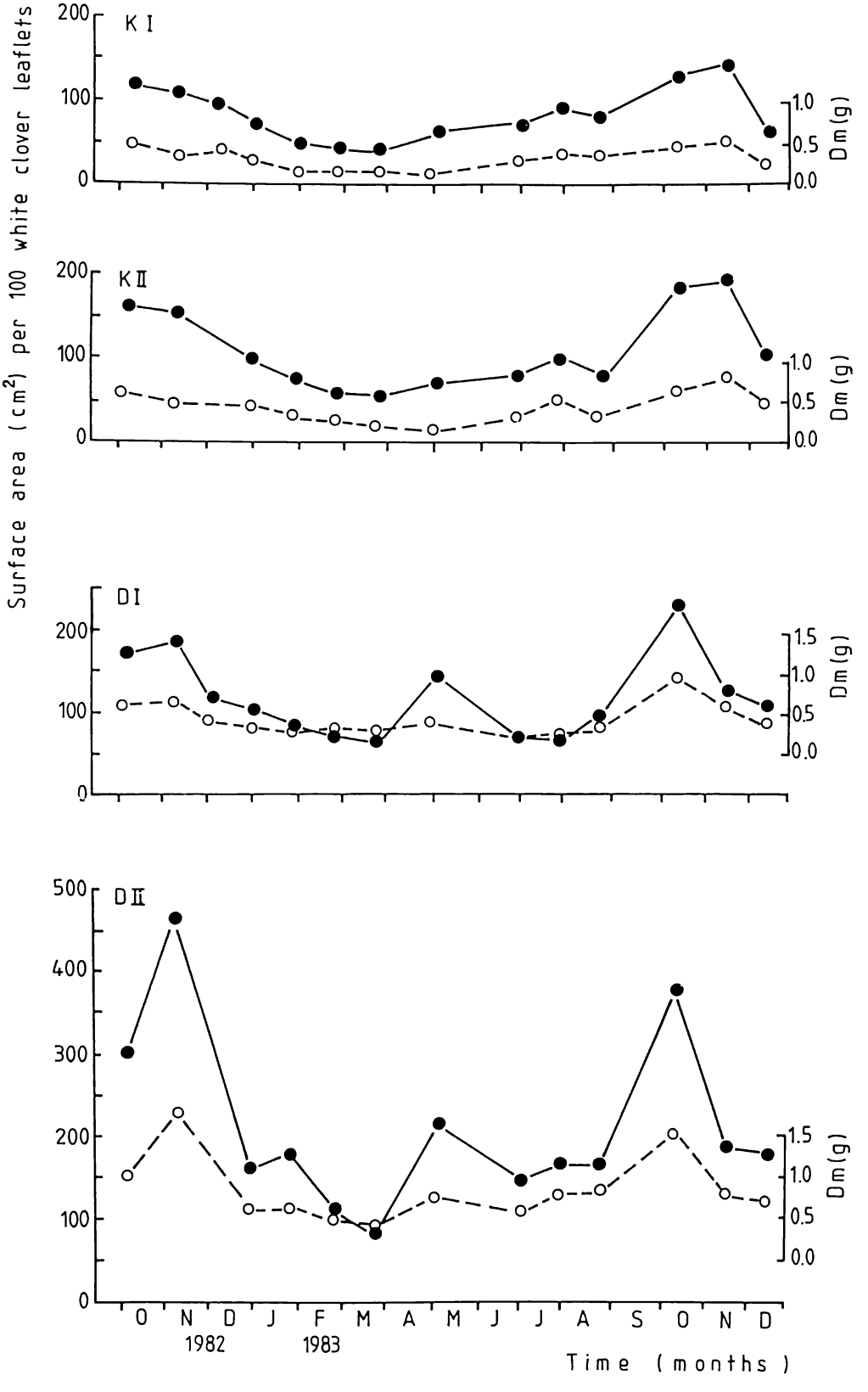


Fig 8.5 Surface area and dry matter weight of white clover leaflets on all locations (o----o = dry matter weight)

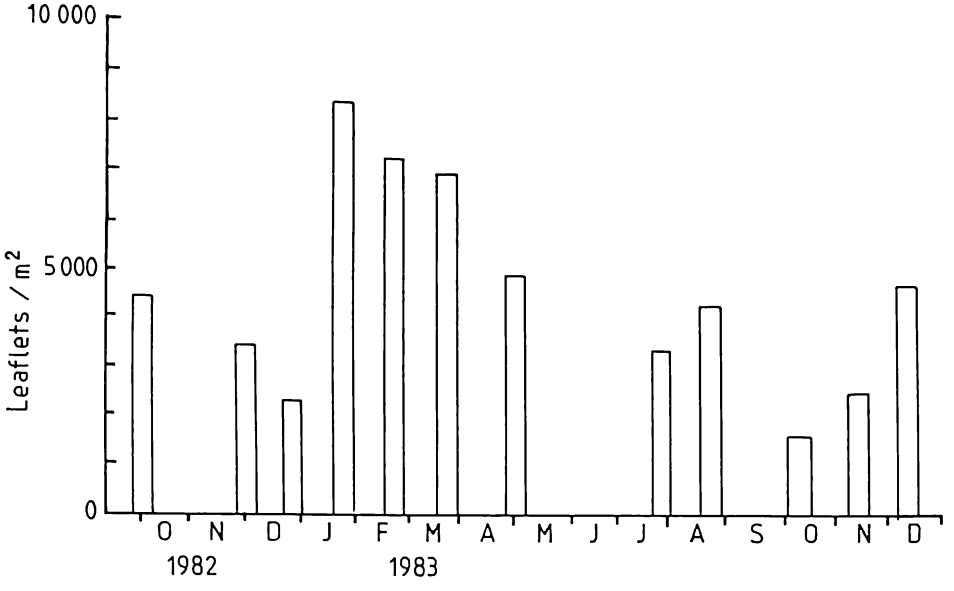


Fig 8.6 Number of white clover leaflets per m^2 in DI (Huntly).

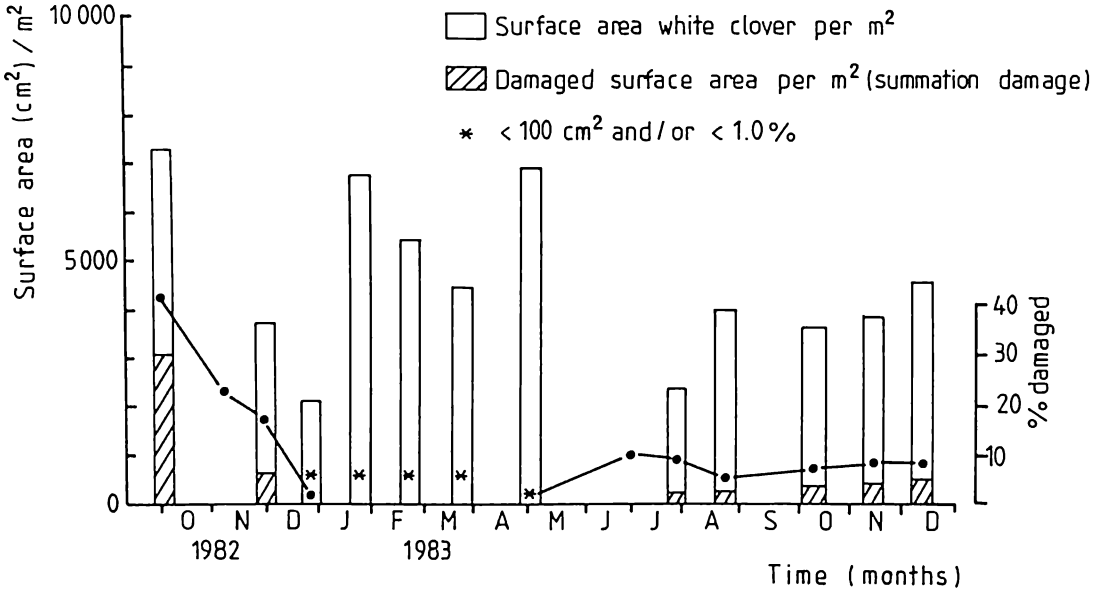


Fig 8.7 Damaged surface area (summation of damage) compared to total surface area per m^2 of white clover leaflets in DI (Huntly).

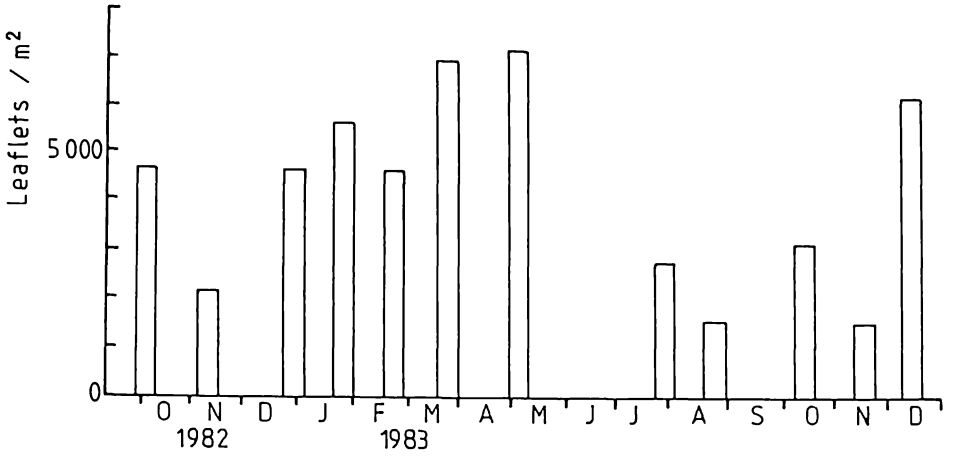


Fig 8.8 Number of white clover leaflets per m^2 in DII (Huntly).

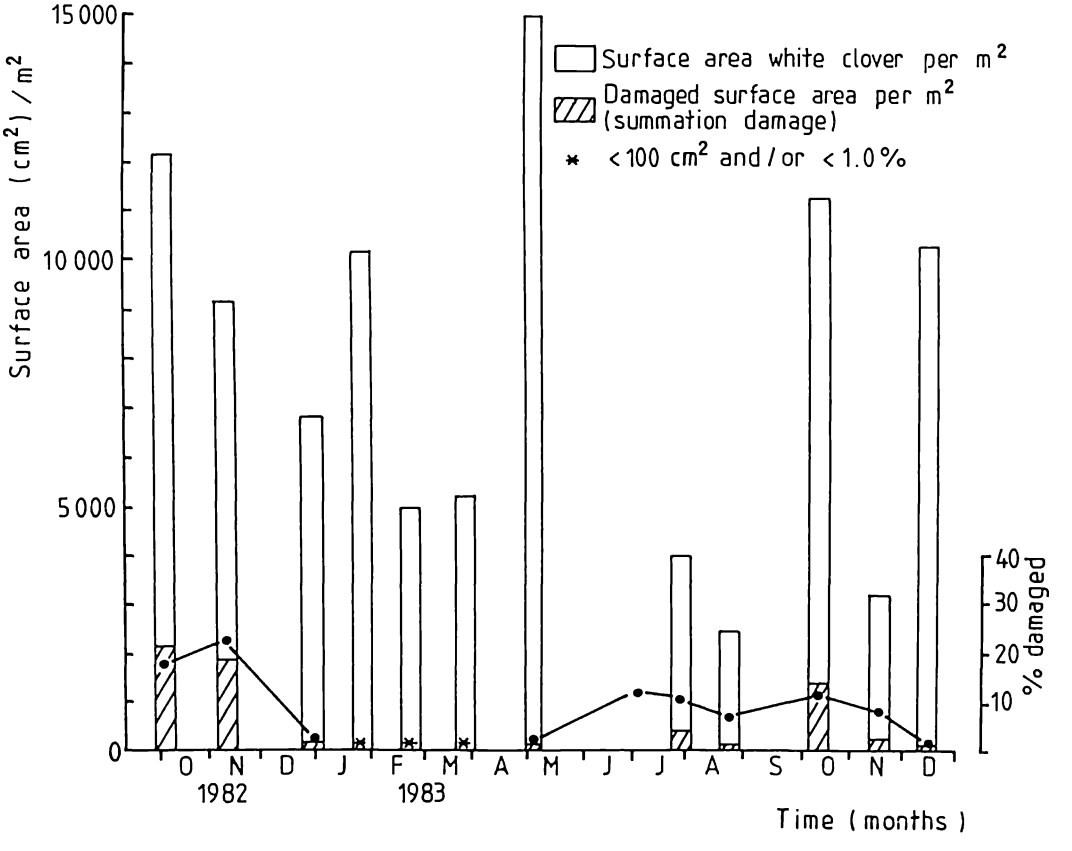


Fig 8.9 Damaged surface area (summation of damage) compared to total surface area per m^2 of white clover leaflets in DII (Huntly).

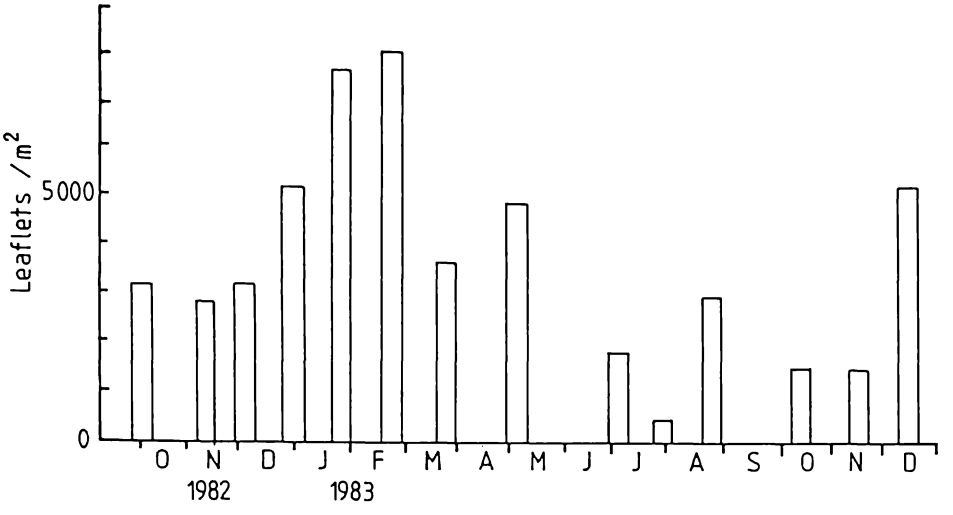


Fig 8.10 Number of white clover leaflets per m^2 in KI (Te Kauwhata).

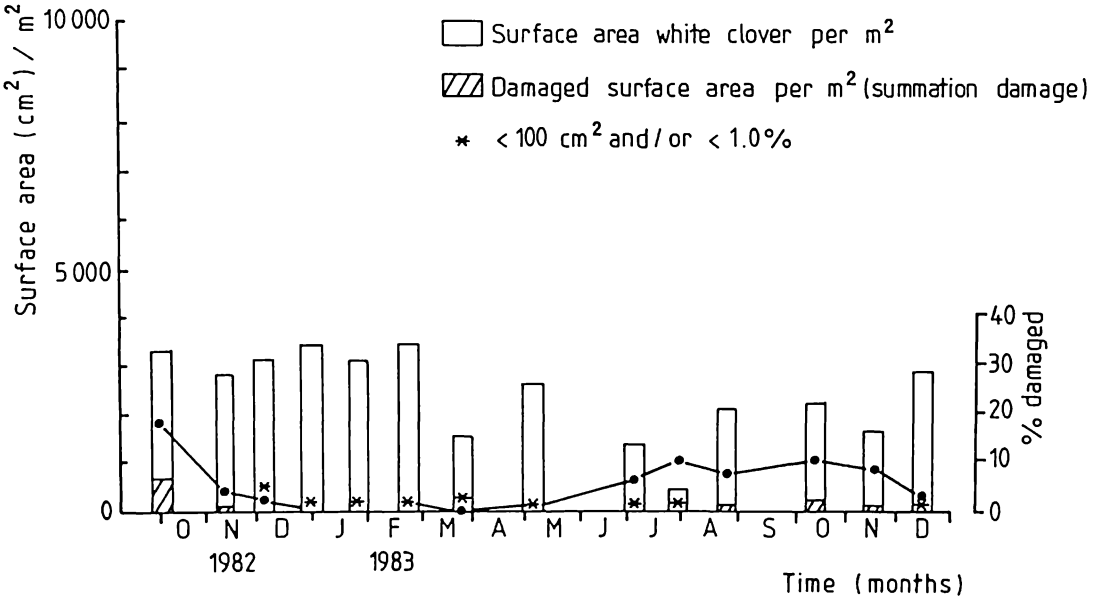


Fig 8.11 Damaged surface area (summation of damage) compared to total surface area per m^2 of white clover leaflets in KI (Te Kauwhata).

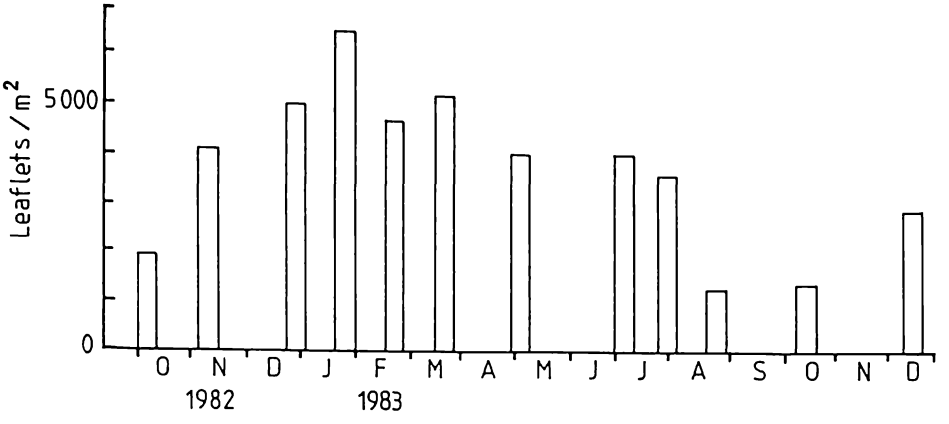


Fig 8.12 Number of white clover leaflets per m^2 in KII (Te Kauwhata).

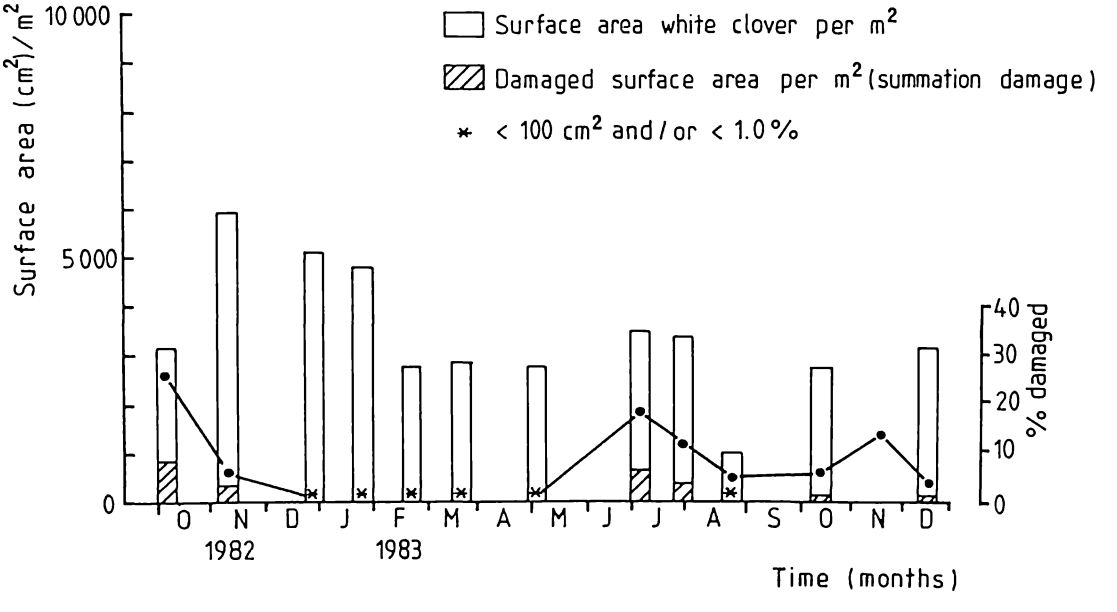


Fig 8.13 Damaged surface area (summation of damage) compared to total surface area per m^2 of white clover leaflets in KII (Te Kauwhata).

data give an insight into the actual level of LSA of white clover per m^2 (Figs 8.7, 8.9, 8.11 and 8.13). At all locations an increase in numbers of leaflets per m^2 (Figs 8.6, 8.8, 8.10 and 8.12) coincided with a decrease of LSA per 100 leaflets. The translation of these figures, however, into LSA per m^2 still shows fluctuations during the year. Figs 8.7, 8.9, 8.11 and 8.13 will be further discussed in Paragraph 8.3.2.

8.3 Assessment of damage on white and red clover plants

8.3.1 Visual observations on damage in the field

An estimate was made by eye of the average damage and the extremes while walking through the paddock on each sampling day. Eyeball assessment is a subjective method and comparison with the standard method of assessment of damage in the laboratory (Paragraph 8.3.2) indicated over-estimation of the damage in the field by a factor 1.5 to 2.0. The technique is also influenced by the climatic conditions on the the day of sampling, sward length and density, and the influence of the season on the vegetation. A paddock with less than 100 % ground cover intensified the feeling of damage whilst a paddock with a good ground cover and good vegetation growth reduced the level of apparent damage. Therefore only a general trend in the development of the damage during the seasons will be discussed. In general, low levels of damage (up to 10 % of the leaf surface area damaged) occurred at the end of April or the beginning of May. By the middle of June leaves with up to 30 % leaf area removed occurred and from July onwards average damage levels equal to 50 % of the leaf area lost were found. The average level of damage stayed at this level but

variability increased and more serious damage occurred as extremes. Most severe damage (more than 80 % of the leaf damaged) occurred during October and at the beginning of November. Damage levels decreased slowly from December onwards and damage was usually absent during the hot summer months (January-March).

8.3.2 Quantitative assessment of damage on field samples in the laboratory

The results of damage assessment on white clover are presented as percentage frequency and cumulative percentage frequency of the different damage levels. Since the figures (Figs 8.14, 8.15, 8.17 and 8.18) speak for themselves, only the general trend will be discussed. The first visible sign of damage normally occurs during May. From then on the damage builds up steadily and peaks in October or November. Both paddocks in Huntly and Te Kauwhata show the same trend. Differences can be found in the levels of damage, however, shown in the cumulative percentage frequency figures. Taking paddock DI, 7 October 1982 (Fig 8.14), as an example, 76 % of the leaflets assessed showed more than 20 % of their LSA damaged and 15 % of the examined leaflets showed 80 % or more damage.

