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THE BIOLOGY AND HOST PLANT RELATIONSHIPS THE GRASS APHID *METOPOLOPHIUM FESTUCAE* (THEOBALD), SUBSPECIES *CEREALIUM*

by

DAVID ROY DENT

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TO MY PARENTS

"An expert is a man who has made all the mistakes which can be made in a very narrow field."

Niels Bohr.

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

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THE BIOLOGY AND HOST PLANT RELATIONSHIPS OF THE GRASS APHID METOPOLOPHIUM FESTUCAE (THEOBALD), SUBSPECIES CEREALIUM

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Metopolophium festucae s.str. is restricted to grasses whilst the subspecies M. festucae cerealium has extended its host range to include cereals. This study considers only M. festucae cerealium. The performance of this aphid on a range of host plants has been considered in terms of antibiotic and antixenotic resistance. Particular emphasis was placed on the comparative resistance of wheat and L. perenne. M. festucae cerealium was more fecund on wheat, produced more alatae and showed more restlessness than on L. perenne. The difference in response on the two host plants implicated the influence of secondary plant substances in wheat. The role of the grassland habitat was considered in relation to density independent induction of alatae and the general life history strategy of this aphid.

The influence of temperature on M. festucae cerealium was investigated, and was found to influence reproductive performance, the induction of alate virginoparae and the morphology of virginoparae. Temperature did not influence the aphid's ovariole number and did not induce the development of any sexual morphs. M. festucae cerealium was considered to be anholocyclic on Gramineae.

The control of M. festucae cerealium in grassland and the implications of its life history strategy for integrated control are discussed.

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CHAPTER ONE

INTRODUCTION

There are more than 500 aphid species in Great Britain (Blackman 1974); of those only two species, Sitobion avenae F. and Metopolophium dirhodum Wlk. are considered to be serious pests of cereals (Gair, Jenkins, Lester 1983). Recently it has become apparent that a third species Metopdophium festucae Theob. (1917) subsp. cerealium. subsp. nov. (Stroyan 1982) may have important consequences for the cereal crop system in the United Kingdom.

The genotype Metopolophium (Mordvilko 1914) has been placed at various times in the genera Aphis, Siphonophora, Macrosiphum, Amphorophora, Aulacorthum, and Acyrthosiphon (Hille Ris Lambers 1947). Metopolophium was at first regarded as a subgenus of Acyrthosiphon, but became a full genus in 1914 with the identification of its well-developed median frontal tubercle as its one constant character which could separate the genera (Hille Ris Lambers 1947).

What is now known as Metopolophium festucae was first identified as Myzus festucae (Theobald 1917) and still recorded as such in 1926 (Theobald 1926). It was called the oat aphid Myzus festucae (Massee 1936) up until 1947 when it was included in the genus Metopolophium as the grass aphid Metopolophium festucae (Hille Ris Lambers 1947).

Metopolophium festucae has two subspecies: M. festucae sensu stricto and M. festucae subsp. cerealium subsp. nov. (Stroyan 1982). M. festucae cerealium has previously been misidentified as Metopolophium graminarium (Mordvilko) (Borner 1952) and as Metopolophium montanum (Hille Ris Lambers 1966; Stroyan 1982).

M. festucae spp. vary in colour between a bright yellow, a reddish brown and a dark olive green, and are monoecious on a wide range of Gramineae, often overlapping the host range of many similar species in the genus. Because of the variation in colour and wide host range of M. festucae spp., its identification and separation from other species in the genus is often difficult. For this reason the main morphological characteristics which separate the various species in the genus, are

mentioned here.

Metopolophium tenerum Hille Ris Lambers apterae can be separated from those of M. festucae spp. by overall size, ratio of siphunculus length to cauda length (h/j), and the function, bmn/afk; where b is the total length of the antennal flagellum; m is the length of the hind tibia; n is the length of tarsal joint II (without claws); a is the total body length; f the length of antennal joint IV and k the length of the apical rostral segment (bmn/afk, Stroyans' nomenclature, 1982). M. festucae tends to be larger than M. tenerum; the ratio h/j is less than for M. tenerum whilst the function bmn/afk is larger in M. festucae. M. tenerum is also restricted to Deschampsia flexuosa (L.) Trin., Festuca rubra L. and Festuca ovina L. as host plants (Prior 1976).

Metopolophium dirhodum is holocyclic and is easily identified by its more elongated body, pale whitish green colour and often prominent dark green spinal stripe (Stroyan 1952).

Metopolophium sabihae Prior. is similar to M. festucae in general appearance, but can be distinguished by its shorter siphunculi (Prior 1976, Stroyan 1982), with weak imbrications and its shorter hairs on the frontal prominences and midfrons (Prior 1976).

Metopolophium albidum H.R.L. is restricted to Arrhenatherum elatius (L.) Beauv ex J. and C. Presl.; its siphunculi are longer and more slender apically than M. festucae spp. (Stroyan 1952, 1982).

The alatae are distinguishable from all but M. sabihae by the distinct dark brown to black pleural intersegmental sclerites and spinopleural bars connecting the pleural sclerites on the dorsum of the abdomen. M. sabihae alatae have a much longer ultimate rostral segment to second hind tarsus (without claws), than M. festucae (Prior 1976).

The difference between the two subspecies of M. festucae is mainly one of size and host range. Both apterous and alate virginoparae of M. festucae cerealium resemble the M. festucae s.str. subspecies, but are on average larger and have longer appendages, and are paler and more yellow, whilst the alatae have a more pronounced pattern of spinopleural

dark bands on the abdominal sclerites (Stroyan 1982). The extent of host overlap in grasses is not known but M. festucae cerealium is found on cereals whilst it is thought that M. festucae sensu stricto is restricted to grass except for transient settlements on cereals.

Since the identification of the two M. festucae subspecies is a recent advance, the following review of the literature concerns the species M. festucae with reference to the individual subspecies when their identity is known.

Distribution and Damage

M. festucae has been recorded in the Neotropical zone of South America (Remaudière 1963; Müller 1965) and the Palaearctic zones of North America (Hille Ris Lambers 1947) and more extensively in Europe and Great Britain (Table 1). In Britain M. festucae has a widespread distribution from Southern England and the Midlands to Central and West Scotland (Table 2).

M. festucae has been recorded at altitudes of 1,750 ft. in Austria (Müller 1968), at 2,125 ft. on Fountains Fell (Prior 1976) and at 3,000 ft. on Sgoran Duhh in Britain (Stroyan 1969).

Records of M. festucae have mostly been associated with the damage it has caused to herbage seed crops and meadow grasses. In the United Kingdom the damage occurs between April and June (Theobald 1917; Massee 1936; Anon 1945; Anon 1950; Stroyan 1952; Gair 1953; Janson 1959; Vickerman 1976), and has been reported for a number of different Gramineae and places (Table 2).

The damage is characterized either by the apical halves of the leaves turning a crimson red (on Poa pratensis L.), a symptom produced also by Sipha spp. on Agrostis spp. (Hille Ris Lambers 1947), or by yellow flecking and purple spotting followed by pronounced yellowing and death of the leaves (Janson 1959).

The damage is thought to be due to aphid numbers rather than virus infection but M. festucae cerealium has been identified as a vector of

Table 1. The worldwide distribution of *M. festucae*

LOCATION	SOURCE OF REFERENCE
North America	Hille Ris Lambers (1947)
Amazon	Müller (1965)
Argentina (a similar form)	Remaudière (1963)
Iceland	Hille Ris Lambers (1955); Prior and Stroyan (1960)
Turkestan	Hill Ris Lambers (1947)
Sweden	Ossiannilsson (1959)
Faroes and Denmark	Heie (1961)
Pyrenees	Remaudière (1958)
Berlin	Börner (1952)
Austria and Rostock	Müller (1968)

Table 2. Distribution records of *M. festucae* damage in Great Britain and the source of reference

LOCATION	DAMAGED HOST PLANT	SOURCE OF REFERENCE
Kent	Winter oats	Massee (1935)
South Wales	Corn crops	Arthur (1944)
Southern England	Meadow grasses	Hille Ris Lambers (1947)
Kent, West Sussex, Middlesex, Oxford, Isle of Wight, Devon, Cardigan, Pembroke, Bedford, Cambridge, Essex, Suffolk, Lancs., Yorks., Staffs., Cheshire and Lincs.	Wheat and oats. *Dactylis*, *Festuca*, *Lolium*, and *Phleum* species	Janson (1957)
Wye and Benenden	*Festuca ovina*, wheat and meadow grasses	Theobald (1923)
Derbyshire	*Alopecurus pratensis* L. *Festuca pratensis* Huds. *Lolium perenne* L.	Gair (1953)
Yorkshire and Lancashire	Herbage seed crops	Warburton (1935) Edwards & Heath (1964)
Scotland	Meadow grasses	Hille Ris Lambers (1947)
Central and West Scotland	Grass crops and *Phleum pratense* L.	Cameron (1945)
Stirlingshire and West Perthshire	Meadows of *Phleum pratense*	Anon (1945)

barley yellow dwarf virus (Plumb 1974) so virus damage cannot be discounted. The numbers of aphids required to cause significant damage of a grass field is approximately 300 m^{-2} (Clements 1980), whilst M. festucae cerealium can reach numbers as high 20,000 m^{-2} (Vickerman 1976).

Life cycle and host plants

The Metopolophium genus consists of one species (M. dirhodum) migrating from Rosa to Gramineae and a number of species including M. festucae which have split off from this cycle and live on Gramineae only (Hille Ris Lambers 1947). M. festucae is monoecious on Gramineae (Table 3) and is the commonest cereal aphid species found on grassland and hedgerow grasses (Hand 1982).

Holocycly in M. festucae appears to be uncommon, overwintering viviparously on various grasses being the norm (Hille Ris Lambers 1947; Stroyan 1952; Gair 1953; Hill 1971; George 1974; Hand 1982). It has been recorded as overwintering viviparously on L. perenne, L. multiflorum, Alopecurus pratensis, and Poa annua (Gair 1953), winter barley and wheat, seedling and mature crop grasses and non crop Gramineae: Poa spp., Bromus sterilis and Arrhenatherum elatius (Hand 1982). Hill (1971) showed that M. festucae cerealium apterae could reproduce at low temperatures and described it as a relatively cold-hardy species, well adapted to reproducing early in the season at low temperatures. The apterous virginoparae overwinter on the lower leaves of the host or on the ground surface beneath the grass canopy (Gair 1953).

Sexual forms of M. festucae have rarely been observed in the field, although the occurence of a red holocyclic race in Rostock was reported by Müller (1968). However, this clone, as well as having a different colour also had a peculiar host range, refusing hosts normally acceptable to M. festucae. Fundatrices have been reported from Poa pratensis, D. flexuosa, B. mollis and wheat by Hille Ris Lambers (1947), and a few males have been produced in the laboratory under conditions of low temperatures and short photoperiod (Hand 1982). Overall however it appears that anholocycly is more important for M. festucae and holocycly occurs only at a very low level.

HOST PLANT	SOURCE OF REFERENCE
Agropyron repens (L.) Beauv.	D. Hille Ris Lambers (1947), Shaw (1964), Hill (1971).
Agrostis stolonifera L.	Shaw (1964), Prior (1976).
Agrostis tenuis. Sibth.	Stroyan (1969), Prior (1976).
Agrostis spp.	Hill (1971).
Alopecurus pratensis L.	Gair (1953), Dean & Luuring (1970), Hill (1971).
Arrhenatherium elatius. Beauv. ex J. & C. Presl.	Hand (1982).
Barley cultivars	Hill (1971), Jones & Dean (1975), Prior (1976), Hand (1982).
Bromus mollis L.	Hille Ris Lambers (1947), Hill (1971).
Bromus sterilis L.	Hand (1982).
Dactylis glomerata L.	Janson (1959), Hill (1971), Prior (1976).
Dactylis spp.	Powell pers. comm. (1982); Singer, Smith, Kendall, March, Mathias, Halfacree (1976).
Deschampsia caespitosa (L.) Beauv.	Shaw (1964), Stroyan (1969), Hill (1971).
Deschampsia flexuosa (L.) Trin.	Hille Ris Lambers (1947), Stroyan (1969), Hill (1971), Prior (1976).
Elymus arenarius L.	Shaw (1964), Hill (1971).
Festuca ovina, var. rubra.	Theobald (1917), Prior (1976).
Festuca pratensis Huds.	Gair (1953), Hill (1971), Muller (1968).
Festuca rubra L.	Stroyan (1969), Dean & Luuring (1970), Hill (1971), Prior (1976).
Festuca spp.	Stroyan (1952), Janson (1959).
Holcus spp.	Prior (1976), Hill (1971).
Lolium multiflorum Lam.	Gair (1953), Hill (1971).
Lolium perenne L.	Dean & Luuring (1970), Prior (1976).
Lolium persicum Boiss. & Hoh.	Shaw (1964).
Lolium spp.	Stroyan (1952), Janson (1959), Shaw (1964), Singer *et al.* (1976).
Oats	Hill (1971), Jones & Dean (1975), Prior (1976), Janson (1959).
Phleum pratense L.	Anon. (1945), Cameron (1945), Shaw (1964), Hill (1971).
Phleum spp.	Anon. (1950), Janson (1959).
Poa annua L.	Gair (1953), Dean & Luuring (1970).
Poa pratensis L.	Hille Ris Lambers (1947).
Poa spp.	Stroyan (1952), Hill (1971), Singer *et al.* (1976).
Wheat	Janson (1959), Hill (1971), Prior (1976), Hand (1982).

Table 3. Host range of *M. festucae*

Overwintering viviparously may be advantageous to this species in springs following mild winters, as it allows a rapid increase in numbers with the spring rise in temperature (Hill 1971; Vickerman 1977). Peak numbers of M. festucae (Vickerman 1977) and alate arrival dates (Sparrow 1974) have been correlated with spring temperatures i.e. warmer springs will bring an earlier alate arrival and higher peak numbers. This relates to information of three severe outbreak years 1949, 1957 and 1974 which are known to have followed a mild winter and an early spring (Anon 1950; Janson 1957, Vickerman 1977, 1978).

Winter and spring weather has been shown to influence an early build-up of cereal aphid numbers but this is also accompanied by a corresponding increase in natural enemies. The warmer weather causes this early appearance of natural enemies which will have abundant prey and hence will keep the cereal aphid populations in check, and by the time they have recovered the cereals will be at a growth stage unsuitable for reproduction (Vickerman 1977).

M. festucae is usually first to be caught in suction traps in the spring (Dean 1973; Robert and Rouze-Jouan 1975, 1976; and Taylor et al. 1977), although mostly in low numbers. This however may be an under-estimation of the timing and numbers of M. festucae flying in spring since higher numbers have been recorded from a suction trap operating at the height of 1.0M as opposed to the 12.2M height of the others (A'Brook 1973). High numbers of M. festucae cerealium can build up very early in spring e.g. up to 6,000m^{-2} on grassland in April 1974 (Vickerman 1976), and severe damage has been reported as early as April (Janson 1957; Anon 1945). The early arrival of M. festucae provides a prey source for many parasites and predators, and they can subsequently cause the population to collapse (Anon 1950; Gair 1953; Hill 1971; Jones & Dean 1975; Singer, Smith, Kendall, March, Mathias, Halfacree 1976; Vickerman 1976), leaving abundant predators and parasites in the grass and cereal crops. These natural enemies may then be present in sufficient numbers to control the later arriving, more harmful cereal aphids.

Natural enemies reported to be responsible for the population

collapse of M. festucae are the parasites Aphidius spp. (Jones and Dean 1975), in particular Aphidius avenae Hal., Aphidius granarius Marsh. (Arthur 1944, 194), Aphidius fabarum Marshall, Asaphes vulgaris (Wlk) and Aphelinus spp. (Gair 1953). The fungal pathogens Entomorpthora planchoniona Corru, E. aphidis Hoffman and E. thaxteriana (Petch) Hall and Bell (Jones and Dean 1975). The only reported predators are the Coccinellidae (Singer et al. 1976; Arthur 1944).

After the collapse of M. festucae cerealium populations in June and early July, little is known about the movement and dispersal of this aphid. The number of alatae caught in suction traps after July decreases markedly and remains low, there being no later autumnal peak as in M. dirhodum and to a lesser extent in S. avenae (Taylor et al 1980). The hosts of this aphid and the reason for such low numbers during this period are unknown, but the numbers of viviparae remain low throughout the winter until the build up once again the following spring.

The relevance of a study of M. festucae cerealium

M. festucae cerealium then is an important aphid to consider for two reasons; firstly it causes damage to grassland and has the potential to damage cereal crops; and secondly it may, through providing a prey source for natural enemies in early spring, be instrumental in preventing outbreaks of other aphids, in cereals during the summer.

Because M. festucae cerealium can cause damage to grassland (Vickerman 1976) it is important to know which type of grassland is most likely to be affected. There are three classes of grassland; by pasture, permanent pasture, rough and hill grazings (Clements 1980; Holmes 1980) with a major characteristic grass species associated with each. A knowledge of the susceptibility of grass species to infestation by M. festucae cerealium is required.

Ryegrass accounts for over 80% of seed sown in the United Kingdom (Williams 1980). M. festucae cerealium has been recorded in numbers as high as $20{,}000m^{-2}$ in ryegrass (Vickerman 1977) and yet the effect of M. festucae cerealium on herbage yield is not known. In years when

outbreaks have occurred an effective control measure for M. festucae on infested pastures has been to cut the grass for silage and hence mechanically remove the aphids (Edwards and Heath 1964). After this initial cut the aphids do not appear to increase substantially in numbers.

M. festucae cerealium is rarely found in large numbers in cereal crops compared with the thousands m^{-2} often encountered in grassland. Little is known of the influence of resistance in wheat on M. festucae cerealium and the effect on yield if and when an outbreak did occur.

M. festucae cerealium reaches peak population levels earlier in spring than the other cereal aphids and hence it may provide an important early prey course for natural enemies. This may be of use for integrated control measures, if conditions can be manipulated to provide a suitable environment for both M. festucae cerealium and its natural enemies. The survival of overwintering populations of M. festucae cerealium and their ability to reproduce at relatively low temperatures on a suitable host growth stage may be factors contributing to the early spring peak.

Little work has been done with M. festucae cerealium and for this reason it is important that this project provides some background life cycle information as well as answering more pertinent questions about the role of this aphid in the grass and cereal systems.

The aims of this project are to determine:-

1. How the early-spring population peak of M. festucae cerealium and its subsequent decline is influenced by the host plant and by temperature.
2. The 'preference' of M. festucae cerealium for selected agricultural grasses and cereals, and their relative importance in its life-history.
3. The influence of the host plant and temperature on morphological characteristics of M. festucae cerealium and to compare morph reproductive biology.
4. The extent to which yield can be reduced by M. festucae cerealium (a) in grassland and (b) by an early infestation in wheat.

CHAPTER TWO

MATERIALS AND METHODS

THE INSECT MATERIAL

A single clone of Metopolophium festucae ssp. cerealium was used for all experiments. All the aphids were derived from a single specimen collected from Burgate Manor Farm, Fordingbridge, Hampshire, during August 1978. The aphids were maintained on three different host plants; wheat cvs Hobbit and Bouquet and Lolium perenne cv. Cropper.

A D.F. Torsion Microbalance, with a sensitivity of 5 µg, was used for all aphid weighings.

THE PLANT MATERIAL

Seedlings used for cultures and experiments were sown in John Innes No.2 compost. Culture and experimental plants were grown in a greenhouse which was maintained at a temperature of 20 with an 8°C range, a minimum of 16 h daylength was maintained with ark lighting when necessary.

Host plant growth stage

The decimal code for the growth stages of cereals (Zadoks, Chang and Konzak 1974; Tottman and Makepeace 1979) was used to describe the growth stages of the grasses. The order of growth stages in grasses is different from that in cereals but the description of events are the same.

The following is a list of all plant material used:-

Wheat	cv.	Bouquet
Wheat	cv.	Hobbit
Oat	cv.	Maris Quest
Lolium perenne	cv.	Cropper
Lolium perenne	cv.	Reveille Tetraploid
Lolium multiflorum	cv.	R.U.P. Lemptal
Lolium multiflorum	cv.	Sabalan Tetraploid

Phleum pratense	cv.	S.48
Festuca arundinacea	cv.	Conway
Festuca pratensis	cv.	S.215
Festuca rubra	cv.	Echo
Dactylis glomerata	cv.	Cambria

CULTURE MAINTENANCE

Culture seedlings were grown in 12 cm pots and were used at growth stage 12 to 13,21 as defined by the decimal code (Zadoks et al. 1974).

The aphids were transferred, with a pooter, to fresh seedlings every seven days.

The aphids and seedlings were kept in perspex boxes in a culture room based on the design of Scopes, Randall and Biggerstaff (1975). The temperature was maintained at 20°C with a range of 2°C and an illumination of 5.8 Wm^{-2} was supplied by 8 'Warmwhite' fluorescent tubes for a 16h photoperiod.

To maintain similar densities on all three hosts and hence control to some extent the influence of crowding on morph determination, a specific volume of aphids were transferred to a known area of seedlings, each week.

The growth rate of the seedlings, of all three hosts used for cultures, was determined by measuring the total leaf area of ssedlings in a culture pot, each day, for a seven day period. The number of aphids per unit area of seedlings was also determined each day. Hence the change in aphid numbers and plant growth rate was estimated throughout the seven days so that for any given day there would be a corresponding aphid density. This provided a standard by which culture densities were compared and maintained over many months.

To check whether similar densities were being maintained, a culture pot removed and the aphid density per unit area of seedling was measured and compared with the standard density for that day in the week. If there was a large difference, the starting volume for the following transfer

would be changed accordingly. In this way aphid density and hence the influence of crowding on morph determination was controlled.

STATISTICAL ANALYSIS

All the data were, where appropriate, tested for a normal distribution using the Kolmogorov-Smirnov one-sample test at P = 0.05. Normality should be assumed unless it is stated otherwise.

CHAPTER THREE

3.1 THE FEEDING POSITION OF APTERAE

3.1.1 The feeding position of apterae on seedling L. perenne

Twenty-five seedlings of L. perenne cv. Cropper were grown in five 13 cm-diameter pots to growth stage 12 (Zadoks et al. 1974), and were then placed in a growth room at 20°C with a range of 3°C. Twenty-five adult apterae were taken from the stock culture of aphids on wheat cv. Bouquet, and an aptera was placed at the base of each seedling. They were then left for 24h. After this time the feeding position of the apterae on the seedlings was recorded. The seedlings were divided into the following feeding positions (I) first unfolded leaf (II) second unfolded leaf (III) third, emerging, leaf (IV) emerging tiller.

Statistical analysis

A chi-squared analysis compared the numbers of apterae at each feeding position.

3.1.2 The feeding position of apterae on leaves of wheat

A wheat (cv. Bouquet) seedling was grown singly in a 13 cm pot after having been vernalized as seed at 5°C for 10 weeks (Cooper 1960). At ear emergence (G.S. 50-51) the wheat was placed in a 20°C growth room.

Thirty apterous adults were taken from the stock culture of aphids on wheat cv. Bouquet and placed at the base of the wheat plant. The pot was placed in a tray of water to prevent the aphids walking off the experiment.

The aphids were left for 24 hours and then their position on wheat was recorded.

Statistical analysis

A chi-squared analysis between the number of apterae at each feeding position was carried out.

3.1.3 The feeding position of apterae on 10 week-old *L. perenne*

A seedling of *L. perenne* cv. Cropper was grown in a seed tray for 10 weeks (G.S. 12, 26) and then placed in a 20°C growth room.

Fifty-five apterae were taken from the stock culture on wheat cv. Bouquet, and placed at the base of the *L. perenne* plant. They were left for 24 hours, and then the feeding position of the apterae was recorded.

Statistical analysis

A chi-squared analysis between the number of apterae at each feeding position was carried out.

3.1.4 The feeding position of aphids on the adaxial and abaxial leaf surfaces of *L. perenne*

Aphids were monitored in clip cages of the design of Williams (1983) to leaves of *L. perenne* cv. Cropper as part of field work (section 3.3.2).

Two hundred cages were placed so the adaxial surface of the leaf was uppermost (normal leaf position) and seventy-five cages were placed with the abaxial leaf surface facing upwards. The numbers of apterous and alate adults, fourth instars, and younger instars on the adaxial and abaxial leaf surfaces were counted.

Statistical analysis

A chi-squared analysis of the relative numbers of aphids on the adaxial and abaxial leaf surfaces, when the leaf was positioned (I) normally and (II) the leaf is inverted, was carried out.

3.2 ANTIBIOSIS EXPERIMENTS

The antibiosis experiments were performed on two growth stages, seedlings (G.S.12 to 13, 21) and plants with elongating stems (G.S. 32), except for L. perenne cv. Cropper for which there was an intermediate growth stage (G.S. 26).

The experiments were carried out in a growth room at a temperature of 20°C.

3.2.1 Seedlings

The grass seedlings under test were L. perenne cvs. Cropper and Reveille tetraploid, L. multiflorum cvs R.V.P. Lemptal and Sabalan tetraploid, P. pratense cv. S.48, F. arundinacea cv. Conway, F. pratensis cv. S.215, F. rubra cv. Echo, D. glomerata cv. Cambria, and the wheat cv. Bouquet and Hobbit and Oat cv. Maris Quest. In each case there were five seedlings per 13 cm diameter pot and only one aphid on each seedling. Seedlings were used between the growth stages 12 to 13, 21, i.e. the second leaf unfolded to third leaf unfolded.

Adult alatae, from a culture maintained on wheat cv. Bouquet, were confined to the second leaf, of the grass under test, by a clip cage (Noble 1958). Each clip cage was held by a wire support.

The adult alatae which had reproduced were removed after 24 hours and nymphs in excess of four per clip cage were removed. The remaining nymphs were placed in individual clip cages after six days, and reared singly to adults.

The nymphal development time and mortality were recorded. The development time is considered here to mean the time from birth to first reproduction.

The number of adult apterae and alatae were recorded and any alatae were then discarded. The adult apterae were removed, weighed and then caged on a fresh second-leaf stage seedling. The number of nymphs produced by each aptera was recorded every three days; the nymphs were then discarded. The adults were transferred to fresh second-leaf-stage (G.S. 12) seedlings every 6 days. The number of nymphs produced by

each adult was recorded for a period of 16 days and then each aptera was removed and reweighed.

Statistical analysis

One-way analysis of variance of development time, adult weight and seven-day fecundity for all twelve Gramineae was carried out, preceded by Bartlett's test for homogeneity of variance. An extension of Duncan's Multiple Range Test for unequal numbers of replicates (Kramer 1956) was carried out.

3.2.2 10 week old (G.S. 26) *L. perenne* cv. Cropper

The experiment was carried out as in 3.2.1 except that the aphids were caged to the lowest green leaf of the main stem.

3.2.3 Stem elongation (G.S. 32)

The host plants under test were *L. perenne* cv. Cropper, *D. glomerata* cv. Cambria, *L. multiflorum* cv. R.V.P. Lemptal, and wheat cv. Bouquet. In each case there were one or two plants to each (13 cm. diameter) pot. The grasses and cereals were used for the experiment between the growth stages 32 to 41.