Although research has been done at Waikato University to establish the influence of LF damage on the acetylene-reduction, as a measurement of nitrogenase activity, it is yet too early to draw any conclusions about the correlation between LSA loss and loss in nitrogen fixation (D. Owens, pers. comm.). Damage levels, however, can be expressed in another way. A summation can be made of the products of percentage frequency and damage (e.g. 50 % of scale 1, 15

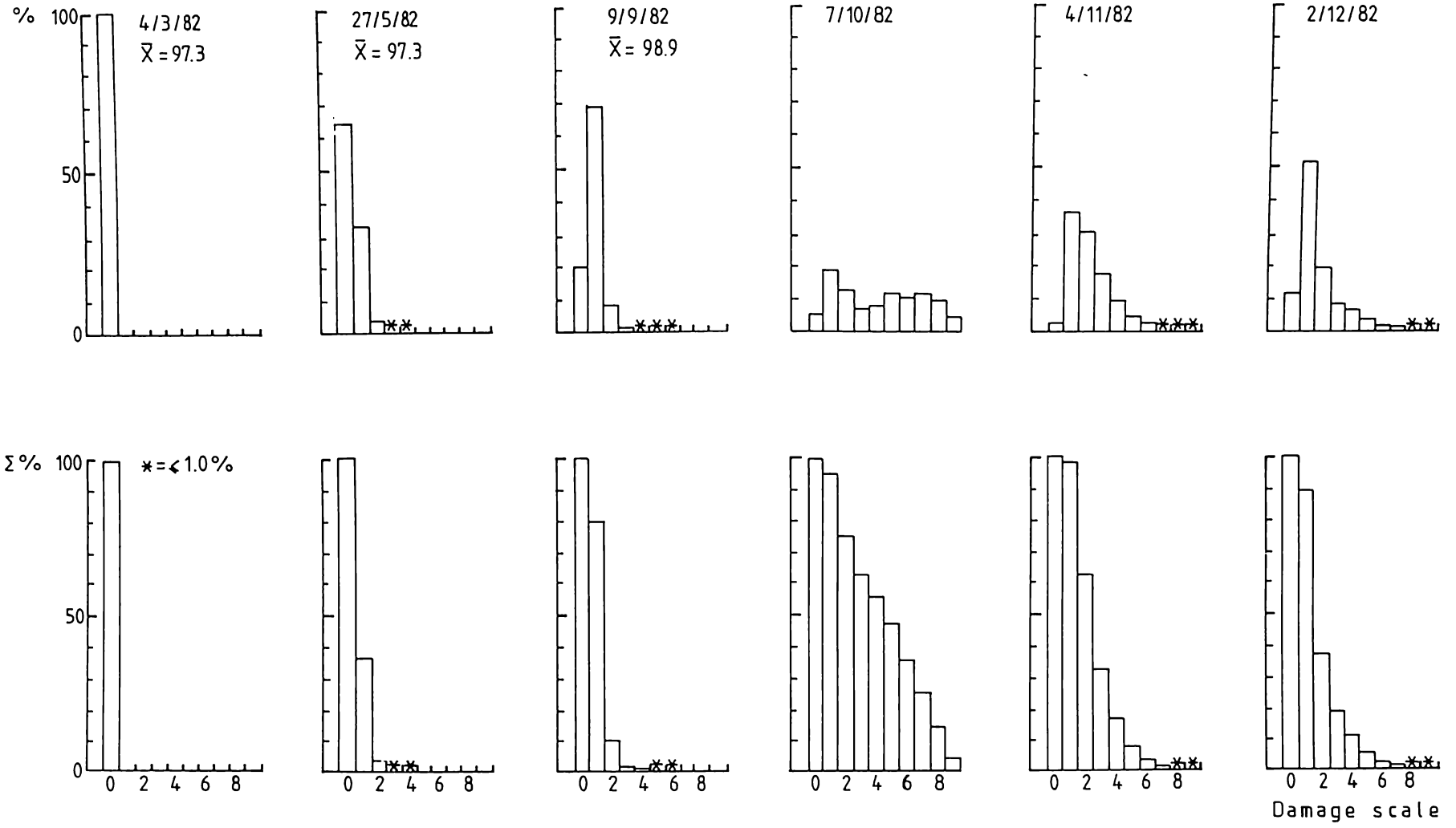


Fig 8.14 Frequency (top) and cumulative frequency (bottom) distribution of the damage on white clover leaflets on a scale of 0 to 9 (90 % damage) in DI (Huntly).

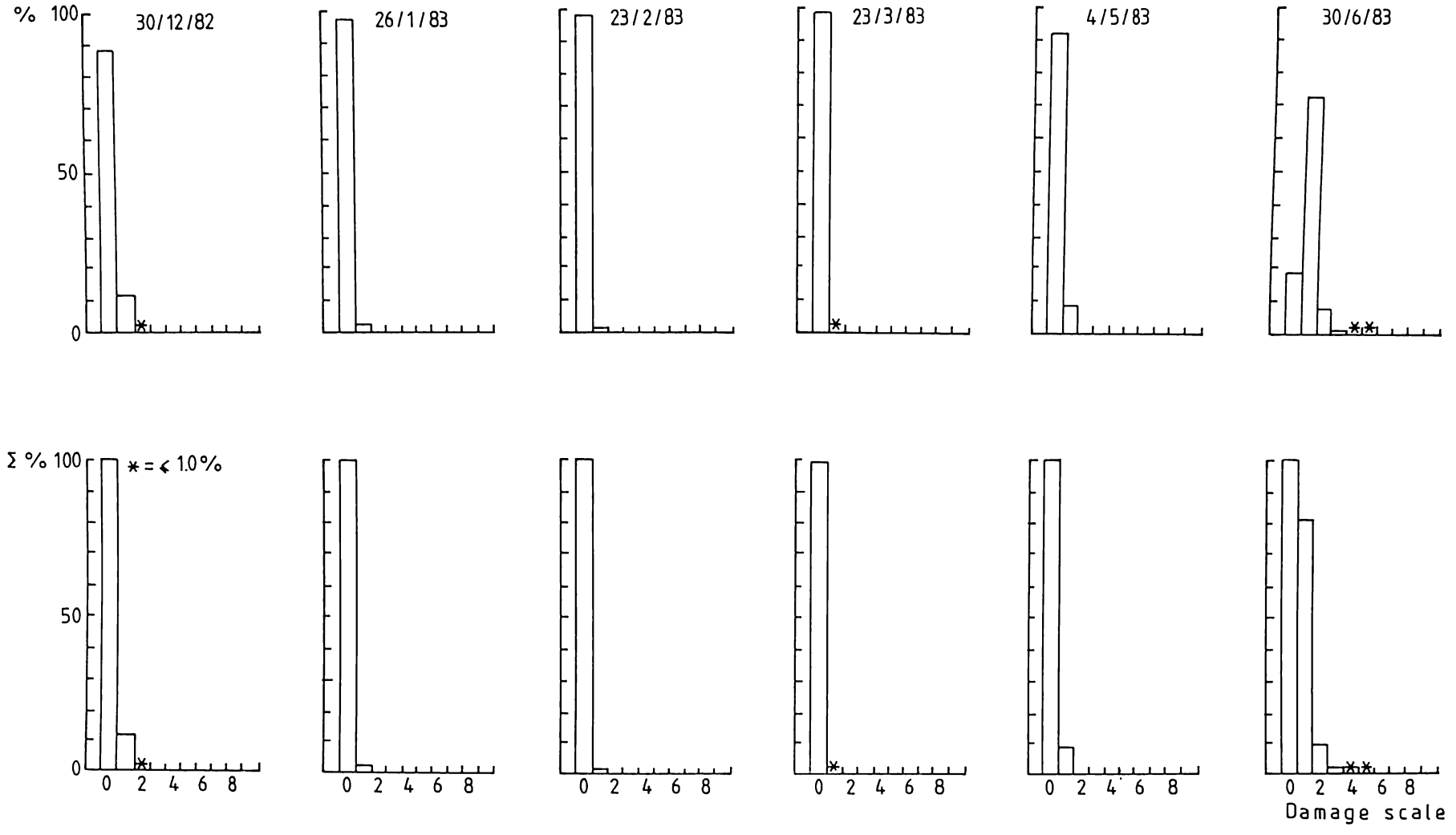


Fig 8.14 Continued.

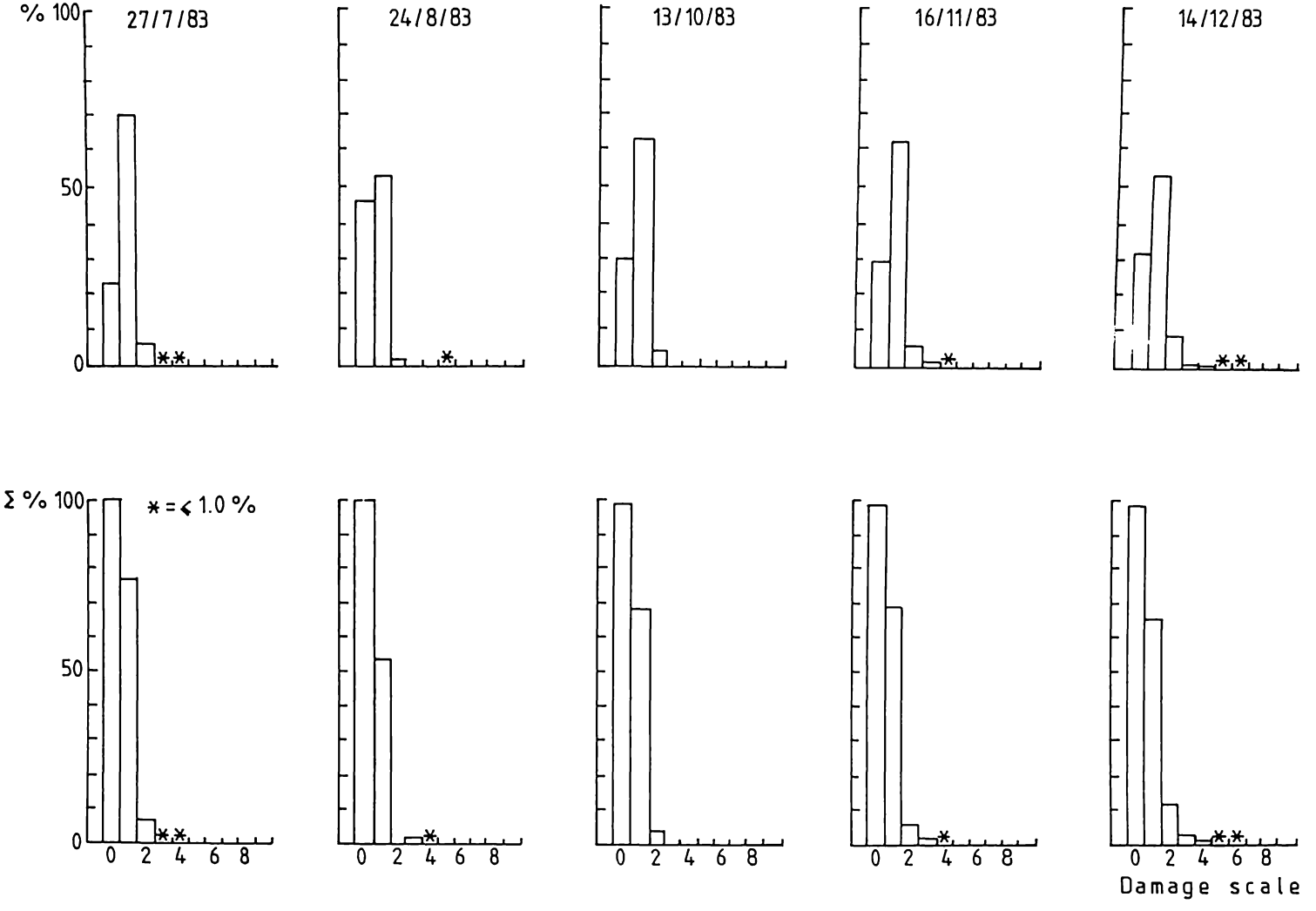


Fig 8.14 Continued.

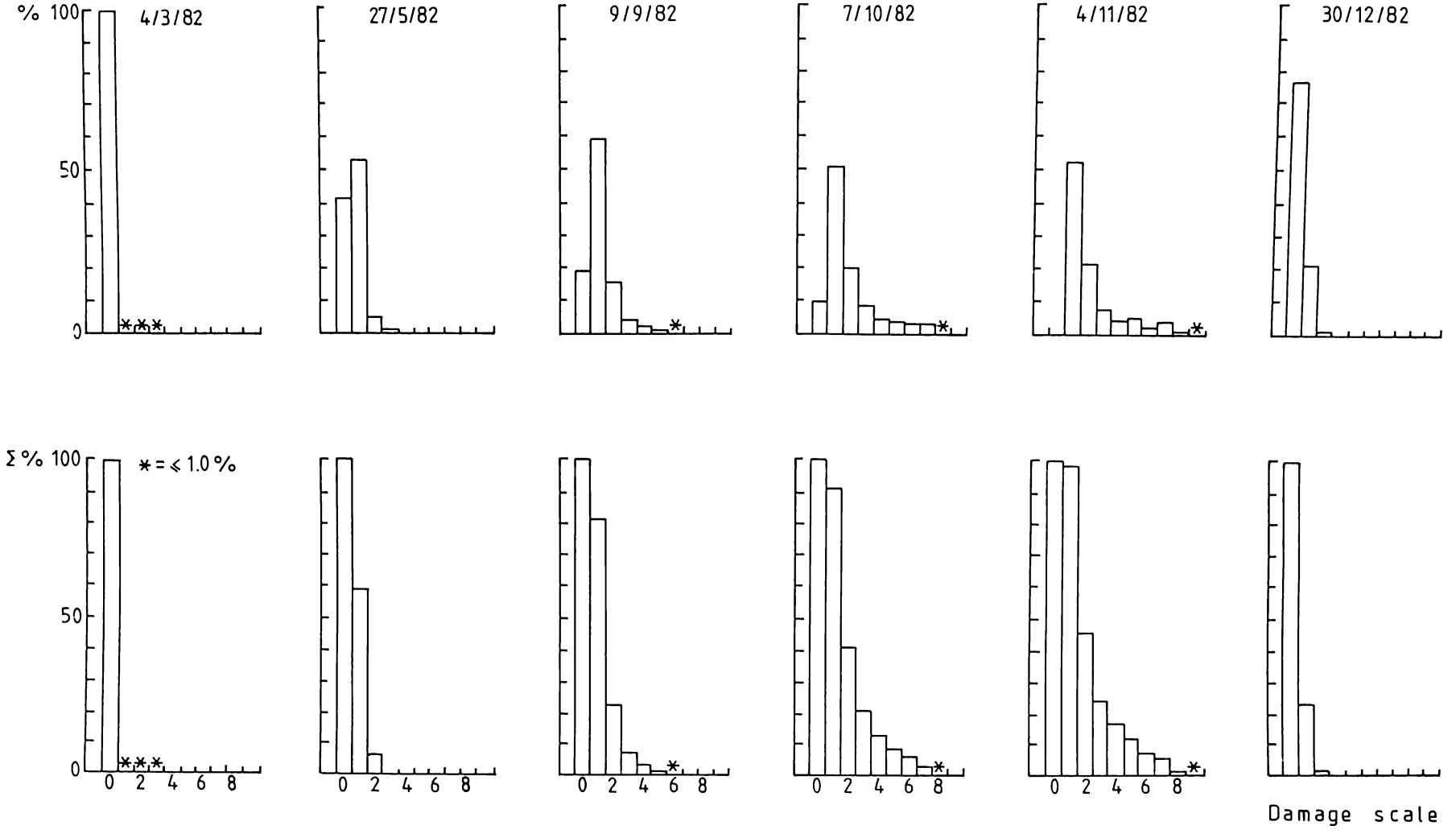


Fig 8.15 Frequency (top) and cumulative frequency (bottom) distribution of the damage on white clover leaflets on a scale of 0 to 9 (90 % damage) in DII (Huntly).

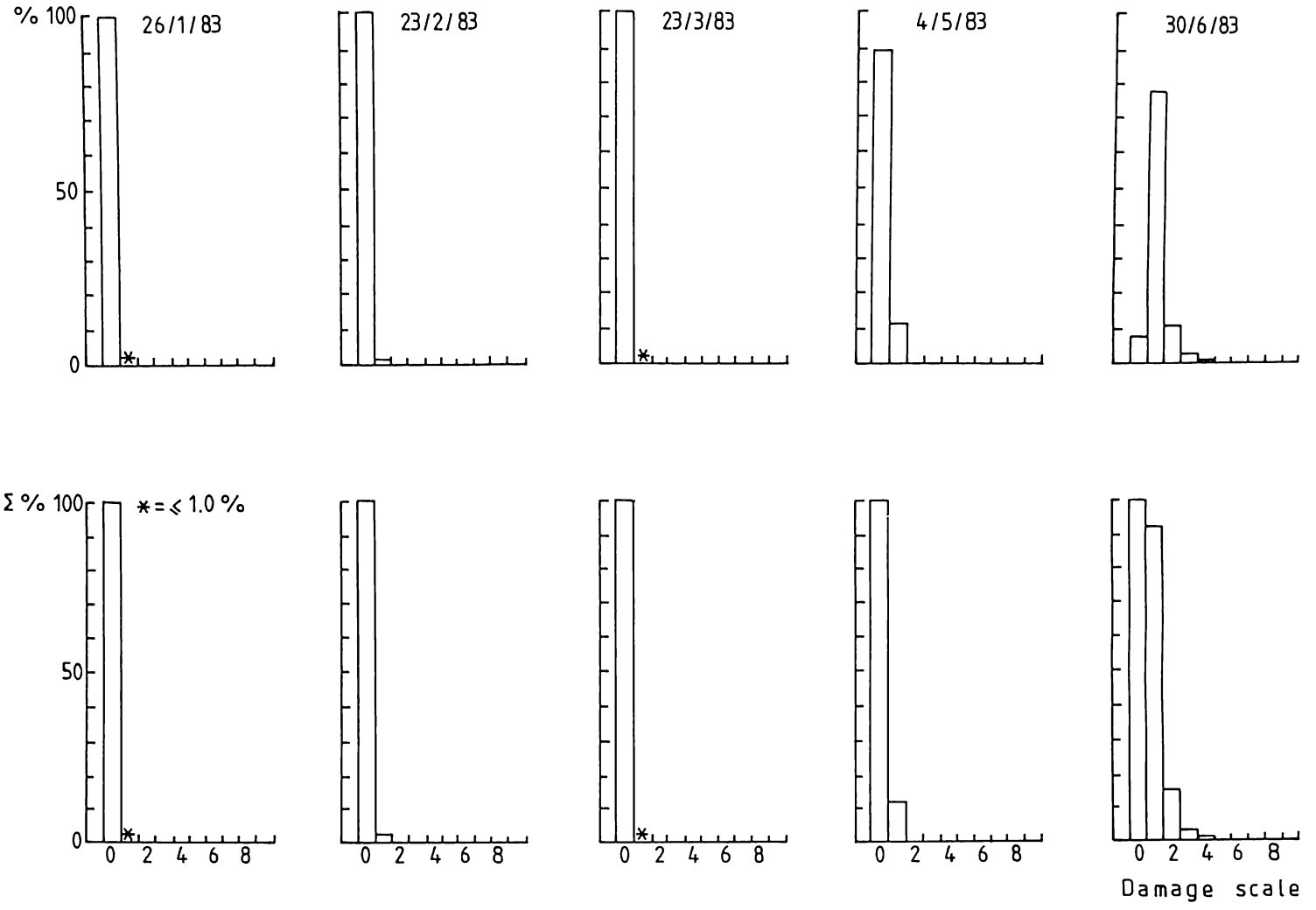


Fig 8.15 Continued.

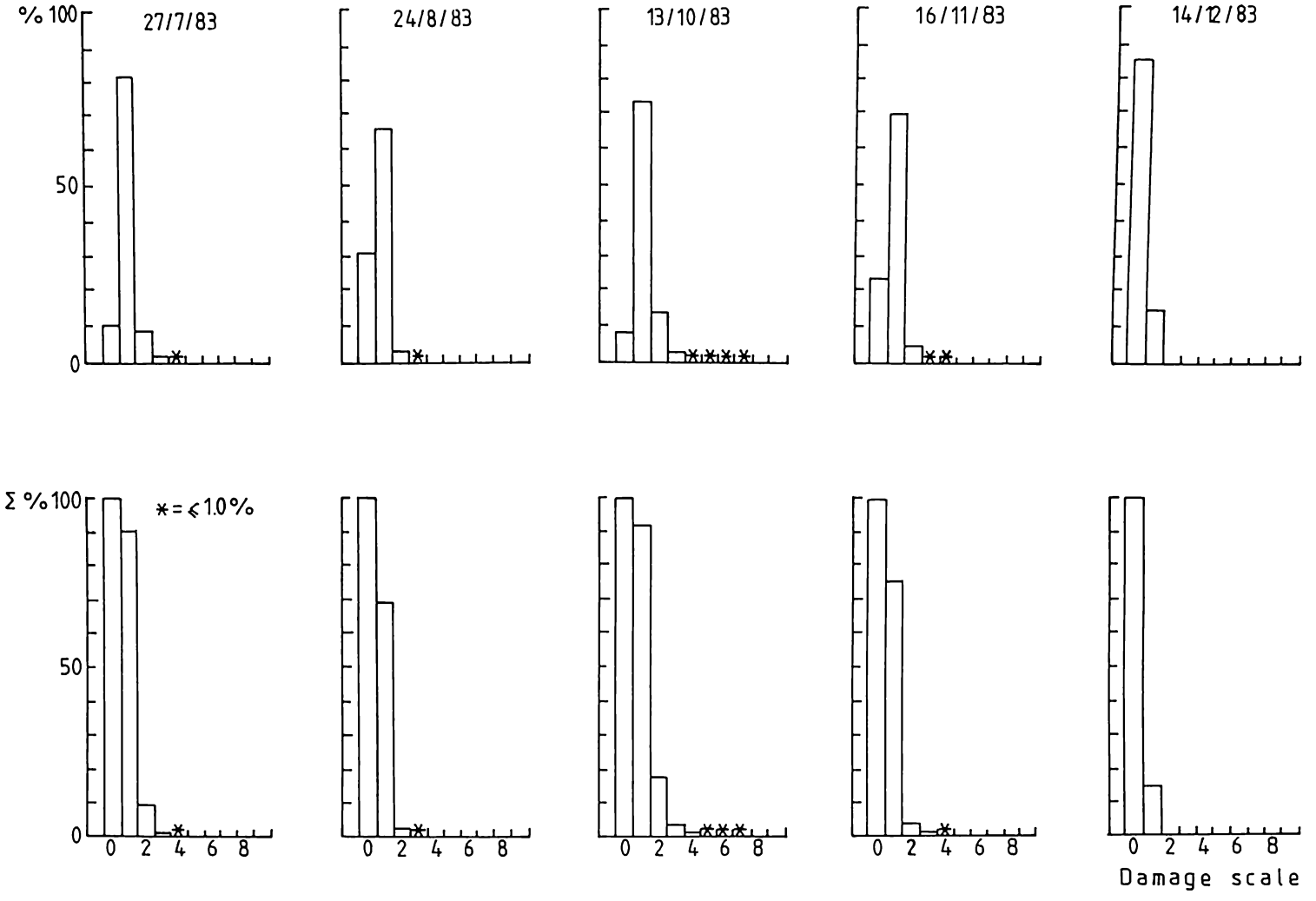


Fig 8.15 Continued.

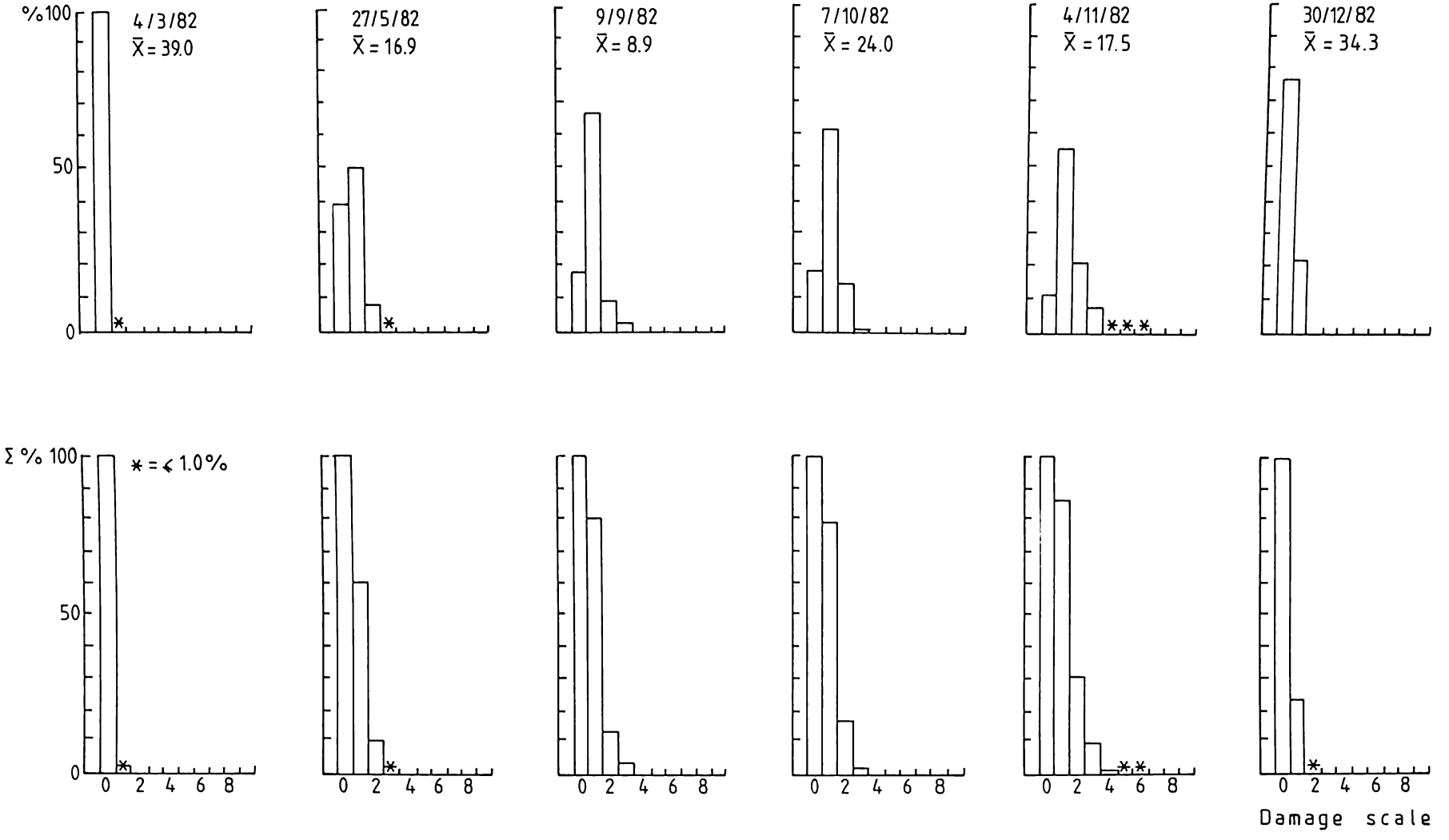


Fig 8.16 Frequency (top) and cumulative frequency (bottom) distribution of the damage on red clover leaflets on a scale of 0 to 9 (90 % damage) in DII (Huntly).

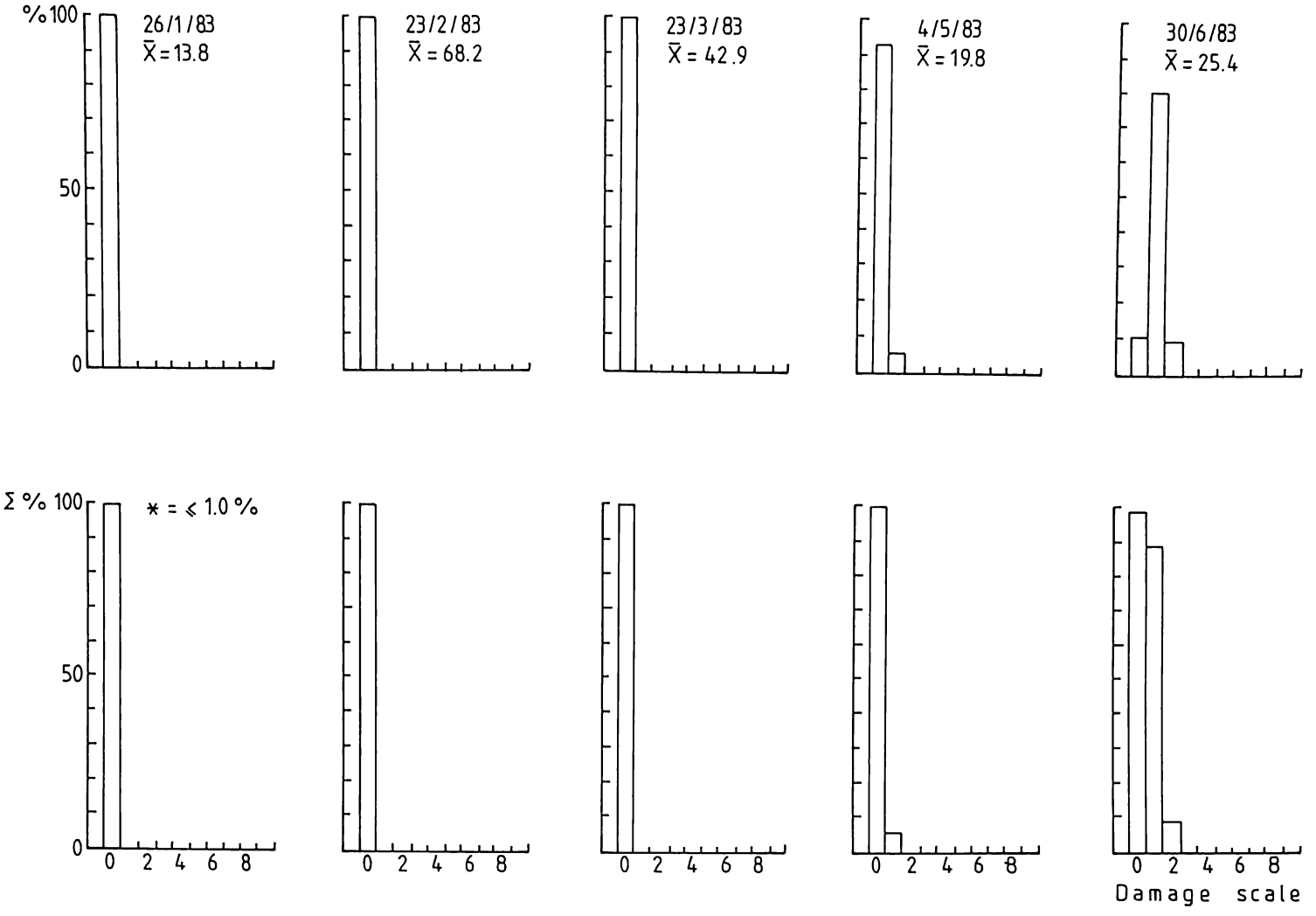


Fig 8.16 Continued.

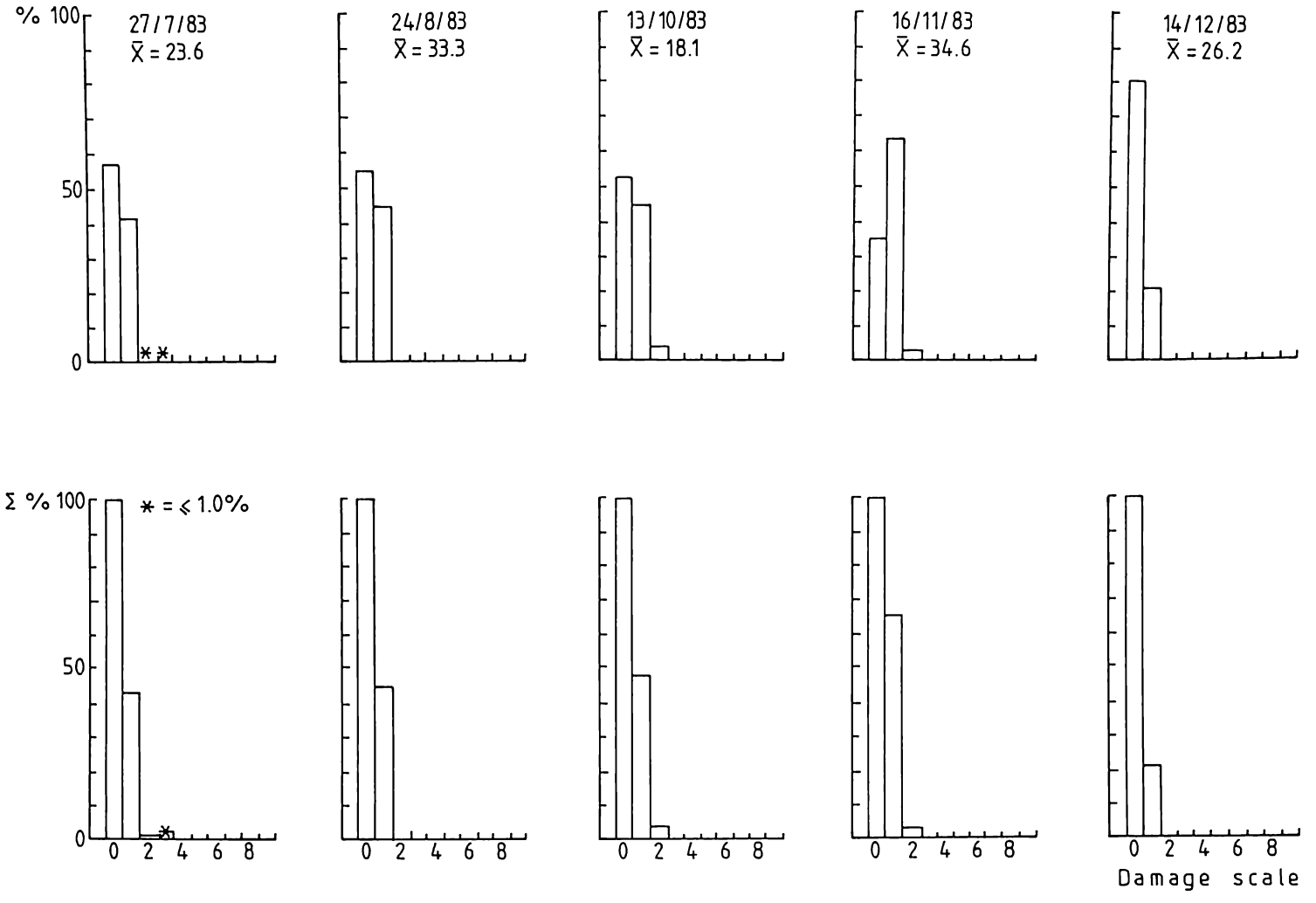


Fig 8.16 Continued.

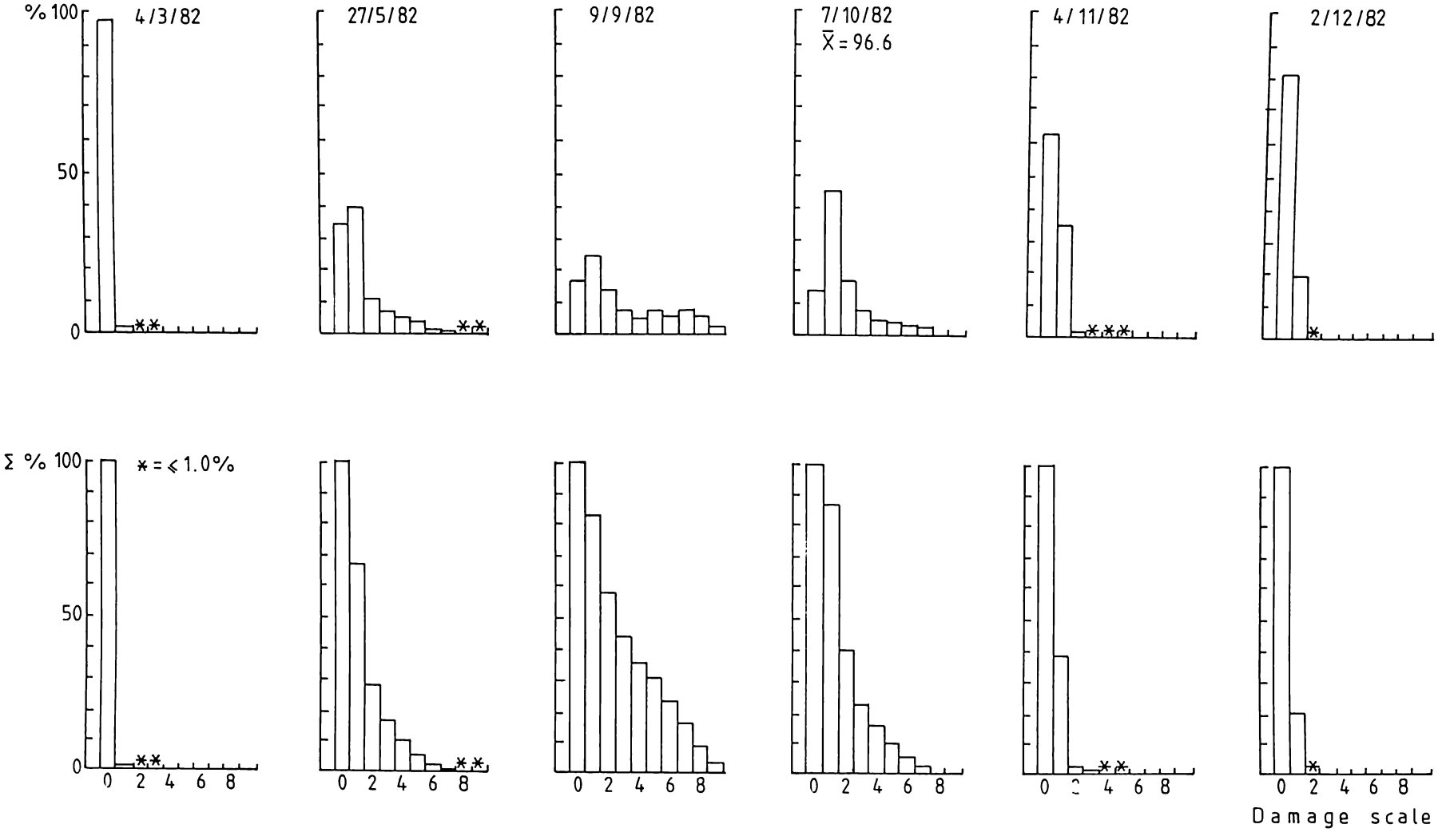
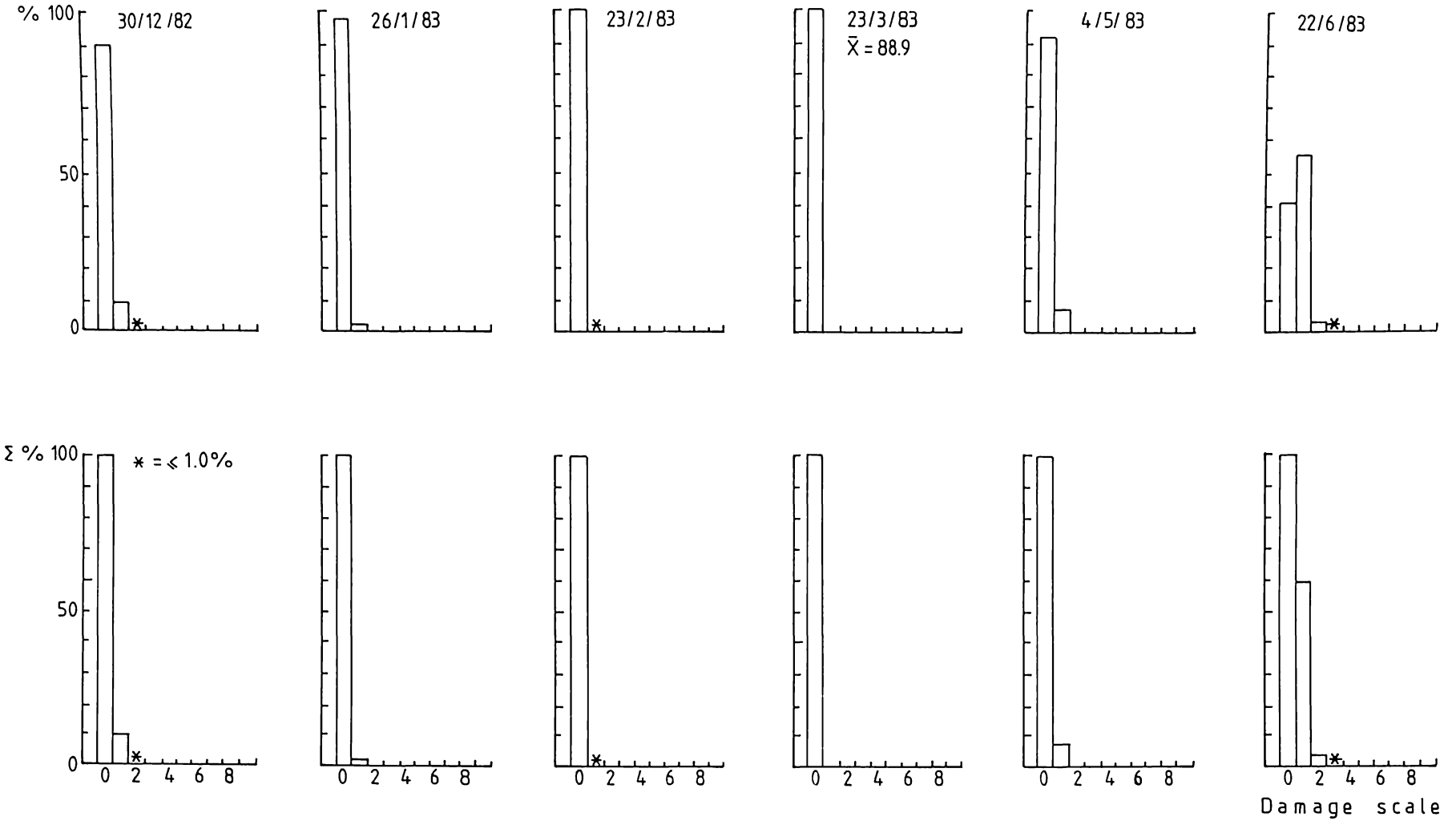


Fig 8.17 Frequency (top) and cumulative frequency (bottom) distribution of the damage on white clover leaflets on a scale of 0 to 9 (90 % damage) in KI (Te Kauwhata).



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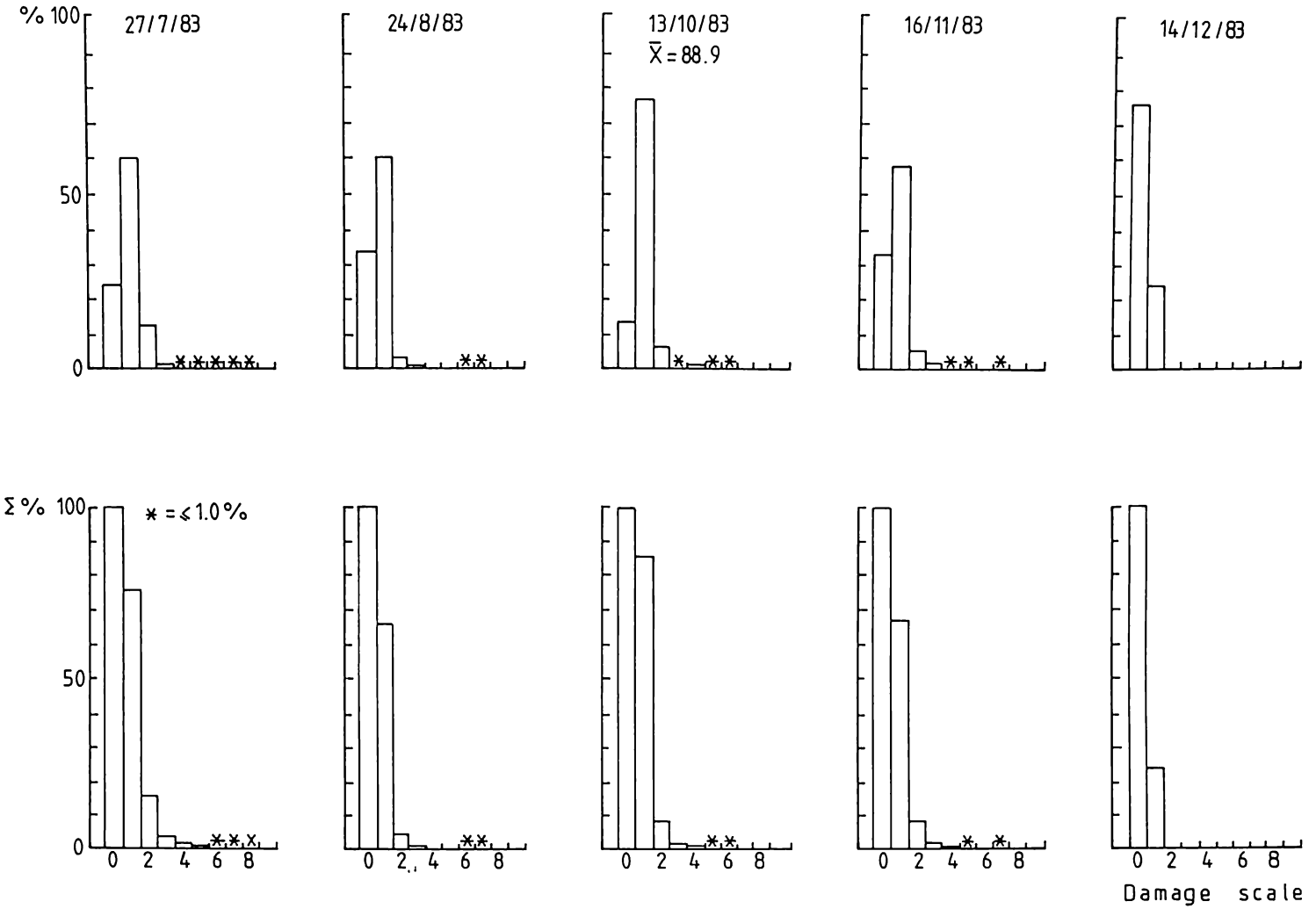

Fig 8.17 Continued.