The experiment was carried out as in 3.2.1 except that the aphids were caged to the lowest green leaf of the elongating stem. In all other ways the experiment was similar 3.2.1.

Statistical analysis

A one-way analysis of variance of the variables development time, adult weight and seven day fecundity for all four host plants was carried out, preceded by Bartlett's test for homogeneity of variance. t-tests using pooled variance estimates were carried out.

A comparison of aphids reared on different growth stages of *L. perenne* cv. Cropper

A one-way analysis of variance of the variables development time,

adult weight and seven-day fecundity for aphids reared on seedlings, was carried out on 10 week old seedlings and stem elongating plants. This was preceded by Bartlett's test for homogeneity of variance. t-tests using separate variance estimates for development time, and pooled variance estimates for adult weight and seven day fecundity were carried out, followed by a regression analysis of seven-day fecundity (y) with adult weight (x) for all three growth stages. A ∞-variance analysis of the regressions was then used to compare the residual variances, slopes and elevations of the reproduction/weight relationship of the three growth stages.

A comparison of aphids reared on the different growth stages of D. glomerata cv. Cambria, L. multiflorum cv. R.V.P. Lemptal, wheat cv. Bouquet.

The statistical analyses for these three host plants were the same as for L. perenne, except that there were only two growth stages. The t-tests were not necessary since the F and t-test are related for only two samples i.e. $F = t^2$.

3.3 A FIELD COMPARISON OF APHID PERFORMANCE FOR APHIDS REARED ON WHEAT, CUT AND UNCUT L. PERENNE

3.3.1 Winter work

Seeds of L. perenne cv. Cropper were sown in ten (13 cm diameter) pots and grown in the Greenhouse to G.S. 12. On September 15 1981 these pots were placed outside to acclimatize for two weeks before aphids from the stock culture were caged to their second leaves. At weekly intervals any nymphs produced were transferred to individual clip cages on fresh seedlings similarly treated.

In early September a 10 x 15M plot was prepared for broadcast sowing of 4 kg of L. perenne cv. Cropper. The seed was lightly raked into the soil. A single application of a broadleaf herbicide was made on 24 March 1982 (ethylester of 2,4-D equivalent to 64 ox 2,4-dichlorophenoxyacetic acid). At this time an area of 450 m^2 was prepared and

wheat cv. Bounty was sown in rows approximately 30 cm apart.

On 6 November 1981 the grass leaves were considered large enough for clip cages to be attached without damage. 60 acclimatised M. festucae cerealium were individually caged to the most recent completely-emerged leaves of the grass i.e. the newest leaves where the ligule was present. A further 100 aphids of mixed morph and instar were caged singly between 10-20 November 1981. These provided the colony from which the subsequent experimental population was built up.

Every 3 days the adult morph, the number of nymphs produced by each adult and the developmental stage (either instar or adult) of each caged aphid were recorded. Approximately every 3 days nymphs produced by the adults of either morph were transferred with a paintbrush to individually-caged leaves. Each aphid was numbered so that lines of descent could be followed.

Recordings of adult reproduction, mortality etc., were made every day, each batch being recorded at 3-day intervals until the 26 April 1982, which marked the end of the 'overwinter' period. Then recordings of all aphids were made on the same day at 3-day intervals.

This overwintering work was unsuccessful due to too small a sample size of aphids. The nymphal mortality after transfer to individual cages was almost 100% (presumably due to interference and low temperature) so that a sufficiently large population could not be established.

3.3.2 Summer work

3.3.2.1 Wheat

On the 17 April 30 adult apterae, 12 adult alatae and 63 first instar nymphs, which had previously been reared on the adjoining L. perenne plot, were transferred to individual clip cages on wheat. Each cage was attached to a newly-unfolded leaf.

Every 3 days the adult morph, the number of nymphs produced by each adult, the development stage (either adult or nymph) of each aphid and aphid mortality were recorded. For the first 15 days any nymphs produced

were transferred with a paintbrush to individual clip cages. Subsequent to this only the number of nymphs required to maintain the sample size were transferred, at any other time the nymphs were removed with a paintbrush and discarded.

The growth stage of the wheat was measured and recorded nine times between 13 April and 19 July. With the onset of stem elongation the criteria for the position of the clip cages changed. A number of aphids were still caged on the newly-emerged leaf, and this continued until the flag leaf emerged. The other aphids were caged on the lowest green leaf. Hence the aphids were, once the ear had emerged, either caged on the flag leaf or the lowest green leaf, of a stem, but only one clip cage per stem.

The temperature was recorded every hour on a Grant's temperature recorder with thermistors placed both in a clip cage and under a foil cover (to measure air temperature) at flag leaf height and at 15 cm above ground level.

The experiment was curtailed on 19 July when all the leaves on the wheat were either dead or dying.

3.3.2.2 Uncut L. perenne

This work was a continuation of the overwintering work. Aphids were clip caged to newly emerged leaves, excluding elongating stems, from 26 April until 3 September.

Growth stage was measured up to and during the first heading. Subsequent to this it was measured in terms of sward height and proportion of flowering. Temperature was measured as described above.

3.3.2.3 Cut L. perenne

A 15 x 15 M strip of the L. perenne plot was cut to a height of 5 cm on 27 May, 12 July and 26 August. Immediately after each cut a number of adults and nymphs were caged to the cut leaves. At 3-day intervals the morality, adult morph, the number of nymphs produced, and the development stage of the aphids were recorded. Also any nymphs

which were produced were transferred with a paintbrush to individual clip cages attached to cut leaves. Their development and mortality were monitored.

The grass height was used as a measure of growth stage and was measured 8 times between 28 May and 4 September.

Clip cage and air temperature were measured at cage height as described above.

Statistical analysis

The intrinsic rate of increase (r_m) (Birch 1948) was used to compare the performance of the aphids on each of the host types and compare performance between the host types. Standard errors of the r_ms were obtained by using the Jackknife Method (Bissell 1977).

3.4 THE INFLUENCE OF CUT GRASS AND TEMPERATURE ON THE REPRODUCTION OF APTERAE

The experiments were carried out in the growth room, at 20°C 360 seedlings of L. perenne cv. Cropper were grown to G.S. 12 and then 180 seedlings were cut 5 cm above soil level. The cuttings were removed. A similar watering regime was used for both cut and uncut seedlings.

3.4.1 The influence of growth stage on reproduction of apterae

20 adult alatae were individually clip caged to the second leaf of an uncut seedling. The procedure for rearing apteriform nymphs was the same as in 3.2.1. Once adult, which was defined by initial reproduction, the aphids were transferred to the second leaf of a freshly-cut seedling. Adult mortality and reproduction were monitored daily and nymphs removed at 3-day intervals for one week. The experiment was compared with one run concurrently using uncut seedlings.

3.4.2 The influence of temperature on development time and weight of aphids reared on cut seedlings

Twenty-four hours previous to cutting the seedlings a further 20

alatae were individually caged on the then uncut second leaf of the L. perenne seedling. Prior to cutting the seedlings, the alatae were removed leaving the nymphs. Again, as in 3.2.1, after six days the nymphs were placed in individual clip cages on cut seedlings, and reared to adults. Nymphal mortality and development time were recorded.

This experiment was run concurrently with another using uncut seedlings.

3.4.3 The influence of temperature and a comparison of development time and weight for aphids reared on cut and uncut seedlings

The experiments 3.4.1 and 3.4.2 were repeated at 15°C and 25°C (with a range of 1°C) with a 16 hour photoperiod in a LEEC cabinet to determine the influence of temperature and cutting on the development and reproduction of M. festucae cerealium.

3.4.4 The influence of temperature on the reproduction of aphids reared on cut and uncut seedlings

Three weeks after the cutting of seedlings the experiment at 20°C was repeated on the now older cut and uncut plants to determine whether the effect of the initial cut had persisted. The aphids were caged on the leaf which had been emerging at the time of the cut. The aphids' development time, adult weight and reproduction were recorded.

Statistical analysis

A one-way analysis of variance, Bartlett's test for homogeneous variance, and t-tests were used to analyse the (I) growth stage effects at 20°C (II) influence of temperature on the development time and adult weight for aphids reared on cut seedlings (III) influence of temperature and a comparison of development time and adult weight for aphids reared on cut and uncut seedlings, and (IV) the influence of temperature on the reproductive performance of apterae reared on cut and uncut seedlings.

CHAPTER FOUR

4.1

Fourth instar alatae were taken from the culture and each was placed in a clip cage, on the second leaf of a seedling of wheat cv.Bouquet. The aphids were observed every 24 h at 16.30 h and any which had moulted were set aside for an experiment the next morning. An experiment was conducted only when there were a minimum of 30 alatae.

At the time of an experiment the minimum age of each adult alate could be 24 h and the maximum possible 44 hours i.e. each aphid was one day old.

4.1

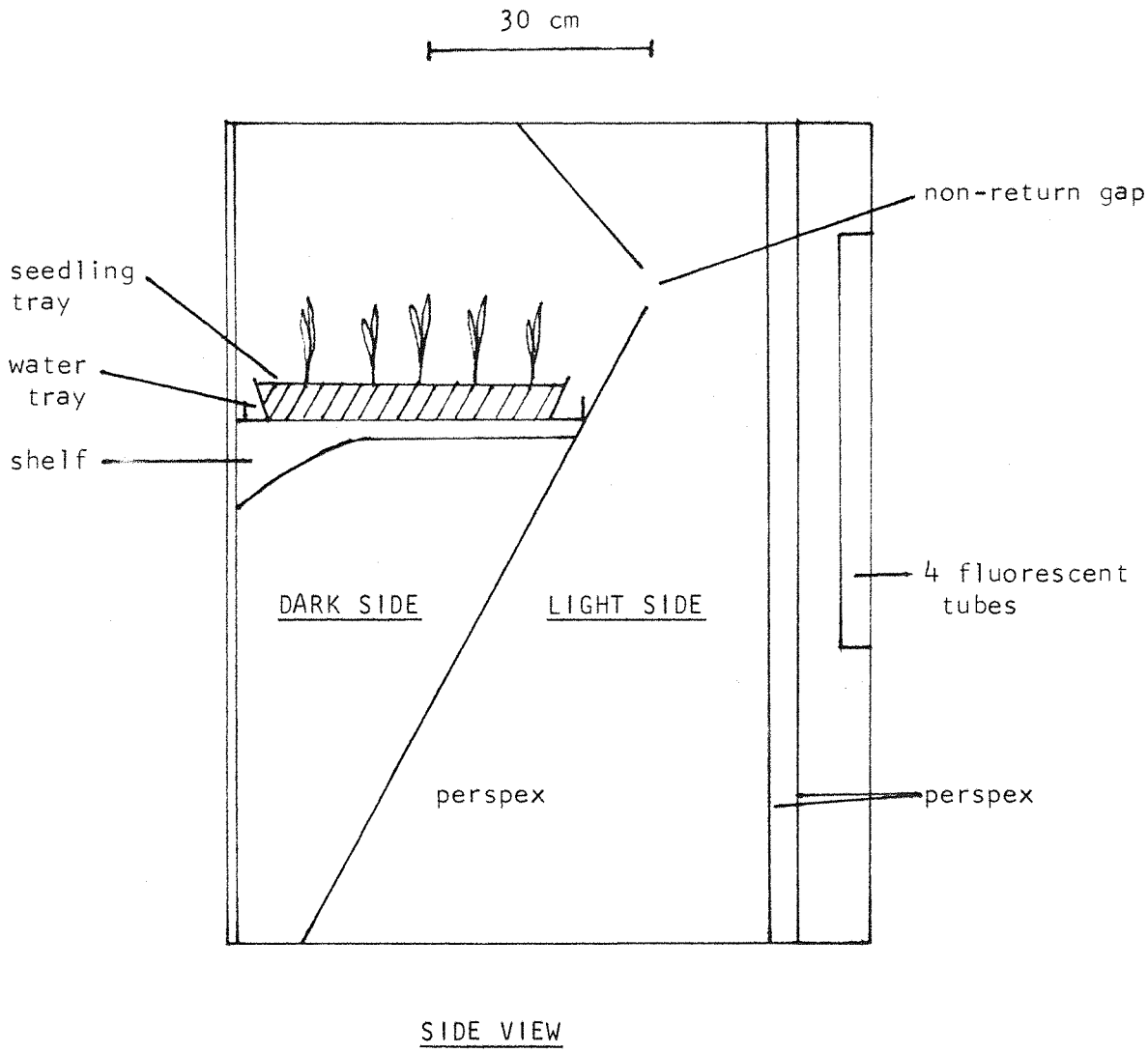
4.1.1 Antixenosis experiments

The number of nymphs produced by each alate whilst caged was recorded. The alatae were maintained under a reversed light cycle and were transferred from the clip cages to the experimental plant under red light. Alatae were removed from the clip cage by allowing them to drop from the cage onto a hand. They were then allowed to walk freely from the hand onto the experimental plant. Any excess interference of the alatae influences their settling behaviour (Kennedy and Booth 1963); this method of transfer was considered to cause least disturbance.

Thirty experimental seedlings were grown in a seed tray (arranged in 6 rows and 5 columns), and were used when the second leaf had unfolded (G.S. 12).

To prevent the alatae walking off the seedlings tree grease was applied around the base of each stem. Alatae were observed to turn around and walk back up the stem whenever coming into contact with the grease. Seedlings were assigned a number between 1 and 30 and each alata randomly allocated a seedling. When each seedling had an alata settled on it the seedling tray was placed in the darkened flight chamber (Fig.1), based on a design by Dixon (1969). The chamber had a 16h photoperiod, the eight hours' darkness allowed time for the aphids to settle.

Fig.1 Flight chamber, based on a design by Dixon (1969)



Twenty-four hours later any aphids which had flown through the non-return gap were collected. The alatae still on the seedlings were removed and the number of nymphs they had produced was recorded. The total number of nymphs left behind by the aphids which had flown was also noted. All alatae were weighed.

The experimental host plants were:

F. rubra	cv. Echo
F. arundinacea	cv. Conway
L. multiflorum	cv. R.U.P. Lemptal
Oat	cv. Maris Quest
L. perenne	cv. Cropper
Wheat	cv. Bouquet

Statistical analysis

(I) Antixenosis experiments: A chi-squared analysis of numbers of alatae flown/not flown for the six emperimental plants was used.

(II) Flight, reproduction and adult weight: All samples of the variables TOTN, EXN, WEIGHT, were assessed by the Kolmorgorov-Smirnov one-sample test for a normal distribution, where TOTN is the total number of nymphs produced by an alate, EXN is the number of nymphs left behind on the experimental plant by alatae whether they have flown or not and WEIGHT is the adult weight after the experiment. EXN were tested using the Mann-Whitney U test for independent samples. The samples of the other variables were analysed with one-way analysis of variance, Bartlett's test for homogeneous variances and t-tests which used a pooled variance estimate. The multiple range test (Kramer 1956) was not valid since the differences between sample sizes were too great and there would have been an increased probability of a significant difference with a subset of ranked means classed as homogeneous by this test.

4.1.2 The influence of ovariole number and large embryo number on flight

The experiment was the same as 4.1.1 except that the experimental seedlings were grown three to a 5 cm pot. Seedlings were assigned a number between 1 and 60 and each alate was randomly allocated a seedling. Each pot was then placed in order of seedling number into the darkened flight chamber. The aphids were transferred from the clip cages to the experimental plants in daylight.

Aphids were reared on wheat cv.Hobbit and were flown from wheat cvs Hobbit and Bouquet, and L. perenne cv.Cropper. Alatae were also reared on wheat cv.Bouquet and flown from the same cultivar.

Ovariole and large embryo dissections: The dissection entailed holding the aphid by the metathorax with one pair of fine forceps and applying distilled water over the abdominal area. The cauda was then gently pulled away using another pair of fine forceps. In this manner the reproductive system was obtained undamaged and the number of ovarioles and large embryos could be easily counted. Large embryos were those embryos having pigmented eyes.

Statistical analysis

Comparisons were made between all flown aphids, the unflown aphids and flown aphids with unflown aphids for the variables adult weight, large embryo number (LEN) and ovariole number. The following tests were used: A Kilmogorov-Smirnov one-sample test for normal distribution, a Mann-Whitney U-test for ovariole number, One-way analysis of variance and Bartlett's test for homogeneity of variances and t-tests were also used with both separate and pooled variance estimates for weight and LEN.

4.2 THE INFLUENCE OF THE HOST PLANT ON SETTLING BEHAVIOUR

This experiment is similar to the experiment by Blackman (1974).

Fourth instar alatae were taken from the culture of Wheat cv.Bouquet and each placed in a clip cage, on the second leaf of a wheat seedling cv. Bouquet. Those alatae which had moulted on the evening before the

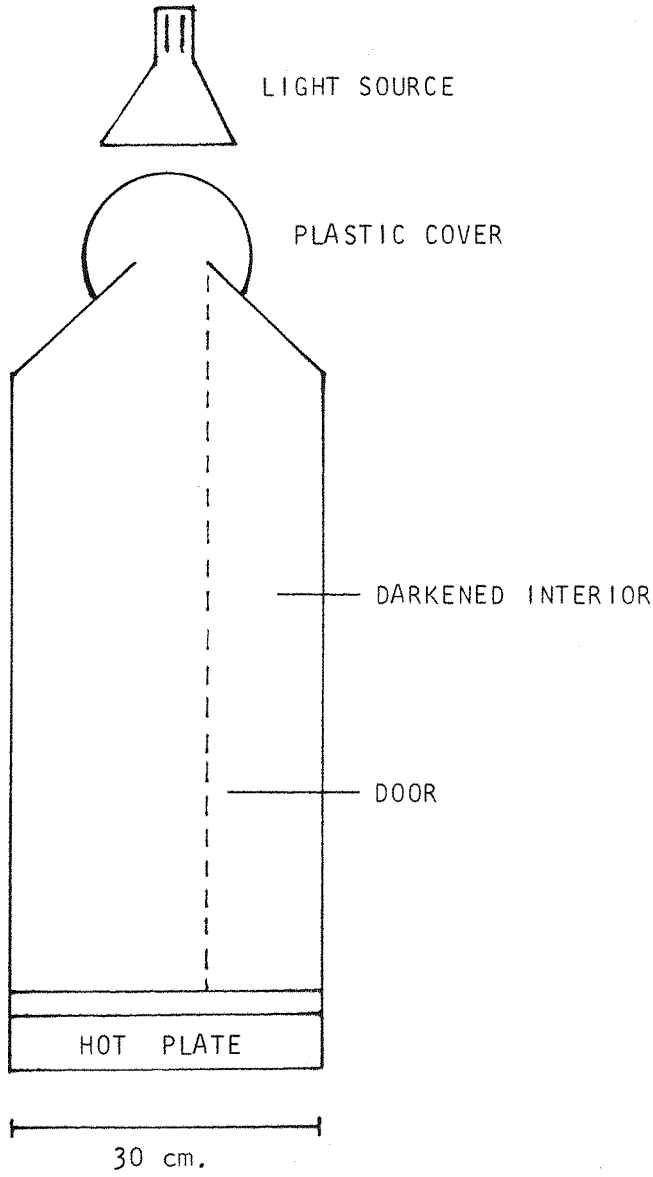


Fig. 2 The chamber which was used for pre-settling flights of alatae. The alatae were dropped onto the warm base from which they would fly to the light. They were collected from the plastic cover

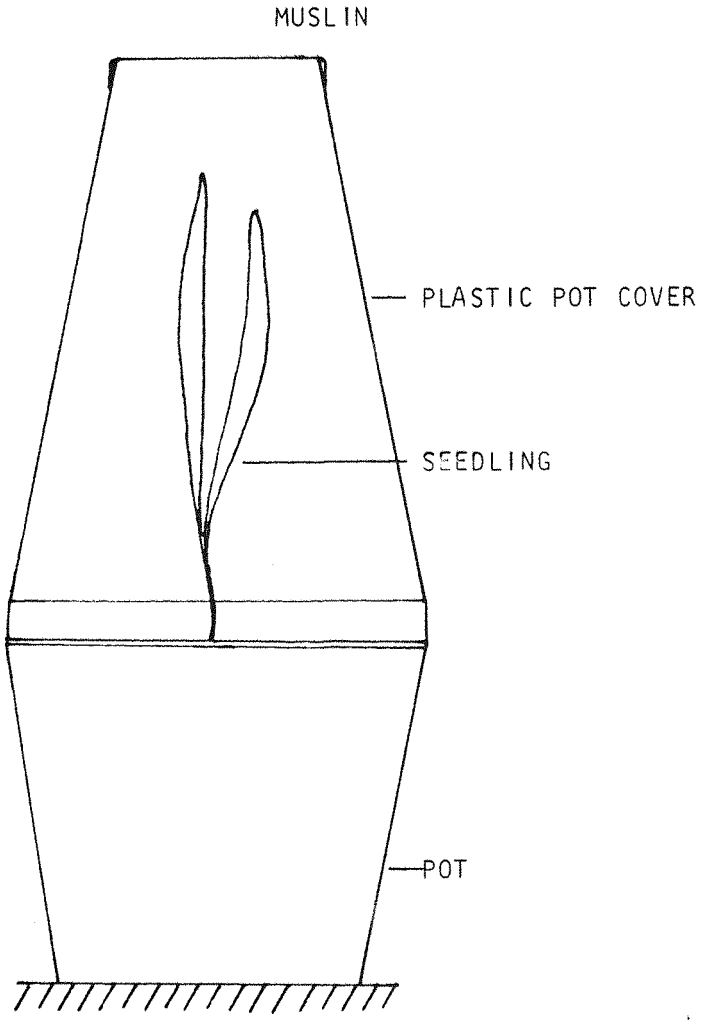


Fig.3 Cylinder cage used for settling experiments (based on a design by Blackman 1974)

experiment were used the next day. Each alate was removed from the cages with a paintbrush and was dropped to the heated base of the chamber (Fig.2). The alatae flew to the illuminated cover and were collected there. They were then induced to fly three more times.

The alatae were then placed in the inverted plastic pot cover (Fig.3) which was then turned upright over the seedling under test.

Three pots with 5 alatae in each was observed at any one time. Each pot contained a single seedling, either L. perenne cv. Cropper or wheat cv. Bouquet.

The alatae were watched continuously and when any settled on a seedling then the number of probes which were made, the duration of probes, walking time and time stopped, were recorded on an event recorder.

Statistical analysis

A chi-squared analysis of the number of probes made on L. perenne and wheat was carried out. A two-way analysis of variance was used to compare the relative times spent probing, walking or stopped on each of the seedlings.

CHAPTER FIVE

5.1 MORPHOMETRICS OF APTEROUS AND ALATE VIRGINOPARAE

5.1.1 Procedure for maceration and clearing aphids

The recommended procedure (Eastop and van Emden 1972) was as follows: the aphids were transferred to a specimen tube and boiled in 90% alcohol for 10 minutes, with a piece of porous pot. The alcohol was decanted off and 10% potassium hydroxide was added and boiled for 10 minutes. The decanted alcohol was re-added, and the resulting liquid poured off; the aphids were then rinsed with fresh alcohol, and gently warmed in a solution of 50 : 50 (w/w) chlorohydrate : crystaline phenol melted together, for 30 minutes. The specimens were stored in this solution until mounted on slides.

The slides were prepared as follows: the clearing solution was drawn off with filter paper. The aphid was set up and a drop of glycerol applied before a cover slip was lowered over the specimen. The slide was then placed in an oven at 60°C for 24 hours.

Aphids were maintained on wheat cv. Bouquet at three temperatures and photoperiods: 20°C, 16h daylength, 10°C, 13½h daylength and 5°C, 10h daylength. A culture was also maintained on wheat cv. Hobbit at 20°C, 16h daylength.

Thirty adult apterae and alatae were taken from each of the cultures and prepared as above. The following morphological characters were measured:-

Antennae:	total length, I + II segment length, III, IV, V and VI segment length, base and process terminalis length, III width and number of rhinaria on III segment.
Stylet:	length of apical rostral segment.
Hind leg:	length of femur and length of tibia, length of I and III tarsal segments.
Siphunculi:	length and width.
Cauda:	length.

Statistical analysis

Canonical Discriminant Function Analysis (CDFA) (Nie, N.H., Hull, C.H., Jenkins, J.F., Steinbrenner, K., Bent, D.H. 1975), between aphids reared under different temperature and light regimes, and aphids reared on two different wheat cultivars was carried out.

5.2 FIELD COLOUR MORPH DATA

These data were kindly provided by Dr W. Vorley. The aphids were collected and identified by Dr Vorley as part of routine sampling for cereal aphids during the summer of 1981. The aphids were taken from crops of L. perenne and wheat (cultivars unknown). They were separated according to colour of the morphs and crop plant.

Statistical analysis

Chi-squared analysis was applied to numbers of red and green aphids

within a crop and a comparison of the relative numbers of each colour morph between crops.

CHAPTER SIX

6.1 MORPH DETERMINATION; THE INFLUENCE OF APHID DENSITY

Seedlings of L. perenne cv. Cropper were grown 5 per 13 cm diameter pot.

Alatae were taken from the stock culture of wheat cv. Bouquet and clip caged to the second leaf of the L. perenne seedlings. After 24h the alatae and all but one of the nymphs which had been produced, were removed. The nymphs were reared to adults, all of which were apterae. These apterae were allowed to produce either 1, 2, 4, 6, 8, 10 or 12 nymphs and were then removed. There were approximately twenty replicates for each density class e.g. there were 20 cages containing 4 nymphs.

Each aphid was transferred to a new seedling every 5 days. Mortality was monitored every day and the final density of aphids per cage at adult moult was recorded. The morph and weight of approximately 20 adults for each density class were recorded. These aphids were called 'generation one', i.e. the first generation experiencing crowded conditions.

An adult from each cage was clip caged to a fresh L. perenne seedling and allowed to produce the same number of nymphs as the density it had experienced during nymphal development, e.g. an aptera having been reared with 3 other nymphs would be allowed to produce 4 nymphs before being removed. These aphids became the second generation of nymphs reared under crowded conditions at densities of 2, 4, 6, 8, 10 or 12 aphids per clip cage. Again the mortality during development, final density at adult moult, numbers of apterae and alatae, and adult weights were recorded.

The area of leaf within 20 clip cages was measured.

Statistical analysis

A comparison of % alatae produced between two generations reared under different density regimes; the starting and finishing densities

were compared with the proportion of alatae produced for Generation 1 and 2 by chi-squared analysis.

The proportion of alatae produced in relation to starting density and final density for Generation 1 and 2 was determined; A regression analysis of the proportion of mothers producing alatae nymphs (y) and rearing density (x). A regression analysis of the proportion of nymphs which were alatae(y) and rearing density (x).

The influence of density on adult weight of apterae and alatae. A one-way analysis of variance of aptera and alata weight in relation to density. The relationship between adult weight and rearing density: A one-way analysis of variance on the weights of all apterae of generation 1 was carried out. This was repeated for alatae of generation 1, apterae of generation 2 and alatae of generation 2. Multiple range tests (Kramer 1956) were used to determine whether any mean weights were significantly different. Multiple range tests were used in preference to t-tests due to the large numbers of samples being compared.