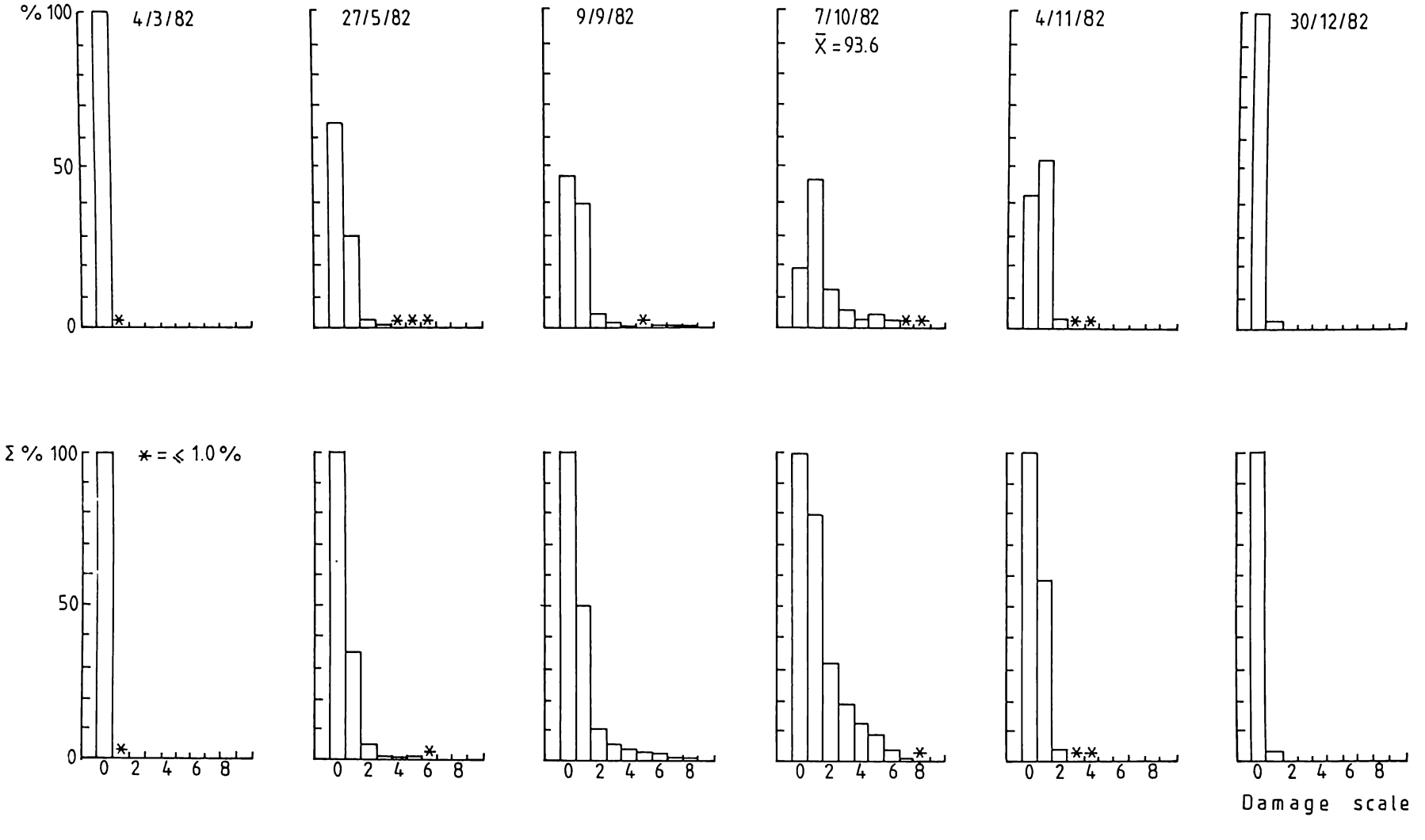

Fig 8.18 Frequency (top) and cumulative frequency (bottom) distribution of the damage on white clover leaflets on a scale of 0 to 9 (90 % damage) in KII (Te Kauwhata).

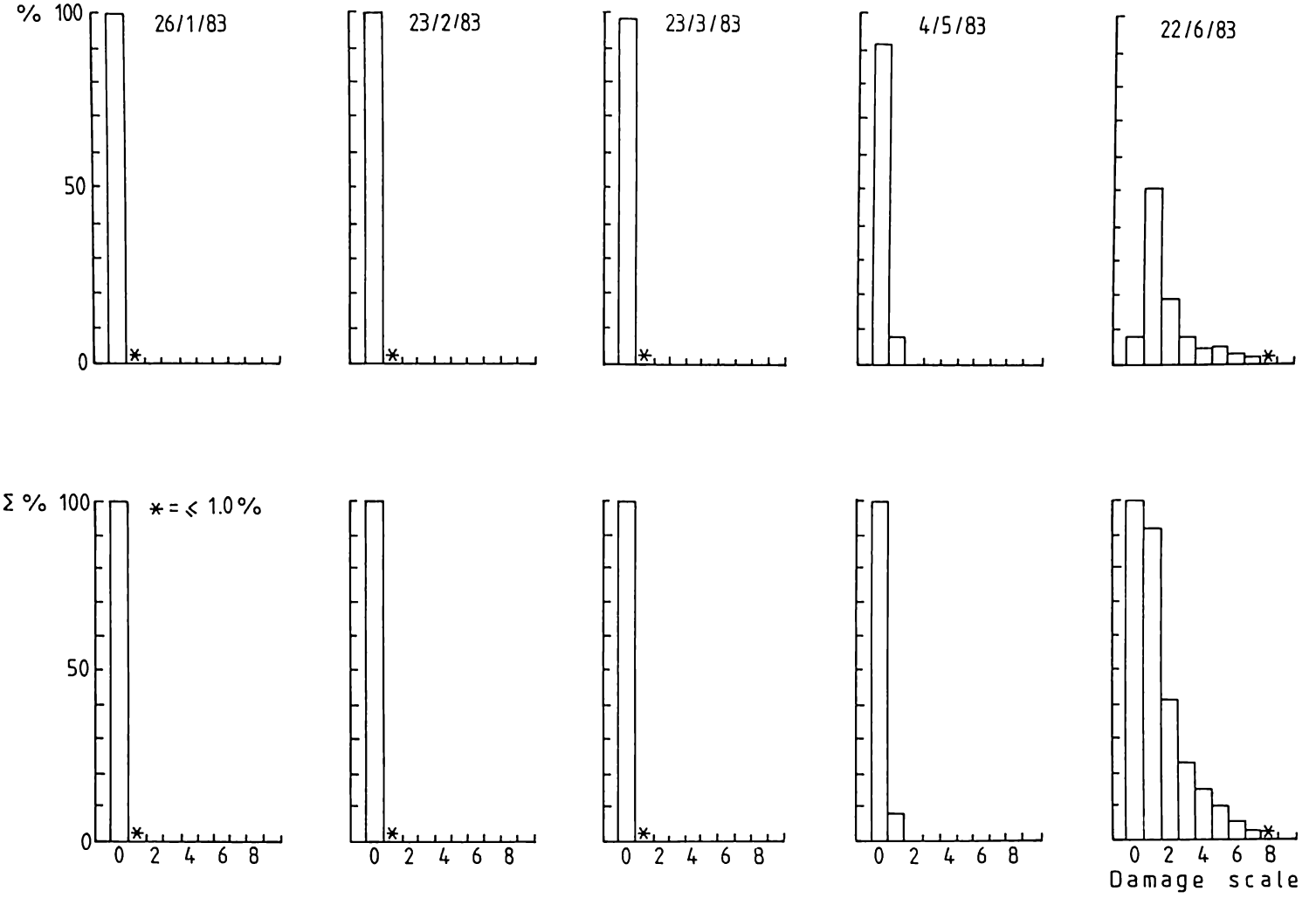

Fig 8.18 Continued.

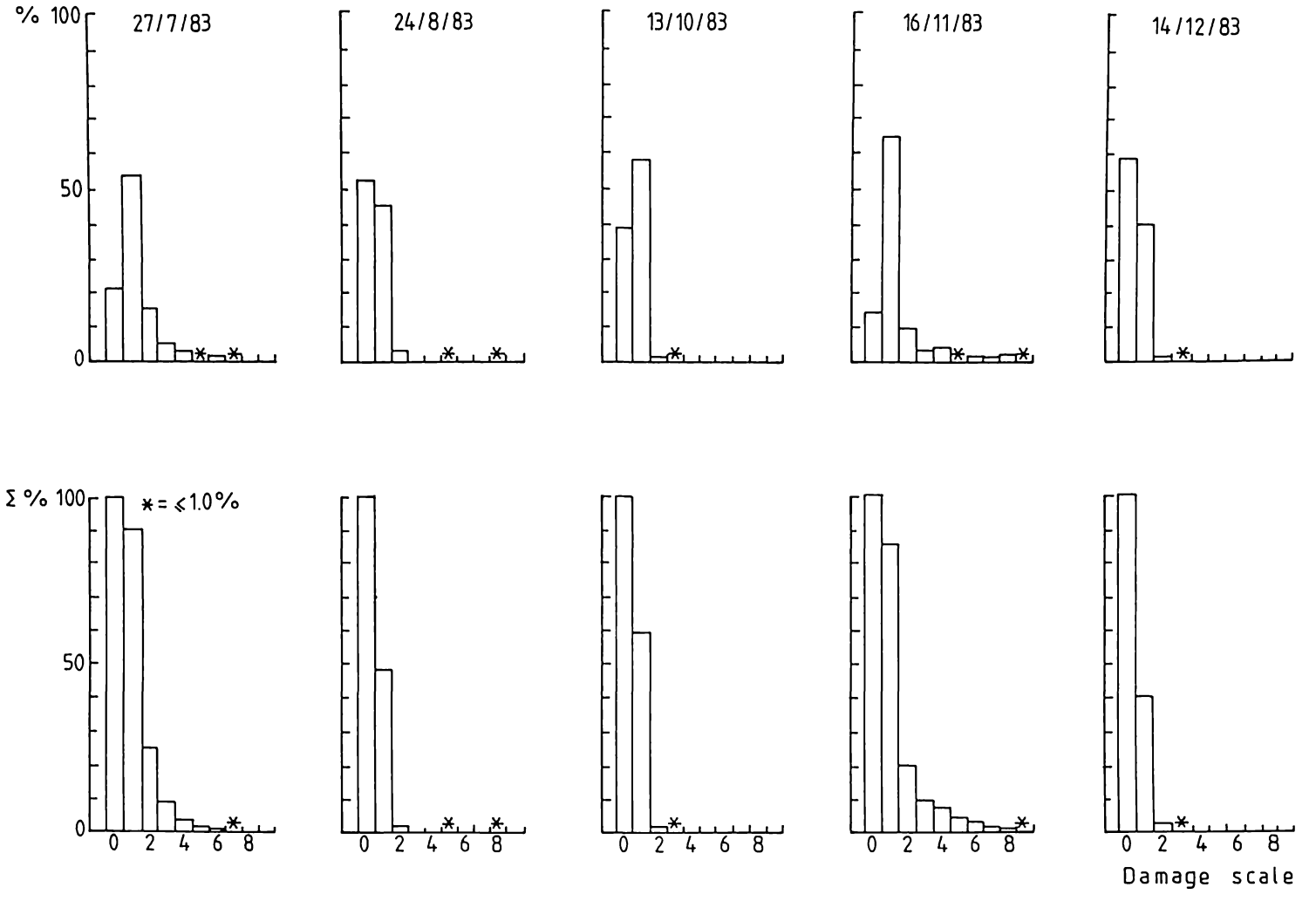

Fig 8.18 Continued.

% of scale 2 and 5 % of scale 3 damage adds up to an equivalent of 9.5 % of the leaflets or LSA lost). The results are given in Figs 8.7, 8.9, 8.11 and 8.13. In Huntly the damage in DI and DII was almost equal, except for the damage in October 1982. DI showed much more damage than DII in October, probably because the paddock was set aside for hay production and not grazed. The same difference, but at a lower level, was found in 1983 when DII was shut up for hay. In both paddocks the damage during the spring in 1982 was more severe than in 1983. In Te Kauwhata the damage in KI was, except for a slight difference in August and October 1983, constantly below that of KII, regardless of the effect of shutting up for hay. As in Huntly, damage during 1982 was more severe than the damage in 1983.

The results of the damage assessment on red clover in DII are presented in Fig 8.16. As with white clover the damage starts to occur during May and builds up to a peak in October and November. The level of damage, however, is much lower on red clover. The highest level of damage found on red clover in 1982 was 60 % of the LSA damaged, but only less than 1 % showed this level of damage. Not more than 1 % of the leaflets assessed showed more than 40 % of their LSA damaged in 1982, and this was even less in 1983. Transferring the results into percentage loss in equivalent leaflets a maximum of 13 % loss occurred in October 1982. The much higher level of damage on white clover compared to red clover may be attributed to the hairy character of the latter.

CHAPTER 9. Histology of damaged white clover leaflets

CONTENTS

CHAPTER 9. Histology of damaged white clover leaflets

9.1 Introduction

The manner of feeding by the LF and the resulting damage to the plants, as well as the fouling of pasture plants with their faeces, has been described in the literature by several authors (*See* Chapter 2). None of these authors, however, examined the damaged leaves and LF droppings at a microscopic level. In the two previous chapters the influence of temperature and photoperiod on the feeding rate of the LF has been studied, and the resulting damage caused by the LF to white and red clover plants in the field assessed. In this chapter a closer examination will be made of a/ the damage done by the LF to white clover leaflets, and b/ LF droppings.

9.2 Histology of white clover leaflets and LF droppings

9.2.1 Methods

Damaged and undamaged white clover leaflets were collected from the field. LF droppings were brushed off into water and mounted on slides. The leaflets were fixed in formalin-aceto-alcohol (F.A.A) and prepared by the parafin-wax method. Sections were cut with a Leitz microtome at a thickness of 15 µm and stained with safranin and fast-green (Johansen, 1940).

9.2.2 Results and discussion

Plate 9a shows a transverse section of a damaged leaflet. Comparing it with an un-damaged leaflet (Plate 9b) it is obvious that all the plant tissue between the veins had been eaten away and that only the lower epidermis was left intact. A close-up of plate 9a (Plate 9c) shows clearly that all the tissue around the vascular bundle was eaten away, but that the latter was not damaged at all. Plates 9d (an overview) and 9e (a close-up of part of a leaflet, cut parallel to the lamina surface), show that all the tissue between the veins had been eaten away but the epidermal layer was kept intact. Plate 9f shows LF faeces, in which cell structures can be easily recognised. Most obviously the cell tissue on the outside seems to be empty while cells on the inside are still intact and containing cell material.

Plates 9a-9e confirm information already presented by other authors in the literature with reference to the damage caused by LF to plants. Microscopic observations of the LF faeces, however, show that the LF possibly only consumes the contents of the cells on the outside that are ruptured during feeding. One of the reasons may be the absence of enzymes for digestion of cell walls, which may well explain the poor utilisation of the available food source and the necessity to consume more than is used. This high rate of consumption becomes apparent when the food consumption is compared with the average body weight of the LF. The results presented in Chapter 7 indicate that a maximum rate of feeding of 7.5 mm^2 per female per day and 2.6 per male per day respectively were achieved at 15 ^{o}C and a photophase of 16 hrs

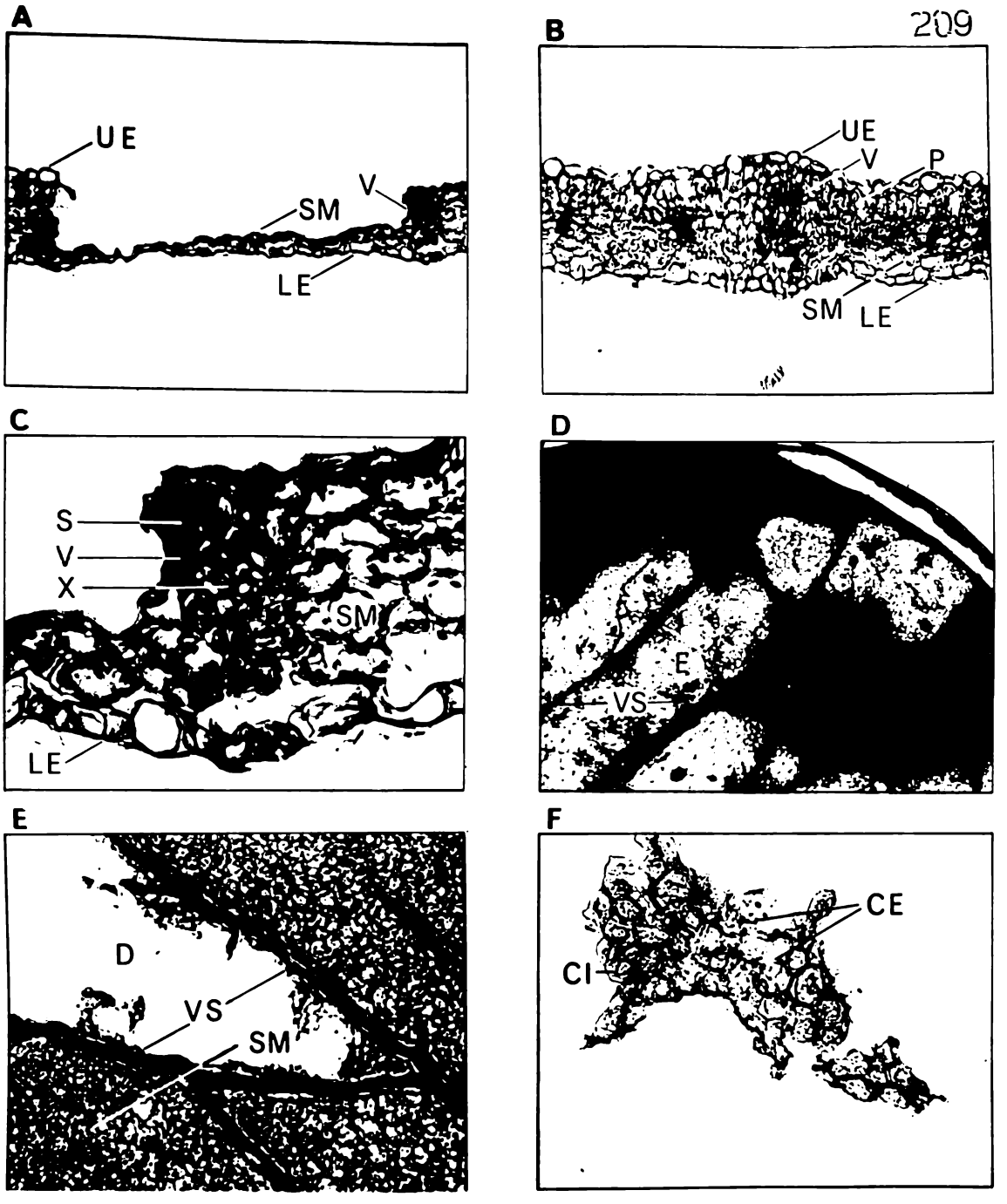

Plate 9.1 Damage done by the lucerne flea to white clover leaflets. A: Transverse section of a leaflet. Plant tissue eaten away between vascular bundles and only lower epidermis plus a few layers of spongy mesophyll left intact. B: Transverse section of an undamaged leaflet. C: Close-up of plate 9a showing that the harder plant tissue (vascular bundle, sclerenchyma and xylem) has been left untouched. D: Overview of part of a leaflet. Damage occurred between the vascular strands and only epidermis left untouched. E: Close-up of part of a leaflet, cut parallel to lamina surface. F: Lucerne flea faeces with intact plant cells containing cell contents, and empty cells.

CE = cells empty; CI = cells intact; D = area damaged by lucerne flea; E = damaged area with only epidermis left intact; LE = lower epidermis; P = palisade layer; S = sclerenchyma; SM = spongy mesophyll; UE = upper epidermis; V = vascular bundle; VS = vascular strand; X = xylem.

light. From the results presented (Appendices 8.5-8.8) an approximate dry matter weight per mm^2 white clover leaflet can be calculated by division of the dry matter weight per 100 leaflets by the surface area per 100 leaflets. This gave a value (mean ± standard error of the mean) of 39 ± 0.78 µg per mm^2 white clover leaflet. A comparison of this with the average weight (Appendix 4.1) of e.g. males (M: 339.1 µg), and second adult female instars (F_2: 665.3 µg) shows that the males eat an equivalent of 30 % of their own body weight per day, and the females 44 %. Since the feeding experiments in Chapter 7 were done with females, covering the three adult instars, the percentage given for the females (F_2) does not reflect an absolute result, but has to be seen as an indication. It presents, nevertheless, a high consumption rate which suggests, in combination with the results from the microscopic observations of LF dropping, a low rate of utilisation of the food source.

CHAPTER 10. General discussion and conclusions

This study was started in March 1981 in response to complaints by farmers in the Huntly-Te Kauwhata area with reference to damage done by the lucerne flea (LF) to their pastures. The purpose of this study was to gain an insight in the biology, seasonal history and population dynamics of LF and provide data to complement a practical programme to control LF, conducted by Ruakura scientists. Apart from a national survey of LF by Dumbleton (1938), no research has been undertaken in New Zealand. This thesis is therefore the first detailed study on the biology and ecology of the LF in New Zealand, and presents the first study of their population dynamics.

LF found during this study were identified as lucerne flea, *Sminthurus viridis* L., equivalent to those found in Europe, Australia and South Africa. The sampling procedures that were developed to collect LF, showed that soil sampling in combination with Tullgren funnel extraction gave good absolute estimates of population density. Comparison of soil sampling with the sweepnet method showed that the latter represented a good relative estimate of population numbers, and a comparison with the pitfall trap method showed that pitfall trap catches could be used as an indication of mobility/activity.

It was found that the LF has three larval, one adult male and three adult female instars in the field. While it is known from the literature that temperature influences the duration of each growth stage, it was found in this study to influence also the number of generations of the LF per year. At both locations the number of degree-days above a lower threshold of 4 ^{o}C was 9 to 12 % higher in 1982 than in 1983, allowing for five generations of LF to develop as opposed

to four in 1983, and causing the presence of more than 41 000 LF per m^2 in October 1982 in one paddock (DI) in Huntly. Apart from Davidson (1934) who mentioned the presence of four generations of LF per year in Australia, more information is not available in the literature to compare these results. Although the average June temperature in the northern half of the North Island of New Zealand resembles that of the south and south-west of Australia, and South Africa, the mean January temperature is lower and the mean precipitation over the summer months higher (Koeppe and De Long, 1958), thus causing LF populations in this study to be present in the field as late as December and to reappear as early as March. It is therefore assumed that LF has an equivalent or higher number of generations per year in the Waikato and South Auckland areas of New Zealand than in Australia and South Africa. A comparison of the life cycle of LF in New Zealand where it aestivates, and Europe where it hibernates shows that LF populations occur in the field in both areas between April and October, an indication of a high level of adaptation.

High population densities in the experimental plots caused a loss in white clover surface area due to LF feeding of between 20 and 40 %. A comparable result, a maximum loss of 20 % in pasture production, was found by Pottinger (1983) in the untreated control in trials conducted on silage crops. One factor that contributed to a high population density and level of damage was the closing of paddocks for hay making or silage. Not only did this extend the presence of the LF population in the field equivalent to the period that the paddock was closed but it also allowed the deposition of diapause eggs for an extended period. This shows that farm management practice can play an important role in the regulation of the LF population and indicates that paddocks where LF are present should not be used for hay making in two consecutive years.

During the study period the LF population had overlapping stages of development as well as generations. The analysis of this type of data is complicated and only a few examples with reference to Collembola exist (*See* Niijima, 1975; Takeda, 1984). In this study a physiological time scale was used to separate the different instar stages and generations, allowing stage-frequency tables to be drawn up and analysed with a method described by Manly (1977b). Using a method equivalent to the k-factor analysis, the number of insects entering each growth stage were compared and the stage most prone to changes in numbers determined. It was found that the LF population was prone to great changes in numbers at the beginning of the immature stage of the life cycle of the males, and the end of the life cycle of the females, but fairly stable at the time that sexual maturity was reached. Thus the survival rate of newly hatched nymphs and ovipositing females was lower than any other growth stage of the LF.

Studies showed that the feeding rate of adult LF was high at a photophase of 12 to 16 hours light and a temperature of 15 to 20 ^{o}C. This indicates a high level of activity in feeding in spring in the field and early summer and agrees with high levels of damage found in October-November. Another factor that may have contributed to the level of damage is the fact that all growth stages of the LF were active during the day and night and that feeding was not restricted to the day time. Microscopic observations of damaged white clover leaves and LF droppings showed that only the contents of the cells that were ruptured during feeding were consumed. This points to a low rate of utilisation of the food source by the LF.

During part of the study period the presence of the predatory mite, *Bdellodes lapidaria*, was established in both paddocks in Huntly. However, the mite was present in such low numbers that no control effect of the mite on LF populations could be established. In 1969 *Bdellodes lapidaria* and *Neomolgus capillatus*, another mite predatory on LF, were released in Western Australia to control the LF population, but it took almost ten years to establish and spread, and regulate the LF population at a significant level (Waterhouse, 1979; Wallace, 1981). Although this may be a good method to control LF in New Zealand in the long term, an alternative will be the use of insecticides. The use of maldison which caused a resurgence of LF populations once frequent spraying of the insecticide had stopped, was the only option until 1983 (Pottinger, 1983). Since then other insecticides have been registered for the control of LF. Experiments done by the author in cooperation with scientists from MAF, Ruakura ARC, Hamilton, showed that insecticides such as fenitrothion, chlorpyrifos and dimethoate exerted 4 to 9 weeks of control after application (Wrenn *et al.*, 1983). Studies into the use of granular insecticides and different application techniques have further improved the control of the LF (Wrenn *et al*, 1984a, b). Attention, however, should be paid to the possible acaricidal effect of some insecticides which may eliminate predatory mites (*See* Wallace, 1954; Pimental and Edwards, 1982).

Since alternative insecticides for the control of the LF are now available in New Zealand, it is up to the farmer to monitor the presence of the LF and time the insecticide application. One problem, however, is to recognise the presence of the LF in the early stages of growth in the field, a problem related to many pests that are small and may be hidden (Clements and Henderson, 1983). An aid to solving this problem is the use of a sweepnet by the farmer to establish the presence of the

LF in the field. It can also be used as a relative measurement of population density since a statistically significant relationship was established in this study between the use of a sweepnet and the soil sampling method. Based on the sweepnet technique, described in this thesis, Pottinger *et al.* (1985) recommend the application of insecticides when catches of 200-500 LF are taken per 6 meter sweep.

An alternative method to control LF may be the use of grazing animals. Recent studies by Pottinger *et al.*, (1985) show that LF populations exposed to heavy grazing pressure in winter, took, on average, four months to recover to pre-grazing levels. The use of grazing animals has been applied and shown to reduce the numbers of insects such as soldier fly (*Inopus rubriceps*) (Dixon and Gerard, 1979; Robertson *et al.*, 1979, 1981), grass grub (*Costelytra zealandica*) (East, 1979) and bluegreen lucerne aphid (*Acyrthosiphon kondoi*) (Penman *et al.*, 1979). Further research will have to be conducted to determine the combination of heavy grazing pressure and the application of insecticides to reduce LF populations to an acceptable level during the year (*See* also Fenemore, 1979; Kain, 1979; Roberts, 1979b; East and Pottinger, 1983).

Other options in reducing the level of damage caused by the LF may be studies on the influence of cyanogenesis in clovers and Lotus spp., and the presence of endophytic fungi in ryegrass on the LF population. Studies have shown that cyanogenesis in white clover and lotus (*See* Corkill, 1940; Melville *et al.*, 1940; Daday, 1954a, 1954b, 1965; Foulds and Grime, 1972a, b) discourages predation by animals such as slugs (Jones, 1962; Dirzo and Harper, 1982a, b) and in bracken predation by locusts (Cooper-Driver and Swain, 1976). Recent studies in New Zealand have shown that the presence of endophytic fungi in tall fescue (*Festuca arundinacea*) and perennial ryegrass (*Lolium perenne*) influenced survival

of larval Argentine stem weevil (*Listronotus bonariensis*) and reduced oviposition on and feeding preference for infected plants by adult Argentine stem weevil (Prestidge *et al.*, 1982; Barker *et al.*, 1983, 1984b; Gaynor *et al.*, 1983, 1984b; Musgrave, 1984). Preliminary observations by the author (not presented in this thesis) indicate that the presence of endophytic fungi in perennial ryegrass may also influence the feeding behaviour of the LF.

This study has provided an insight into some aspects of the biology and seasonal history of the LF. Based on 1/ the development of a sweepnet technique (Chapter 3), 2/ the results of the life history and population dynamics studies (Chapter 4), and 3/ the damage assessment scale (Chapter 8) Ruakura scientists have been able to construct an effective, low cost and simple LF management programme (R.P. Pottinger, pers. comm.; Pottinger *et al.*, 1985).

APPENDICES

CONTENTS

Appendix 3.1 Percentage representation of Orders caught with the soil sampling method on different data on both locations.

Order	Paddock															
	DI Date				DII Date				KI Date				KII Date			
	[&]A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Arhropleona	55.5	29.8		76.8	70.4	79.9	72.6	70.8	13.6	2.5	41.4	45.7	17.0	32.5	64.5	62.1
Acari	22.5	56.5		17.4	9.7	11.7	7.6	12.0	55.7	50.9	32.2	25.1	70.0	63.6	27.6	30.5
Araneae	*	*		0	*	*	0	*	*	*	*	*	*	*	*	*
Coleoptera	*	1.3		*	*	1.1	*	*	*	*	*	*	*	*	1.1	2.4
Diptera	*	*		*	2.7	*	*	1.3	2.7	*	0	2.2	2.7	*	*	1.1
Homoptera[!]	19.0	*		1.9	15.1	*	2.7	1.6	21.6	*	3.1	3.3	6.8	*	2.9	1.0
Heteroptera[!]	0	*		0	0	*	*	0	0	*	*	0	0	*	1.1	0
Hymenoptera	*	*		*	0	*	1.4	*	2.7	1.0	1.2	*	*	*	*	*
L. Holometabola	1.5	1.2		*	1.8	4.5	*	*	2.5	11.1	*	*	2.5	*	*	*
Orthoptera	0	0		0	0	0	0	0	0	0	0	0	0	*	0	0
Thysanoptera	0	*		2.1	0	*	12.5	12.0	0	1.3	19.4	21.6	0	*	*	1.7
Chilopoda[$]	0	8.1		*	0	*	1.2	*	0	31.4	*	*	*	1.1	0	0
Others	*	*		*	0	0	*	*	*	*	0	0	0	0	0	0
Number of individuals	137.2	112.6		97.7	98.8	109.3	57.1	49.8	85.5	127.9	89.1	184.7	96.4	262.9	99.2	110.7

$: Class; !: Suborder; [&]A: 15/10/81; B: 07/01/82; C: 05/04/82; D: 22/07/82; L: larvae; *: less than 1.0 %

Appendix 3.2 Percentage representation of Orders caught with the sweepnet method on different data on both locations.

Order	Paddock DI Date				DII Date				KI Date				KII Date			
	&A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Arhropleona	0	*	2.7	6.0	0	0	2.4	24.3	0	0	0		0	0	1.1	
Acari	0	0	*	0	0	0	0	0	0	0	0		0	0	0	
Araneae	*	0	58.2	1.5	0	0	26.8	1.3	0	1.2	5.7		0	*	19.7	
Coleoptera	*	*	4.4	*	*	0	2.4	0	*	8.4	2.2		1.3	2.2	0	
Diptera	88.2	99.0	13.2	81.4	76.7	98.8	55.0	70.6	72.9	88.7	65.9		92.6	91.2	48.5	
Homoptera!	10.3	0	8.4	10.4	21.6	0	1.2	3.8	25.6	0	9.1		6.1	0	4.6	
Heteroptera!	0	0	6.6	0	0	0	6.0	0	0	*	10.8		0	0	15.6	
Hymenoptera	*	*	6.2	0	*	1.1	6.2	0	1.1	*	2.9		0	5.3	8.1	
L. Holometabola	0	0	0	0	0	0	0	0	0	0	0		0	0	0	
Orthoptera	0	0	0	0	0	0	0	0	0	1.0	3.4		0	*	2.3	
Thysanoptera	0	0	0	0	0	0	0	0	0	0	0		0	0	0	
Chilopoda$	0	0	0	0	0	0	0	0	0	0	0		0	0	0	
Others	0	0	0	0	0	0	0	0	0	0	0		0	*	0	
Number of individuals	20.6	45.2	25.2	29.7	12.9	31.1	9.1	8.7	29.1	46.1	19.6		33.0	25.2	19.2	

$: Class; !: Suborder; &A: 15/10/81; B: 07/01/82; C: 05/04/82; D: 22/07/82; L: larvae; *: less than 1.0 %

Appendix 3.3 Percentage representation of Orders caught with the pitfall trap method on different data on both locations.

Order	Paddock DI Date				DII Date				KI Date				KII Date			
	[&]A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Arhropleona	91.0	69.4	78.4	97.2	89.9	74.6	84.5	98.5	52.0	35.1	27.5	72.2	72.2	22.1	42.8	88.5
Acari	*	7.0	*	*	*	4.5	*	*	22.2	29.9	9.7	14.0	15.1	47.3	23.3	5.2
Araneae	*	3.4	4.1	*	*	4.1	6.8	*	1.8	18.5	4.7	*	1.8	5.8	4.0	*
Coleoptera	4.5	2.8	*	*	1.1	2.5	*	*	1.3	5.7	*	*	1.2	2.0	1.7	*
Diptera	1.3	6.7	1.8	1.1	1.0	7.0	1.6	*	1.5	2.9	2.3	3.5	1.7	4.2	3.2	2.0
Homoptera[!]	1.3	2.8	1.3	*	6.9	2.1	*	*	20.4	*	4.5	6.2	7.8	11.5	2.2	2.4
Heteroptera[!]	*	*	*	0	0	*	*	0	*	*	2.2	*	*	0	1.0	0
Hymenoptera	*	2.9	1.5	*	*	1.4	2.5	*	*	1.5	1.7	*	*	2.0	1.5	*
L. Holometabola	*	1.2	0	*	*	1.0	*	0	*	*	*	*	*	*	*	*
Orthoptera	0	3.4	1.4	*	*	2.4	1.8	0	0	4.9	25.3	*	0	4.0	18.9	0
Thysanoptera	0	*	9.2	*	0	0	*	*	0	0	19.7	2.4	0	*	0	*
Chilopoda[$]	*	*	*	0	0	*	0	0	0	*	0	0	0	*	0	*
Others	*	*	*	0	*	*	0	0	*	*	1.7	*	*	0	1.1	0
Number of individuals	397.4	238.2	292.7	717.3	565.2	374.4	251.3	1036.5	371.6	261.8	249.3	353.1	361.1	399.0	226.9	298.0

$: Class; !: Suborder; [&]A: 15/10/81; B: 07/01/82; C: 05/04/82; D: 22/07/82; L: larvae; *: less than 1.0 %

Appendix 3.4.a Weekly and cumulative degree-days in Huntly at a zero development threshold of 4 °C.

Date	Σ°D	°D	Date	Σ°D	°D	Date	Σ°D	°D
810723	23		820107	110		820624	2157	(34)
810730	73	(46)	820114	213	(102)	820701	2198	(41)
810806	113	(40)	820121	328	(115)	820708	2229	(31)
810813	155	(42)	820128	446	(118)	820715	2257	(28)
810820	186	(31)	820204	576	(130)	820722	2303	(46)
810827	229	(43)	820211	685	(109)	820729	2338	(35)
810903	259	(30)	820218	802	(117)	820805	2390	(52)
810910	318	(59)	820225	936	(134)	820812	2439	(49)
810917	317	(53)	820304	1065	(129)	820819	2481	(42)
810924	426	(55)	820311	1179	(114)	820826	2531	(50)
811001	491	(65)	820318	1279	(100)	820902	2583	(52)
811008	559	(68)	820325	1379	(100)	820909	2639	(56)
811015	616	(57)	820401	1479	(100)	820916	2700	(61)
811022	678	(62)	820408	1571	(92)	820923	2768	(68)
811029	743	(65)	820415	1652	(81)	820930	2843	(75)
811105	815	(72)	820422	1726	(74)	821007	2910	(67)
811112	904	(89)	820429	1789	(63)	821014	2984	(74)
811119	994	(90)	820506	1836	(47)	821021	3030	(46)
811126	1080	(86)	820513	1900	(64)	821028	3084	(54)
811203	1179	(99)	820520	1963	(63)	821104	3169	(85)
811210	1280	(101)	820527	2026	(63)	821111	3260	(91)
811217	1373	(93)	820603	2064	(38)	821118	3330	(70)
811224	1488	(115)	820610	2101	(37)	821125	3414	(91)
811231	1612	(124)	820617	2123	(22)	821202	3495	(81)

Σ°D= cumulative °D

Appendix 3.4.a Continued.

Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D
821209	3582	(87)	830526	1676	(40)	831110	2894	(101)
821216	3677	(95)	830602	1721	(45)	831117	2964	(70)
821223	3767	(99)	830609	1767	(46)	831124	3031	(67)
821230	3861	(85)	830616	1808	(41)	831201	3101	(70)
830106	93		830623	1848	(40)	831208	3196	(95)
830113	198	(105)	830630	1889	(41)	831215	3280	(84)
830120	276	(78)	830707	1912	(23)	831222	3357	(77)
830127	354	(78)	830714	1952	(40)	831229	3436	(79)
830203	442	(88)	830721	1975	(23)			
830210	524	(82)	830728	1997	(22)			
830217	619	(95)	830804	2050	(53)			
830224	715	(96)	830811	2101	(51)			
830303	801	(86)	830818	2130	(29)			
830310	902	(101)	830825	2165	(35)			
830317	999	(97)	830901	2202	(37)			
830324	1104	(105)	830908	2260	(58)			
830331	1189	(85)	830915	2320	(60)			
830407	1262	(73)	830922	2370	(50)			
830414	1330	(68)	830929	2428	(58)			
830421	1420	(90)	831006	2497	(69)			
830428	1490	(70)	831013	2548	(51)			
830505	1544	(54)	831020	2615	(67)			
830512	1594	(50)	831027	2708	(93)			
830519	1636	(42)	831103	2793	(85)			

$\Sigma^{o}D$= cumulative ^{o}D

Appendix 3.4.b Weekly and cumulative degree-days in Huntly at a zero development threshold of 7 °C.

Date	Σ°D	°D	Date	Σ°D	°D	Date	Σ°D	°D
810723	14		820107	90		820624	1665	(20)
810730	42	(28)	820114	171	(81)	820701	1688	(23)
810806	65	(23)	820121	265	(94)	820708	1704	(16)
810813	90	(25)	820128	362	(97)	820715	1719	(15)
810820	108	(18)	820204	471	(109)	820722	1746	(27)
810827	133	(25)	820211	559	(88)	820729	1768	(22)
810903	150	(17)	820218	655	(96)	820805	1801	(33)
810910	187	(37)	820225	768	(113)	820812	1830	(29)
810917	219	(32)	820304	876	(108)	820819	1855	(25)
810924	254	(35)	820311	969	(93)	820826	1885	(30)
811001	298	(44)	820318	1048	(79)	820902	1918	(33)
811008	346	(48)	820325	1127	(79)	820909	1955	(37)
811015	383	(37)	820401	1206	(79)	820916	1996	(41)
811022	424	(41)	820408	1277	(71)	820923	2045	(49)
811029	470	(46)	820415	1337	(60)	820930	2099	(54)
811105	522	(52)	820422	1390	(53)	821007	2145	(46)
811112	589	(52)	820429	1433	(43)	821014	2198	(53)
811119	658	(69)	820506	1464	(31)	821021	2224	(26)
811126	723	(65)	820513	1508	(44)	821028	2258	(34)
811203	802	(79)	820520	1550	(42)	821104	2322	(64)
811210	881	(79)	820527	1592	(42)	821111	2392	(70)
811217	953	(72)	820603	1613	(42)	821118	2441	(49)
811224	1048	(95)	820610	1635	(22)	821125	2504	(63)
811231	1150	(102)	820617	1645	(10)	821202	2565	(61)

Σ°D= cumulative °D

Appendix 3.4.b Continued

Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D
821209	2631	(66)	830526	1249	(23)	831110	2042	(80)
821216	2705	(74)	830602	1276	(27)	831117	2091	(49)
821223	2783	(78)	830609	1305	(29)	831124	2138	(47)
821230	2847	(64)	830616	1329	(24)	831201	2187	(49)
830106	72		830623	1351	(22)	831208	2226	(75)
830113	156	(84)	830630	1370	(19)	831215	2325	(63)
830120	213	(57)	830707	1382	(12)	831222	2380	(55)
830127	270	(57)	830714	1406	(24)	831229	2439	(59)
830203	337	(67)	830721	1417	(11)			
830210	398	(61)	830728	1428	(11)			
830217	472	(74)	830804	1461	(33)			
830224	547	(75)	830811	1491	(30)			
830303	612	(65)	830818	1506	(15)			
830310	692	(80)	830825	1525	(19)			
830317	768	(76)	830901	1547	(22)			
830324	852	(84)	830908	1585	(38)			
830331	916	(64)	830915	1627	(42)			
830407	968	(52)	830922	1655	(28)			
830414	1018	(50)	830929	1694	(39)			
830421	1086	(68)	831006	1742	(48)			
830428	1137	(51)	831013	1779	(37)			
830505	1172	(35)	831020	1826	(47)			
830512	1202	(30)	831027	1898	(72)			
830519	1226	(24)	831103	1962	(64)			

$\Sigma^{o}D$= cumulative ^{o}D

Appendix 3.4.c Weekly and cumulative degree-days in Huntly at a zero development threshold of 10 °C.

Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D
810723	5		820107	69		820624	1206	(8)
810730	19	(14)	820114	129	(60)	820701	1215	(9)
810806	28	(9)	820121	202	(73)	820708	1221	(6)
810813	39	(11)	820128	278	(76)	820715	1225	(4)
810820	47	(8)	820204	366	(88)	820722	1238	(13)
810827	59	(12)	820211	434	(68)	820729	1248	(10)
810903	67	(8)	820218	508	(74)	820805	1246	(16)
810910	85	(18)	820225	601	(93)	820812	1278	(14)
810917	99	(14)	820304	687	(86)	820819	1290	(12)
810924	117	(18)	820311	760	(73)	820826	1304	(14)
811001	141	(24)	820318	818	(58)	820902	1321	(17)
811008	170	(29)	820325	876	(58)	820909	1342	(21)
811015	191	(21)	820401	934	(58)	820916	1366	(24)
811022	216	(25)	820408	984	(50)	820923	1397	(31)
811029	243	(27)	820415	1024	(40)	820930	1431	(43)
811105	275	(32)	820422	1059	(35)	821007	1457	(26)
811112	321	(46)	820429	1087	(28)	821014	1490	(33)
811119	370	(49)	820506	1104	(17)	821021	1503	(13)
811126	414	(44)	820513	1130	(26)	821028	1521	(18)
811203	472	(58)	820520	1154	(24)	821104	1564	(43)
811210	531	(59)	820527	1176	(22)	821111	1613	(49)
811217	582	(51)	820603	1186	(10)	821118	1644	(31)
811224	655	(73)	820610	1196	(10)	821125	1687	(43)
811231	737	(82)	820617	1198	(2)	821202	1730	(43)

$\Sigma^{o}D$= cumulative ^{o}D

Appendix 3.4.c Continued.

Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D
821209	1776	(46)	830526	844	(10)	831110	1285	(59)
821216	1829	(53)	830602	855	(11)	831117	1316	(31)
821223	1886	(57)	830609	870	(15)	831124	1345	(29)
821230	1929	(43)	830616	881	(11)	831201	1376	(31)
830106	51		830623	891	(10)	831208	1430	(54)
830113	114	(63)	830630	899	(8)	831215	1473	(43)
830120	150	(36)	830707	903	(4)	831222	1508	(35)
830127	187	(37)	830714	914	(11)	831229	1547	(39)
830203	233	(46)	830721	918	(4)			
830210	273	(40)	830728	921	(3)			
830217	327	(54)	830804	938	(17)			
830224	380	(53)	830811	951	(13)			
830303	426	(46)	830818	964	(7)			
830310	485	(59)	830825	974	(10)			
830317	541	(56)	830901	995	(21)			
830324	603	(62)	830908	1018	(23)			
830331	647	(44)	830915	1032	(14)			
830407	680	(33)	830922	1053	(21)			
830414	712	(32)	830929	1081	(28)			
830421	759	(47)	831006	1101	(20)			
830428	799	(32)	831013	1132	(31)			
830505	811	(20)	831020	1182	(50)			
830512	824	(13)	831027	1226	(44)			
830519	834	(10)	831103	1285	(59)			

$\Sigma^{o}D$= cumulative ^{o}D

Appendix 3.5.a Weekly and cumulative degree-days in Te Kauwhata at a zero development threshold of 4 °C.

Date	Σ°D	°D	Date	Σ°D	°D	Date	Σ°D	°D
810723	52	(25)	820107	121		820624	2234	(38)
810730	103	(51)	820114	234	(113)	820701	2271	(37)
810806	146	(43)	820121	359	(125)	820708	2296	(25)
810813	197	(51)	820128	482	(123)	820715	2318	(22)
810820	236	(39)	820204	617	(135)	820722	2358	(40)
810827	289	(53)	820211	739	(122)	820729	2392	(34)
810903	324	(35)	820218	869	(130)	820805	2444	(52)
810910	370	(46)	820225	1009	(140)	820812	2490	(46)
810917	422	(52)	820304	1146	(137)	820819	2531	(41)
810924	478	(56)	820311	1263	(117)	820826	2582	(51)
811001	540	(62)	820318	1369	(106)	820902	2627	(45)
811008	616	(76)	820325	1478	(109)	820909	2673	(46)
811015	669	(53)	820401	1586	(108)	820916	2728	(55)
811022	736	(67)	820408	1687	(101)	820923	2793	(65)
811029	814	(78)	820415	1774	(87)	820930	2862	(69)
811105	885	(71)	820422	1852	(78)	821007	2923	(61)
811112	979	(94)	820429	1894	(42)	821014	2989	(66)
811119	1071	(92)	820506	1947	(53)	821021	3045	(56)
811126	1159	(88)	820513	2009	(62)	821028	3103	(58)
811203	1269	(110)	820520	2065	(56)	821104	3189	(86)
811210	1376	(107)	820527	2116	(51)	821111	3284	(95)
811217	1477	(101)	820603	2146	(30)	821118	3352	(68)
811224	1601	(124)	820610	2178	(32)	821125	3434	(82)
811231	1736	(135)	820617	2196	(18)	821202	3517	(83)

Σ°D= cumulative °D

Appendix 3.5.a Continued.

Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D
821209	3608	(91)	830526	1765	(41)	831110	3009	(95)
821216	3700	(92)	830602	1818	(53)	831117	3181	972)
821223	3800	(100)	830609	1872	(54)	831124	3148	(67)
821230	3883	(83)	830616	1926	(54)	831201	3221	(73)
830106	92		830623	1959	(33)	831208	3324	(103)
830113	190	(98)	830630	2007	(48)	831215	3412	(88)
830120	284	(94)	830707	2034	(27)	831222	3495	(83)
830127	377	(93)	830714	2067	(33)	831229	3574	(79)
830203	473	(96)	830721	2084	(17)			
830210	566	(93)	830728	2100	(16)			
830217	665	(99)	830804	2152	(52)			
830224	771	(106)	830811	2204	(52)			
830303	867	(96)	830818	2232	(28)			
830310	969	(102)	830825	2273	(41)			
830317	1065	(96)	830901	2312	(39)			
830324	1171	(106)	830908	2371	(59)			
830331	1259	(88)	830915	2435	(64)			
830407	1335	(76)	830922	2490	(55)			
830414	1410	(66)	830929	2551	(61)			
830421	1491	(90)	831006	2624	(73)			
830428	1559	(68)	831013	2688	(64)			
830505	1622	(63)	831020	2755	(67)			
830512	1679	(57)	831027	2838	(83)			
830519	1724	(45)	831103	2914	(76)			

$\Sigma^{o}D$= cumulative ^{o}D

Appendix 3.5.b Weekly and cumulative degree-days in Te Kauwhata at a zero development threshold of 7 °C.