A regression analysis between adult weight and density was performed. A covariance analysis compared the residual variances between apterae of generation 1 and 2, a comparison was also made between alatae of generation 1 and 2.

6.2 A COMPARISON OF THE REPRODUCTION OF APTEROUS AND ALATE VIRGINOPARAE

60 apterae and 60 alatae of generation 2 were weighed and individually clip caged to the second leaf of L. perenne seedlings (G.S. 12). The number of nymphs produced by each aphid was recorded daily for 20 days.

Statistical analysis

A Kolmogorov-Smirnov one sample test was used. A Mann-Whitney U-test for independent samples was used to compare apterae and alatae weight. A one-way analysis of variance was performed between apterae and alatae weight and fecundity over 7 days, 10 days, 15 days and

20 days. Bartlett's test for homogeneity of variances was used for all variables. t-tests using separate variance estimates compared apterae and alatae weight and reproduction. Regression analysis of fecundity with weight and a covariance analysis with apterae and alatae as covariates were performed.

CHAPTER SEVEN

7.1 THE INFLUENCE OF TEMPERATURE AND PHOTOPERIOD ON NYMPHAL DEVELOPMENT TIME, ADULT WEIGHT AND REPRODUCTION

The temperatures and photoperiods chosen for this study correspond to those mean temperatures and photoperiods experienced in the field during early April, i.e. 10°C, 13½h daylength, mid May 13°C, 16h daylength and June 15°C and 16 hrs daylength.

LEEC cabinets were used and the temperature range was as follows: at 10°C ± 1°C, 13°C ± 1½ and 15°C ± 1°C.

Both the experimental and culture plants and aphids used at low temperatures were acclimated. All plants used for the 15°C experiment were grown at 15°C and 16h daylight. The aphids were also cultured at this temperature on wheat cv. Bouquet. The experimental host plant was L. perenne cv. Cropper. The wheat culture seedlings for the 10°C experiment were first grown at 15°C for 10 days and were then transferred to a 10°C cabinet for a further 6 days before aphids were placed on them. Experimental L. perenne seedlings were grown at 15°C for 20 days and then transferred to a 10°C cabinet and allowed to acclimate for 8 days before use. An aphid culture was maintained on wheat cv. Bouquet at 10°C. The following procedure was used to measure development time and reproduction at 10°C, 13°C and 15°C: 25 alatae were individually caged to the second leaf of the L. perenne seedlings (G.S. 12). Alatae which had reproduced were removed after 24 hours. The nymphs were then placed in individual cages and reared to adults. The nymphal development time and mortality were recorded. The number of adult apterae and alatae were recorded and at 13°C and 15°C the alatae were discarded. The

alatae reared at 10°C were kept and treated in a way similar to apterae for the rest of the experiment. The adult aphids were weighed and then caged on the second leaf of a new L. perenne seedling (G.S. 12). The number of nymphs produced by each adult was recorded every 3 days at 13°C and 15°C and every day at 10°C. Reproduction was measured for 7 days at 13°C and 15°C and for 20 days at 10°C.

Statistical analysis

A Bartlett's test for homogeneity of variances and a one-way analysis of variance were used to compare development times, adult weights and 7-day fecundities at 10°C, 13°C, 15°C and 20°C. The 20°C data were obtained from 3.2. Separate variance estimates were used for t-tests of development time and adult weight, pooled variance estimates were used for 7-day fecundity at all temperatures. Regression analyses of development time (y), adult weight (y) and 7-day fecundity (y) with temperature were carried out.

Apterae and alatae reproduction at 10°C. A one-way analysis of variance to compare apterae and alatae development times, weight, 7-day, 10-day, 15-day and 20-day fecundity were carried out. A regression analysis of 7-day, 10-day, 15-day and 20-day fecundity with adult weight for apterae and alatae was carried out.

7.2 APTERAE AND ALATAE OVARIOLE NUMBER

Cultures of aphids were maintained on wheat cv. Bouquet at 10°C, 15°C and 20°C. Apterae and alatae were taken from each of the cultures, were weighed and dissected for ovariole number. The L.E.N. was also recorded (see 4.2).

Statistical analysis

Kolmorgorov-Smirnov one-sample test was carried out for weight, L.E.N. and ovariole number. A one-way analysis of variance was also carried out to compare the weights of apterae and alatae reared at different temperatures. This was repeated for L.E.N. t-tests using separate variance estimates were used to compare the effect of temperature on weight and L.E.N. of apterae and alatae; a comparison of apterae and alatae weights and L.E.N.s was also made.

CHAPTER EIGHT

8.1.1 Grass yield experiment

This field experiment involved the use of 6 2 x 2 x 2M field cages; three were used as controls and the others as experimental treatments.

The cages were erected on a two-year-old L. perenne cv.Cropper field on 7 April 1983. The control cages were spaced alternately between the experimental cages and were sprayed with pyrethrum and then pirimor to remove any naturally-occurring aphid population.

During December a number of apterous M. festucae were removed from the culture and placed in glass vials. The nymphs produced after 24 hours were virus-free and were placed on wheat seedlings to form the basis of the infestations.

After 4 weeks at 20°C under normal culture conditions the aphids were transferred to wheat seedlings maintained at 15°C and 16h daylength. 7 days later these were transferred to wheat seedlings maintained at 10°C and 13½h daylength for two weeks to complete acclimation. The aphid-infested seedlings were then cut and transferred to the field cages. As the wheat cuttings died the aphids moved into the grass sward. Each experimental cage had a similar starting density of aphids.

Estimation of aphid increase was made by clearing 10 cm^2 patches of grass using shears, and then vacuum-net sampling the cut area. The cut grass was then taken back to the laboratory and the numbers of M. festucae counted. The 'D-vac.' samples were also sorted and the numbers of M. festucae present added to those from the grass cuttings.

The growth stage of the grass was measured in terms of grass height. This was estimated from the height of the cuttings which were used to determine the number of M. festucae present in the field cages. Aphid/grass samples were taken from 21 April to 27 May.

8.2 WHEAT YIELD EXPERIMENT

This experiment involved the use of 6 2 x 2 x 2m field cages. The cages were erected on a wheat winter cv. Rapier field on 7 April. The cages were sprayed as in 8.1.1. The acclimation and infestation of the aphids in the cages was also the some as for the L. perenne experiment (8.1.1).

Aphid increase was measured by a direct count of aphids per stem, for 100 stems per cage. The growth stage of the wheat was measured at the time of sampling.

The last sample was made on 14 June, and the cages were removed on 18 June.

The ears of wheat from both experimental and control cages were to be removed on 10 August. The grain was to be used to determine the extent of yield reduction due to M. festucae. However without my prior knowledge the wheat crop was harvested a day early and the subsequent experiment ruined.

CHAPTER THREE

THE REPRODUCTION AND DISTRIBUTION OF APTEROUS VIRGINOPARAE OF METOPOLOPHIUM FESTUCAE CEREALIUM

INTRODUCTION

Numbers of M. festucae cerealium are usually low on cereals; for this reason little is known about its feeding site (Vickerman and Wratten 1979). Dean (1974) however suggested that there might be a preference for the lower leaves of cereals.

The only reference to the feeding site of M. festucae cerealium on grasses was the large numbers of virginoparae found on the lower leaves of grasses during the winter 1951-52 (Gair 1953).

It is important to determine the preferred feeding site of M. festucae cerealium on both cereals and grasses otherwise subsequent measurements of aphid performance could be misleading.

Many researchers have studied resistance in cereals and grasses to aphids. The type of research falls into two categories; the use of antibiosis and antixenosis to test resistance of cultivars of cereals important to agricultural (Markkula and Roukka 1972; Dewar 1977; Lowe 1978, 1980; Kay, Wratten and Stokes 1981; Lee 1981; Lowe 1982) or detailed studies, often unrelated to resistance requirements of the reproductive biology and life history of cereal aphid species (Orlob 1961; Markkulla and Myllymäki 1963; Robinson and Sze-Jhi Hsu 1963; Adams and Drew 1964; Pettersson 1971; Dixon 1971; Dean 1973; Kieckhefer and Stone 1978; Watt 1979; Leather and Dixon 1981; Watt 1981; Watt and Dixon 1981; Leather and Dixon 1982a). The majority of studies have been of the latter type and have been carried out on the important cereal aphid species S. avenae, M. dirhodum and Rhopalosiphum padi (L.). For each of these species it has been shown that the species of host and even cultivars influence aphid performance. Often this work has been carried out on seedlings (Adams and Drew 1964; Dean 1974; Markkula and Roukka 1972) and it has become increasingly evident that measurements should be made on the stage of the plant on which the aphid thrives best (Watt 1979); several studies have compared aphid performance at a

number of growth stages (Watt 1979; Watt and Dixon 1981; Watt 1981; Leather and Dixon 1981; Leather and Dixon 1982a).

Although M. festucae has been cited as occuring on 32 Gramineae little work has been done to compare the relative resistance of these hosts to M. festucae cerealium. Hill (1971) compared the performance of M. festucae cerealium on 3 cereals and 3 grasses and found that cereals were somewhat better hosts than grasses. However the experiments were carried out in an insectary and hence were subject to fluctuating temperatures, making subsequent comparisons between aphid species difficult.

Stroyan (1982) also compared the performance of M. festucae cerealium on a number of Gramineae including cereals but neglected to give details except to say his ranking did not agree with that of Hill (1971).

M. festucae cerealium has been recorded on a number of important agricultural grasses. The important grasses used in leys are: L. perenne, L. multiflorum, D. glomerata, P. pratense, F. pratensis and F. arundinacea (Hubbard 1978; Williams 1980; NIAB 1980/81), whilst F. rubra is important in permanent pasture (Williams 1980).

A study of the reproductive performance of M. festucae cerealium on these agricultural grasses and on cereals has been undertaken here. The influence of antibiosis was compared at two growth stages: seedlings and at stem elongation. It is at this growth stage on both grasses and cereals that M. festucae cerealium reaches peak population levels in the field (Carrillo, pers.comm.). L. perenne is a particularly important agricultural grass, being the most widely sown grass in Britain (NIAB 1980/81), and for this reason the reproductive performance of M. festucae cerealium was compared at 3 growth stages of this species. L. perenne is known to be a suitable host for M. festucae cerealium since numbers of 3,000m^{-2} (Carrillo, pers.comm.) and as high as 20,000m^{-2} (Vickerman 1977) have been recorded in the field. A field comparison was made of antibiosis on L. perenne and wheat to look at seasonal variation in reproductive performance on these two hosts.

Grass in the United Kingdom is either used for grazing or cut for silage or hay. An average of 3-4 cuts are made in summer, depending

on the grass species and cultivars and weather conditions. The first cut for a L. perenne crop (an early heading cultivar) is made on 20-25 May; the grass would normally flower on 15-20 May hence the grass is cut soon after anthesis. The cutting of the crop and the timing of the cut have important implications for the aphid's population dynamics. Grazing has been shown to reduce populations in grass (Carrillo pers.comm.) and in lucerne (Penman, Rohitha, White and Smallfield 1979) whilst cutting for silage has been used to remove M. festucae cerealium during severe outbreaks on ley pasture (Edwards and Heath 1964).

The management of grassland therefore has important consequences for M. festucae cerealium populations; the development of grasses is stopped at anthesis, a large biomass is removed and hence there are dramatic changes in the microclimate; this process is repeated until late summer/autumn. The influence of these changes was studied by comparing the reproductive performance of M. festucae cerealium on uncut grass and grass cut and managed as if for silage production.

The aims of this present work were to investigate

(I) the preferred feeding site on grass and wheat

(II) the influence of antibiotic resistance in seedlings of 12 grass spp.

(III) the influence of antibiotic resistance in 4 grass spp. at stem elongation

(IV) the reproductive performance of apterous and alate virginoparae on wheat, cut and uncut L. perenne

(V) to assess the influence of temperature and growth stage on apterous and alate virginoparae reared on cut L. perenne.

RESULTS

3.1 THE FEEDING POSITION OF APTERAE ON A RANGE OF HOST PLANTS

3.1.1 Seedling L. perenne w. Cropper

The distribution of apterae on the leaves of seedlings was unequal ($\chi^2 = 16$; d.f = 3; $P < 0.005$) the largest number of apterae on the second

Fig.1 THE DISTRIBUTION OF ADULT APTERAE ON LEAVES OF (a) A 3 WEEK OLD AND (b) A 10 WEEK OLD *L. perenne* PLANT. E, LEAF EMERGING; T, FIRST LEAF AXIL TILLER; ( ), NUMBER OF APHIDS

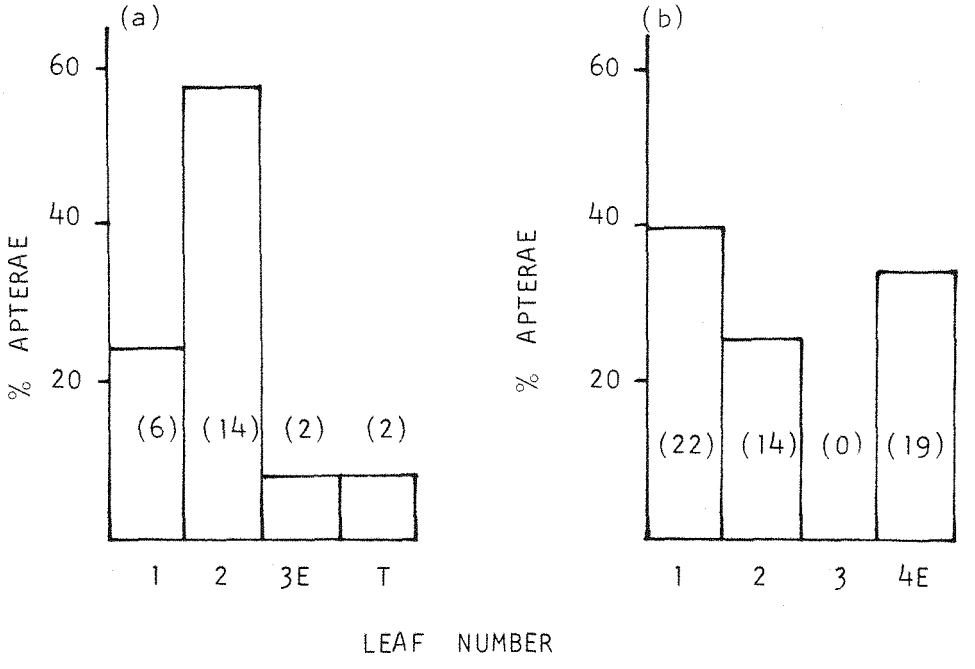
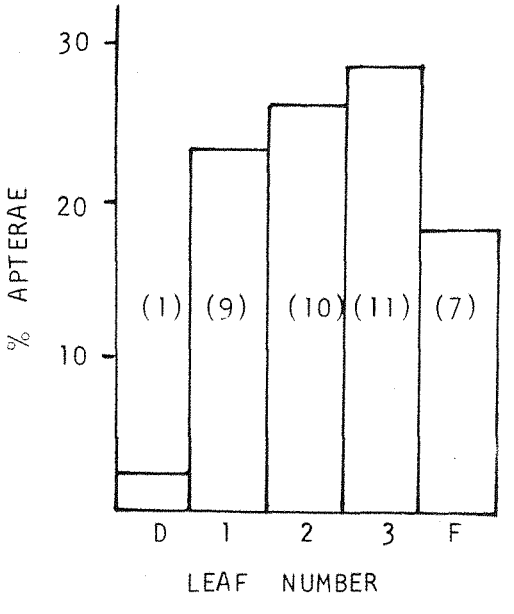


Fig.2 THE DISTRIBUTION OF ADULT APTERAE ON A MATURE WHEAT PLANT (G.S. 50.51); D, DEAD LOWER LEAVES; F, FLAG LEAF. ( ), NUMBER OF APHIDS



unfolded leaf (Fig.1a). A subsequent chi-squared analysis without the value for the second leaf (χ^2 = 3.20; d.f = 2; $0.10 < P > 0.25$) shows that the distribution of the remaining apterae were evenly distributed. The high value of chi-squared obtained initially (χ^2 = 16) can be ascribed to the second leaf having a higher proportion of the aphids, the other three classes not deviating significantly from the expected equiprobabilities.

Apterae therefore have a preference for feeding on the second leaf of a L. perenne seedling (G.S. 12).

3.1.2 Leaves of wheat cv. Hobbit

The apterae were equally distributed on all the leaves of the wheat plant (χ^2 = 8.31; d.f = 4; $P > 0.05$) (Fig.2). The numbers on the flag leaf were lower than on the other leaves, but not significantly so.

3.1.3 10 week old L. perenne cv. Cropper

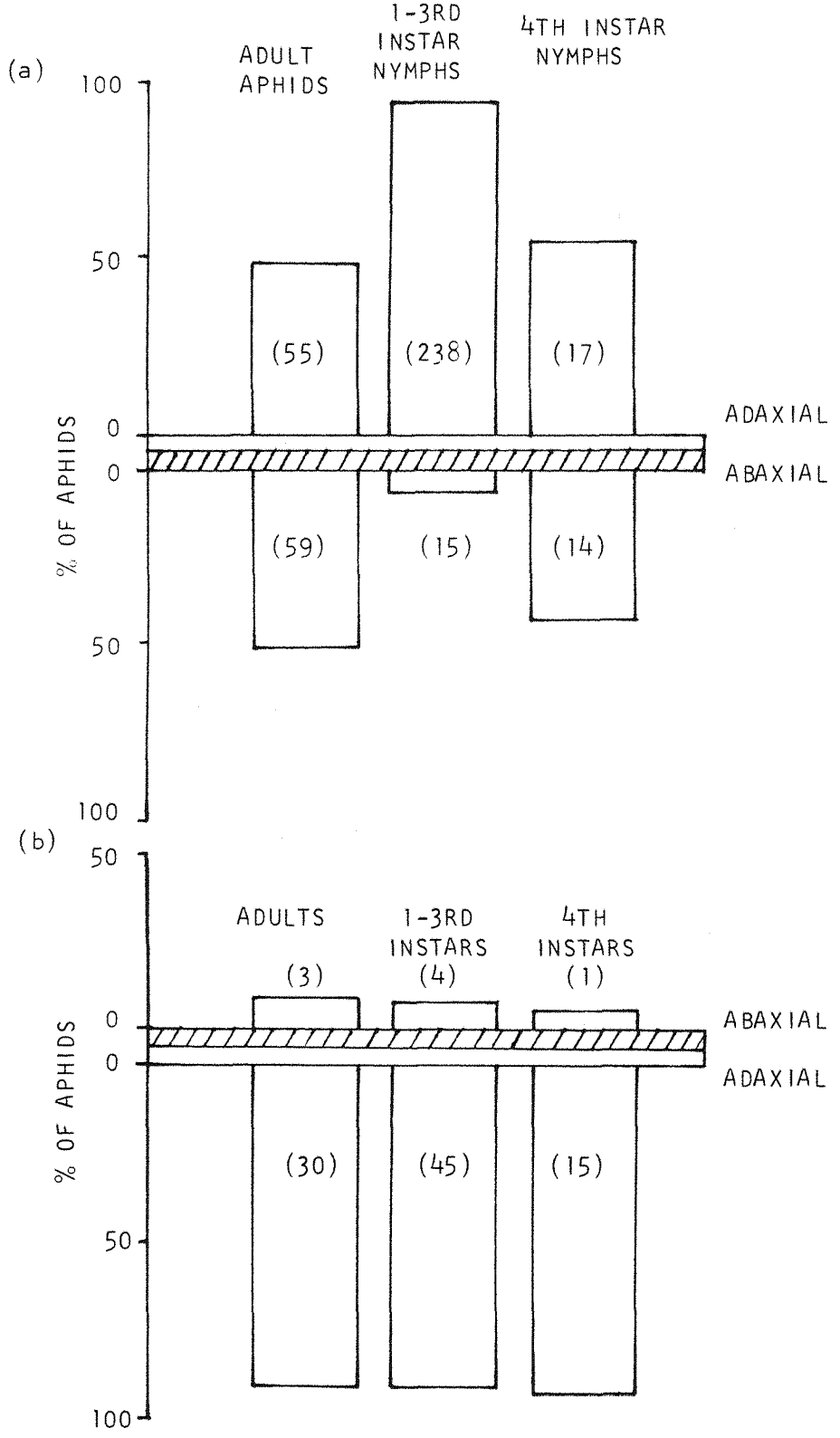
The apterae on the 10 week old plant were not evenly distributed on all leaves (χ^2 = 0.71; d.f = 3; $P < 0.005$; this test included the third leaf which had no aphids feeding on it, however the expected value was > 1 (Snedecor & Cochran 1978), therefore the test was valid). The aphids showed a 'preference' for the first, second and emerging fourth leaf, with no aphids feeding on the third leaf (Fig.1.6). A subsequent chi-squared analysis, excluding the value for the third leaf, (χ^2 = 1.78; d.f = 2; $0.25 < P > 0.50$) showed that the remaining alatae were evenly distributed. The high chi-squared value obtained initially (χ^2 = 20.71) can be ascribed to a deficiency of aphids on the third leaf.

The apterae therefore showed a non-preference for the third leaf of a 10 week old L. perenne plant.

3.1.4 Adaxial or abaxial leaf surfaces of L. perenne cv. Cropper

The distribution of aphids on the adaxial and abaxial leaf surfaces differed according to the instar of the aphid, and to the orientation of the leaf (Figs.3a and b).

Fig.3 THE DISTRIBUTION OF APHIDS ON THE ADAXIAL AND ABAXIAL SURFACES OF NORMALLY ORIENTATED (a) OR (b) INVERTED LEAVES. THE NUMBERS IN BRACKETS REFER TO THE TOTAL NUMBER OF APHIDS RECORDED ON A LEAF SURFACE.



3.1.4.1 A normally orientated leaf (adaxial surface facing upwards)

The distribution of aphid instars on the adaxial and abaxial leaf surfaces in unequal (χ^2 = 105.9; d.f = 2; $P < 0.005$). The lower instars (first to third instars) showed a preference for the adaxial leaf surfaces (Fig.3a). Subsequent chi-squared analysis of the numbers of aphids on each surface for each aphid class showed the distribution of adults and fourth instars not to differ significantly from equality (χ^2 = 0.14; d.f = 1; $0.500 > P < 0.750$ and χ^2 = 0.290, d.f = 1, $0.50 > P < 0.75$ respectively). The chi-squared value for the lower instars (χ^2 = 223; d.f = 1; $P < 0.005$) showed that these nymphs were distributed significantly differently from equality; the lowest instars are concentrated on the adaxial leaf surface.

3.1.4.2. An inverted leaf (abaxial surface facing upwards)

The distribution of aphids on the adaxial and abaxial leaf surfaces homogeneous (χ^2 = 0.1174; d.f = 2; $0.900 > P < 0.95$). A chi-squared analysis of the numbers of aphids on each surface, for each aphid class, showed the distribution of all aphids significantly different from equality. The chi-squared values were 22.08, 34.30, 12.25 with d.f = 1 and $P < 0.005$ for adults, lower instars and fourth instars respectively. When the leaf is inverted all aphid classes show a preference for adaxial leaf surface (Fig. 3b).

3.2 ANTIBIOSIS EXPERIMENTS

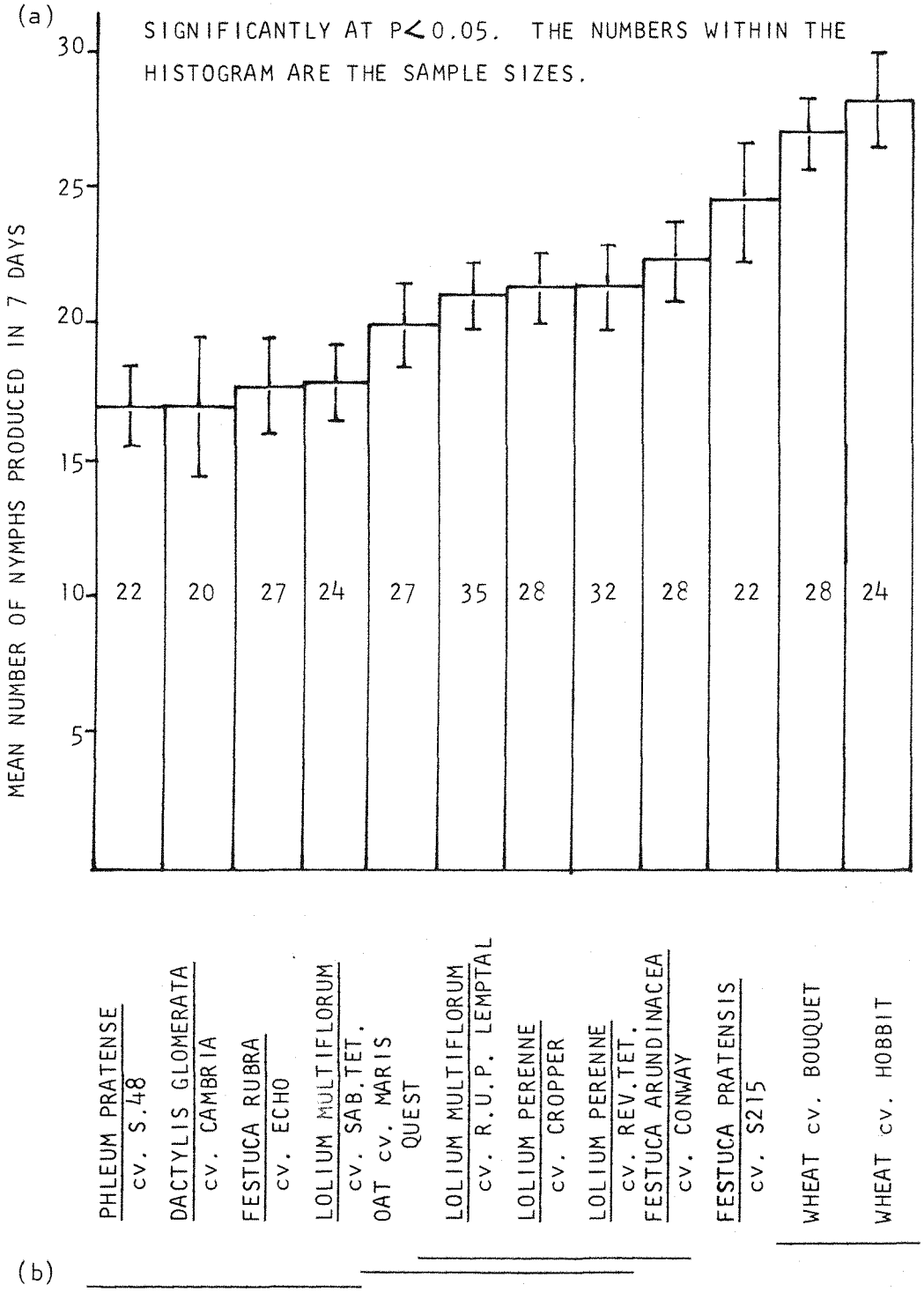
3.2.1 Seedlings

The 7-day fecundity of apterae on wheat cv. Hobbit was higher than on the other host grasses, and differed from that of apterae on *P. pratense*, which had the lowest fecundity, 40% fewer nymphs (Fig.4). Apterae were most fecund on the wheat cultivars whilst the oat cv. Maris Quest had a 7-day fecundity of 19.96, 29% fewer nymphs than wheat cv. Hobbit. Two of the grasses of the genus *Festuca*, *F. pratense* and *F. arundinacea* cv. Conway were two of the less resistant grasses whilst a third species *F. rubra* cv. Echo showed a high level of resistance. The

Fig.4

(a) THE MEAN NUMBER OF NYMPHS PRODUCED BY APTEROUS APHIDS ON 12 DIFFERENT HOST SEEDLINGS, WITH 99% CONFIDENCE LIMITS.

(b) A MULTIPLE RANGE TEST; ANY HOSTS UNDERSCORED BY THE SAME LINE EXHIBIT SIMILAR ANTIBIOTIC RESISTANCE i.e. THE MEAN NUMBER OF NYMPHS PRODUCED ON EACH HOST DOES NOT DIFFER SIGNIFICANTLY AT $P < 0.05$. THE NUMBERS WITHIN THE HISTOGRAM ARE THE SAMPLE SIZES.



common agricultural grasses L. perenne and L. multiflorum showed intermediate levels of resistance (Fig.4).

A one-way analysis of variance showed there to be significant differences ($F = 34.023$, d.f = 11,305, $P < 0.001$) between the means of 7-day fecundity for apterae on the 12 Gramineae. A multiple range test (Fig.4b) showed that there are roughly four levels of resistance ($P < 0.05$), (I) the two wheat cultivars, (II) F. pratensis cv. S215, (III) F. arundinacea cv. Conway, the three Lolium species/cultivars and oat cv. Maris Quest and the most resistant group, (IV) including L. multiflorum cv. Sab.Tet., F. rubra cv. Echo, D. glomerata cv. Cambria and P. pratense cv. S.48.

A one-way analysis of the variance of development times and weights of the apterae on the 12 Gramineae showed there to be significant differences ($F = 50.157$, and $F = 50.906$ with d.f = 11,305, $P < 0.001$ respectively) between means. When the mean development times and weights were ranked the order of means did not directly correspond with those of fecundity, i.e. a high fecundity did not necessarily correspond to a short development time and high weight (Fig.5a and b). Apterae on the two wheat cultivars had the highest mean weights but only apterae on the cultivar Hobbit exhibited a relatively short development time. The grass which showed most resistance to reproduction, P. pratense cv. S.48, also produced apterae with the lowest mean weight. The apterae reared on the fescues, F. pratensis and F. arundinacea were relatively heavy and had the shortest development times. The apterae reared on the oat cv. Maris Quest had the fourth highest mean weight but also had the longest development time of 12.66 days. The main agricultural grasses, the Lolium species/cultivars showed intermediate levels of resistance for weight and development times.

3.2.2 A comparison of antibiosis on 3 growth stages of L. perenne cv. Cropper

The apterae reared on three growth stages of L. perenne had significantly different 7-day fecundity ($F = 6.474$, $P < 0.01$) and development times ($F = 183.37$, $P < 0.001$). The weights of adults at

01. Lolium perenne cv. Cropper

02. Phleum pratense cv. S.48

03. Festuca arundinacea cv. Conway

04. Wheat cv. Hobbit

05. Dactylis glomerata cv. Cambria

06. Festuca pratensis cv. S.215

07. Wheat cv. Bouquet

08. Lolium multiflorum cv. R.U.P. Lemptal

09 Lolium multiflorum cv. Sab. Tet.

10. Lolium perenne cv. Rev.Tet.

11. Festuca rubra cv. Echo

12. Oats cv. Maris Quest.

(a)

DEVELOPMENT TIME

	1	2	3	4	5	6	7	8	9	10	11	12
	03	06	04	01	02	08	07	10	05	11	09	12
$\bar{X}$	9.78	9.95	10.25	10.32	10.59	10.62	11.01	11.18	11.35	11.66	12.33	12.66

(b)

ADULT WEIGHT

	1	2	3	4	5	6	7	8	9	10	11	12
	02	11	09	05	08	01	03	10	12	06	04	07
$\bar{X}$	.571	.574	.607	.622	.709	.738	.770	.798	.902	.972	.990	1.228

Fig.5 Multiple range tests for (a) developments times and (b) adult weights of aphids reared on 12 different host Gramineae Means ($\bar{x}$) underscored by the same line are not significantly different at $P<0.05$.

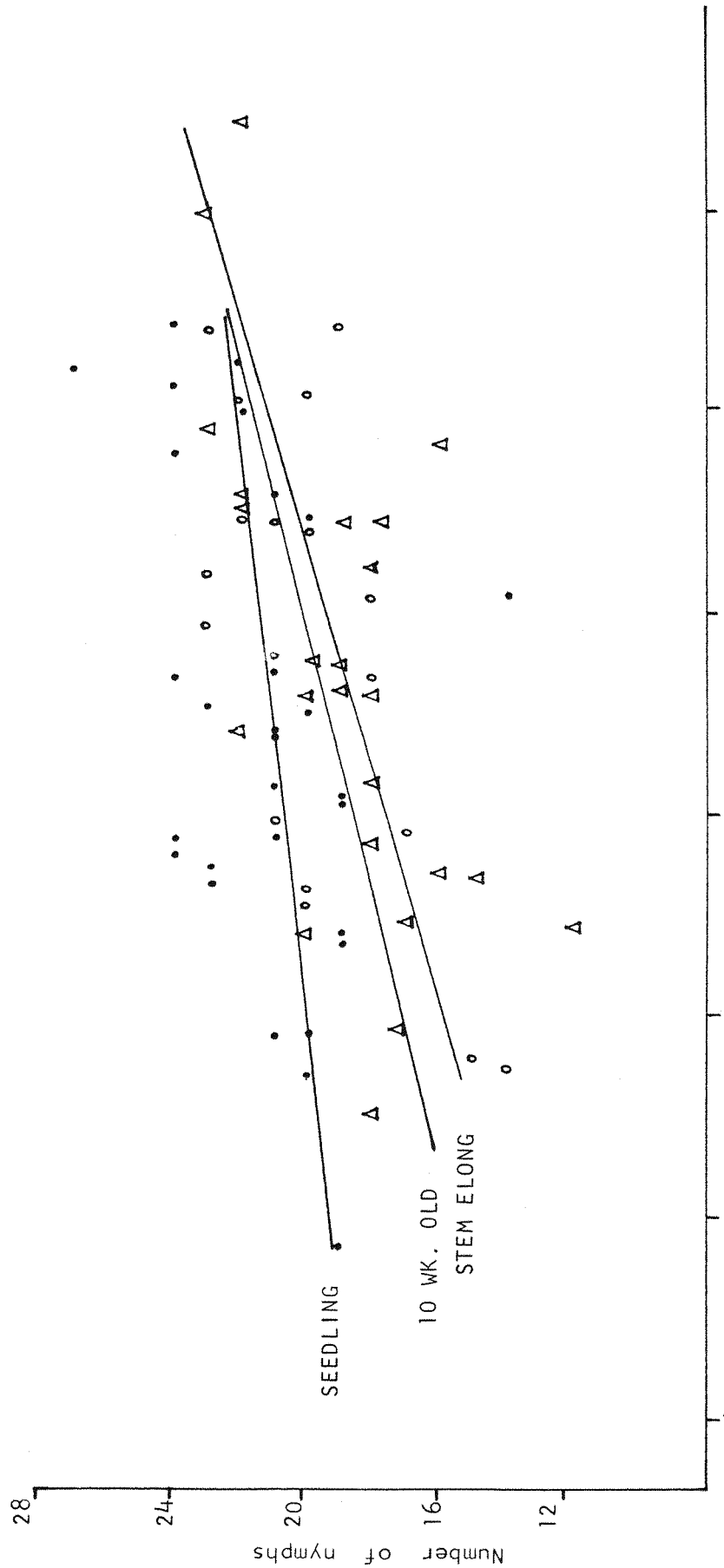


Fig.6 The relationship between fecundity during the first 7 days of adult life and adult weight (mg) on (•) young seedlings (Δ) 10-week old seedlings and (o) lower leaves of elongating stems for Lolium perenne cv. Cropper.

eclosion were not significantly different ($F = 0.696$, $P > 0.05$). The 7-day fecundity of apterae reared on seedlings ($\bar{x} = 21.3$, S.E. = 0.48) was significantly different from 10-week old plants ($\bar{x} = 18.6$, $s = 0.62$; $t = 3.51$, $P < 0.001$) and stem elongating plants ($\bar{x} = 19.8$, S.E. = 0.62; $t = 1.97$, $P < 0.05$). There was no significant difference between the 7-day fecundity of apterae reared on 10 week old plants and stem elongating plants. The development times of apterae reared on the three growth stages were all significantly different from each other at $P < 0.01$. The apterae reared on seedlings had the shortest development time (days; $\bar{x} = 10.3$, S.E. = 0.08) followed by the aphids on stem elongating plants ($\bar{x} = 12.4$, S.E. = 0.24). The mean development time of aphids on the 10-week old plants was 14.8 (S.E. = 0.20).

On each growth stage, large aphids give birth to more nymphs than small ones (Fig.6). A covariance analysis of the relationships between fecundity and weight for the different growth stages indicated that the regression lines had a common slope ($F = 2.435$, d.f = 2.71, $P > 0.05$; the residual variances were homogeneous $\chi^2 = 0.1399$, d.f = 2, $P > 0.05$). The elevation of the lines however was significantly different ($F = 20.95$, d.f = 2.71, $P < 0.01$) (Table 1). The apterae reared on seedlings had a higher reproductive rate than those on 10-week old and stem elongating plants.

3.2.3 A comparison of antibiosis on two growth stages for *D. glomerata* cv. Cambria, *L. multiflorum* cv. R.U.P. Lemptal and wheat cv. Bouquet

3.2.3.1 *D. glomerata* cv. Cambria

The apterae reared on the seedlings and stem elongating plants had significantly different 7-day fecundities ($F = 11.756$, $P < 0.001$) and development times ($F = 21.89$, $P < 0.001$). The weights of adults at eclosion were not significantly different ($F = 1.883$, $P = 0.179$).

The 7-day fecundity of apterae on seedlings ($\bar{x} = 16.95$, S.E. = 0.980) was greater than that of apterae on stem elongating plants ($\bar{x} = 12.56$, S.E. = 2.943), whilst the development time was less ($\bar{x} = 11.35$, S.E. = 0.209, and $\bar{x} = 14.12$, S.E. = 0.611 respectively).

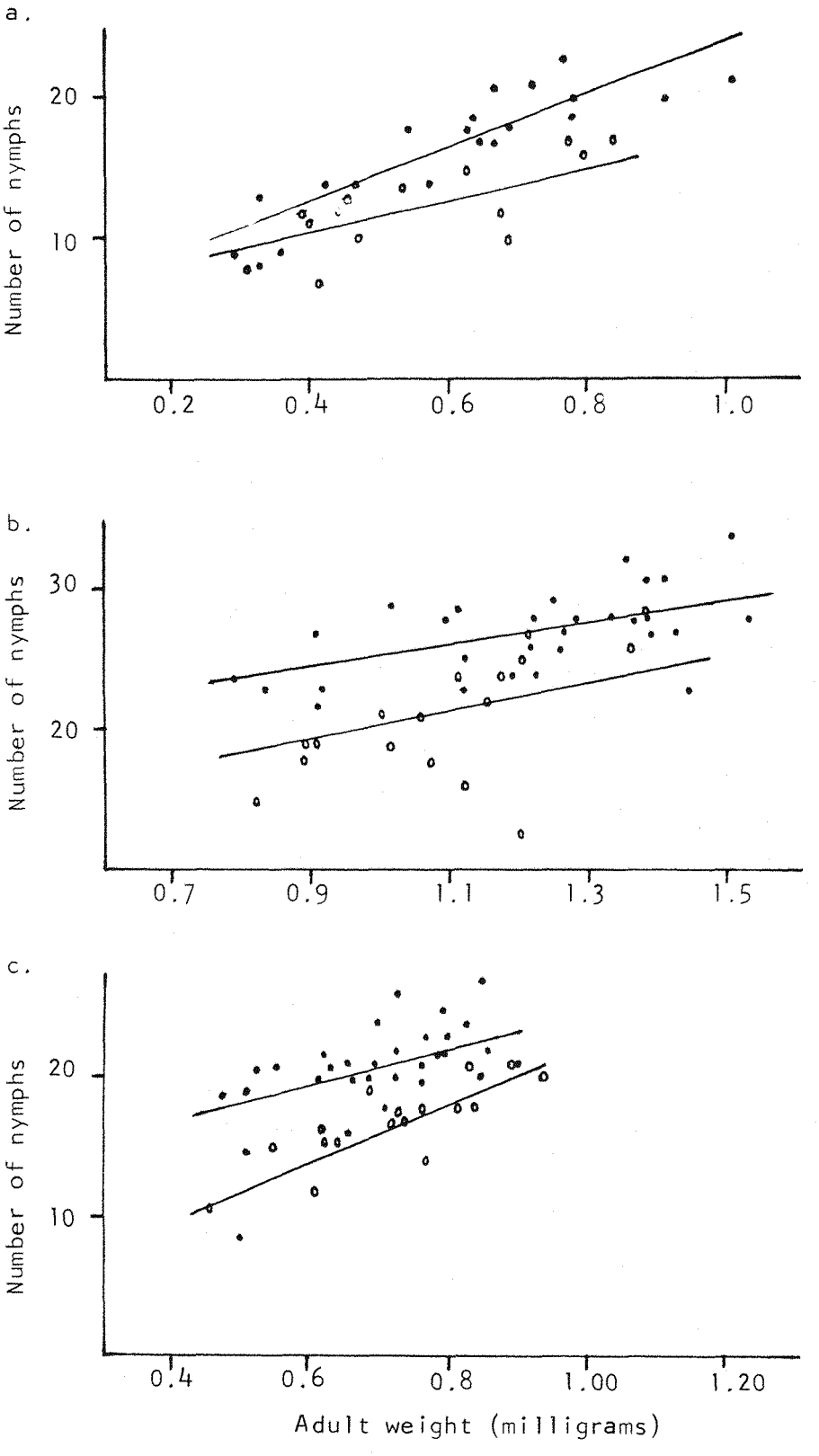


Fig.7 The relationship between fecundity during the first 7 days of adult life and adult weight (mg) life on young seedlings (•) and lower leaves of elongating stems (o) for (a) Dactylis glomerata cv. Cambria; (b) wheat cv. Bouquet; (c) Lolium multiflorum cv. R.U.P. Lemptal

Table 1. The relationship between the number of nymphs produced during the first 7 days of adult life (y) and adult weight (x) for *M. festucae* on a number of host plants and growth stages.

Hostplant	growth stage	regression lines fitted from the results
L. perenne cv. Cropper	seedling	$y = 15.21 + 8.232x$ ($n = 28$, $r = 0.386$, $P < 0.05$)
	10 wk. old	$y = 5.398 + 17.365x$ ($n = 26$, $r = 0.685$, $P < 0.01$)
	stem elongation	$y = 8.010 + 15.162$ ($n = 18$, $r = 0.656$, $P < 0.01$)
D. glomerata cv. Cambria	seedling	$y = 5.111 + 19.02x$ ($n = 20$, $r = 0.867$, $P < 0.001$)
	stem elongation	$y = 6.436 + 11.436x$ ($n = 16$, $r = 0.673$, $P < 0.01$)
Wheat cv. Bouquet	seedling	$y = 17.95 + 7.483x$ ($n = 28$, $r = 0.521$, $P < 0.05$)
	stem elongation	$y = 10.31 + 10.132x$ ($n = 20$, $r = 0.500$, $P < 0.05$)
L. multiflorum	seedling	$y = 1.606 + 20.82x$ ($n = 17$, $r = 0.835$, $P < 0.001$)
	stem elongation	$y = 1.606 + 20.82x$ ($N = 17$, $r = 0.835$, $P < 0.001$)

On both growth stages, large aphids give birth to more nymphs than small aphids (Fig.7a). A covariance analysis of the relationship between fecundity and weight for the two growth stages indicated that the regression lines had a common slope ($F = 3.218$, $d.f = 1.32$, $P > 0.05$; the residual variances were homogeneous $F = 1.008$, $d.f = 14.18$, $P > 0.05$). The elevation of the lines was significantly different ($F = 13.898$, $d.f = 1.32$, $P < 0.01$). The apterae which were reared on seedlings had a higher reproductive rate than those reared on stem elongating plants.

3.2.3.2. Wheat cv. Bouquet

The apterae reared on the seedlings and stem elongating plants had significantly different 7-day fecundities ($F = 38.396$, $P < 0.001$), weights ($F = 8.838$, $P < 0.004$) and development times ($F = 50.951$, $P < 0.001$).

The 7-day fecundity and weight of apterae on seedlings ($\bar{x} = 27.14$, S.E. = 0.541 and $\bar{x} = 1.22$, S.E. = 0.199 respectively) were greater than for apterae reared on stem elongating plants ($\bar{x}$ 7-day fecundity = 21.00, S.E. = 0.897 and $\bar{x}$ wt = 1.06, S.E. = 0.044). The development time of apterae on seedlings was less ($\bar{x} = 11.10$, S.E. = 0.079) than apterae reared on stem elongating plants ($\bar{x} = 12.7$, S.E. = 0.25).

A covariance analysis of the relationship between fecundity and weight for the two growth stages indicated that the regression lines had a common slope ($F = 0.3481$, $d.f = 1,44$, $P > 0.05$; the residual variances were homogeneous, $F = 2.053$, $d.f = 18.26$, $P > 0.05$).

The elevation of the lines was significantly different ($F = 24.275$, $d.f = 1.44$, $P < 0.01$), indicating that those aphids reared on seedlings had a higher reproductive rate than apterae reared on stem-elongating plants.

3.2.3.3 *L. multiflorum* cv. R.U.P. Lemptal

The apterae reared on the seedlings and stem elongating plants had significantly different 7-day fecundities ($F = 26.984$, $P < 0.001$) and development times ($F = 82.462$, $P < 0.001$). The weights of adults at

eclosion were not significantly different ($F = 0.014$, $P = 0.904$).

The 7-day fecundity of apterae on seedlings ($\bar{x} = 21.00$, S.E. = 0.487) was greater than for apterae on stem elongating plants ($\bar{x} = 16.29$, S.E. = 0.830), whilst the development time was less ($\bar{x} = 10.67$, S.E. = 0.646; $\bar{x} = 13.70$, S.E. = 0.435 respectively).

A covariance analysis of the relationship between fecundity and weight for the two growth stages indicated that the regression lines had a common slope ($F = 2.263$, d.f = 1.49, $P > 0.05$; the residual variances were homogeneous, $F = 1.656$, d.f = 33.15, $P > 0.05$). The elevations were significantly different ($F = 45.50$, d.f = 1.49, $P < 0.01$), indicating that apterae reared on seedlings have a higher reproductive rate than apterae reared on stem-elongating plants.

3.2.4 A comparison of antibiosis on stem elongating D. glomerata cv. Cambria, wheat cv. Bouquet, L. multiflorum cv. R.U.P. Lemptal and L. perenne cv, Cropper

A one-way analysis of variance of all three variables, 7-day fecundity, weight and development time gave significant F values at $P < 0.05$.

The development time variances were heterogeneous.

The apterae which had the longest development times e.g. on D. glomerata (Fig.8) had a tendency to be smaller and less fecund. The weights of apterae on L. multiflorum and L. perenne were not significantly different ($t = 1.76$, d.f = 33, $P > 0.05$). Adults on the wheat weighed nearly twice those on D. glomerata.

The 7-day fecundity of apterae reared on the wheat and L. perenne were not significantly different ($t = 1.05$, d.f = 36, $P > 0.05$). Both wheat and L. perenne were significantly less resistant than D. glomerata and L. multiflorum at $P < 0.05$ (Fig.8c).

a.

DEVELOPMENT TIME (DAYS)

	L. perenne cv. Cropper	Wheat cv. Bouquet	L. multiflorum cv. R.V.P. Lemptal	D. glomerata cv. Cambria
$\bar{x}$	12.44	12.75	13.07	14.125

b.

ADULT WEIGHT (mg)

	D. glomerata cv. Cambria	L. multiflorum cv. R.V.P. Lemptal	L. perenne cv. Cropper	Wheat cv. Bouquet
$\bar{x}$	0.535	0.705	0.779	1.055

c.

FECUNDITY (7 DAYS)

	D. glomerata cv. Cambria	L. multiflorum cv. R.V.P. Lemptal	L. perenne cv. Cropper	Wheat cv. Bouquet
n	16	17	18	20
$\bar{x}$	12.56	16.29	19.83	21.00

Fig.8 Differences between (a) development time $P < 0.05$; (b) adult weight $P < 0.001$; (c) 7-day fecundity $P < 0.005$ for aphids reared on the lowest leaves of D. glomerata, L. multiflorum, L. perenne, and wheat (G.S. 50-51). Means ($\bar{x}$) underscored by the same line are not significantly different. The sample size (n) for each host is shown in (c).

3.3 A FIELD COMPARISON OF ANTIBIOSIS ON WHEAT, CUT AND UNCUT *L. perenne*

3.3.2 Wheat

The mean number of nymphs produced in 3 days by apterae on the lower leaves of wheat increased from 1.0 ± 0.2 nymphs on 26 April to 6.0 ± 0.35 nymphs on 17 May (Fig.9). The 3-day fecundity remained at approximately 5 nymphs per mother until the 5 June when reproduction decreased; it was accompanied by a corresponding increase in mortality. In early July the 3-day fecundity reached its highest level: 8.0 S.E. 0.78 nymphs per mother. The r_m value of the aphid cohort at this time (0.64 S.E. 0.026) was significantly different at $P < 0.05$ from the other three cohorts established earlier in the season (Fig.10). This can be attributed to a decrease in mean generation time rather than an increase in reproductive rate (Table 2).

Cohorts of aphids were established on the emerging leaves of stem elongating wheat on 11 June. A large proportion of alatae were produced (Fig.11), and the 3-day fecundity of apterae and alatae was measured. Apterae produced a larger number of nymphs than alatae (Fig.9) although the difference in r_m values were not significant at $P < 0.05$ ($r_m = 0.55$, S.E. = 0.022 and $r_m = 0.50$, S.E. = 0.023 for apterae and alatae respectively).

The apterae reared on the emerging leaves of stem-elongating wheat had a higher 3-day fecundity than apterae on the lower leaves. The alatae however produced a similar number of nymphs as the apterae on the lower leaves.

The apterae reared on the flag leaves reached a peak 3-day fecundity of 11.22 nymphs on 10 June when fecundity had decreased for apterae on emerging leaves and the lower leaves of wheat. However the cohort with the largest r_m (0.92, S.E. = 0.157) was established on the 16 June. This r_m was significantly different at $P < 0.05$ from all the rates of increase of other cohorts on the flag leaves (Table 3), and occurred during the milky-ripe stage (G.S. 70-79) of grain development.

Apterae of the 16 June flag leaf cohort had a significantly different

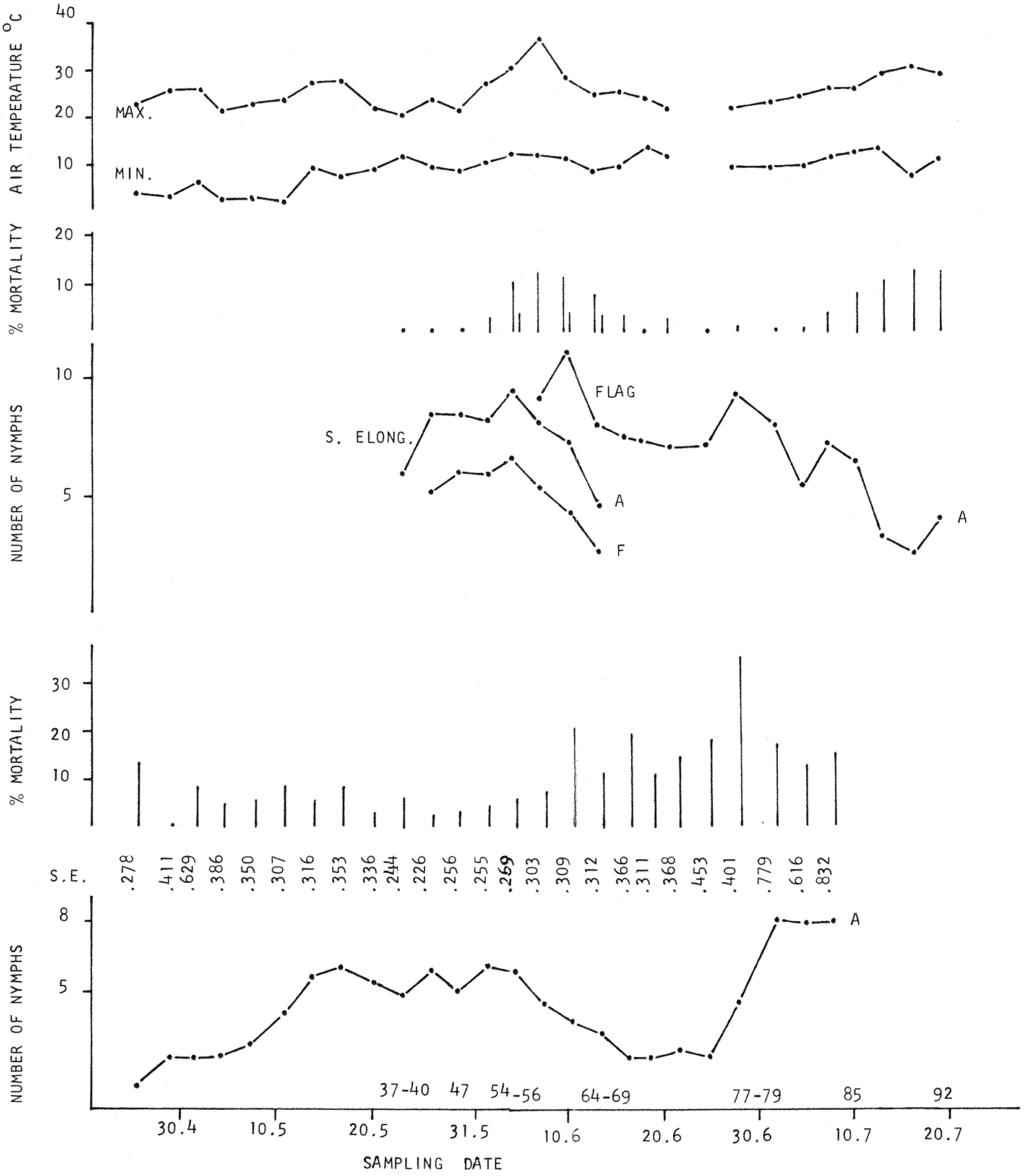


Fig.9 The reproductive performance and % mortality of apterae (A) and alatae (F) reared in clip cages on the lower and upper leaves of wheat cv. Bounty. Growth stages are numbered above the x axis. FLAG, Flag leaves and S. ELONG; upper unfolded leaves.