Date	Σ°D	°D	Date	Σ°D	°D	Date	Σ°D	°D
810723	25	(12)	820107	100		820624	1748	(22)
810730	57	(32)	820114	192	(92)	820701	1767	(19)
810806	81	(24)	820121	296	(104)	820708	1778	(11)
810813	112	(31)	820128	398	(102)	820715	1788	(10)
810820	134	(22)	820204	512	(112)	820722	1811	(23)
810827	166	(32)	820211	613	(101)	820729	1832	(21)
810903	185	(19)	820218	722	(109)	820805	1864	(32)
810910	211	(26)	820225	841	(119)	820812	1890	(26)
810917	242	(31)	820304	957	(116)	820819	1913	(23)
810924	278	(36)	820311	1053	(96)	820826	1944	(31)
811001	319	(41)	820318	1138	(85)	820902	1970	(26)
811008	374	(55)	820325	1226	(88)	820909	1999	(29)
811015	408	(34)	820401	1313	(87)	820916	2034	(35)
811022	454	(46)	820408	1393	(80)	820923	2080	(46)
811029	509	(55)	820415	1459	(66)	820930	2129	(49)
811105	560	(51)	820422	1516	(57)	821007	2168	(39)
811112	633	(73)	820429	1544	(28)	821014	2213	(45)
811119	703	(70)	820506	1578	(34)	821021	2248	(35)
811126	771	(68)	820513	1621	(43)	821028	2298	(50)
811203	860	(89)	820520	1657	(36)	821104	2363	(65)
811210	945	(85)	820527	1686	(29)	821111	2438	(75)
811217	1026	(81)	820603	1701	(15)	821118	2485	(47)
811224	1129	(103)	820610	1719	(18)	821125	2545	(60)
811231	1243	(114)	820617	1726	(7)	821202	2608	(63)

Σ°D= cumulative °D

Appendix 3.5.b Continued.

Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D
821209	2678	(70)	830526	1328	(24)	831110	2133	(73)
821216	2748	(70)	830602	1361	(33)	831117	2185	(52)
821223	2827	(79)	830609	1397	(36)	831124	2232	(47)
821230	2889	(62)	830616	1431	(34)	831201	2284	(52)
830106	71		830623	1448	(17)	831208	2366	(82)
830113	149	(78)	830630	1476	(28)	831215	2433	(67)
830120	222	(73)	830707	1489	(13)	831222	2494	(61)
830127	294	(72)	830714	1508	(19)	831229	2553	(59)
830203	368	(74)	830721	1514	(6)			
830210	441	(73)	830728	1521	(7)			
830217	512	(71)	830804	1553	(32)			
830224	598	(86)	830811	1584	(31)			
830303	672	(74)	830818	1598	(14)			
830310	753	(81)	830825	1621	(23)			
830317	829	(76)	830901	1642	(21)			
830324	914	(85)	830908	1682	(40)			
830331	981	(67)	830915	1726	(44)			
830407	1036	(55)	830922	1760	(34)			
830414	1082	(46)	830929	1800	(40)			
830421	1151	(69)	831006	1852	(52)			
830428	1199	(48)	831013	1896	(44)			
830505	1241	(42)	831020	1943	(47)			
830512	1277	(36)	831027	2005	(62)			
830519	1304	(27)	831103	2060	(55)			

$\Sigma^{o}D$= cumulative ^{o}D

Appendix 3.5.c Weekly and cumulative degree-days in Te Kauwhata at a zero development threshold of 10 °C.

Date	Σ°D	°D	Date	Σ°D	°D	Date	Σ°D	°D
810723	7	(3)	820107	79		820624	1295	(8)
810730	23	(16)	820114	150	(71)	820701	1301	(6)
810806	33	(10)	820121	233	(83)	820708	1304	(3)
810813	47	(14)	820128	314	(81)	820715	1306	(2)
810820	56	(9)	820204	407	(93)	820722	1316	(10)
810827	71	(15)	820211	487	(80)	820729	1326	(10)
810903	78	(7)	820218	575	(88)	820805	1340	(14)
810910	87	(9)	820225	673	(98)	820812	1352	(12)
810917	101	(14)	820304	768	(95)	820819	1361	(9)
810924	119	(18)	820311	843	(75)	820826	1374	(13)
811001	141	(22)	820318	907	(64)	820902	1386	(12)
811008	176	(35)	820325	974	(67)	820909	1400	(14)
811015	194	(18)	820401	1040	(66)	820916	1418	(18)
811022	220	(26)	820408	1099	(59)	820923	1446	(28)
811029	256	(36)	820415	1144	(45)	820930	1474	(28)
811105	287	(31)	820422	1182	(38)	821007	1495	(21)
811112	339	(52)	820429	1199	(17)	821014	1520	(25)
811119	389	(50)	820506	1217	(18)	821021	1537	(17)
811126	435	(46)	820513	1242	(25)	821028	1561	(24)
811203	503	(68)	820520	1260	(18)	821104	1606	(45)
811210	568	(65)	820527	1274	(14)	821111	1659	(53)
811217	627	(59)	820603	1280	(6)	821118	1687	(28)
811224	709	(82)	820610	1286	(6)	821125	1727	(40)
811231	802	(93)	820617	1287	(1)	821202	1771	(44)

Σ°D= cumulative °D

Appendix 3.5.c Continued.

Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D	Date	$\Sigma^{o}D$	^{o}D
821209	1820	(49)	830526	923	(9)	831110	1360	(53)
821216	1869	(49)	830602	940	(170	831117	1392	(32)
821223	1927	(58)	830609	960	(20)	831124	1422	(30)
821230	1968	(41)	830616	977	(17)	831201	1455	(33)
830106	50		830623	983	(6)	831208	1516	(61)
830113	108	(58)	830630	995	(12)	831215	1563	(47)
830120	160	(52)	830707	999	(4)	831222	1603	(40)
830127	211	(51)	830714	1007	(80	831229	1642	(39)
830203	265	(54)	830721	1008	(1)			
830210	316	(51)	830728	1009	(1)			
830217	375	(59)	830804	1024	(15)			
830224	439	(64)	830811	1036	(12)			
830303	493	(54)	830818	1041	(5)			
830310	553	(60)	830825	1050	(9)			
830317	608	(55)	830901	1059	(9)			
830324	672	(64)	830908	1081	(22)			
830331	719	(47)	830915	1107	(26)			
830407	753	(34)	830922	1124	(17)			
830414	782	(290	830929	1146	(22)			
830421	829	(47)	831006	1177	(31)			
830428	859	(30)	831013	1202	(25)			
830505	883	(24)	831020	1232	(30)			
830512	901	(18)	831027	1273	(41)			
830519	914	(130	831103	1307	(34)			

$\Sigma^{o}D$= cumulative ^{o}D

Appendix 4.1 Average body length (μm) and weight (μg) plus the SEM for all the immature and mature instars of the LF in Huntly (DI, DII) and Te Kauwhata (KI, KII).

	Body length			Weight			Body length			Weight		
	n	x	SEM	n	x	SEM	n	x	SEM	n	x	SEM
DI							DII					
L_1 [$]	146	323	± 3	126	16	± 1	174	328	± 4	140	21	± 1
L_2	124	453	± 6	120	36	± 2	83	478	± 8	82	47	± 2
L_3	172	650	± 9	166	116	± 5	205	658	± 8	197	121	± 5
M	441	983	± 8	438	357	± 6	421	965	± 8	415	360	± 7
F_1	110	888	± 12	105	276	± 9	98	873	± 12	98	274	± 10
F_2	362	1235	± 9	357	651	± 11	376	1233	± 8	361	692	± 11
F_3	117	1503	± 19	117	1203	± 38	133	1543	± 17	132	1286	± 39
KI							KII					
L_1	140	310	± 4	69	18	± 1	123	313	± 3	72	19	± 1
L_2	95	433	± 5	78	35	± 2	82	443	± 7	75	44	± 2
L_3	172	600	± 7	148	95	± 4	127	645	± 12	118	125	± 7
M	350	920	± 49	329	303	± 7	249	940	± 11	242	337	± 10
F_1	99	853	± 14	85	247	± 10	70	865	± 15	68	271	± 11
F_2	284	1223	± 9	263	641	± 11	212	1228	± 11	208	676	± 13
F_3	122	1570	± 17	119	1290	± 39	110	1563	± 21	108	1368	± 46

$= immature and mature instars; n = number of replicates, x = mean, SEM = standard error of the mean

Appendix 4.2.a The average number of LF per m^2 and the SEM in Huntly (DI, DII) during 1981, 1982 and 1983, using the big and the small soil corer.

Date	DI		DII	
	Big corer	Small corer	Big corer	Small corer
1981				
23/07	598 ± 155		1000 ± 223	
06/08	3197 ± 1333		1501 ± 300	
20/08	2487 ± 511		1857 ± 514	
03/09	908 ± 310		2549 ± 810	
17/09	4405 ± 709		4907 ± 1308	
01/10	4324 ± 1917		3294 ± 1429	
15/10	7768 ± 1670		10289 ± 1829	
29/10	2901 ± 689		4026 ± 882	
12/11	27 ± 18		6195 ± 1798	
26/11	Shut up for hay making		0	
10/12	27 ± 18		13 ± 13	
23/12	27 ± 18		27 ± 18	
1982				
07/01	27 ± 27		0	
21/01		Soil too dry		
04/02		Soil too dry		
18/02		Soil too dry		
04/03	0		24 ± 24	
18/03	149 ± 63		46 ± 23	
02/04	321 ± 40		298 ± 110	
15/04	Soil too dry		326 ± 95	
28/04		Soil too dry		
13/05	1598 ± 271		1007 ± 211	

Appendix 4.2.a Continued.

Date	DI		DII	
	Big corer	Small corer	Big corer	Small corer
27/05	1857 ± 567		2196 ± 519	
10/06	3321 ± 727		4379 ± 1209	
24/06	2522 ± 433		908 ± 143	
08/07	3133 ± 1349		1200 ± 189	
22/07	2387 ± 398		4466 ± 885	
05/08	6733 ± 2068		4519 ± 1241	
19/08	16414 ± 3580		6880 ± 307	
02/09	14560 ± 3570		9768 ± 2890	
15/09	12810 ± 1737		12700 ± 4571	
30/09	19435 ± 1770	19883 ± 4209	10261 ± 1342	16952 ± 3208
14/10	13249 ± 3006	9288 ± 1204	18690 ± 5117	21672 ± 8222
28/10	32099 ± 8743	41318 ± 11436	24007 ± 6333	18288 ± 2382
11/11	1654 ± 464	248 ± 91	3133 ± 633	745 ± 251
25/11	4466 ± 1168	612 ± 217	11359 ± 2738	592 ± 134
09/12	3606 ± 1109	822 ± 375	2358 ± 675	745 ± 363
23/12	231 ± 48	153 ± 112	109 ± 24	115 ± 64
1983				
06/01	Soil too dry			
20/01	40 ± 21	Stopped	0	Stopped
04/02	Soil too dry			
17/02	13 ± 13		95 ± 34	
03/03	Soil too dry			
17/03	650 ± 298		31 ± 31	
31/03	Soil too dry			
14/04	4812 ± 2718	3113 ± 908	4880 ± 2462	2561 ± 926

Appendix 4.2.a Continued.

Date	DI		DII	
	Big corer	Small corer	Big corer	Small corer
28/04	1274 ± 355	726 ± 239	1369 ± 350	554 ± 89
12/05	1952 ± 630	631 ± 151	1007 ± 85	363 ± 117
26/05	1668 ± 486	2271 ± 961	3199 ± 961	1300 ± 612
09/06	1681 ± 335	2808 ± 771	3104 ± 628	975 ± 254
23/06		No sampling		
07/07	1748 ± 516		2562 ± 694	
21/07	406 ± 110		949 ± 189	
04/08	6222 ± 1347		5319 ± 2073	
18/08	5612 ± 875		9462 ± 3472	
01/09	1952 ± 556		6181 ± 1296	
15/09	2440 ± 903		4826 ± 1115	
29/09	3904 ± 758		2928 ± 599	
13/10	14518 ± 1225		5070 ± 2162	
27/10	6032 ± 792		14844 ± 2553	
10/11	3470 ± 806		1220 ± 437	
24/11	1410 ± 309		473 ± 104	
08/12	931 ± 128		87 ± 44	
21/12	379 ± 96		0	

Appendix 4.2.b The average number of LF per m^2 and the SEM in Te Kauwhata (KI, KII) during 1981, 1982 and 1983, using the big and the small soil corer.

Date	KI		KII	
	Big corer	Small corer	Big corer	Small corer
1981				
09/07	439 ± 284		0	
23/07	1025 ± 387			
06/08	610 ± 156		40 ± 29	
20/09	963 ± 417		82 ± 29	
03/09	2074 ± 605		0	
17/09	298 ± 111		13 ± 13	
01/10	1666 ± 216		162 ± 95	
15/10	1315 ± 294		153 ± 71	
29/10	162 ± 92		0	
12/11	488 ± 168		54 ± 29	
26/11	420 ± 246		95 ± 52	
10/12	Shut up for hay making		0	
23/12	0		27 ± 18	
1982				
07/01	0		0	
21/01		Soil too dry		
04/02		Soil too dry		
18/02		Soil too dry		
04/03	13 ± 13		0	
18/03	325 ± 101		13 ± 13	
02/04	488 ± 188		27 ± 18	
15/04	759 ± 325		31 ± 18	
28/04	326 ± 76		52 ± 37	
13/05	2372 ± 582	1166 ± 212	204 ± 71	

Appendix 4.2.b Continued.

Date	KI		KII	
	Big corer	Small corer	Big corer	Small corer
27/05	5586 ± 841	3192 ± 697	312 ± 71	
10/06	6601 ± 538	8485 ± 2690	610 ± 278	
24/06	1138 ± 515	1300 ± 518	217 ± 109	
08/07	11066 ± 3927	11887 ± 8373	1387 ± 622	
22/07	7590 ± 3094	5217 ± 1352	1966 ± 1244	
05/08	7600 ± 1391	5198 ± 1362	800 ± 266	
19/08	3053 ± 521	3134 ± 610	1774 ± 1440	
02/09	3640 ± 1160	3708 ± 540	1307 ± 134	
15/09	4978 ± 845	7430 ± 447	1476 ± 143	
30/09	6588 ± 1309	10492 ± 1914	5856 ± 1717	
14/10	4650 ± 1164	3402 ± 893	3619 ± 888	
28/10	2941 ± 861	2351 ± 922	3606 ± 1415	
11/11	600 ± 195	134 ± 38	540 ± 156	
25/11	583 ± 89	344 ± 81	692 ± 268	
09/12	379 ± 126	209 ± 74	122 ± 35	
23/12	0	0	0	
1983				
06/01		Soil too dry		
20/01	0	Stopped	0	
04/02		Soil too dry		
17/02	0		0	
03/03		Soil too dry		
17/03	0		13 ± 7	
31/03	0		40 ± 29	
14/04	284 ± 76		95 ± 44	

Appendix 4.2.b Continued.

Date	KI		KII	
	Big corer	Small corer	Big corer	Small corer
28/04	190 ± 82		231 ± 89	
12/05	623 ± 210		583 ± 206	
26/05	623 ± 183		1843 ± 444	
09/06	636 ± 163		1870 ± 697	
23/06	1532 ± 345		3809 ± 1509	
07/07	1058 ± 162		1396 ± 426	
21/07	2168 ± 914		1302 ± 1061	
04/08	1695 ± 555		1030 ± 231	
18/08	3307 ± 893		2278 ± 837	
01/09	1247 ± 281		488 ± 113	
15/09	1044 ± 231		610 ± 151	
29/09	637 ± 216		4975 ± 1590	
13/10	5774 ± 1491		1504 ± 398	
27/10	1451 ± 283		3240 ± 748	
10/11	1274 ± 534		3620 ± 1249	
24/11	326 ± 149		867 ± 411	
08/12	122 ± 45		217 ± 83	
21/12	0		0	

Appendix 4.3 Pasture mamagement in Huntly.

	DI	DII
810812	Sulphate of ammonia, 100 kg/ha (F)	Idem
811020	2-4 DB, 2 l/ha (W)	
811003	Closed for hay making	
811104	30 % potassic super phosphate, 400 kg/ha (F)	Idem
811109	$Dimethoate, 80 g.a.i./ha (LF)	
811117		Topped pasture
811118		Maldison, 100 g.a.i./ha (LF)
811127	Cut for hay	
820503		15 % potassic super phosphate, 300 kg/ha (F)
821013	Lime, 1200 kg/ha (F)	Idem
821021		Shut up for hay making
821107	Topped	
821110	Diazinon, 48 g.a.i./ha (LF) ;MCPA, 500 ml/ha (W)	Idem Idem
821124	Potash, 200 kg/ha; Causmag, 100 kg/ha; trace elements (F)	
821201		Cut for hay
830515	Chlorpyrifos, 120 g.a.i./ha (LF); 2-4 DC, 100 ml/ha (W)	Idem
830930		Chlorpyrifos, 160 g.a.i./ha (LF); shut up for silage
831101		Cut for silage
831220	Potash, 100 kg/ha (F)	Idem

F: fertilizer; LF: insecticide against LF; W: weedkiller; $: sprayed on experimental plots.

Appendix 4.4 Pasture mamagement in Te Kauwhata.

811014	Shut up for hay making	
811028	$Maldison, 100 g.a.i./ha (LF)	Idem
811104	Potassic super phosphate, 400 kg/ha (F)	Idem
811215	Cut for hay	
821009		Shut up for hay making
821015	Potassic super phosphate, 500 kg/ha (F)	Idem
821020	$Maldison, 100 g.a.i./ha (LF)	Idem
821202		Cut for hay
830314	Potassic super phosphate, 400 kg/ha (F)	Idem
830706	2-4 D, (W) Chlorpyrifos, 100 g.a.i./ha (LF)	Idem
830822		Urea, 25 kg/ha (F)
831002		Shut up for hay making
831015	Maldison, 100 g.a.i./ha (LF)	Idem
831103		Cut for hay

F: fertilizer; LF: insecticide against LF; W: weedkiller; $: sprayed on experimental plots.

Appendix 4.5 Number of the different immature and mature instars per m^2 in DI on different sampling dates in 1982 and 1983.

Date	Instars						
	L_1	L_2	L_3	M	F_1	F_2	F_3
1982							
08/07/82	0	63	832	1072	191	955	63
22/07	0	0	145	1122	145	832	195
05/08	0	0	955	2344	407	2188	955
19/08	331	1349	1660	7079	0	2692	3631
02/09	5012	2089	1175	2951	891	1479	1175
16/09				no data			
30/09	0	0	389	4266	1175	12303	1175
14/10	263	525	0	3715	0	6025	2630
28/10	16596	2570	1905	2570	0	3890	4467
11/11	0	100	646	372	135	302	132
25/11	0	631	1072	1514	457	724	91
09/12	72	0	0	1585	145	1660	145
23/12/82	0	0	40	0	76	115	0
06/01/83	0	0	0	0	0	0	0
1983							
03/03/83	0						
17/03	646	0	0	0	0	0	0
31/03				no data			
14/04	2884	1349	0	288	0	0	288
28/04	0	151	102	331	25	661	0
12/05	39	155	78	389	309	589	389
26/05	832	67	100	468	135	68	0
09/06	501	537	468	100	34	0	34
23/06				no data			
07/07	0	0	69	794	138	661	69
21/07	48	24	8	178	8	81	56
04/08	123	372	123	3631	617	372	1000
18/08	112	0	447	2570	891	676	891
01/09	275	550	603	234	118	195	0
15/09	0	49	245	724	148	1122	148
29/09	78	309	78	1318	78	1318	708
13/10	1175	2042	1445	4365	1175	2344	2042
27/10	0	603	1585	1585	2042	240	0
10/11	69	0	138	1585	275	1259	138
24/11	28	141	427	513	224	56	28
08/12	0	0	0	389	37	501	0
22/12	0	0	0	0	0	0	0

Appendix 4.6 Number of the different immature and mature instars per m^2 in DII on different sampling dates in 1982 and 1983.

Date	Instars						
	L_1	L_2	L_3	M	F_1	F_2	F_3
1982							
08/07/82	269	195	98	245	72	245	98
22/07	0	724	1175	1096	182	1096	275
05/08	0	91	646	2188	182	550	912
19/08	0	282	1950	1950	562	1413	832
02/09	0	0	398	4169	398	3162	1778
16/09				no data			
30/09	3715	1445	1230	1660	407	813	1023
14/10	1862	3020	7413	1479	0	3715	1122
28/10	191	955	4786	6310	0	7762	2399
11/11	0	129	337	1148	257	891	129
25/11	93	457	3236	3020	229	4571	0
09/12	0	0	141	933	0	1175	0
23/12/82	0	0	10	10	0	89	0
06/01/83	0	0	0	0	0	0	0
1983							
03/03/83	0	0	0	0	0	0	0
17/03	36	0	0	0	0	0	0
31/03				no data			
14/04	4467	295	98	0	0	0	0
28/04	55	81	355	245	138	490	0
12/05	60	20	41	245	182	204	263
26/05	1349	0	65	832	129	380	447
09/06	1660	562	741	62	0	0	62
23/06				no data			
07/07	51	204	407	724	562	562	51
21/07	0	0	58	363	38	417	76
04/08	0	107	0	2138	214	1585	1288
18/08	191	0	0	2291	380	2291	4365
01/09	0	245	2239	1862	617	741	490
15/09	389	575	776	1072	871	1072	98
29/09	59	59	234	933	174	1000	468
13/10	100	0	0	2138	302	1820	708
27/10	3236	589	3548	3891	2692	891	0
10/11	123	245	468	295	0	49	49
24/11	0	10	19	209	85	151	0
08/12	0	0	0	62	0	23	0
22/12	0	0	0	0	0	0	0

Appendix 7.1 The influence of the photoperiod on the feeding rate of female LF. Feeding rate is expressed as mm^2 eaten per individual per day (mean ± SEM). For level of significance between treatments, see text.

Photoperiod (hours light)	10 °C	15 °C	20 °C
0	2.16 ± 0.23 (n=29)	4.04 ± 0.35 (n=29)	6.96 ± 1.06 (n=14)
8	1.53 ± 0.18 (n=17)	3.72 ± 0.44 (n=17)	3.67 ± 0.53 (n=12)
12	3.38 ± 0.31 (n=23)	5.85 ± 0.55 (n=23)	6.47 ± 0.53 (n=24)
16	3.80 ± 0.27 (n=11)	7.52 ± 0.75 (n=17)	7.36 ± 0.86 (n=6)
24	1.87 ± 0.16 (n=7)	3.27 ± 0.27 (n=7)	3.35 ± 0.27 (n=6)

Appendix 7.2 The influence of the photoperiod on the feeding rate of male LF. Feeding rate is expressed as mm^2 eaten per individual per day (mean ± SEM). For level of significance between treatments, see text.

Photoperiod (hours light)	10 °C	15 °C	20 °C
0	0.56 ± 0.14 (n=12)	1.81 ± 0.27 (n=12)	2.27 ± 0.32 (n=15)
8	0.67 ± 0.14 (n=9)	1.79 ± 0.18 (n=9)	1.31 ± 0.22 (n=10)
12	0.46 ± 0.20 (n=4)	1.82 ± 0.20 (n=5)	2.16 ± 0.33 (n=8)
16	1.60 ± 0.39 (n=6)	2.58 ± 0.62 (n=6)	2.45 ± 0.46 (n=8)
24	0.55 ± 0.09 (n=4)	0.88 ± 0.12 (n=4)	1.22 ± 0.27 (n=4)

Appendix 7.3 The influence of the temperature on the feeding rate of the female LF. Feeding is expressed as mm^2 eaten perindividual per day (mean ± SEM). For significance between treatments, See text.

Temperature	hours light 0	8	12	16	24
10 °C	2.16 ± 0.23 (n=29)	1.53 ± 0.18 (n=17)	3.38 ± 0.31 (n=23)	3.80 ± 0.27 (n=11)	1.87 ± 0.16 (n=7)
15 °C	4.04 ± 0.35 (n=29)	3.72 ± 0.44 (n=17)	5.85 ± 0.55 (n=23)	7.52 ± 0.75 (n=17)	3.27 ± 0.38 (n=7)
20 °C	6.96 ± 1.06 (n=14)	3.67 ± 0.53 (n=12)	6.47 ± 0.53 (n=24)	7.36 ± 0.86 (n=6)	3.35 ± 0.27 (n=6)

Appendix 7.4 The influence of the temperature on the feeding rate of the male LF. Feeding is expressed as mm^2 eaten per individual per day (mean ± SEM). For significance between treatments, see text.

Temperature	hours light 0	8	12	16	24
10 °C	0.56 ± 0.14 (n=12)	0.67 ± 0.14 (n=9)	0.46 ± 0.20 (n=4)	1.60 ± 0.39 (n=6)	0.55 ± 0.09 (n=4)
15 °C	1.81 ± 0.27 (n=12)	1.79 ± 0.18 (n=9)	1.82 ± 0.20 (n=5)	2.58 ± 0.62 (n=6)	0.88 ± 0.12 (n=4)
20 °C	2.27 ± 0.32 (n=15)	1.31 ± 0.22 (n=10)	2.16 ± 0.33 (n=8)	2.45 ± 0.46 (n=8)	1.22 ± 0.27 (n=4)

Appendix 7.5 The influence of time on the feeding rate of third instar LF at different temperatures. Feeding is expressed as mm^2 eaten per individual per period and per day ± SEM. For level of significance between periods, see text.

Period	10 °C		15 °C		20 °C	
	Feeding per period	Feeding per day	Feeding per period	Feeding per day	Feeding per period	Feeding per day
1	1.83 ± 0.21 (n=9)	0.61 ± 0.07	2.52 ± 0.39 (n=9)	0.84 ± 0.13	3.87 ± 0.48 (n=9)	1.29 ± 0.16
2	1.41 ± 0.18 (n=9)	0.47 ± 0.06	3.93 ± 0.30 (n=9)	1.31 ± 0.10	7.35 ± 0.72 (n=9)	2.45 ± 0.24
3	2.01 ± 0.24 (n=9)	0.67 ± 0.08	7.02 ± 0.75 (n=9)	2.34 ± 0.25	11.64 ± 1.74 (n=9)	3.88 ± 0.58
4	5.70 ± 0.91 (n=7)	1.50 ± 0.24	13.19 ± 1.79 (n=9)	3.47 ± 0.47	17.48 ± 2.09 (n=5)	4.60 ± 0.55
5	3.65 ± 1.79 (n=6)	1.14 ± 0.56	13.82 ± 1.02 (n=9)	4.32 ± 0.32		
6	5.36 ± 1.48 (n=5)	1.41 ± 0.39	12.58 ± 2.32 (n=8)	3.31 ± 0.61		
7	11.07 ± 1.41 (n=5)	3.46 ± 0.44	8.00 ± 2.85 (n=5)	2.50 ± 0.89		
8	12.84 ± 1.06 (n=3)	3.38 ± 0.28	13.60 ± 3.84 (n=4)	3.58 ± 1.01		

Appendix 8.1 Percentage representation of the major pasture components in DI (Huntly) based on dry matter (DM) weight (per 0.09 m^2). Results given as mean ± SEM.

Date	Grasses			White clover			Weeds	Total
	Alive	Dead	Total	Alive	Dead	Total		DM(g)
1982 04/03	87.7 ± 2.02			9.7 ± 1.35			2.6 ± 1.60	7.82 ± 0.52
27/05	85.7 ± 2.32			11.2 ± 1.71			3.1 ± 1.12	5.26 ± 0.37
09/09	74.0 ± 5.60			20.9 ± 4.55			5.1 ± 1.80	8.81 ± 1.36
07/10	75.6 ± 5.62			17.0 ± 4.30			7.4 ± 4.91	15.10 ± 1.99
11/11	paddock just topped							
02/12	52.1 ± 4.39	36.6 ± 3.23	88.7 ± 2.15	6.2 ± 1.16	1.2 ± 0.31	7.5 ± 1.42	3.9 ± 1.81	16.23 ± 1.40
31/12	74.6 ± 2.71	16.2 ± 2.13	90.8 ± 3.14	7.5 ± 2.52			1.7 ± 0.75	12.45± 7.04
1983 26/01	60.1 ± 4.13	22.8 ± 1.97	82.9 ± 3.57	13.8 ± 2.35			3.3 ± 1.48	16.46 ± 1.42
23/02	57.5 ± 6.05	18.2 ± 2.98	75.7 ± 6.31	21.6 ± 5.17			2.7 ± 1.74	9.95 ± 1.39
23/03	59.4 ± 5.03	17.9 ± 1.82	77.3 ± 4.98	21.2 ± 5.01			1.5 ± 0.62	10.61 ± 1.25
04/05	69.3 ± 4.47			26.4 ± 3.50			4.3 ± 1.79	7.37 ± 1.30
30/06	no cutting							
27/07	89.4 ± 2.61			8.8 ± 2.00			1.8 ± 0.98	10.23 ± 0.53
24/08	81.1 ± 3.58			16.0 ± 3.48			2.9 ± 1.13	8.00 ± 0.71
13/10	85.7 ± 3.26			11.6 ± 2.17			2.7 ± 1.37	12.64 ± 1.64
16/11	65.8 ± 2.33	20.7 ± 1.86	86.5 ± 1.61	12.8 ± 1.51			0.7 ± 0.29	9.50 ± 1.01
14/12	76.9 ± 5.13	4.4 ± 1.20	81.3 ± 5.14	13.5 ± 3.72			5.2 ± 1.64	11.71 ± 1.40

Appendix 8.2 Percentage representation of the major pasture components in DII (Huntly) based on dry matter (DM) weight (per 0.09 m^2). Results given as mean ± SEM.

	Grasses			White (Red) clover			Weeds	Total
Date	Alive	Dead	Total	Alive	Dead	Total		DM(g)
1982	73.6 ±			21.2 ±			1.7 ±	6.81 ±
04/03	3.48			3.27			0.99	0.29
				(3.5 ± 0.99)				
27/05	58.5 ±			38.2 ±			1.6 ±	5.88 ±
	3.08			3.36			0.33	0.30
				(1.7 ± 0.56)				
09/09	59.7 ±			38.8 ±			1.2 ±	19.39 ±
	5.95			5.81			0.40	1.73
				(0.3 ± 0.09)				
07/10	71.7 ±			25.9 ±			1.4 ±	14.10 ±
	5.48			5.52			0.34	0.98
				(1.0 ± 0.48)				
11/11	89.0 ±			10.3 ±			0.4 ±	36.60 ±
	3.09			2.81			0.22	3.66
				(0.3 ± 0.19)				
02/12				Just cut for hay				
31/12	51.1 ±	28.1 ±	79.2 ±	15.4 ±	0.8 ±	16.2 ±	1.8 ±	12.11 ±
	4.07	6.85	4.47	4.38	0.78	4.46	0.84	1.22
				(2.8 ± 1.35)				
1983	53.9 ±	21.8 ±	75.7 ±	20.6 ±			0.3 ±	13.26 ±
26/01	2.98	2.05	2.86	2.87			0.16	1.00
				(3.4 ± 1.63)				
23/02	46.4 ±	31.0 ±	77.4 ±	20.3 ±			0.5 ±	9.24 ±
	4.01	3.29	4.38	4.08			0.42	0.63
				(1.8 ± 1.20)				
23/03	49.6 ±	26.4 ±	76.0 ±	22.9 ±			0.5 ±	11.68 ±
	5.06	3.94	4.56	4.40			0.22	1.06
				(0.6 ± 0.51)				
04/05	61.0 ±			36.5 ±			1.5 ±	13.47 ±
	5.74			5.99			0.53	1.21
				(1.0 ± 0.54)				
30/06				no cutting				
27/07	82.3 ±			16.7 ±			1.0 ±	12.32 ±
	2.53			2.23			0.96	1.96
				(0)				
24/08	90.1 ±			9.7 ±			0.1 ±	11.35 ±
	2.52			2.48			0.06	1.10
				(0.1 ± 0.10)				
13/10	75.7 ±			19.4 ±			1.5 ±	22.75 ±
	4.50			3.17			0.48	2.08
				(3.4 ± 2.35)				
16/11	31.7 ±	43.8 ±	75.4 ±	22.3 ±			1.1 ±	4.86 ±
	3.42	3.79	4.88	4.55			0.71	0.29
				(1.1 ± 1.10)				
14/12	60.5 ±	3.1 ±	63.6 ±	26.3 ±	0.8 ±	27.1 ±	0.5 ±	13.30 ±
	6.98	1.90	7.40	6.07	0.20	6.24	0.33	1.23
				(8.8 ± 5.42)				

Appendix 8.3 Percentage representation of the major pasture components in KI (Te Kauwhata) based on dry matter (DM) weight (per 0.09 m^2). Results given as mean ± SEM.

Date	Grasses			White clover			Weeds	Total DM(g)
	Alive	Dead	Total	Alive	Dead	Total		
1982 04/03	69.6 ± 4.42			20.1 ± 1.75			10.3 ± 4.49	5.64 ± 0.39
27/05	79.2 ± 2.92			12.4 ± 0.97			8.4 ± 2.86	4.09 ± 0.11
09/09	87.8 ± 2.53			7.6 ± 1.67			4.6 ± 1.56	11.00 ± 1.13
07/10	82.7 ± 3.79			10.5 ± 2.57			6.8 ± 2.02	12.10 ± 1.25
11/11	80.4 ± 3.42			14.0 ± 2.41			5.6 ± 1.25	7.11 ± 1.16
02/12	63.4 ± 4.00	20.3 ± 3.27	83.7 ± 4.07	11.2 ± 3.18	1.4 ± 0.59	12.6 ± 3.47	3.7 ± 1.47	16.17 ± 5.17
31/12	51.0 ± 4.13	22.1 ± 3.86	73.1 ± 3.61	16.8 ± 2.23	2.1 ± 0.52	18.9 ± 2.17	8.0 ± 2.39	7.45 ± 1.90
1983 26/01	48.7 ± 3.15	30.0 ± 4.56	78.7 ± 5.21	18.0 ± 4.27			3.3 ± 1.41	4.95 ± 0.80
23/02	46.6 ± 3.46	24.0 ± 2.78	70.6 ± 4.98	20.4 ± 3.82			9.0 ± 2.67	5.27 ± 0.88
23/03	68.4 ± 4.37	15.7 ± 2.82	84.1 ± 3.88	8.2 ± 2.11			7.7 ± 2.29	7.35 ± 0.93
04/05	75.2 ± 6.69			8.3 ± 2.91			16.5 ± 4.07	6.17 ± 0.85
22/06	81.9 ± 4.73			7.3 ± 2.47			10.8 ± 3.94	6.76 ± 0.61
27/07	87.0 ± 3.71			2.7 ± 1.20			10.3 ± 3.02	6.37 ± 0.88
24/08	88.9 ± 3.68			8.1 ± 3.27			3.0 ± 1.21	9.88 ± 0.93
13/10	86.9 ± 3.81			10.1 ± 3.17			3.0 ± 0.99	7.74 ± 0.78
16/11	59.3 ± 5.69	26.3 ± 4.44	85.6 ± 2.93	9.3 ± 1.84			5.1 ± 1.53	8.10 ± 1.42
14/12	59.7 ± 3.92	15.1 ± 2.56	74.8 ± 5.88	18.0 ± 5.04			7.2 ± 2.69	9.18 ± 1.71

Appendix 8.4 Percentage representation of the major pasture components in KII_2 (Te Kauwhata) based on dry matter (DM) weight (per 0.09 m^2). Results given as mean ± SEM.

Date	Grasses			White clover			Weeds	Total DM(g)
	Alive	Dead	Total	Alive	Dead	Total		
1982 04/03	84.1 ± 1.56			13.5 ± 1.38			2.4 ± 0.51	5.44 ± 0.19
27/05	84.1 ± 2.00			14.2 ± 1.99			1.7 ± 0.42	3.70 ± 0.36
09/09	89.1 ± 1.89			10.1 ± 1.96			0.8 ± 0.45	12.64 ± 1.48
07/10	89.2 ± 2.14			10.2 ± 2.09			0.5 ± 0.27	11.29 ± 1.81
11/11	82.9 ± 3.37			13.1 ± 2.66			4.1 ± 1.62	14.83 ± 2.19
02/12	Just cut for hay							
31/12	48.0 ± 4.09	29.9 ± 1.53	77.9 ± 3.69	20.4 ± 3.81	0.44 ± 0.19	20.8 ± 3.78	1.3 ± 0.91	9.84 ± 0.51
1983 26/01	56.4 ± 3.93	22.8 ± 1.68	79.2 ± 4.02	19.4 ± 3.65			1.2 ± 0.96	9.46 ± 0.50
23/02	54.8 ± 2.89	27.4 ± 3.25	82.2 ± 3.78	16.6 ± 3.45			1.3 ± 0.69	7.26 ± 0.55
23/03	57.3 ± 3.10	31.2 ± 3.94	88.5 ± 3.92	12.1 ± 3.88			0.6 ± 0.30	10.39 ± 1.22
04/05	86.5 ± 2.98			11.4 ± 3.06			2.1 ± 0.71	5.66 ± 0.45
22/06	91.1 ± 1.17			8.1 ± 0.75			0.8 ± 0.56	16.00 ± 1.46
27/07	88.0 ± 2.50			9.6 ± 2.48			2.4 ± 0.86	15.95 ± 0.68
24/08	95.8 ± 0.91			3.6 ± 0.76			0.6 ± 0.28	11.81 ± 1.17
13/10	92.7 ± 1.74			6.6 ± 1.57			0.7 ± 0.47	12.65 ± 1.09
16/11	no cutting							
14/12	41.8 ± 4.19	43.2 ± 3.82	85.0 ± 3.30	14.5 ± 3.32			0.5 ± 0.44	9.50 ± 0.81

Appendix 8.5 Data on weight and leaf surface area (LSA) of 100 white clover leaflets, number of leaflets and LSA per m^2 plus percentage and actual LSA lost due to damage in DI (Huntly). Mean ± SEM are given.

Date	Weight/100 leaflets (g)	$LSA/100 leaflets	Leaflets per m^2	LSA per m^2 (cm^2)	LSA lost %	LSA lost cm^2
1982 07/10	0.58 ± 0.04	172.5 ± 8.3	4362 ± 815	7344 ± 1342	42.2	3099 ± 566
04/11	0.66 ± 0.03	188.1 ± 7.4			22.0	
02/12	0.42 ± 0.05	116.6 ± 11.4	3442 ± 725	3670 ± 838	16.4	602 ± 137
31/12	0.36 ± 0.04	102.8 ± 6.9	2275 ± 607	2162 ± 491	1.2	26 ± 6
1983 26/01	0.31 ± 0.02	85.5 ± 4.9	8692 ± 1824	6796 ± 1070	0.3	20 ± 3
23/02	0.30 ± 0.01	78.0 ± 2.4	7240 ± 1786	5450 ± 1288	0.1	&1
23/03	0.30 ± 0.02	65.4 ± 3.8	6794 ± 1473	4389 ± 907	0.1	&1
04/05	0.39 ± 0.03	146.4 ± 8.7	4824 ± 587	6907 ± 759	0.8	55 ± 6
30/06	0.26 ± 0.03	70.0 ± 6.7			9.2	
27/07	0.29 ± 0.02	71.0 ± 4.2	3450 ± 773	2359 ± 515	8.4	198 ± 43
24/08	0.39 ± 0.04	101.9 ± 6.6	4239 ± 979	3941 ± 939	5.6	221 ± 53
13/10	0.96 ± 0.06	234.6 ± 15.4	1518 ± 325	3666 ± 875	7.3	268 ± 64
16/11	0.58 ± 0.05	144.3 ± 20.9	2415 ± 426	3834 ± 734	8.0	307 ± 59
14/12	0.38 ± 0.04	110.4 ± 7.4	4589 ± 1202	4559 ± 985	8.5	388 ± 84

&1: less than 10 cm^2; $: expressed in cm^2

Appendix 8.6 Data on weight and leaf surface area (LSA) of 100 white clover leaflets, number of leaflets and LSA per m^2 plus percentage and actual LSA lost due to damage in DII (Huntly). Mean ± SEM are given.

Date	Weight/100 leaflets (g)	$LSA/100 leaflets	Leaflets per m^2	LSA per m^2 (cm^2)	LSA lost %	LSA lost cm^2
1982 07/10	1.02 ± 0.13	303.8 ± 25.8	4642 ± 1140	12188 ± 2338	17.7	2175 ± 414
04/11	1.79 ± 0.18	468.3 ± 43.6	2144 ± 698	9142 ± 2955	21.2	1938 ± 626
02/12			Just cut for hay			
31/12	0.62 ± 0.06	160.3 ± 11.8	4608 ± 1552	6897 ± 2466	2.4	166 ± 59
1983 26/01	0.62 ± 0.03	180.8 ± 8.5	5602 ± 655	10263 ± 1330	0.03	&1
23/02	0.47 ± 0.02	113.4 ± 6.6	4635 ± 1063	5094 ± 1120	0.1	&1
23/03	0.41 ± 0.03	83.2 ± 7.0	6854 ± 1817	5260 ± 1190	0.02	&1
04/05	0.75 ± 0.04	217.1 ± 10.2	7136 ± 1075	15044 ± 2145	1.1	165 ± 24
30/06	0.53 ± 0.04	149.0 ± 12.0			11.2	
27/07	0.80 ± 0.09	164.4 ± 17.4	2831 ± 471	4098 ± 306	10.1	414 ± 31
24/08	0.80 ± 0.15	163.1 ± 16.1	1642 ± 442	2484 ± 551	7.2	179 ± 40
13/10	1.53 ± 0.11	379.4 ± 20.8	3183 ± 542	11368 ± 1698	11.8	1341 ± 200
16/11	0.77 ± 0.06	202.7 ± 16.3	1578 ± 341	3214 ± 749	8.4	270 ± 63
14/12	0.70 ± 0.05	176.4 ± 10.7	6138 ± 1620	10406 ± 2427	1.5	156 ± 36

&1: less than 10 cm^2; $: expressed in cm^2

Appendix 8.7 Data on weight and leaf surface area (LSA) of 100 white clover leaflets, number of leaflets and LSA per m^2 plus percentage and actual LSA lost due to damage in KI (Te Kauwhata). Mean ± SEM are given.

Date	Weight/100 leaflets (g)	$LSA/100 leaflets	Leaflets per m^2	LSA per m^2 (cm^2)	LSA lost %	LSA lost cm^2
1982 07/10	0.46 ± 0.07	116.5 ± 18.7	3192 ± 804	3324 ± 774	18.2	605 ± 141
04/11	0.35 ± 0.03	108.4 ± 6.6	2780 ± 385	2904 ± 329	4.2	122 ± 14
02/12	0.38 ± 0.04	97.9 ± 6.5	3256 ± 332	3192 ± 370	2.0	64 ± 7
31/12	0.30 ± 0.02	70.1 ± 3.3	5208 ± 1372	3542 ± 946	1.0	35 ± 10
1983 26/01	0.17 ± 0.03	48.9 ± 5.2	7698 ± 3010	3094 ± 995	0.3	&1
23/02	0.18 ± 0.01	43.5 ± 3.2	8061 ± 2854	3483 ± 1177	0.02	&1
23/03	0.18 ± 0.01	43.2 ± 2.1	3672 ± 821	1604 ± 388	0	0
04/05	0.14 ± 0.02	63.0 ± 4.9	4880 ± 1789	2669 ± 850	0.8	21 ± 7
22/06	0.28 ± 0.02	76.0 ± 3.7	1823 ± 626	1401 ± 488	6.4	90 ± 31
27/07	0.38 ± 0.04	91.5 ± 9.7	542 ± 246	417 ± 174	10.0	42 ± 17
24/08	0.39 ± 0.10	85.3 ± 16.5	2925 ± 1331	2087 ± 875	7.4	154 ± 65
13/10	0.53 ± 0.03	150.9 ± 9.9	1460 ± 348	2269 ± 571	10.1	229 ± 58
16/11	0.56 ± 0.06	131.9 ± 13.1	1395 ± 334	1654 ± 378	8.1	134 ± 31
14/12	0.28 ± 0.03	62.3 ± 5.0	5200 ± 1478	2826 ± 720	2.4	68 ± 17

&1: less than 10 cm^2; $: expressed in cm^2

Appendix 8.8 Data on weight and leaf surface area (LSA) of 100 white clover leaflets, number of leaflets and LSA per m^2 plus percentage and actual LSA lost due to damage in KII (Te Kauwhata). Mean ± SEM are given.

Date	Weight/100 leaflets (g)	$LSA/100 leaflets	Leaflets per m^2	LSA per m^2 (cm^2)	LSA lost %	LSA lost cm^2
1982 07/10	0.59 ± 0.05	167.7 ± 12.0	1958 ± 318	3332 ± 606	25.9	863 ± 157
04/11	0.48 ± 0.04	152.1 ± 8.8	4050 ± 879	5945 ± 1277	6.3	375 ± 81
02/12			Just cut for hay			
31/12	0.44 ± 0.02	102.4 ± 4.5	5080 ± 833	5179 ± 795	0.2	10 ± 2
1983 26/01	0.33 ± 0.03	78.1 ± 4.2	6593 ± 1247	4882 ± 820	0.02	&1
23/02	0.28 ± 0.01	61.1 ± 1.6	4623 ± 892	2817 ± 546	0.08	&1
23/03	0.25 ± 0.02	57.6 ± 2.5	5188 ± 1544	2866 ± 824	0.06	&1
04/05	0.19 ± 0.02	74.4 ± 4.3	4006 ± 1142	2825 ± 786	0.8	23 ± 6
22/06	0.35 ± 0.01	87.7 ± 4.0	4004 ± 403	3513 ± 368	18.8	660 ± 69
27/07	0.52 ± 0.07	105.0 ± 9.7	3662 ± 1367	3426 ± 1072	12.2	418 ± 131
24/08	0.36 ± 0.05	85.4 ± 7.5	1267 ± 290	1016 ± 189	5.1	52 ± 10
13/10	0.67 ± 0.04	193.5 ± 19.0	1371 ± 290	2782 ± 719	6.2	172 ± 45
16/11	0.86 ± 0.07	183.1 ± 14.0			14.1	
14/12	0.53 ± 0.03	111.8 ± 5.6	2804 ± 657	3268 ± 934	4.3	141 ± 40

&1: less than 10 cm^2; $: expressed in cm^2

Appendix 8.9 Damage assessment on white clover samples taken from DI (Huntly). Damage assessed on a scale of 0 to 9. Results are presented as percentage frequency (mean ± SEM) and cumulative percentage frequency.