Table 2. The $\underline{r}_m$ values and LSD for cohorts of apterae reared on the lower leaves of wheat. $\underline{r}_m$ values underscored by the same line are not significantly different at $P > 0.05$. Ro = reproductive rate: G, cohort mean generation time.

Date cohort established	Ro	G	$\underline{r}_m$ (jackknife)	S.E.	LSD
21.4.82	43.93	12.88	0.341	0.008	
26.4.82	44.90	11.44	0.384	0.012	
2.5.82	45.92	11.43	0.386	0.011	
19.6.82	29.77	5.959	0.637	0.026	

Table 3. The $\underline{r}_m$ values and LSD test for cohorts of apterae reared on the flag leaves of wheat. $\underline{r}_m$ values underscored by the same line are not significantly different at $P > 0.05$. Ro and G as Table 2.

Date established	Ro	G	$\underline{r}_m$ (jackknife)	S.E.	LSD
10.6.82	59.00	7.809	0.607	0.010	
2.6.82	64.90	8.010	0.667	0.017	
29.5.82	76.34	8.546	0.676	0.008	
16.6.82	111.61	5.84	0.918	0.157	

value from an alatae cohort established at the same time (alatae r_m = 0.54, S.E. = 0.022).

Apterae reared on the flag leaves (cohort 16 June) had significantly different intrinsic rates of increase (at $P < 0.05$) from apterae reared on the lower leaves (cohort 19 June) (Tables 2 & 3). Intrinsic rates of increase however did not differ significantly for alatae reared on the two types of leaf. The mortality of aphids was higher on the lower leaves than the flag leaves.

The proportion of alatae per cohort differed for the lower leaves and the flag leaves (Fig.11). All the cohorts established on the lower leaves or emerging leaves after 1 May produced large proportions of alatae, compared with the number of cohorts and the proportion of alatae produced on the flag leaves.

Regression analyses were carried out on the relationship between temperatures inside clip cages on the lower leaves and the flag leaves and standard air temperatures. The temperatures were highly correlated ($r = 0.933$, d.f = 1, 46, $P < 0.001$; $r = 0.962$, d.f = 1, 46, $P < 0.001$ for lower and flag leaves respectively), and the slopes differed from 1.0 by 0.0016 and 0.0876 for the lower leaf and flag leaf clip cages. Hence the temperatures experienced by aphids in the clip cages were similar to air temperatures.

3.3.3 L. perenne (uncut)

The mean number of nymphs produced in 3 days by apterae on the lower leaves of L. perenne steadily increased from 2.0 nymphs in early May to 5.0 nymphs in early June. The numbers declined and then increased again at the end of June. The 3-day fecundity then fluctuated between a minimum 4.0 nymphs to a maximum 10 nymphs per mother. A steady decline in the number of nymphs produced by the apterae occurred in mid-August (Fig.13). Mortality was highest during early June and mid August.

The highest r_m achieved was 0.64 S.E. = 0.016 by a cohort established

Fig.10 The r_m (Jackknife) values for apterae reared in clip cages on leaves of wheat cv. Bounty and the lower leaves of L. perenne. The width of each histogram is the age of the oldest individual within the cohort.

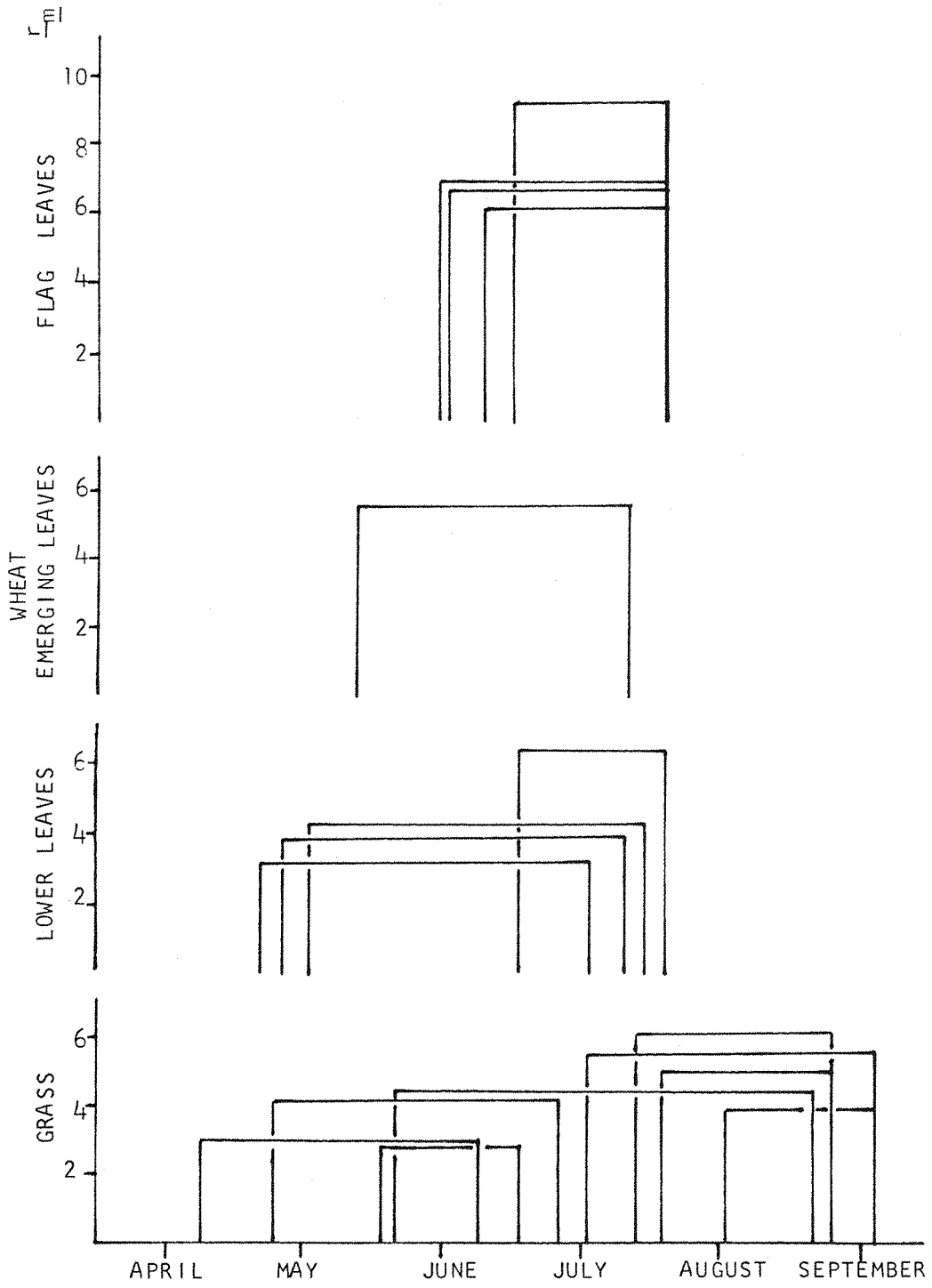


Fig.11 The proportion of alatae produced for each cohort of aphids reared in clip cages on the leaves of wheat and L. perenne. ↓ ; a cohort which produced no alatae. S. ELONG; aphids reared on the emerging leaf of stem elongating wheat

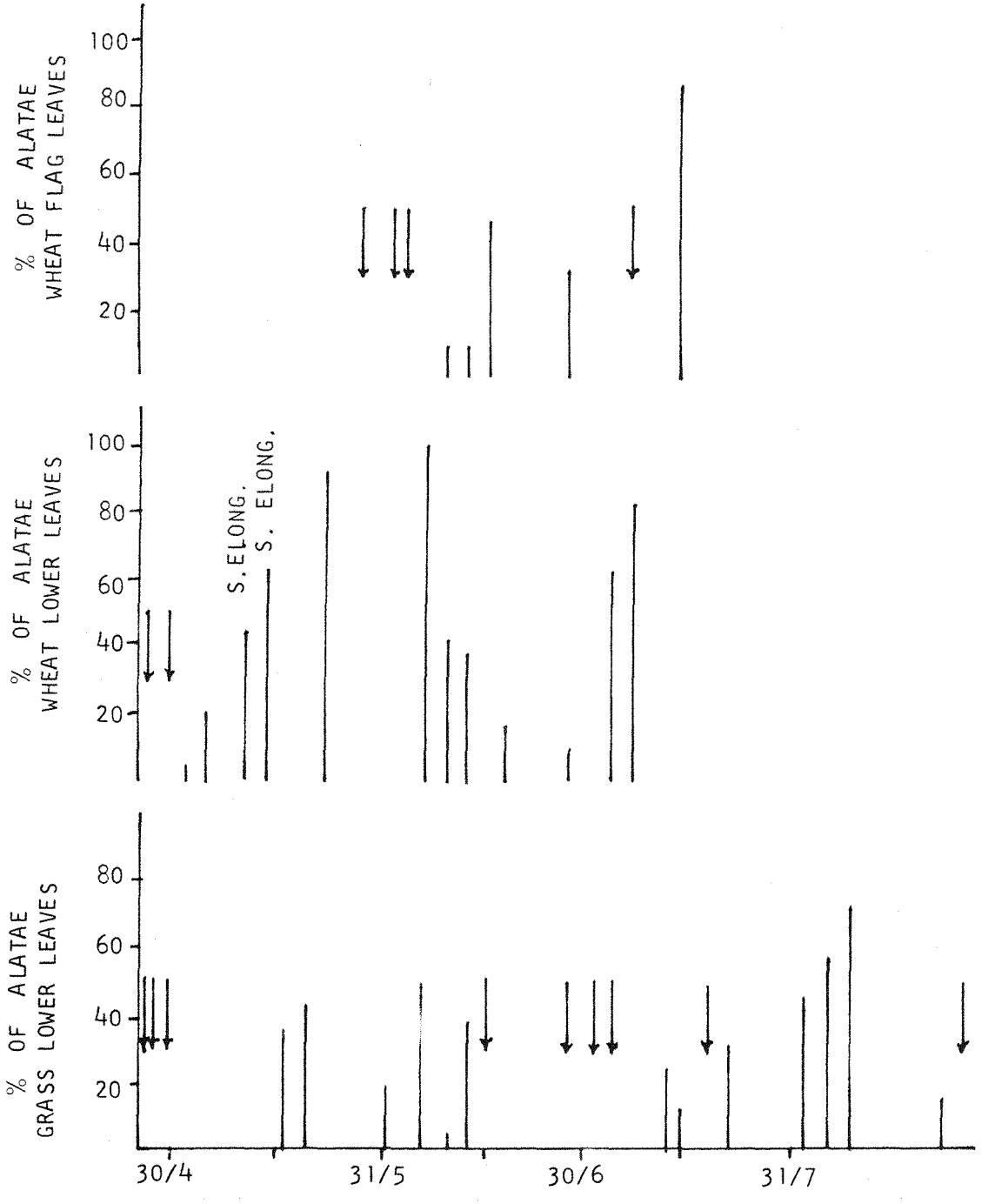


Fig.12 The $\underline{r}_m$ (jackknife) values for apterae reared in clip cages on leaves of wheat and the lower leaves of L. perenne. The width of each histogram is the age of the oldest individual for each cohort

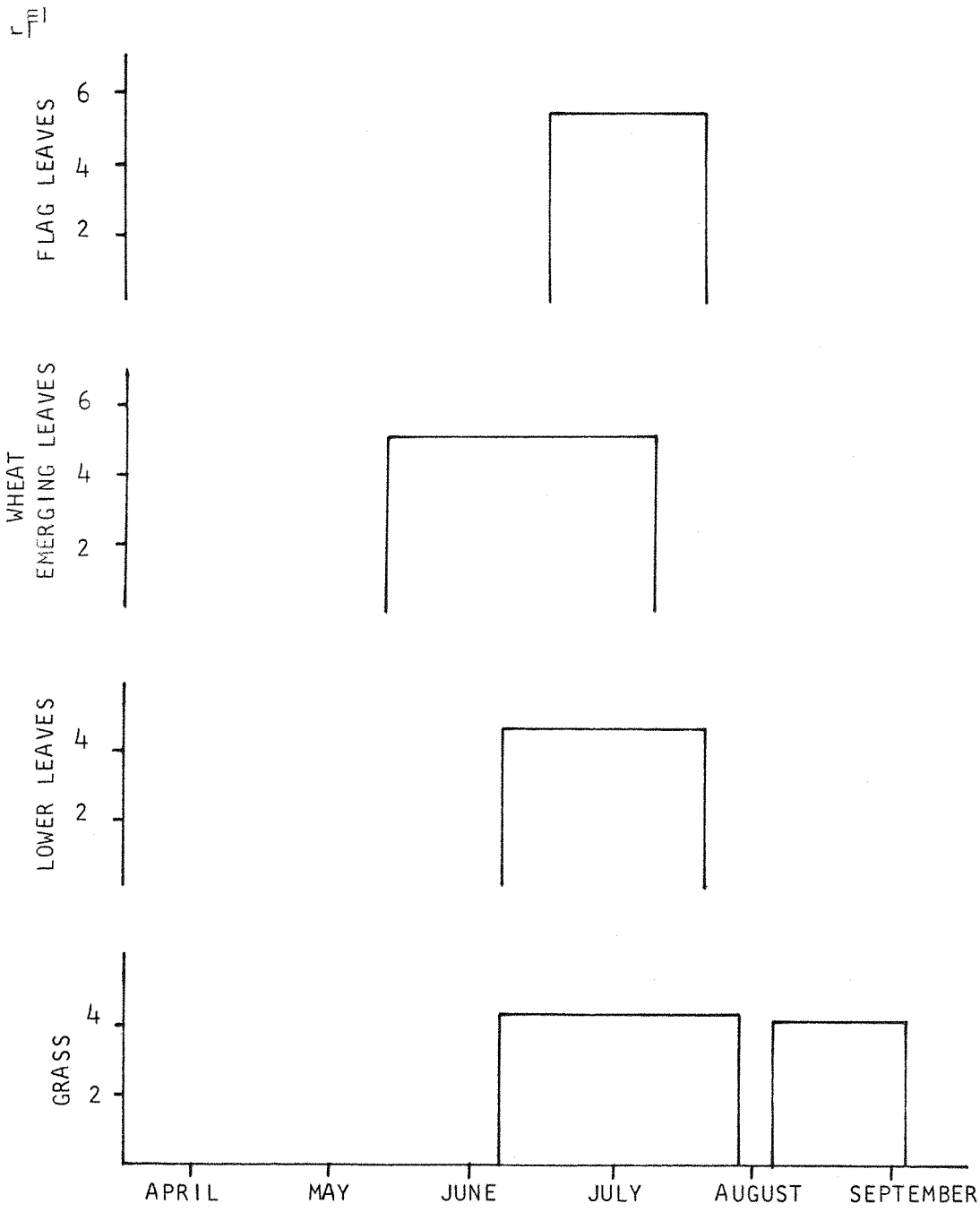


Table 4. The $\underline{r}_m$ values and LSD test for cohorts of apterae reared on the lower leaves of grass L. perenne. $\underline{r}_m$ values underscored by the same line are not significantly different at $P > 0.05$. Ro and G as Table 2.

Date cohort established	Ro	G	$\underline{r}_m$ (Jackknife)	S.E.	LSD
17.5.82	6.50	6.82	0.286	0.034	
8.4.82	24.47	11.80	0.297	0.011	
23.8.82	12.86	7.10	0.393	0.033	
23.4.82	41.95	10.52	0.408	0.065	
7.6.82	20.48	8.37	0.436	0.025	
19.7.82	22.57	6.74	0.496	0.027	
2.7.82	40.39	8.19	0.551	0.033	
13.7.82	41.62	6.63	0.616	0.016	

on 13 July (Table 4). The lowest $\frac{r}{m}$ values were for cohorts established early in the summer (April and May) and a cohort established in late August (Fig.10). The $\frac{r}{m}$ values of two alatae cohorts established on 7 June and 2 August were not significantly different at $P > 0.05$ (Fig.12).

Alatae were produced at two distinct times on grass (Fig.11); for cohorts established between 16 May to 14 June and between 14 July to the end of the experiment, the proportion of alatae produced during the latter time were higher.

3.3.4 L. perenne (cut)

Subsequent to the cut on the first two of the three occasions the number of nymphs produced by apterae markedly decreased (Fig.13). On the third cut which occurred during August the 3-day fecundity increased initially and then steadily decreased. The 3-day fecundity of the aphids on the cut grass at this time was greater than for uncut grass. Mortality on the first two cuts was very high but was low for the third cut (Fig.13).

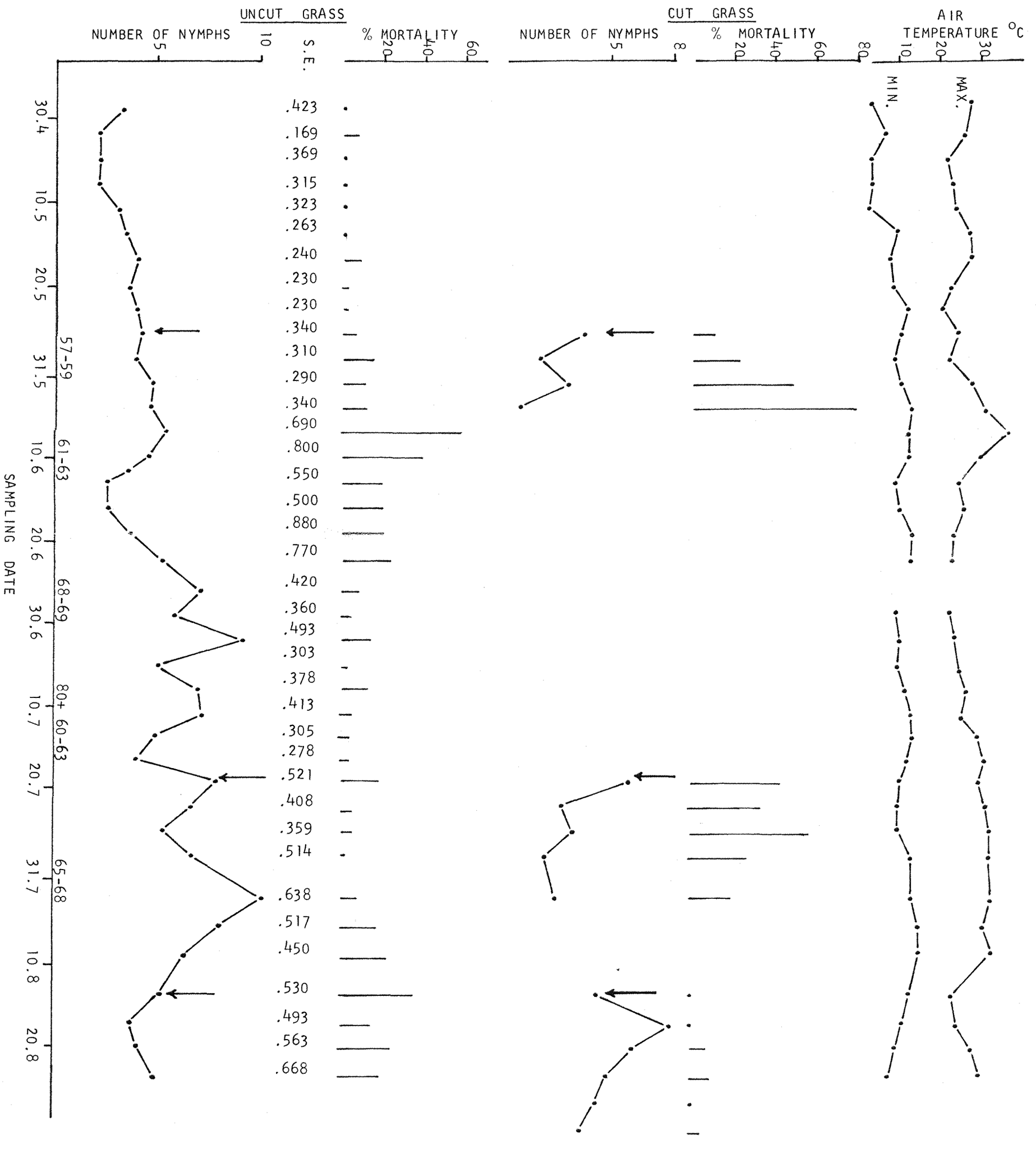
A regression and correlation analysis was carried out of the relationship between temperatures inside clip cages on cut and uncut grass and standard air temperatures. The relationships were highly significant ($r = 0.962$, d.f = 1,46, $P < 0.001$; $r = 0.986$, d.f = 1,46, $P < 0.001$, for cut and uncut grass respectively); and the slopes differed from 1.0 by 0.465 and 0.061 for the cut and uncut grass clip cages. Hence the temperatures experienced by aphids in clip cages on cut grass were half as much again as the standard air temperature.

3.3.5 A comparison of antibiosis in wheat and L. perenne

The 3-day fecundity of apterae on wheat during May and early June was higher than for apterae reared on grass. The fecundities of apterae on both hosts are similar during late June and early July (Figs.9, 10). The highest mortalities occur at different times for aphids reared on wheat and grass.

On grass the highest mortality occurs during early June (G.S. 61-68)

Fig.13 The reproductive performance and % mortality of apterae reared in clip cages on uncut and cut L. perenne cv. Cropper. Growth stages are numbered above the x axis. The arrows indicate time of cut.



and at the end of August (Fig.13), whilst on wheat the highest mortalities occurred from 10 June to 10 July on the lower leaves (G.S. 64-85) and during early June (G.S. 54-56) and mid July (G.S. 85-92) on the flag leaves. The mortality on the flag leaves was less than the mortality on the lower leaves.

During late April the intrinsic rate of natural increase of apterae reared on grass was significantly different from the rate for apterae on wheat ($\underline{r_m}$ = 0.41 ± 0.065; $\underline{r_m}$ = 0.34, ± 0.008 for apterae on grass and wheat respectively) (Fig.10). For cohorts established during early June, the apterae on the flag leaves of wheat had significantly higher $\underline{r_m}$ values ($\underline{r_m}$ = 0.44 ± 0.025; $\underline{r_m}$ = 0.61 ± 0.010; $P < 0.05$, for apterae on grass and wheat respectively). The alatae cohorts established at the same time were also significantly different; once again the alatae reared on wheat (flag leaves) had significantly higher rm values at $P < 0.05$ ($\underline{r_m}$ = 0.43 ± 0.032 on grass compared with $\underline{r_m}$ = 0.53 ± 0.022 on wheat). The alatae reared on the lower leaves of wheat were not significantly different at P = 0.05 to the $\underline{r_m}$ of alatae reared on grass.

The $\underline{r_m}$ values of apterae reared on the lower leaves of wheat and on grass during June were significantly different at $P < 0.05$. The $\underline{r_m}$ of apterae on wheat (0.064 ± 0.026) was higher than that of apterae on grass (0.55 ± 0.033).

3.4 THE INFLUENCE OF CUT GRASS AND TEMPERATURE ON APTERAE REPRODUCTION, WEIGHT AND DEVELOPMENT TIME

3.4.1 The influence of growth stage at 20°C

The 7-day fecundity of apterae reared on uncut seedlings was significantly different from that of apterae on cut seedlings (t = 7.02, d.f = 48, $P < 0.001$) (Fig. 14C). The apterae reared on 10-week old plants which had been either cut or left uncut as seedlings produced similar numbers of nymphs in 7 days (t = -1.39, d.f = 31, P = 0.176). A comparison of 7-day fecundity of apterae reared on cut seedlings and 'cut' 10-week old plants showed no significant difference (t = 1.06,

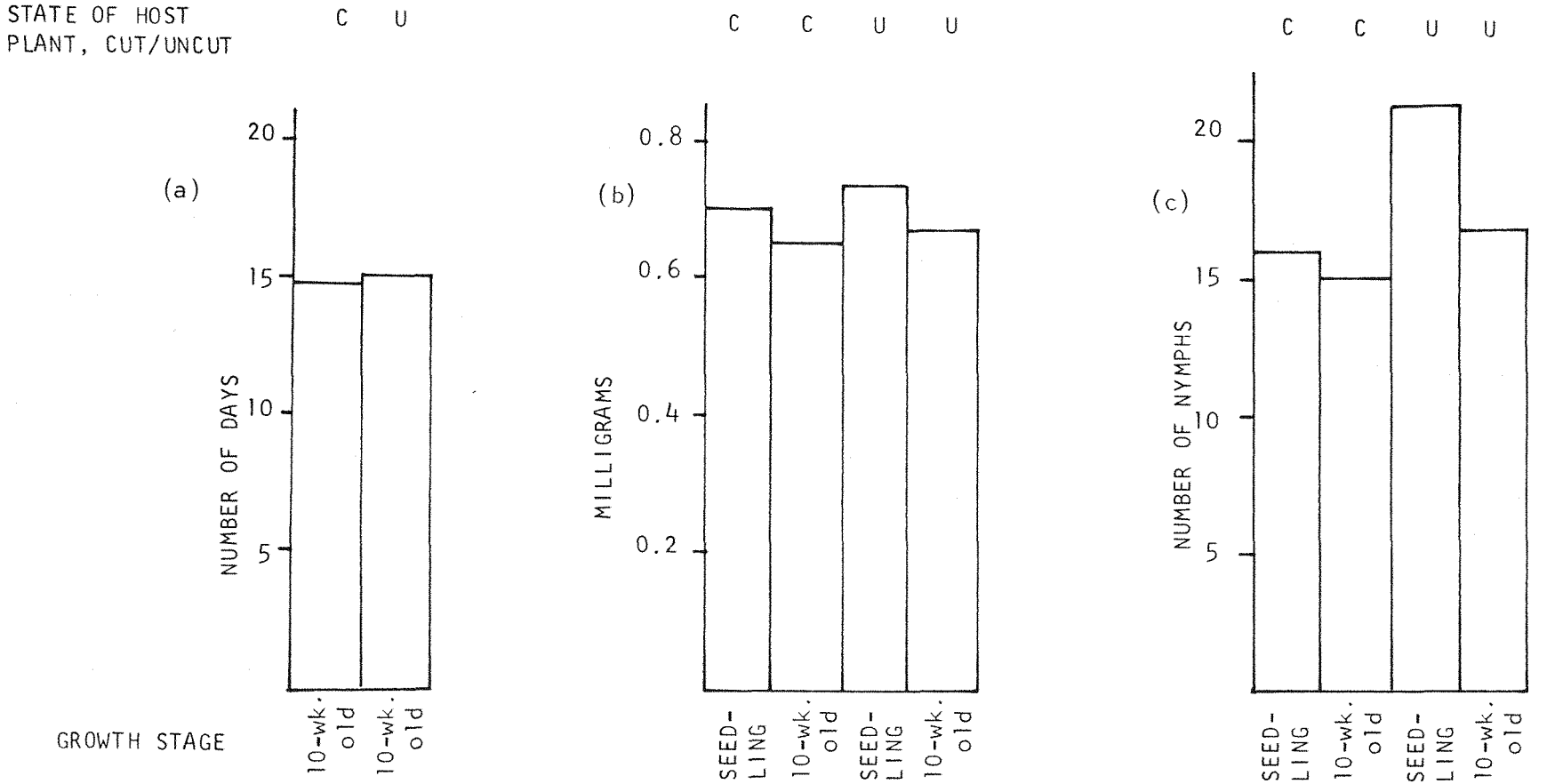


Fig.14 The development time (a), adult weight (b) and fecundity after 7 days of adult life (c), for apterae reared on cut and uncut L. perenne cv. Cropper. The aphids' performance was compared on seedlings and 6-week old plants. The numbers in the histogram (b) are the respective sample sizes. The standard errors from left to right are: 0.23, 0.148; 0.029, 0.028, 0.022, 0.033; 0.568, 0.745, 0.477, 0.868

d.f = 41, P = 0.294) whilst apterae reared on uncut seedlings and uncut 10-week old plants had 7-day fecundities which were significantly different ($t = -4.90$, d.f = 38, $P < 0.001$) (Fig.14c). Cutting seedlings decreases the 7-day fecundity of apterae; an older growth stage has a similar effect.

The development times of apterae reared on cut and uncut 10-week old plants were not significantly different at P = 0.05 (Fig.14a). The weights of adult apterae reared on cut/uncut seedlings and 10-week old plants were not significantly different at P = 0.05 (Fig.14b).

3.4.2 The influence of temperature on development time and adult weight for aphids reared on cut seedlings

The development times of apterae reared on cut seedlings decreased with increasing temperature (Fig.15b). All development times at each temperature were significantly different at $P < 0.001$ ($15^{o}C/20^{o}C$, $t = 8.66$, d.f = 47.68; $15^{o}C/25^{o}C$, $t = 21.12$, d.f = 37.29; $20^{o}C/25^{o}C$, $t = 13.41$, d.f = 50.15).

Adult weights of apterae reared on cut seedlings were influenced by temperature (Fig.15a), with weight decreasing with an increase in temperature. Adults reared at $15^{o}C$ and $25^{o}C$ had significantly different weights (at $P < 0.05$), and adults reared at $20^{o}C$ and $25^{o}C$ differed at P = 0.063. The weights of adults reared at $15^{o}C$ and $20^{o}C$ were not significantly different at P = 0.065.

3.4.3 The influence of temperature and a comparison of development time and adult weight for aphids reared on cut and uncut seedlings

An analysis of variance on development times of apterae reared on cut and uncut seedlings at $15^{o}C$ and $20^{o}C$ showed that the development times were significantly different at $P < 0.001$ ($F = 92.74$). A similar analysis of variance on adult weights showed there to be no significant difference ($F = 1.546$, $P = 0.207$), (Fig.16a). The development times of apterae on cut and uncut seedlings at $15^{o}C$ were not significantly different at $P > 0.05$, whilst the development times of apterae reared

Fig.15 The adult weight (mg) (a) and development time (days) (b), for apterous nymphs reared on cut L. perenne seedlings at 15°C, 20°C and 25°C. The standard errors from left to right were (a) 0.316, 0.330, 0.176, (b) 0.281, 0.224, 0.148.

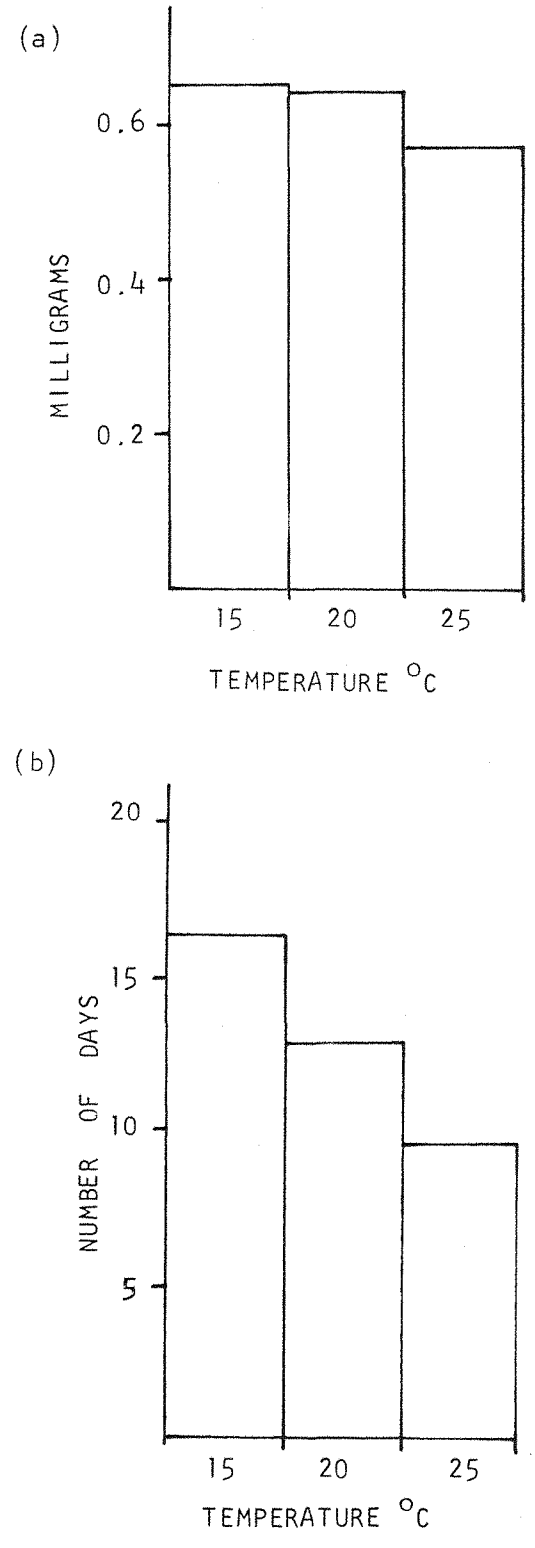
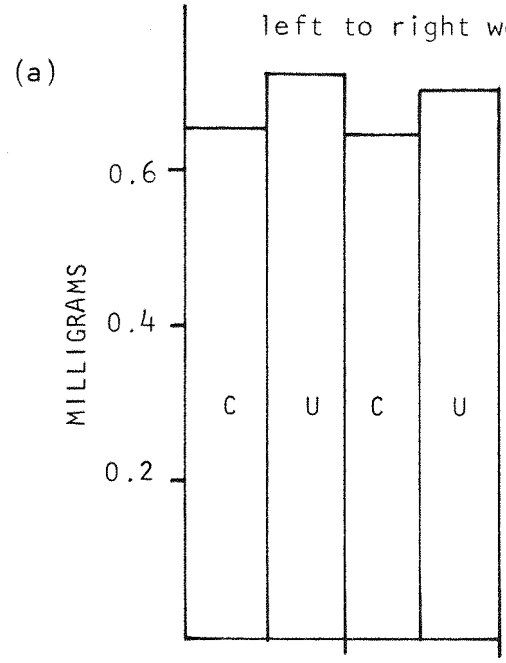
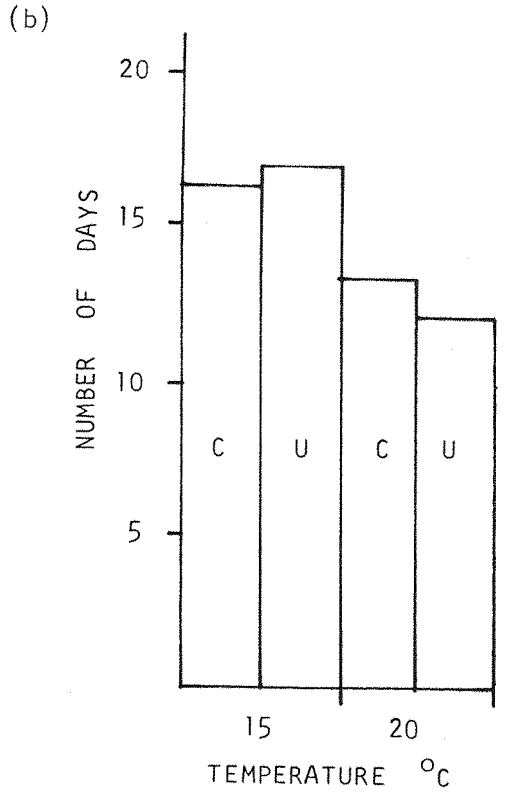


Fig.16 The adult weight (mg) (a), and development time (days) (b), of apterous nymphs reared on cut (c) and uncut (u) seedlings of L. perenne at 15°C and 20°C. The standard errors from left to right were (a) 0.031, 0.028, 0.033, 0.029, (b) 0.281, 0.228, 0.224, 0.196.





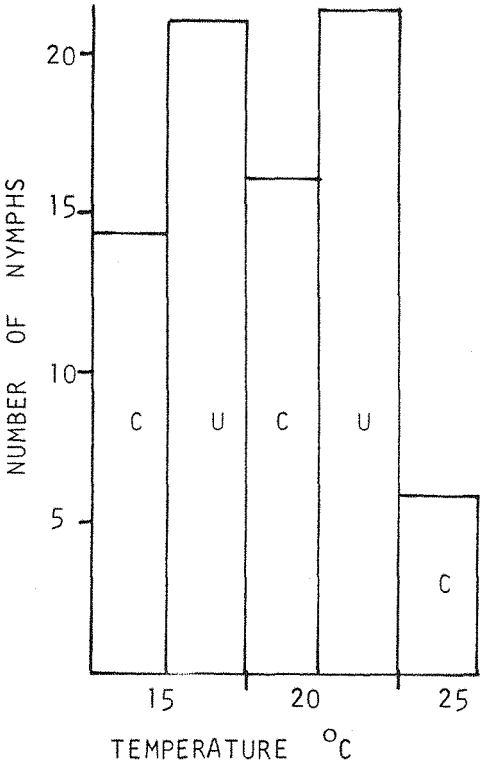
on cut and uncut seedlings at 20°C were significantly different ($t = 3.61$, $d.f = 49$, $P < 0.001$). The development times of apterae reared at 20°C for both cut and uncut seedlings were less than for apterae reared on cut and uncut seedlings at 15°C. The difference was significant at $P < 0.05$.

3.4.4 The influence of temperature on reproduction of aphids reared on cut and uncut seedlings

The apterae reared on uncut seedlings at 15°C and 20°C produced a greater number of nymphs in 7 days than their counterparts reared on cut seedlings (Fig.17). The difference was significant at $P < 0.001$ ($t = 8.32$, $d.f = 51$; $t = 7.02$, $d.f = 48$ for apterae reared at 15°C and 20°C respectively). The 7-day fecundity of apterae reared at 20°C on cut seedlings was significantly higher than the 7-day fecundity of apterae reared at 15°C ($t = 2.11$, $d.f = 45$, $P < 0.05$). The 7-day fecundity of apterae reared on uncut seedlings at 20°C and 15°C was not significantly different ($P = 0.703$).

The 7-day fecundity of apterae reared on cut seedlings at 25°C was significantly less than that of apterae on cut seedlings at 15°C and 20°C ($P < 0.001$).

Fig.17 The fecundity after 7 days of adult life for apterae living on cut (c) and uncut (u) L. perenne seedlings at 15°C and 20°C and cut seedlings at 25°C. The standard errors from left to right were: 0.725, 0.443, 0.568, 0.477, 0.603.



DISCUSSION

The feeding sites of M. festucae cerealium

It was important to know the preferred feeding site of M. festucae cerealium so that this information could be utilized in later measurements of aphid reproductive performance. This was especially true for the antibiosis assessment on seedling grasses. Clip cages were attached to the second unfolded leaf, the preferred feeding site of M. festucae cerealium on this growth stage.

The suggestion by Dean (1974a) that M. festucae cerealium preferred the lower leaves of heading wheat has not been substantiated here. The apterae were evenly distributed over the leaves of the wheat plant, although fewer apterae were found on the flag leaf.

Each cereal aphid species show specific feeding site preferences, S.avenae on the ear (Wratten 1975), M. dirhodum on the flag and lower leaves (Dean & Luuring 1970) and R. padi on the lower leaves (Dean 1974). The feeding site is important in relation to the type and amount of damage that can be caused by the aphids (Vickerman & Wratten 1979). M. festucae cerealium appears to have the same feeding site preference as M. dirhodum. M. dirhodum has caused 7% yield loss with peak populations of 69 aphids per stem (Wratten 1975); M. festucae cerealium then may have the potential to cause a similar yield loss, if numbers reach sufficiently high levels.

The apterae on the tillering L. perenne showed a distinct non-preference for feeding on the most recently unfolded third leaf, whilst preferring to feed on the lower and emerging leaves. The highest numbers of apterae were found on the first leaf which was in the process of senescing, and the emerging leaves, which were actively growing (Fig.1b). The preference for senescing leaves could explain the reference of Gair (1953) of virginoparae on the lower leaves of the grass sward; however the low winter temperatures could also have contributed to this feeding site preference.

When the leaves of L. perenne are inverted, all instars and adults show a preference for feeding on the inverted adaxial surface. This could be due to any combination of the following factors; a characteristic of the adaxial leaf surface, light and/or gravity.

However when the leaf is normally orientated with the adaxial surface uppermost the feeding site preference of the lower instar nymphs remains the same i.e. the adaxial surface. This suggests there is some characteristic of the adaxial leaf surface which is more attractive to the lower instars than to fourth instars and adults.

The stylet length of nymphs is smaller than adult aphids (Pollard 1973) and this could restrict the depth of penetration or the size of phloem bundles available for penetration (Dixon and Logan 1973) by nymphs.

A thick cuticle has been suggested as hindering the feeding behaviour of Aphis fabae nymphs (Davidson 1923). The lower surface of grass leaves have a thicker cuticle than the adaxial surface, and it could be that nymphs cannot penetrate the thick cuticle. However it is not known whether M. festucae cerealium penetrates the leaf lamina or stoma to feed, so this is only conjecture. The presence of a cuticle can also prevent an insect from gaining an adequate grip on a leaf except at the margins (Edwards and Wratten 1980). M. festucae cerealium adults were observed to grip the leaf blade by the edges when they were feeding on the inverted surface. The nymphs may not be able to feed on the abaxial surface when it is normally orientated since they cannot grip the cuticle. However nymphs can feed on the inverted adaxial surface which has less cuticle and leaf ridges onto which the nymphs can hold.

There is some circumstantial evidence to suggest that the fourth instars and adults may feed on the lower surface of leaves to avoid predators (Carrillo, pers.comm.). Earwigs which prey on M. festucae cerealium are able to walk and move only on the upper surface of a leaf (normally the adaxial surface). Any aphids they find on this surface they will consume. M. festucae cerealium fourth instars and adults

can avoid predation by feeding on the underside of the leaf. If both adults and nymphs have a preference for the adaxial surface but by feeding on the adaxial surface there is an increased choice of predation then this would explain the response shown in Fig.3a and b.

Antibiosis: Laboratory

Stroyan (1982) remarked that one of the distinguishing features which separates M. festucae s. str. from M. festucae cerealium is the propensity with which M. festucae cerealium colonizes cereals. This study like those of Hill (1971) and Stroyan (1982) has shown that M. festucae cerealium is more fecund on wheat than on other grass hosts. However the ranking of fecundity achieved here differs from the ranking given by Hill (1971), and presumably differs also from those of Stroyan (1982). Hill (1971) showed that the fecundity on wheat and oats was not significantly different, whilst in this study apterae reared on oats were much less fecund than those on wheat. P. pratense also ranked high as a susceptible host in Hill's work, whilst here it is the most resistant grass to M. festucae cerealium. The differences between the two resistance rankings can be attributed to differences in cultivars and the use by Hill of an insectary.

Differences in the reproductive performance of an aphid species between growth stages is often not consistent for a number of different host plants (Leather and Dixon 1982a; 1982b), but with M. festucae cerealium this was not the case. The fecundity of apterae on the stem elongating plants was consistently less than for apterae reared on seedlings, although the ranking of fecundities was the same as for seedlings, i.e. apterae were most fecund on wheat followed by L. perenne, L. multiflorum and D. glomerata. The ranking of adult weights was also the same for stem elongating plants and seedlings.

Leather and Dixon (1982a) reared R. padi on a number of seedling grasses and measured 7-day fecundity. For all the grasses (except F. pratensis) which they compared that overlapped with the host range studied here, the mean fecundity was higher than that achieved by

M. festucae cerealium. The ranking of resistance for the grasses differed for the two aphid species. Both species have high fecundities on L. perenne and lowest on D. glomerata. P. pratense is more susceptible to R. padi than to M. festucae cerealium; the other grasses also differ in susceptibility. Also the mean weights of R. padi were lower than the lowest mean weight of the apterae of M. festucae cerealium.

Leather and Dixon (1981) state that R. padi can achieve reproductive rates of up to 40 nymphs in 7 days after a development period of 6-7.5 days on cereals and compare this with a reproductive rate of 35 nymphs in 7 days after 8.5 days' development time for S. avenae (Watt 1979). During this study the highest reproductive rate in 7 days achieved by M. festucae cerealium on cereals was 27 nymphs with a development time of 11 days. M. festucae cerealium clearly does less well on cereals than either S. avenae and R. padi and also less well than R. padi on grasses.

This difference in reproductive performance on cereals may help to explain why M. festucae cerealium is less abundant on cereals than either S. avenae or M. dirhodum.

Antibiosis: Field

During late April the apterae reared on L. perenne were more fecund and had a higher intrinsic rate of increase than apterae reared on the lower leaves of wheat. Normally, in the laboratory and for the rest of the fieldwork, apterae were more fecund on wheat. This suggests that the ability to reproduce on any particular host may be dependent on environmental conditions (Leather & Dixon 1982a).

The peak fecundity was reached on wheat at anthesis but the decline in fecundity was not as rapid as that of S. avenae (Watt 1979). There was also a corresponding increase in fecundity indicating that the apterae may be responding in the same way to similar growth stages on different host plants. However there would be less reason for M. festucae cerealium to respond to the growth stage of grass than to growth stage of cereals. Within a grass sward there is a continuous production of new tillers, mature and senescing leaves as well as flowering stems.

An aphid has an unlimited supply of preferred feeding sites; in the case of M. festucae cerealium these are the senescing leaves and newly-emerging leaves.

Without the influence of population density the timing of alate production on L. perenne and on wheat were completely different. Alatae on L. perenne were produced in two specific groups, (G.S. 57-59 and 65-68 respectively) perhaps as a response to host growth stage. On wheat alatae were produced with every cohort established on the lower leaves. The production of alatae is normally associated with a deterioration in plant quality and subsequent alate emigration; if this were the case with M. festucae cerealium on wheat then the plants were in a poor condition for most of the summer. In culture on wheat, M. festucae cerealium has always produced larger numbers of alatae than on L. perenne.

The fecundity of apterae on wheat is greater than that of alatae, therefore there is no great advantage in producing alatae unless it is to enhance dispersal. There is a host plant effect which seems to stimulate production of alatae on wheat to a greater extent than on grass.

S. avenae has been shown to colonize grasses sequentially according to their state of development (Watt 1979); the production of alatae increased as aphid density increased on each of the hosts. M. festucae cerealium could be responding in a similar way and produces alatae in response to specific host plant stimuli and host growth stage.

The influence of cut grass

There has been very little work that follows the fate of invertebrate populations before and after a sequence of cuts on grassland managed for conservation of silage. Most of the work done has been concerned with the numbers of species and numbers of individuals present in the grass sward at the conclusion of a grazing and/or cutting régime (Curry 1978; Curry and Tuohy 1978; Henderson and Clements 1977, 1979;

Morris 1978, 1979; Morris and Lakhani 1979). Work by Penman et al (1979) has shown that a selective grazing management can significantly reduce the impact of the blue green lucerne aphid (Acyrthosiphum kondoi) on lucerne crops in New Zealand. No work of this kind has been carried out in this country despite the low numbers of aphids apparently required to cause significant yield loss to grassland (Henderson and Clements 1979).

The decrease in fecundity and the increase in mortality caused by cutting the grass is sufficient to explain the effectiveness of cutting as a control for M. festucae outbreaks in grassland (Edwards and Heath 1964). The laboratory experiments showed that even without the influence of water stress, cut seedlings significantly influenced both fecundity and development time. An increase in temperature has been shown to decrease the development times of M. dirhodum, R. padi and S. avenae on leaf disks (Dean 1974b), although no work has been done on cut grasses. The fecundity, development times and adult weight decrease with very high temperatures; similar results were recorded by Murdie (1969) and Dean (1974b).

The aphids which are left on the sward after a cut for silage are on a host which is probably suffering from water stress, and the aphid is then exposed to more extreme temperature changes. The combined effect of host water stress and temperature on aphid reproduction and development time (Wearing and van Emden 1967; Murdie 1969; Dean 1974b) would be sufficient marked to reduce aphid populations on recently cut grassland.

CHAPTER FOUR

THE REPRODUCTION, FLIGHT AND SETTLING BEHAVIOUR OF ALATE VIRGINOPARAE

INTRODUCTION

Aphids exhibit a great plasticity in morphology and behaviour which allows rapid population increase in suitable environments and escape from less favourable ones.

Apterous virginoparae are the aphid morph which has a high reproductive potential whereas alatae have extra roles including dispersal, emigration and escape from natural enemies (Schaefers 1972).

Alatae are classically thought of as being produced in response to unfavourable conditions such as crowding (Toba, Paschke, and Friedman 1967; Awram 1968; Dixon, Burns and Wangboonkong 1968; Shaw 1970, 1973; Dixon and Glen 1971; Sunderland and Mittler 1971; Dixon 1972; Watt and Dixon 1981), a change in hostplant condition/nutrition (Mittler and Dadd 1966; Dadd 1968; Sutherland 1969; Mittler and Kleinjan 1970; Mittler and Kunkle 1971; Dixon 1972; Schaefers 1972), photoperiod and temperature (Kenten 1955; Schaefers and Judge 1971); however an alternative function of alatae is dispersal of the aphid when its host is most suitable (Schaefers and Judge 1972; Schaefers 1972). This role of alatae in the dispersal of aphids between favourable hosts has rarely been considered despite work which has suggested that alatae continue to fly between larvipositions (Johnson 1953; Johnson 1958; Dent unpublished). Further, the role of alatae in dispersal and host selection is often overlooked in studies of host-plant resistance even though alatae must play a greater part than apterae in the selection between plant species (Kennedy and Booth 1950), i.e. non-preference, see below.

Plant resistance has three fundamental components: (a) nonpreference (the use of the term non-preference has now been replaced by 'antixenosis' (Kogan and Ortman 1978), but their meanings are synonymous) (b) antibiosis and (c) tolerance (Painter 1951). The emphasis in work on aphids has been to study antibiosis either to obtain life cycle information or for rapid, often laboratory-based, screening cultivars for agricultural use (Ch.3). There have been very few studies of antixenosis on cereal

aphids with the exception of the work of Leather and Dixon (1982b) and Walters and Carter (1981). The former study looked at the preference of alate and apterous R. padi for a number of grasses and the latter at for preference of alate S. avenae for different growth stages of cereals.

In assessing alate host-finding behaviour it is important to take into account alate age and larviposition history as these have been shown to influence the flight response of A. fabae (Johnson 1957) and S. avenae (Dent unpublished), whilst alate movement in M. dirhodum and S. avenae are influenced by the number of nymphs produced (Dean 1973). The weight of adult alatae has also been shown to influence aphid flight behaviour. Large alatae of D. platanoidis have been shown to have a greater wing loading and fly more frequently (although shorter distances) than do the smaller more migrant alatae (Dixon 1974), whilst a greater proportion of migrant alatae are found among small rather than large alatae of A. fabae (Shaw 1974).

The number of ovarioles is another factor related to alate flight behaviour and varies according to the species and morph of the aphid. Wellings, Leather and Dixon (1980) have shown for a range of aphids (not including M. festucae) that individuals within a species having a higher number of ovarioles, are potentially more fecund and reproduce at a greater rate than individuals with fewer ovarioles. They related the variation in ovariole number to a programmed anticipation of predictable changes in habitat, which so optimized the reproductive success of the aphid in a changing environment. Alate morphs are normally produced in greater number during less favourable conditions (Shaw 1970b, 1970c and 1973), e.g. high densities. These conditions may vary in severity and persistance, therefore it would be an advantage if alatae could optimise their dispersal and reproductive effort in anticipation of these conditions. Work by Leather and Walters (unpublished) on R. padi and Dent (unpublished) on S. avenae showed a positive relationship between the number of ovarioles and alatae take-off time (the time from when the alate was first on the platform until subsequent flight) from a non-host surface. Those alatae with a large number of ovarioles were more reluctant to fly than alatae with few ovarioles. If an aphid

colony was experiencing unfavourable conditions alate nymphs would be produced which would have a low ovariole number and would subsequently leave the colony as migrants; under more favourable conditions any alatae produced would either have the ability to fly and reproduce and/or an inability to fly but a large potential for reproduction. Ovariole number, then, essentially determines the 'apterousness' of alatae.

The interaction between flight and settling behaviour is important for host finding in aphids (Wiktelius 1982). Settling behaviour has been studied to explain differing levels of damage (Parry 1971), the transmission of virus (Wiktelius 1982), and differences in host preferences (Müller 1958) as well in relation to duration of flight (Johnson 1957; Wiktelius 1982; Kennedy and Booth 1963a, 1963b). Host-preference may be explained by the settling behaviour of alatae. M. festucae cerealium is found more on grassland than on cereal crops and yet in the laboratory M. festucae cerealium was more fecund on wheat than any of the grasses (Ch.3). The settling behaviour of alatae may help explain the differences in numbers found on the wheat and grass crops.

The aims of the present work are to:

(I) determine the extent of the alate flight response to a selected number of host plants (antixenosis experiment).

(II) study the relationship between alate flight and the number of nymphs produced by alatae on different host plants.

(III) determine the relationship between alate flight and ovariole number.

(IV) compare the settling behaviour of alatae on L. perenne cv. Cropper and wheat cv. Bouquet.

RESULTS

4.1 ANTIXENOSIS EXPERIMENT: THE INFLUENCE OF THE HOST PLANT ON ALATAE FLIGHT.

The proportion of alatae taking off from the six host plants F. rubra, F. arundinacea, L. multiflorum, oats, L. perenne, and wheat were

significantly different (χ^2 = 53.613, d.f. = 5, $P < 0.005$). The proportion of alatae taking off from F. rubra and F. arundinacea was much larger than that from the other host plants (Fig.1). A subsequent chi-squared analysis showed that the proportions leaving L. multiflorum, oats, L. perenne and wheat were similar (χ^2 = 9.044, d.f = 3, $0.25 < P > 0.05$), and the heterogeneity in the initial chi-squared was caused by the differing response of F. rubra and F. arundinacea.

The relative proportions of alatae taking off and remaining on F. rubra and F. arundinacea were not significantly different (χ^2 = 3.352, d.f = 1 $0.10 < P > 0.05$). More alatae remained on oats than any of the other host plants (Fig.1).

Data were collected for each host plant over 2 days and a chi-square analysis was performed to see if the flight response differed for each host plant between the 2 days. The data were homogeneous between days for all host plants (Table 1).

A number of alatae were lost during the experiment and they could not be accounted for.