	Damage scale										Average number of leaflets (n=9)
Date	0	1	2	3	4	5	6	7	8	9	
4/3/1982											
mean ±	100										97.2 ±
s.e.											2.18
% cum.	100										
27/5											
mean ±	64.4 ±	32.7 ±	2.7 ±	0.1 ±	0.1 ±						97.1 ±
s.e.	3.25	2.79	0.71	0.11	0.11						2.08
% cum.	100	35.6	2.9	0.2	0.1						
9/9											
mean ±	20.2 ±	69.4 ±	8.1 ±	1.5 ±	0.3 ±	0.3 ±	0.1 ±				98.9 ±
s.e.	2.63	4.14	1.50	0.67	0.33	0.24	0.11				1.11
% cum.	100	79.7	10.3	2.2	0.7	0.4	0.1				
7/10											
mean ±	5.3 ±	19.0 ±	12.9 ±	7.1 ±	8.0 ±	11.8 ±	10.8 ±	11.2 ±	9.6 ±	5.0 ±	100.7 ±
s.e.	1.04	2.48	1.38	0.76	1.65	1.01	1.26	0.93	2.29	2.23	0.55
% cum.	100	95.4	76.4	63.5	56.4	48.4	36.6	25.8	14.6	5.0	
4/11											
mean ±	2.1 ±	35.9 ±	29.8 ±	16.6 ±	8.8 ±	3.9 ±	1.9 ±	0.6 ±	0.4 ±	0.1 ±	100
s.e.	0.69	4.11	1.69	1.97	1.56	0.78	0.46	0.27	0.33	0.10	
% cum.	100	98.0	62.1	32.2	15.7	6.9	3.0	1.1	0.5	0.1	
2/12											
mean ±	11.4 ±	51.2 ±	18.9 ±	7.8 ±	5.8 ±	2.6 ±	1.1 ±	0.9 ±	0.2 ±	0.1 ±	100
s.e.	2.77	4.72	1.90	1.52	2.35	0.73	0.51	0.51	0.15	0.11	
% cum.	100	88.6	37.4	18.5	10.7	4.9	2.3	1.2	0.3	0.1	
30/12											
mean ±	87.9 ±	12.0 ±	0.1 ±								100
s.e.	2.30	2.29	0.11								
% cum.	100	12.1	0.1								
26/1/1983											
mean ±	97.4 ±	2.6 ±									100
s.e.	0.58	0.58									
% cum.	100	2.6									

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.9 Continued. For text, see previous page.

Date	Damage scale 0	1	2	3	4	5	6	7	8	9	Average number of leaflets (n=9)
23/2											
mean ±	98.6 ±	1.4 ±									100
s.e.	0.44	0.44									
% cum.	100	1.4									
23/3											
mean ±	99.2 ±	0.8 ±									100
s.e.	0.32	0.32									
% cum.	100	0.8									
4/5											
mean ±	91.6 ±	8.4 ±									100
s.e.	1.19	1.19									
% cum.	100	8.4									
30/6											
mean ±	19.1 ±	71.8 ±	7.7 ±	1.0 ±	0.3 ±	0.1 ±					100
s.e.	4.04	2.09	2.57	0.53	0.33	0.11					
% cum.	100	80.9	9.1	1.4	0.4	0.1					
27/7											
mean ±	23.3 ±	70.1 ±	5.8 ±	0.6 ±	0.2 ±						100
s.e.	2.77	2.43	0.88	0.34	0.22						
% cum.	100	76.7	6.6	0.8	0.2						
24/8											
mean ±	45.8 ±	53.1 ±	1.0 ±		0.1 ±						100
s.e.	4.60	4.33	0.41		0.11						
% cum.	100	54.2	1.1		0.1						
13/10											
mean ±	31.4 ±	64.0 ±	4.6 ±								100
s.e.	2.74	2.74	0.90								
% cum.	100	68.6	4.6								
16/11											
mean ±	29.7 ±	62.7 ±	6.2 ±	1.1 ±	0.3 ±						100
s.e.	1.59	1.56	1.27	0.45	0.24						
% cum.	100	70.3	7.6	1.4	0.3						
14/12											
mean ±	33.3 ±	53.8 ±	9.9 ±	1.4 ±	1.1 ±	0.3 ±	0.1 ±				100
s.e.	3.02	2.88	1.55	0.97	0.35	0.24	0.11				
% cum.	100	66.6	12.8	2.9	1.5	0.4	0.1				

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.10 Damage assessment on white clover samples taken from DII (Huntly). Damage assessed on a scale of 0 to 9. Results are presented as percentage frequency (mean ± SEM) and cumulative percentage frequency.

	Damage scale										Average number of leaflets (n=9)
Date	0	1	2	3	4	5	6	7	8	9	
4/3/1982											
mean ±	99.7 ±	0.1 ±	0.1 ±	0.1 ±							100
s.e.	0.33	0.11	0.11	0.11							
% cum.	100	0.3	0.2	0.1							
27/5											
mean ±	41.2 ±	52.6 ±	5.1 ±	1.1 ±							100
s.e.	3.24	2.47	0.88	0.63							
% cum.	100	58.8	6.2	1.1							
9/9											
mean ±	19.3 ±	58.6 ±	15.0 ±	4.2 ±	1.8 ±	1.0 ±	0.1 ±				100
s.e.	2.65	4.88	2.30	1.50	0.81	0.67	0.11				
% cum.	100	80.7	22.1	7.1	2.9	1.1	0.1				
7/10											
mean ±	8.9 ±	50.7 ±	20.2 ±	7.9 ±	3.9 ±	3.1 ±	2.9 ±	2.4 ±	0.1 ±		100
s.e.	1.76	5.56	1.27	1.09	0.89	1.47	1.54	1.66	0.11		
% cum.	100	91.2	40.5	20.3	12.4	8.5	5.4	2.5	0.1		
4/11											
mean ±	2.0 ±	52.6 ±	21.8 ±	7.3 ±	4.3 ±	4.9 ±	2.1 ±	3.8 ±	1.1 ±	0.4 ±	100
s.e.	0.71	8.56	2.96	2.48	1.74	1.95	1.29	1.82	0.89	0.44	
% cum.	100	97.9	45.3	23.5	16.2	11.9	7.0	4.9	1.1	0.4	
2/12											
mean ±											
s.e.					cut for hay						
% cum.											
30/12											
mean ±	77.2 ±	21.4 ±	1.3 ±								100
s.e.	1.96	1.47	0.90								
% cum.	100	22.7	1.3								
26/1/1983											
mean ±	99.7 ±	0.3 ±									100
s.e.	0.33	0.33									
% cum.	100	0.3									

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.10 Continued. For text, see previous page.

Date	Damage scale 0	1	2	3	4	5	6	7	8	9	Average number of leaflets (n=9)
23/2											
mean ±	98.6 ±	1.4 ±									100
s.e.	0.50	0.50									
% cum.	100	1.4									
23/3											
mean ±	99.8 ±	0.2 ±									100
s.e.	0.22	0.22									
% cum.	100	0.2									
4/5											
mean ±	88.9 ±	11.1 ±									100
s.e.	1.47	1.47									
% cum.	100	11.1									
30/6											
mean ±	7.6 ±	77.5 ±	11.2 ±	2.6 ±	1.1 ±						99.2 ±
s.e.	1.80	4.02	2.86	1.73	0.73						0.52
% cum.	100	92.4	14.9	3.7	1.1						
27/7											
mean ±	9.6 ±	80.8 ±	8.4 ±	1.0 ±	0.2 ±						100
s.e.	1.88	1.98	1.64	0.37	0.22						
% cum.	100	90.4	9.6	1.2	0.2						
24/8											
mean ±	30.9 ±	66.1 ±	2.9 ±	0.1 ±							100
s.e.	3.83	3.22	0.99	0.11							
% cum.	100	69.1	3.0	0.1							
13/10											
mean ±	7.7 ±	74.0 ±	14.0 ±	2.8 ±	0.9 ±	0.4 ±	0.1 ±	0.1 ±			100
s.e.	2.03	4.18	2.94	1.01	0.35	0.29	0.11	0.11			
% cum.	100	92.3	18.3	4.3	1.5	0.6	0.2	0.1			
16/11											
mean ±	23.9 ±	70.6 ±	4.6 ±	0.3 ±	0.67 ±						100
s.e.	3.00	2.82	0.93	0.33	0.37						
% cum.	100	76.2	5.6	1.0	0.7						
14/12											
mean ±	84.9 ±	15.1 ±									100
s.e.	1.37	1.37									
% cum.	100	15.1									

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.11 Damage assessment on red clover samples taken from DII (Huntly). Damage assessed on a scale of 0 to 9. Results are presented as percentage frequency (mean ± SEM) and cumulative percentage frequency.

	Damage scale										Average number of leaflets (n=9)
Date	0	1	2	3	4	5	6	7	8	9	
4/3/1982											
mean ±	99.6 ±	0.4 ±									39.0 ±
s.e.	0.41	0.42									2.18
% cum.	100	0.4									
27/5											
mean ±	39.6 ±	51.0 ±	9.0 ±	0.5 ±							16.9 ±
s.e.	7.53	7.52	5.11	0.45							2.08
% cum.	100	60.5	9.5	0.5							
9/9											
mean ±	19.1 ±	68.1 ±	9.9 ±	2.9 ±							8.8 ±
s.e.	2.94	7.35	5.00	2.13							3.10
% cum.	100	80.9	12.8	2.9							
7/10											
mean ±	20.0 ±	63.2 ±	15.3 ±	1.6 ±							24.0 ±
s.e.	2.86	3.94	4.44	0.38							17.75
% cum.	100	80.1	16.9	1.6							
4/11											
mean ±	12.4 ±	56.3 ±	21.8 ±	8.4 ±	0.4 ±	0.4 ±	0.2 ±				17.6 ±
s.e.	7.32	9.51	8.20	4.16	0.40	0.40	0.20				14.35
% cum.	100	87.5	31.2	9.4	1.0	0.6	0.2				
2/12											
mean ±											
s.e.				cut for hay							
% cum.											
30/12											
mean ±	76.7 ±	22.6 ±	0.7 ±								34.3 ±
s.e.	4.65	4.57	0.75								22.06
% cum.	100	23.3	0.7								
26/1/1983											
mean ±	100										13.8 ±
s.e.											11.41
% cum.	100										

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.11 Continued. For text, see previous page.

Date	Damage scale 0	1	2	3	4	5	6	7	8	9	Average number of leaflets (n=9)
23/2											
mean ±	100										68.2 ±
s.e.											12.91
% cum.	100										
23/3											
mean ±	100										42.9 ±
s.e.											13.68
% cum.	100										
4/5											
mean ±	95.1 ±	4.9 ±									19.8 ±
s.e.	1.64	1.64									10.33
% cum.	100	4.9									
30/6											
mean ±	10.1 ±	80.7 ±	9.2 ±								25.4 ±
s.e.	3.17	3.18	4.95								10.70
% cum.	100	89.9	9.2								
27/7											
mean ±	57.4 ±	41.6 ±	0.3 ±	0.7 ±							23.6 ±
s.e.	17.09	16.84	0.25	0.75							14.48
% cum.	100	42.6	1.0	0.7							
24/8											
mean ±	55.0 ±	45.0 ±									33.3 ±
s.e.	11.72	11.72									12.82
% cum.	100	45.0									
13/10											
mean ±	52.6 ±	43.7 ±	3.7 ±								18.1 ±
s.e.	14.05	12.80	2.34								6.65
% cum.	100	47.4	3.7								
16/11											
mean ±	34.5 ±	63.5 ±	2.0 ±								34.6 ±
s.e.	2.01	3.07	2.02								19.67
% cum.	100	65.5	2.0								
14/12											
mean ±	79.4 ±	20.6 ±									26.2 ±
s.e.	7.70	7.69									11.59
% cum.	100	20.6									

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.12 Damage assessment on white clover samples taken from KI (Te Kauwhata). Damage assessed on a scale of 0 to 9. Results are presented as percentage frequency (mean ± SEM) and cumulative percentage frequency.

	Damage scale										Average number of leaflets (n=9)
Date	0	1	2	3	4	5	6	7	8	9	
4/3/1982											
mean ±	97.8 ±	1.9 ±	0.2 ±	0.1 ±							100
s.e.	1.04	0.73	0.22	0.11							
% cum.	100	2.2	0.3	0.1							
27/5											
mean ±	33.7 ±	38.9 ±	11.2 ±	6.9 ±	4.6 ±	3.2 ±	0.7 ±	0.2 ±	0.1 ±		100
s.e.	3.87	3.43	1.34	1.20	1.32	1.02	0.29	0.22	0.11		
% cum.	100	65.8	26.9	15.7	8.8	4.2	1.0	0.3	0.1		
9/9											
mean ±	17.0 ±	25.1 ±	13.8 ±	8.3 ±	5.0 ±	7.6 ±	6.0 ±	7.7 ±	5.9 ±	3.6 ±	100
s.e.	2.33	3.87	2.34	1.04	1.13	1.19	0.94	2.80	2.75	2.17	
% cum.	100	82.9	57.8	44.0	35.7	30.7	23.1	17.1	9.4	3.6	
7/10											
mean ±	14.6 ±	45.7 ±	16.9 ±	7.7 ±	4.9 ±	4.3 ±	3.3 ±	2.6 ±			96.6 ±
s.e.	3.18	4.76	1.95	1.14	0.97	1.33	1.38	1.43			3.44
% cum.	100	85.4	39.7	22.8	15.1	10.2	5.9	2.6			
4/11											
mean ±	62.4 ±	35.1 ±	1.4 ±	0.6 ±	0.2 ±	0.2 ±					100
s.e.	4.42	4.02	0.50	0.34	0.22	0.22					
% cum.	100	37.5	2.4	1.0	0.4	0.2					
2/12											
mean ±	80.3 ±	19.1 ±	0.6 ±								100
s.e.	2.52	2.61	0.18								
% cum.	100	19.7	0.6								
30/12											
mean ±	90.3 ±	9.2 ±	0.5 ±								100
s.e.	2.30	2.29	0.11								
% cum.	100	12.1	0.1								
26/1/1983											
mean ±	97.2 ±	2.8 ±									100
s.e.	0.70	0.71									
% cum.	100	2.8									

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.12 Continued. For text, see previous page.

Date	Damage scale 0	1	2	3	4	5	6	7	8	9	Average number of leaflets (n=9)
23/2											
mean ±	98.8 ±	0.2 ±									100
s.e.	0.15	0.15									
% cum.	100	0.2									
23/3											
mean ±	100										88.9 ±
s.e.											11.11
% cum.	100										
4/5											
mean ±	92.3 ±	7.7 ±									100
s.e.	1.56	1.56									
% cum.	100	7.7									
30/6											
mean ±	40.9 ±	55.3 ±	3.1 ±	0.7 ±							100
s.e.	7.04	6.48	0.82	0.37							
% cum.	100	59.1	3.8	0.7							
27/7											
mean ±	24.0 ±	60.0 ±	12.6 ±	1.7 ±	0.7 ±	0.6 ±	0.2 ±	0.2 ±	0.2 ±		100
s.e.	2.07	2.82	2.26	0.55	0.33	0.38	0.15	0.15	0.15		
% cum.	100	76.0	16.0	3.4	1.7	1.0	0.6	0.4	0.2		
24/8											
mean ±	34.2 ±	60.7 ±	3.4 ±	1.1 ±			0.4 ±	0.1 ±			100
s.e.	5.26	5.21	0.77	0.31			0.34	0.11			
% cum.	100	65.7	5.0	1.6			0.5	0.1			
13/10											
mean ±	14.0 ±	76.5 ±	7.0 ±	0.6 ±	1.0 ±	0.6 ±	0.3 ±				88.9 ±
s.e.	2.91	2.85	1.87	0.50	0.68	0.38	0.25				11.11
% cum.	100	86.0	9.5	2.5	1.9	0.9	0.3				
16/11											
mean ±	33.2 ±	57.6 ±	6.1 ±	1.9 ±	0.6 ±	0.3 ±		0.2 ±			100
s.e.	3.90	2.94	1.43	0.92	0.38	0.24		0.22			
% cum.	100	66.7	9.1	3.0	1.1	0.5		0.2			
14/12											
mean ±	75.9 ±	24.1 ±									100
s.e.	2.43	2.43									
% cum.	100	24.1									

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.13 Damage assessment on white clover samples taken from KII (Te Kauwhata). Damage assessed on a scale of 0 to 9. Results are presented as percentage frequency (mean ± SEM) and cumulative percentage frequency.

	Damage scale										Average number of leaflets (n=9)
Date	0	1	2	3	4	5	6	7	8	9	
4/3/1982											
mean ±	99.4 ±	0.6 ±									100
s.e.	0.24	0.24									
% cum.	100	0.6									
27/5											
mean ±	65.3 ±	30.0 ±	2.8 ±	1.0 ±	0.3 ±	0.3 ±	0.2 ±				100
s.e.	6.05	3.94	1.41	0.88	0.33	0.33	0.22				
% cum.	100	34.6	4.6	1.8	0.8	0.5	0.2				
9/9											
mean ±	48.9 ±	40.1 ±	5.3 ±	1.4 ±	1.2 ±	0.4 ±	0.9 ±	0.7 ±	1.0 ±		100
s.e.	5.40	3.20	1.65	0.93	0.80	0.34	0.68	0.44	0.88		
% cum.	100	51.0	10.9	5.6	4.2	3.0	2.6	1.7	1.0		
7/10											
mean ±	20.6 ±	48.2 ±	12.7 ±	6.8 ±	3.5 ±	5.2 ±	2.5 ±	0.8 ±	0.2 ±		93.6 ±
s.e.	5.34	4.82	2.76	2.33	1.42	2.20	1.53	0.56	0.20		4.28
% cum.	100	79.9	31.7	19.0	12.1	8.7	3.5	1.0	0.2		
4/11											
mean ±	42.2 ±	53.7 ±	3.4 ±	0.6 ±	0.1 ±						100
s.e.	4.99	4.76	0.87	0.33	0.10						
% cum.	100	57.8	4.1	0.7	0.1						
2/12											
mean ±											
s.e.				cut for hay							
% cum.											
30/12											
mean ±	97.6 ±	2.4 ±									100
s.e.	1.07	1.07									
% cum.	100	2.4									
26/1/1983											
mean ±	99.8 ±	0.2 ±									100
s.e.	0.22	0.22									
% cum.	100	0.2									

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 8.13 Continued. For text, see previous page.

Date	Damage scale 0	1	2	3	4	5	6	7	8	9	Average number of leaflets (n=9)
23/2											
mean ±	99.2 ±	0.8 ±									100
s.e.	0.43	0.43									
% cum.	100	0.8									
23/3											
mean ±	99.4 ±	0.6 ±									100
s.e.	0.24	0.24									
% cum.	100	0.6									
4/5											
mean ±	91.9 ±	8.1 ±									100
s.e.	3.93	1.31									
% cum.	100	8.1									
22/6											
mean ±	8.1 ±	50.7 ±	18.8 ±	7.7 ±	4.5 ±	4.8 ±	2.9 ±	1.7 ±	0.7 ±		100
s.e.	2.30	5.38	2.96	1.39	1.16	1.67	1.03	0.81	0.24		
% cum.	100	91.8	41.1	22.3	14.6	10.1	5.3	2.4	0.7		
27/7											
mean ±	20.8 ±	54.2 ±	15.3 ±	5.1 ±	2.3 ±	0.8 ±	1.0 ±	0.4 ±			100
s.e.	3.69	2.05	2.35	1.32	0.71	0.36	0.50	0.34			
% cum.	100	79.1	24.9	9.6	4.5	2.2	1.4	0.4			
24/8											
mean ±	52.3 ±	45.3 ±	2.1 ±			0.1 ±			0.1 ±		100
s.e.	2.91	2.82	0.68			0.11			0.11		
% cum.	100	47.6	2.3			0.2			0.1		
13/10											
mean ±	39.7 ±	58.8 ±	1.4 ±	0.1 ±							100
s.e.	5.52	5.35	0.47	0.11							
% cum.	100	60.3	1.5	0.1							
16/11											
mean ±	14.0 ±	65.2 ±	9.6 ±	2.8 ±	3.3 ±	0.8 ±	1.3 ±	1.2 ±	1.6 ±	0.2 ±	100
s.e.	2.94	4.91	1.92	0.78	1.05	0.55	0.90	1.10	1.56	0.22	
% cum.	100	86.0	20.8	11.2	8.4	5.1	4.3	3.0	1.8	0.2	
14/12											
mean ±	58.9 ±	39.7 ±	1.2 ±	0.2 ±							100
s.e.	5.54	5.17	0.68	0.22							
% cum.	100	41.1	1.4	0.2							

mean ± s.e.: mean ± standard error of the mean; % cum.: cumulative percentage

Appendix 10.1 Synopsis of conclusions

CHAPTER 3.

- There was a linear relationship between the surface area covered by the different sized soil corers used in this study, and the number of LF caught.

- There was a significant correlation between the number of LF caught with a sweepnet and a soil corer.

- There was a significant relationship between the locomotory activity of the LF as indicated by pitfall trap catches, and the population density of the LF, determined by soil sampling.

CHAPTER 4.

- Based on the frequency distribution of the measurement of the head width of the LF, three larval instars, two adult male and three adult female instars are recognised. Since the difference between the peak in numbers of the first and second adult male instar is very small, they were grouped together and referred to as the adult male instar.

- Adult male LF were smaller and lighter in weight than adult female LF.

- The population of the LF built up steadily from March or April onwards to reach a peak in numbers in October or November, after which the numbers declined to a very low or zero level in December.

- Rainfall played an important role in the hatching of diapause eggs in the field and influenced the survival of first instar larvae.

- The accumulated temperature (degree-days) above a zero development threshold of 4 ^{o}C determines the number of generations of the LF per year.

- There were five generations of LF in 1982, and four in 1983 at Huntly.

- In the paddocks that were shut for hay production the number of LF remained at the same level or increased.

- In the paddocks that were cut for hay the number of LF leveled out or dropped considerably.

- Although the temperature influenced the hatching of the diapause eggs, during laboratory trials in 1983 and 1984 no specific temperature could be established within the range of temperature from 10 to 20 ^{o}C, that would significantly induce or inhibit the hatching of the diapause eggs.

- Watering of the diapause egg samples twice a week, as opposed to once a week, did not influence the speed of hatching at 15 and 20 ^{o}C, but significantly reduced the speed of hatching at 10 ^{o}C.

- LF populations had overlapping stages of development as well as generations during the study period.

- The overall sex ratio (M : F) of LF in the field was 1 : 1.43, not significantly different from a 1 : 1 sex ratio.

- LF populations were prone to great changes in number at the beginning of the immature stage of the life cycle of the males and the end of the life cycle of the females, but fairly stable at the time that sexual maturity was reached.

- The locomotory activity of the LF, as indicated by pitfall trap catches, differed from day to day and all growth stages that were present in the field during the period of the experiments contributed, proportionally to their presence at the moment of sampling, to the total LF activity.

- No statistical significance could be found between the daily LF activity and the daily temperature, expressed as degree-days, or daily rainfall.

- The locomotory activity of the LF took place during the day as well as the night.

CHAPTER 5.

- The mite *Bdellodes lapidaria*, predatory on the LF, was found on the study sites near Huntly.

- Due to their presence in very low numbers, no control effect with reference to the LF, or Symphypleona in general, could be attributed to the predatory mite.

- No other predators or parasites of the LF were found during this study.

CHAPTER 7.

- Adult female LF eat significantly more than adult male LF.

- At a constant temperature of 10, 15 and 20 ^{o}C adult female LF eat significantly more white clover leaflets at a photophase of 12 hrs light and 16 hrs light, than at a short day length or total light or dark.

- Although the same tendencies, found for the adult female LF, were also present in the feeding activity of the males, statistically significant differences in feeding between the photoperiods only occurred in a few cases.

- At a constant photophase of 0, 8, 12 and 16 hours light, adult female LF eat significantly more when the temperature was increased from 10 to 15 and 20 ^{o}C.

- A significant increase in the feeding rate of adult males, when the temperature was increased from 10 to 15 and 20 ^{o}C, could only be established at a photophase of 0, 8 and 12 hours light.

- The outcome of the feeding trials suggest that some feeding activity may occur at night under field conditions.

- It was found for the third instar larvae and the first and second adult instars that the feeding activity increased significantly with age.

CHAPTER 8.

- Severe damage done by the LF reduced the leaflet surface area of the white clover plants in the field by up to 40 % during the study period.

- White clover plants with more than 90 % of their leaflet surface area damaged, were observed in October and November of 1982 and 1983.

CHAPTER 9.

- The LF is a wasteful feeder.

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