The alatae had left the host but the number re-captured did not related to the numbers flown. A chi-squared analysis was performed between the numbers lost for each host plant. χ^2 = 3.823, d.f = 5, $0.75 < P > 0.05$; thus there was no significant difference between the numbers of alatae lost during each trial.

4.2 FLIGHT, REPRODUCTION AND ALATE WEIGHT

4.2.1 For each host plant a comparison between alatae which did and did not fly

The weights of the alatae which did and did not fly were not significantly different at P = 0.05. Hence the weights of the alatae were not influencing the differences in the flight response.

The total number of nymphs produced by alatae (i.e.the number of nymphs produced on the wheat culture plants plus the number of nymphs produced on the experimental plant) which did and did not fly were

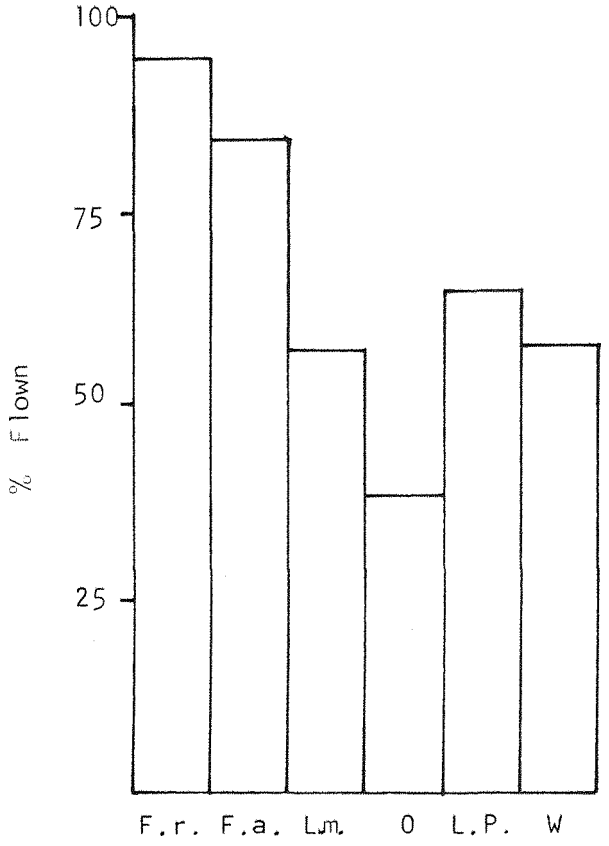


Fig.1 The percentage of alatae which flew from the experimental host plants: F.r. Festuca rubra cv. Echo; F.a., Festuca arundinacea cv. Conway; Lolium multiflorum cv. R.V.P. Lemptal; Oats cv. Maris Quest; Lolium perenne cv. Cropper; wheat cv. Bouquet.

Table 1. The chi-squared values and associated probabilities used to test whether the flight response data collected over two days were homogeneous. d.f = 1

Hostplant	χ^2	P
F. rubra	0.389	$0.750 < P > 0.50$
L. perenne	0.008	$P > 0.90$
F. arundinacea	0.036	$0.90 < P > 0.75$
wheat	0.012	$P > 0.90$
oats	0.070	$0.90 < P > 0.75$
L. multiflorum	0.095	$0.90 < P > 0.75$

significantly different at $P < 0.05$ on all the hosts except F. rubra ($t = 1.87$, $P = 0.67$) and wheat ($t = 0.30$, $P = 0.767$).

The number of nymphs produced on the experimental seedlings, by alatae which did not fly differed significantly from the numbers of nymphs produced by alatae which did fly at $P < 0.05$; except for alatae flying from L. perenne and wheat. The number of nymphs left behind by alatae on these hosts did not significantly differ ($z = -1.870$, $P = 0.0615$; $z = -0.084$, $P = 0.932$ for L. perenne and wheat respectively) from the number of nymphs produced by alatae which did not fly. This suggested that the alatae which did fly from L. perenne and wheat, took off late in the experiment after producing as many nymphs as was possible in the time.

4.2.2 A between-host-plant comparison of alatae which did not fly

The weights of the alatae on F. rubra were significantly different from the weights of alatae on L. perenne ($t = 2.22$, $P = 0.036$) and on wheat ($t = 2.36$, $P = 0.025$); the weights of all the other alatae were not significantly different at $P = 0.05$.

The total number of nymphs produced, and the number of nymphs produced on the experimental plants, by alatae which did not fly, were not significantly different at $P = 0.05$.

4.2.3 A between-host-plant comparison of alatae which did fly

The weights of alatae which did take off were significantly different between host plants (Table 10). The alatae which took off from wheat were heaviest and those taking off from oats were the lightest.

The total number of nymphs produced and the number of nymphs left on the experimental plants by alatae were significantly different (Table 10). The alatae which flew from the wheat left the largest number of nymphs behind and alatae taking off from F. rubra left the lowest number. The number of nymphs left behind by alatae on L. perenne and wheat were not significantly different; also the number of nymphs produced by alatae which did and did not take off were not significantly

different (4.2.1). When this is considered in conjunction with the proportions of alatae taking off from each host plant (Table 1) it then becomes apparent that the flight/reproduction strategy of alatae on L. perenne and wheat was different from the alatae on the other hosts. The alatae on L. perenne and wheat produce a large number of nymphs and then a high proportion (approximately 60%) take off. This was in contrast for example to alatae which flew from L. multiflorum (the proportion taking off was the same as wheat), where the number of nymphs left behind was on average just over one nymph per alata.

4.3 THE INFLUENCE OF OVARIOLE NUMBER AND THE NUMBER OF LARGE EMBRYOS ON FLIGHT

4.3.1 For each host plant a comparison between alatae which did and did not fly

The weights of alatae which did and did not fly from wheat cv. Bouquet (reared on Hobbit) and wheat cv. Bouquet (reared on Bouquet) were significantly different at $P < 0.05$ (Table 2). There were no consistent differences in weight between alatae which did and did not fly. There were no significant differences between the mean ovariole numbers of the alatae which did and did not fly from all the host plants (Table 2). The alatae which did take off had a significantly higher number of large embryos than those which did not fly (Table 2). This could be an inherent characteristic i.e. alatae with large embryo numbers tend to fly, or it could be that the alatae which had flown had not reproduced before flight, therefore they had more large embryos.

Regression analyses of ovariole number on weight and large embryo number on weight were not significant.

4.4 THE INFLUENCE OF THE HOST PLANT ON SETTLING BEHAVIOUR

4.4.1 The time spent walking, stationary and probing on wheat and L. perenne

A two-way analysis of variance of the data showed there to be no

Table 14. The difference between means of (a) alate weight and (b) the mean number of nymphs produced before flight N; also the percentage of alatae which did fly from each host species (% F). Host abbreviations as in Figure 1. Means underscored by the same line are not significantly different at P = 0.05.

(a) WEIGHT

	0	F.a.	L.m.	F.r.	L.p.	w
$\bar{x}$	0.464	0.477	0.504	0.523	0.527	0.533

(b) NUMBER OF NYMPHS

	F.r	F.a.	L.m.	0	L.p.	w
% F	94.7	84.2	57.1	38.3	64.8	57.8
$\bar{x}$ N	0.982	1.156	1.277	1.608	2.230	2.972

Table 2. A comparison of weight, LEN and ovariole number between alatae which did and did not fly from a number of host plants. Comparisons were made using the t-test for weight and L.E.N.; a Mann Whitney U test was used for ovariole number.

HOST PLANT	$\bar{x}$ not flown	$\bar{x}$ flown	t	P
WEIGHT				
wheat cv. Hobbit	0.512	0.548	1.32	0.193
wheat cv. Bouquet	0.483	0.401	2.47	0.018
L. perenne	0.444	0.476	1.30	0.199
wheat cv. Bouquet (reared on Bouquet)	0.727	0.630	3.06	0.004
LEN				
wheat cv. Hobbit	6.891	10.428	5.88	0.0001
wheat cv. Bouquet	7.137	8.300	2.35	0.024
L. perenne	6.440	9.375	5.88	0.0001
wheat cv. Bouquet (reared on Bouquet)	10.551	12.57	3.60	0.001
OVARIOLE NUMBER				
			z	
wheat cv. Hobbit	9.478	9.357	-0.489	0.05
wheat cv. Bouquet	9.862	10.000	-0.287	0.05
L. perenne	9.880	9.750	-0.225	0.05
wheat cv. Bouquet (reared on Bouquet)	9.862	9.904	-0.304	0.05

significant difference in the way time was allocated by alatae on the two host plants. The data were extremely variable and for this reason they were analysed in terms of relative proportions (Fig.2).

The time spent probing by alatae on the adaxial leaf surface of L. perenne (88%) was slightly longer than that on wheat (81%). The time spent walking and stationary was greater on the wheat (Fig.2).

The allocation of time on the abaxial surface was completely different for alatae on each host. Alatae on L. perenne spent more time walking than probing (55% and 37% respectively) compared with than on wheat (26% and 65% respectively). If it is assumed that an alate is more likely to be restless and walk more on a less preferred host or leaf surface and spend more time probing on a preferred host or leaf surface then alatae 'prefer' the abaxial surface of wheat more than the same surface of L. perenne.

The total proportion of time spent probing was greater on L. perenne (88%) than on wheat (77%). The time spent walking and stationary on wheat was greater than on L. perenne (Figure 2).

The proportion of probes made by alatae on the adaxial surface was much greater on L. perenne than on wheat (Figure 3). Alatae on wheat made 31% of their probes on the abaxial surface. Alatae on wheat also made more probes on the stem (14%) than did alatae on L. perenne (7.5%).

DISCUSSION OF METHODS

Work by Kennedy and Booth (1963) made it clear that the type of procedure used for alate flight experiments was critical if there was to be no bias in the results. There are two main areas of importance (I) previous flight experience and (II) interference of the aphids.

The alatae of some species reject the host on which they were born (Kring 1972) and flight mature aphids (recently moulted alatae capable of flight) are more likely to settle on a host plant if they have previously taken flight (Johnson 1958; Dixon 1971). Alatae in this experiment were given no previous flight experience; however aphids

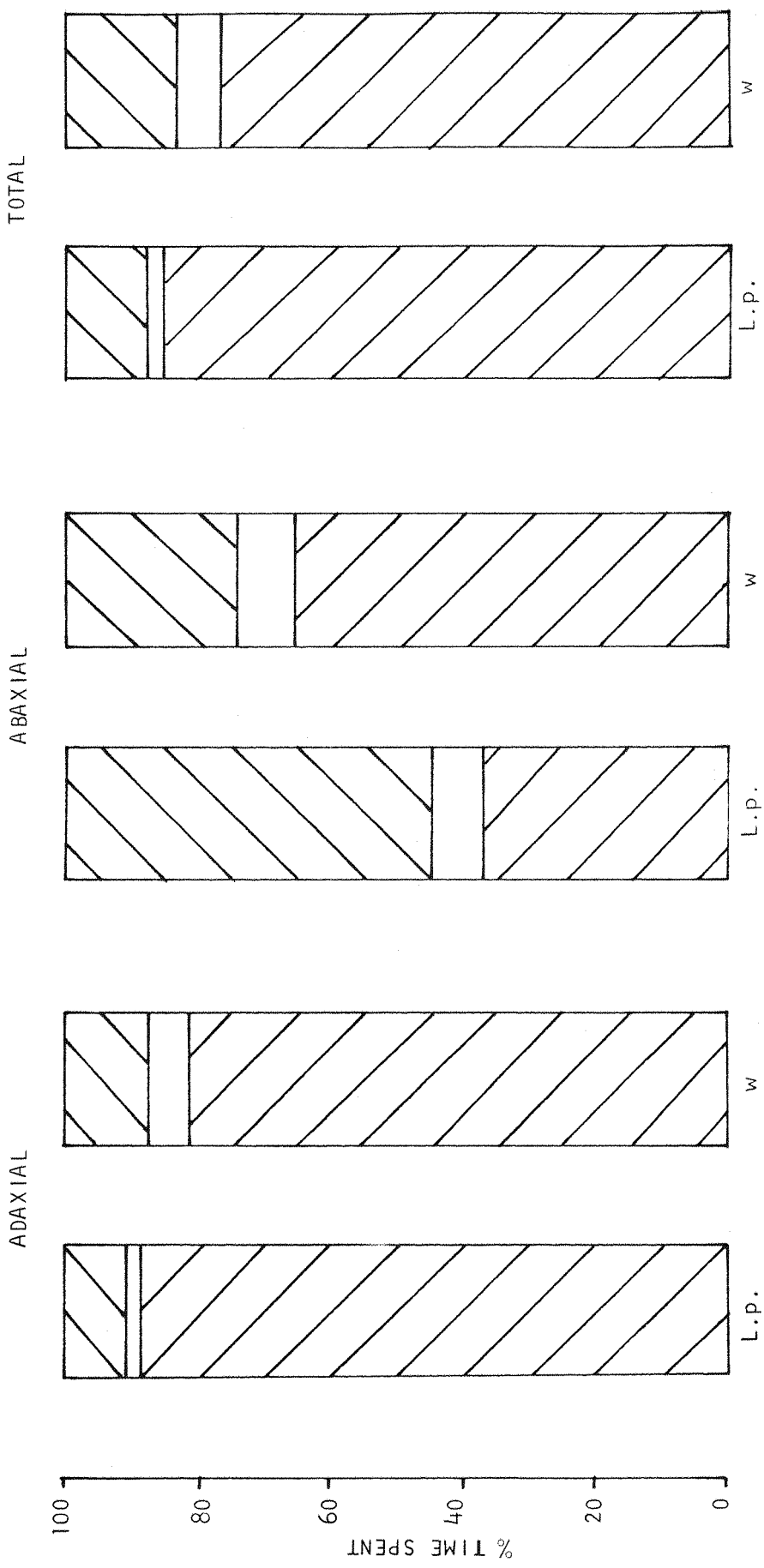


Fig.2 The proportion of time spent by settling alatae probing ▨, stationary □, and walking ▨ on the adaxial and abaxial leaf surfaces of Lolium perenne L.p. and wheat seedlings w.

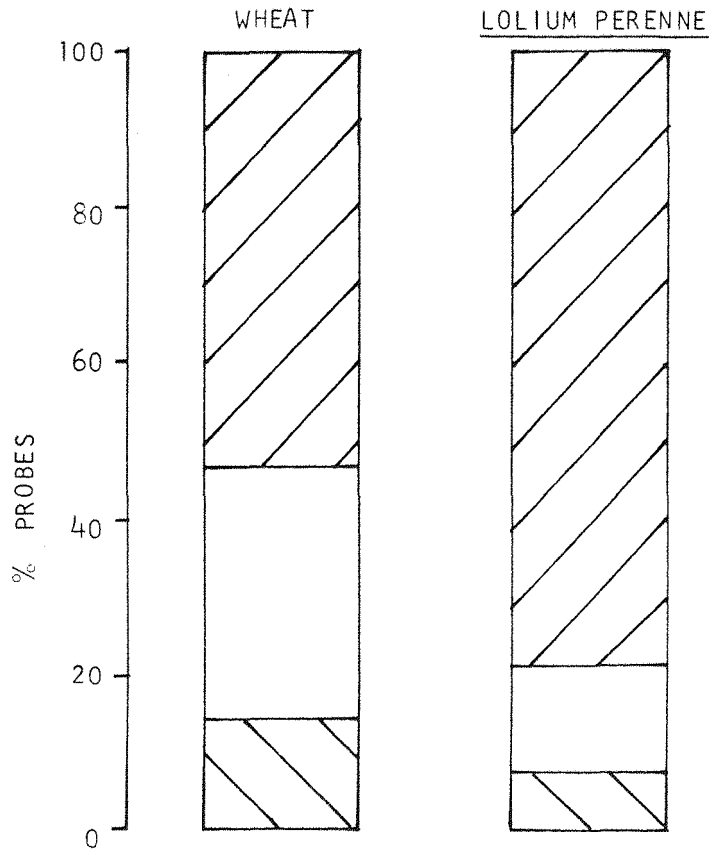


Fig.3 Proportion of probes made by alatae on a. ▨ adaxial and b. □ abaxial leaf surfaces and c. ▧ stems of wheat and Lolium perenne seedlings

which are confined to the host plant may reproduce (and hence have released the settling response) without first engaging in locomotory activity (Johnson 1958). Hence all the alatae used in this experiment had 'settled' on the 'culture' plant before being used for the experiment.

Excessive handling of alatae enhances their settling response (Kennedy and Booth 1963); the transfer of alatae to the flight chamber was carried out without the use of a paintbrush (see Ch.2) and hence did not unduly interfere with the aphid. The alatae were placed in a darkened flight chamber because this increased the settling response and was equivalent in effect to a long flight of several hours (Johnson 1958). The flight response exhibited in this experiment was an expression of alate reselection after they had been given every opportunity to settle.

Alatae which have landed on a favourable host may or may not settle to feed and will often return to flight (Johnson 1958; Müller 1958; Kring 1972); they will take off from a favourable host even after having produced nymphs (Johnson 1958; Müller 1958; Shaw 1970b). Alatae accumulate on a particular host because they have a prolonged stay on a suitable host and depart from a less suitable one (Müller 1958; Kring 1972). Antixenosis experiments with alatae must take into account this transient flight/settling behaviour. The numbers of alatae present on a host at any particular time may not truly reflect the alate preference (see Leather and Dixon 1982b) unless the activity of the alatae on the host and the number of nymphs produced are recorded as well (see Walters and Carter 1981).

Antixenosis was measured here as the numbers of alatae taking off as opposed to the numbers settling (Leather and Dixon 1982; Walters and Carter 1981) because the proportion of alatae which actually settle is often very low (Holt pers.comm.). The number of nymphs produced by alatae was also recorded.

DISCUSSION

The proportion of alatae taking off from oats was lower than that for any of the other plants tested, suggesting a preference for this host. However, the proportion of alatae leaving the different host plants should only be considered in conjunction with the number of nymphs produced before take off, since alatae will even take off from suitable hosts (see above).

The larger number of alatae which flew from F. rubra and F. arundinacea left few nymphs behind which suggests that these hosts were unsuitable for colonization. Alatae spend less time on unsuitable hosts (Müller 1958; Kring 1972) and this was reflected in the greater number of nymphs produced by alatae which did not fly compared with those that did. The exceptions to this were the numbers of nymphs produced by alatae which did and did not fly from F. rubra and wheat. The number of nymphs produced by alatae on F. rubra was very low and this suggested an antibiotic as well as an antixenotic influence. Subsequently few alatae remained, the majority flying. The alatae which flew from wheat produced as many nymphs as the alatae which did not fly. The alatae had stayed on the wheat for a longer duration than alatae on the other host plants. The large number of nymphs left behind suggested that wheat was a preferred host. Flight may have been stimulated by an unsatisfactory host flavour (Kennedy and Booth 1951).

The number of nymphs left behind by alatae which flew from wheat and L. perenne were not significantly different (Fig.2), although the number of nymphs produced by alatae which did fly from L. perenne were significantly less than the numbers produced by alatae which did not fly. The alatae taking off from L. perenne are dispersing from a suitable host which allows colonization of other similar hosts before the loss of the ability to fly. The host plants of M. festucae cerealium are both temporally and spatially abundant and there would be ample opportunity for successful colonization by alatae.

There was no difference in ovariole number between alatae which did and did not fly. The ovariole number of M. festucae cerealium does not seem to influence take-off behaviour as it does for S. avenae

(Dent unpub.) and R. padi (Walters and Leather unpub.). The variation in ovariole number and its influence on the drive of alatae to fly was thought (Walters and Leather unpublished; Dent unpublished) to explain Shaw's division of alatae into migrants, flyers and non flyers (Shaw 1970, 1973). Migrants (fly without reproduction) have a low ovariole number, non flyers (reproduce but do not fly) have a high ovariole number and flyers (reproduce and then fly) have an intermediate ovariole number.

M. festucae cerealium shows no significant difference in ovariole number between flying and non flying alatae, which suggest that the alatae were not divided into migrants, flyers and non flyers. Alatae of M. festucae cerealium have a modal ovariole number of 10 (with a range of 8 to 10) which was greater than the modal values for alate exules of M. dirhodum and R. padi (modal values of 6 and 4 respectively with a range of 4 to 10) (Wellings, Leather and Dixon 1980). M. festucae cerealium alatae have a higher reproductive potential than either M. dirhodum and R. padi but apparently less flexibility with which to exploit a changing environment.

Alatae which settled on either L. perenne or wheat were observed to make an initial probe on landing; this initial probe has been observed in A. fabae (Müller 1958; Kennedy and Booth 1963) Brevicoryne brassicae (L). (Wensler 1962) and R. padi (Wiktelius 1982). This brief probe may be important in determining whether or not a host is suitable. The less suitable the host plants are for permanent colonization the more restless the aphids will be before settling down (Johnson 1958). A restless aphid spends more time walking and makes more probes (Wiktelius 1982). The alatae of M. festucae cerealium on wheat spend more time walking but spending less time probing than alatae on L. perenne. The difference in time spent walking and probing suggests a slight preference of M. festucae cerealium for L. perenne. M. festucae cerealium had an obvious preference for the adaxial surface of L. perenne with fewer probes made and more time spent walking on the abaxial leaf surface (Ch.3). Alatae also preferred the adaxial leaf surface of wheat, although the preference was less marked than that of alatae on L. perenne.

CHAPTER FIVE

MORPHOMETRICS OF APTEROUS AND ALATE VIRGINOPARAE

INTRODUCTION

The production of the morphs of an insect species are controlled ultimately by its gene complement, but gene action can be modified by the environment (Murdie 1969). The seasonal development of the different morphs is initiated primarily by changes in the external environment, whilst internal changes in aphids govern the responsiveness of the aphid to changes in its environment (Dixon 1973).

It is known that of the environmental factors which influence aphids, temperature, daylength and nutritional quality of the host plant are important for inducing morphological changes whereas genetic and clonal differences influence the aphid's response to its environment (Dixon 1973; Hand 1982).

Morphological differences between aphid morphs are often very small (Hille Ris Lambers 1966), but it has been shown that if a large number of aphid characters are used in the identification then morphs can be readily separated (Hand 1982).

Hand (1982) studied the variation between aphid morphs of different cereal aphid species using multivariate analysis techniques. The approach he developed showed clear morphological separation of aphids which are often difficult to classify e.g. M. festucae cerealium and M. dirhodum. Hand stated "The results from these multivariate analyses suggest that these methods could be a very useful tool for aphidologists, both for the separation of species and of morphs". Hand had studied the variation between morphs but it was obvious from his work and from that of Murdie (1969) that there was considerable variation within morphs.

Temperature was found to influence the morphology of Acyrthosiphon pisum Harris virginoparae (Murdie 1969), whilst rearing density influenced only the size of the aphid. Temperature may be an important influence of any seasonal variation on within-morph differences in morphological

character (Hand 1982).

Considerable colour variation often occurs within one species and may alter according to the time of year or temperature (Blackman 1974). The only reference to a distinct colour morph of M. festucae was of a red holocyclic race in Rostock (Müller 1968); however observations of seasonal colour changes in M. festucae cerealium have been made here.

The aims of this work are to:

(I) determine whether temperature influences the morphology of apterous and alate virginoparae.

(II) consider colour variation of M. festucae cerealium in the light of aphid samples collected from fields of wheat and L. perenne.

CANONICAL DISCRIMINANT FUNCTION ANALYSIS AND ITS INTERPRETATION

The purpose of discriminant analysis is to examine how far it is possible to distinguish between members of various groups on the basis of observations made on them (Marriott 1974). Discriminant analysis is an ordinary analysis of variance within and between groups which has been extended for multivariate observations. Canonical analysis is analogous to regression analyses.

The analysis provides:

(I) Tests of significance for differences in the values of the variables between the groups. The overall test of significance is based on Wilks' criterion (Marriott 1974). If there is little correlation between the two sets of variables, then Wilks' Lambda is near unity. However if they are closely correlated i.e. there is a high degree of separation, then Wilks' Lambda becomes small i.e. tending towards zero.

(II) Allocation rules, for identifying further individuals as belonging to one of the groups on the basis of the values of the variables. These rules are expressed in terms of discriminant functions. A large discriminant function indicates that a variable is making

an important contribution to the axis; if the values are approximately the same then it indicates that individuals in one group are merely larger than those in the other group, whereas a range of values (especially if they have different signs) indicates that the individuals differ in their ratios i.e. their shapes (Nie, Hull, Jenkins, Steinbrenner, Bent 1975).

(III) Estimates of the probability of correct allocation given as the percentage correctly classified (Nie et al. 1975).

RESULTS

5.1 THE INFLUENCE OF TEMPERATURE ON THE MORPHOLOGY OF APTEROUS AND ALATE VIRGINOPARAE

5.1.1 A comparison of the morphology of (I) apterae and (II) alatae reared at 5°C with 10h daylength and at 10°C and 13½h daylength

(I) The proportion of the variance explained by the groups was low i.e. the canonical correlation coefficient (c) = 0.580 (the square of the canonical correlation coefficient c^2 is analogous to the r^2 used in regression analyses). Only 76% of cases were correctly classified which means that there was a large overlap in the characteristics of the groups (Fig.1). There were only three pairs of variables which were important for separating the two groups (Table 1). The standardised coefficients (Table 1) were all similar which suggests that the small differences which were separating the groups were mainly due to variation in aphid size.

(II) A higher proportion of the variance was explained by the groups (c^2 = 0.636) but only 85% of the cases were correctly classified (Fig.2). There were 8 pairs of variables which significantly separated the groups, the most important being the length of the base of the IV antennal segment and the length of the tibia, having standardised coefficient values of 0.964 and 0.772 respectively (Table 2). The standardised coefficients also varied in their size and sign indicating that the groups were separated by their shape rather than their size.

List of abbreviations used in Tables 1-7

Abbreviation	Description
TOTAL	Antennae : total length
FIRST	" : length of segments I & II
THIRD	" : length of segment III
FOURTH	" : length of segment IV
FIFTH	" : length of segment V
SIXTH	" : length of segment VI
BASE	" : width of basal segment
PROC	" : length of process terminalis
WIDTH	" : width of third segment
RHIN	" : number of rhinaria on third segment
ARS	Stylet : length of apical rostral segment
FEMUR	Hind leg : length of femur
TIBIA	" " : length of tibia
TARONE	" " : length of second tarsus segment
TARTWO	" " : length of third tarsus segment
SIPHL	Siphunculi: length of siphunculi
SIPHW	" : width of siphunculi
CAUDA	Cauda : length of cauda

Table 1. Results of Canonical Discriminant Function Analysis of apterous virginoparae reared at 5°C and 10h photoperiod compared with apterae reared at 10°C, 13½h photoperiod. The Standardised Coefficient is the Standardised Canonical Discriminant Function Coefficient.

Variables	Wilks' Lambda	Significance Levels	Standardised Coefficient
BASE	0.7864	$P < 0.001$	0.49191
PROC.	0.7059	$P < 0.001$	0.5001
RHIN	0.6631	$P < 0.001$	0.4372

Table 2. Results of Canonical Discriminant Function Analysis of alatae virginoparae reared at 5°C and 10h photoperiod compared with alatae reared at 10°C and 13½h photoperiod.

Variables	Wilks' Lambda	Significance Levels	Standardised Coefficient
RHIN	0.6111	$P < 0.001$	0.4670
BASE	0.4695	$P < 0.001$	0.9643
PROC	0.4530	$P < 0.001$	0.4286
THIRD	0.4332	$P < 0.001$	-0.5324
ARS	0.4188	$P < 0.001$	-0.3712
TIBIA	0.4000	$P < 0.001$	0.7724
FOURTH	0.3750	$P < 0.001$	-0.4932
TARTWO	0.3631	$P < 0.001$	-0.2812

Fig.1 Canonical Discriminant Function Analysis on apterous virginoparae reared at 5°C and 10h photoperiod ▨ and 10°C and 13½h photoperiod □ .
▲ = Group centroids

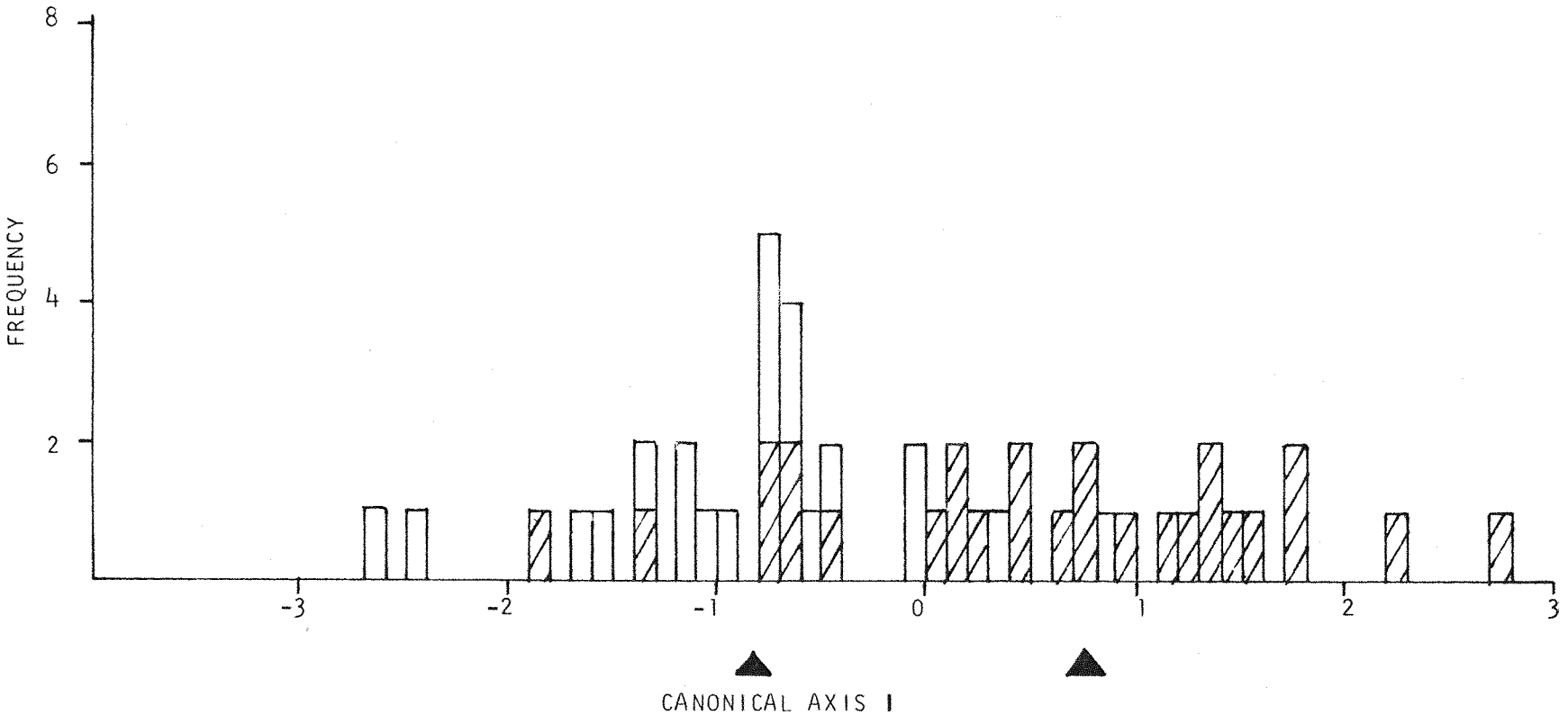
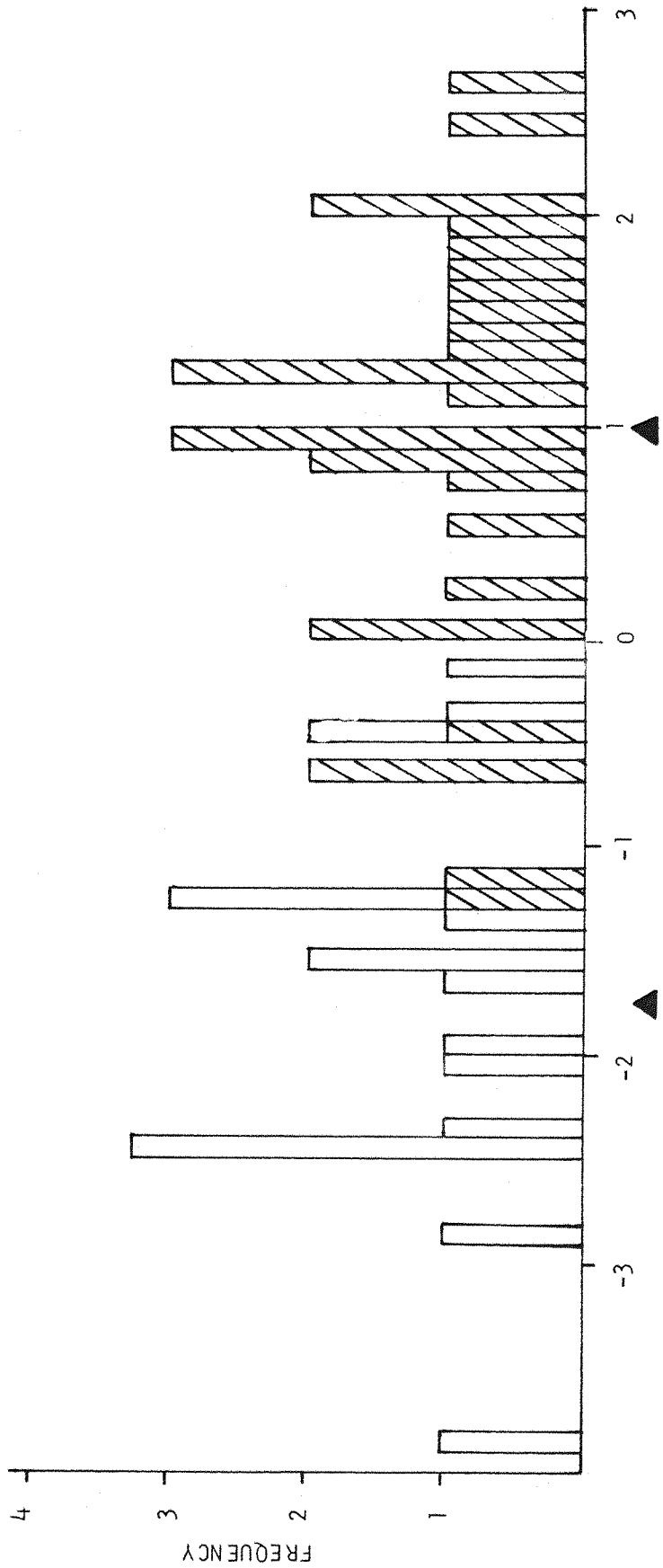


Fig.2. Canonical Discriminant Function Analysis on alatae virginoparae reared at 5°C, 10h photoperiod ▨ and 10°C, 13½h photoperiod □ .
▲ = Group centroids



The alatae unlike the apterae did have different shapes as a result of being reared at temperatures of $5^{o}C$ and $10^{o}C$.

5.1.2 A comparison of the morphology of (I) apterae and (II) alatae reared at $5^{o}C$ with 10h daylength and $20^{o}C$ with 16h daylength

(I) A high proportion of the variance was explained by the two groups ($c^2 = 0.804$), and 95.7% of the cases were correctly classified, i.e. there was little overlap between the two groups (Fig.3). There were 8 variables which significantly separated the groups, the most important being the length of the siphunculi, having a standardised coefficient of 2.19 (Table 3). The standardised coefficients were heterogeneous with different signs indicating clear morphometric differences between the apterae reared at the two temperatures.

(II) The proportion of the variance explained by the groups was only 68% ($c^2 = 0.680$); however 93.6% of the cases were correctly classified (Fig.4). The length of the siphunculi and length of the third and fourth antennal segments were the mostimportant characteristics used for separating the groups (Table 4). The standardised coefficients were heterogeneous in size and sign.

The apterae and alatae reared at the two temperatures have different morphological characteristics.

5.1.3 A comparison of the morphology of (I) apterae and (II) alatae reared at $10^{o}C$ with $13\frac{1}{2}$h daylength and $20^{o}C$ 16h daylength

(I) A high proportion of the variance was explained by the groups ($c^2 = 0.810$) and 100% of the cases were correctly classified i.e. there was complete separation of the groups (Fig.5). The high degree of separation was also indicated by the low Lambda value (0.189) (Table 5). The characteristics contributing most to the separation of the groups were the length of the tibia, the length of the third antennal segment and the length of the siphunculi, which had standardised coefficients of 0.904, -0.977 and 0.862 respectively. The size and signs of the standardised coefficients were heterogeneous i.e. apterae reared under

Table 3. Results of Canonical Discriminant Function Analysis of apterous virginoparae reared at 5°C with 10h photoperiod in comparison with apterae reared at 20°C, 16h photoperiod. Standardised coefficient is the Standardised Canonical Discriminant Function Coefficient

Variables	Wilks' Lambda	Significance Levels	Standardised Coefficient
SIPHL	0.5318	P < 0.001	2.190
THIRD	0.4076	P < 0.001	-1.918
TARTWO	0.3614	P < 0.001	-1.0596
TIBIA	0.2809	P < 0.001	0.8219
WIDTH	0.2530	P < 0.001	0.6937
ARS	0.2182	P < 0.001	-0.5278
FOURTH	0.2069	P < 0.001	0.5759
SECOND	0.1937	P < 0.001	-0.3747

Table 4. Results of Canonical Discriminant Function Analysis of alatae virginoparae reared at 5°C 10h photoperiod in comparison with alatae reared at 20°C, 16h photoperiod.

Variables	Wilks' Lambda	Significance Levels	Standardised Coefficient
THIRD	0.4808	P < 0.001	0.7359
TIBIA	0.4300	P < 0.001	0.6215
BASE	0.4032	P < 0.001	-0.4822
SIPHL	0.3822	P < 0.001	-0.9568
FOURTH	0.3310	P < 0.001	0.7257
TARTWO	0.3170	P < 0.001	0.2683

Fig.3. Canonical Discriminant Function Analysis of apterous virginoparae reared at 5°C, 10h photoperiod ▨ and 20°C, 16h photoperiod □.

▲ = Group centroids

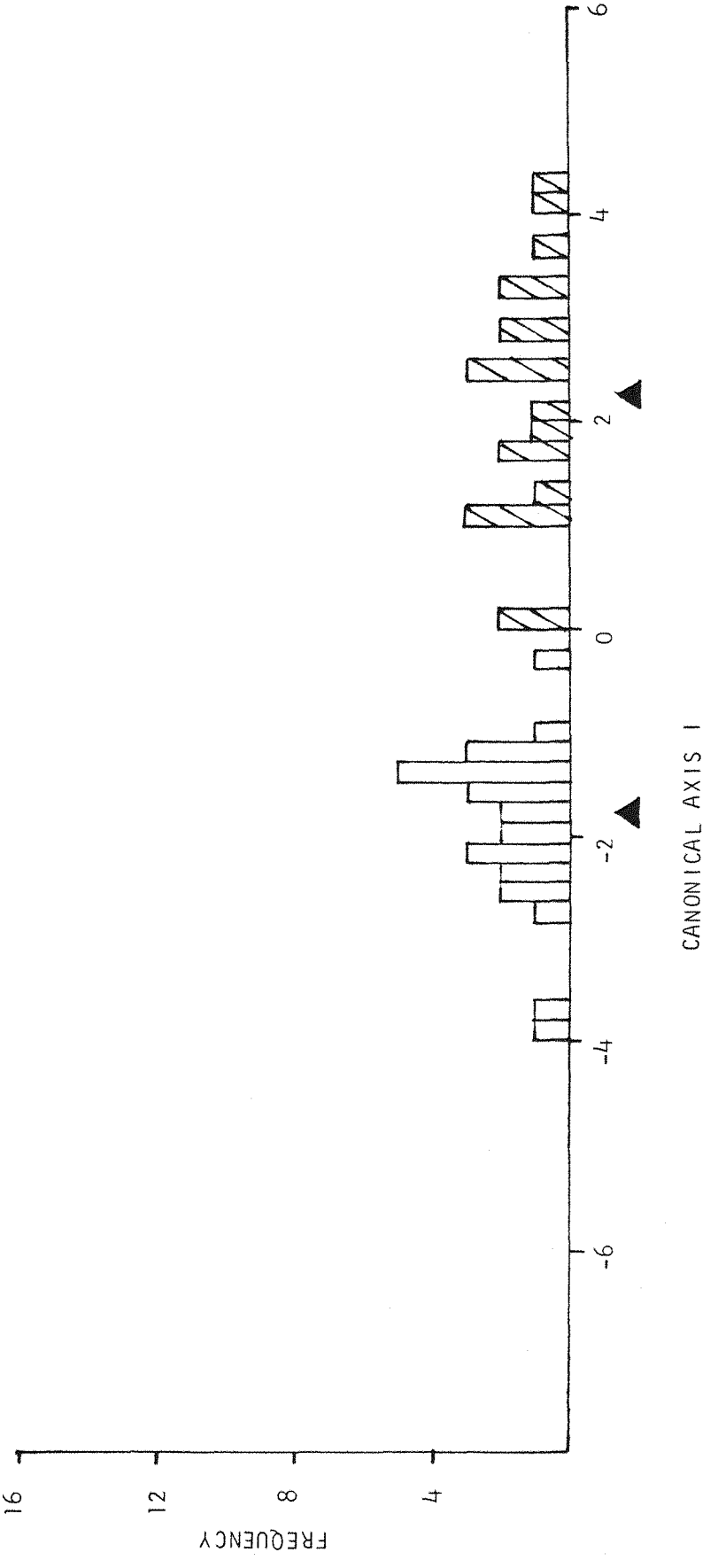


Fig.4. Canonical Discriminant Function Analysis on alatae virginoparae reared at 5°C, 10h photoperiod ▨ and 20°C, 16h photoperiod □ .
▲ = Group centroids

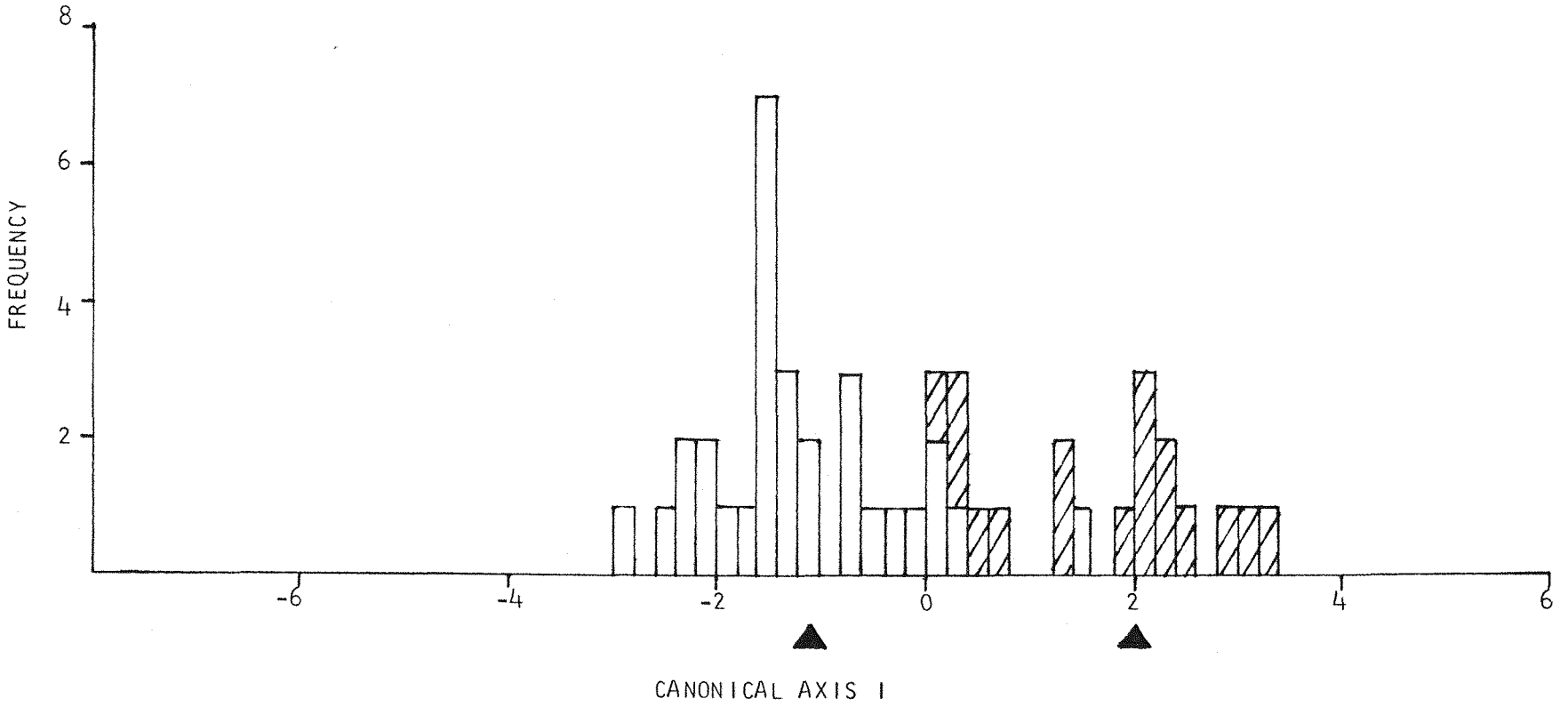


Table 5. Results of Canonical Discriminant Function Analysis of apterous virginoparae reared at 10°C and 10h photoperiod compared with apterae reared at 20°C and 16h photoperiod. The Standardised Coefficient is the Standardised Canonical Discriminant Function Coefficient.

Variables	Wilks' Lambda	Significance Level	Standardised Coefficient
CAUDA	0.2987	$P < 0.001$	0.5808
THIRD	0.2745	$P < 0.001$	-0.9779
SIPHL	0.2435	$P < 0.001$	0.8622
TARTWO	0.2252	$P < 0.001$	-0.7071
TIBIA	0.2026	$P < 0.001$	0.9041
RHIN	0.1956	$P < 0.001$	0.2850
SIPHW	0.1895	$P < 0.001$	0.2302

Table 6. Results of Canonical Discriminant Function Analysis of alatae virginoparae reared at 10°C and 10h photoperiod compared with alatae reared at 20°C and 16h photoperiod.

Variables	Wilks' Lambda	Significance Level	Standardised Coefficient
FOURTH	0.2853	$P < 0.001$	0.5204
RHIN	0.2393	$P < 0.001$	0.3179
FEMUR	0.2175	$P < 0.001$	0.5421
CAUDA	0.1964	$P < 0.001$	-0.6586
THIRD	0.1832	$P < 0.001$	0.3471
SIPHL	0.1718	$P < 0.001$	-0.5840
PROC	0.1639	$P < 0.001$	0.4596
FIFTH	0.1537	$P < 0.001$	0.4760
TARTWO	0.1466	$P < 0.001$	-0.3751
SIPHW	0.1396	$P < 0.001$	0.2891
TARONE	0.1365	$P < 0.001$	0.1850

Fig.5. Canonical Discriminant Function Analysis on apterous virginoparae reared at 10°C, 13½h photoperiod ▨ and 20°C, 16h photoperiod □ .
▲ = Group centroids

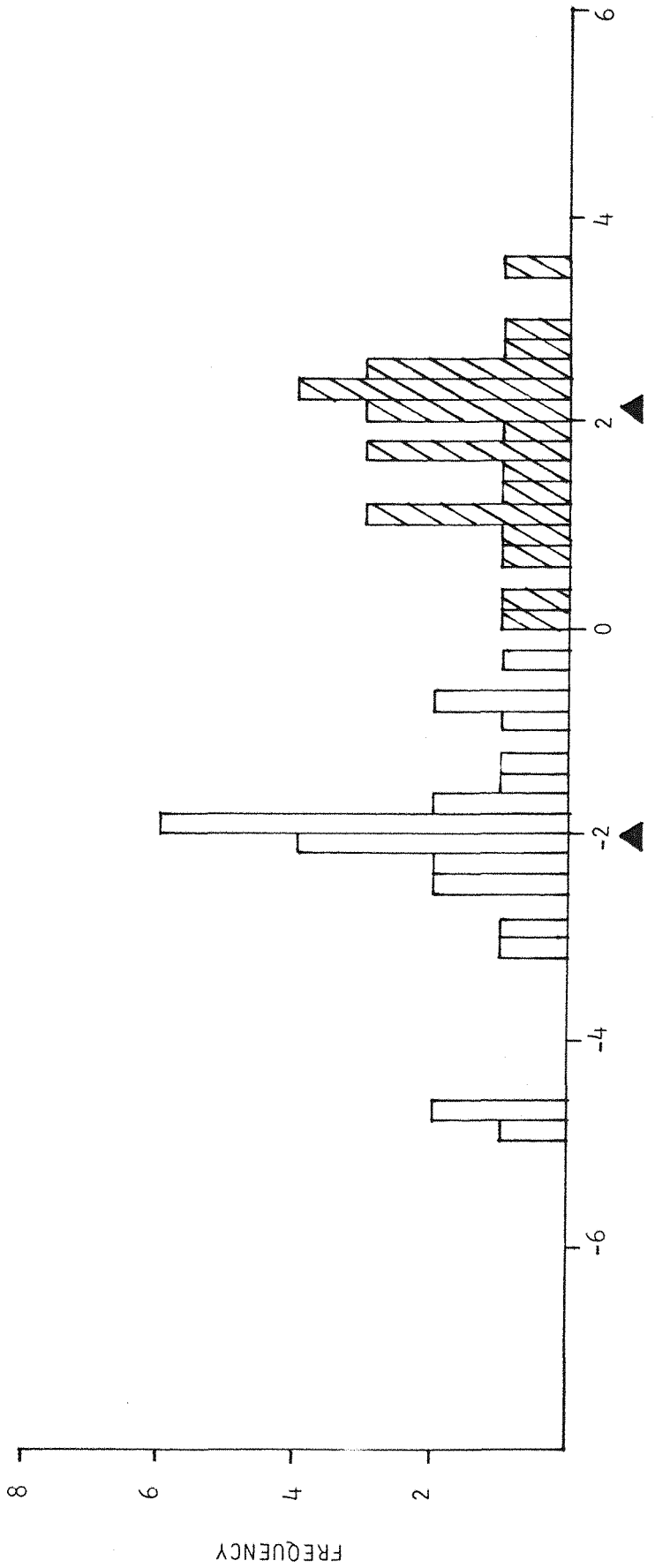
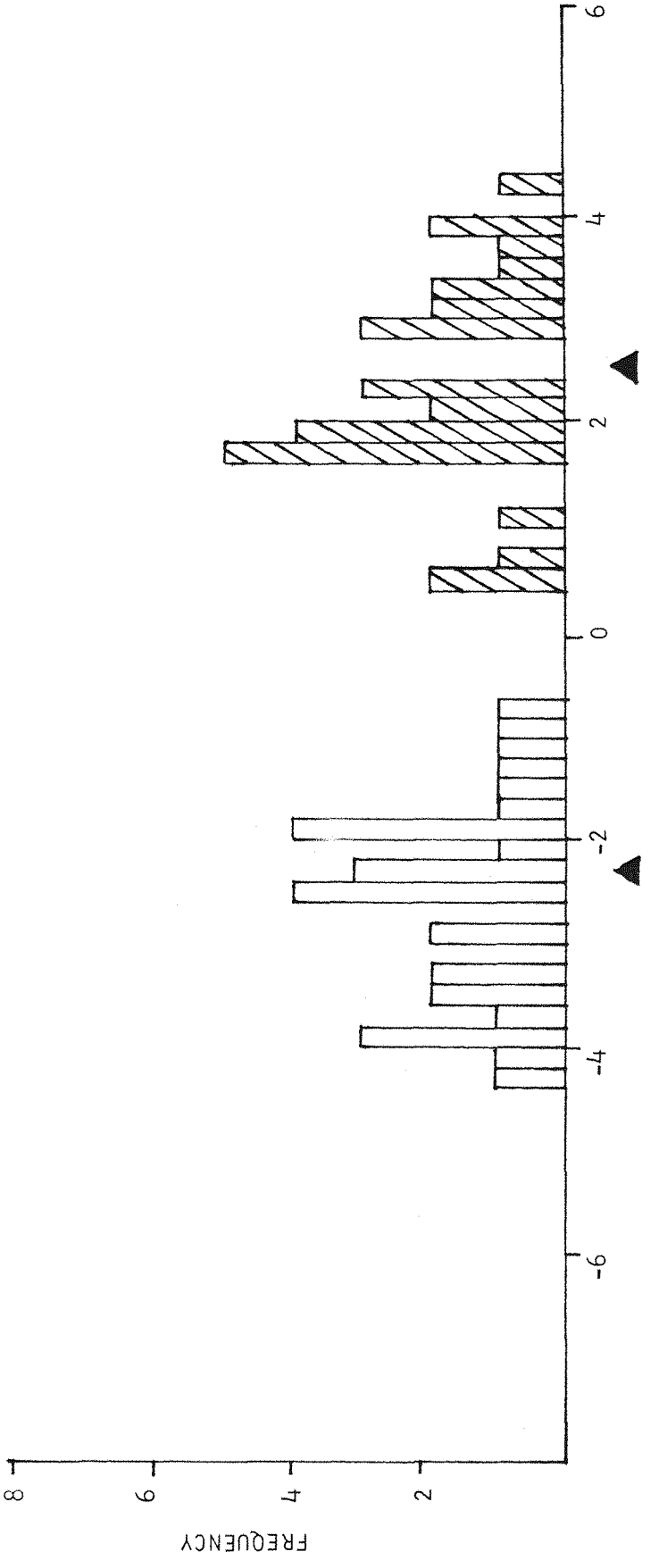


Fig.6. Canonical Discriminant Function Analysis on alatae virginoparae reared at 10°C, 13½h photoperiod ▨ and 20°C, 16h photoperiod □ .

▲ = Group centroids



these two temperatures exhibited distinct morphological differences which were not related to differences in size.

(II) A high proportion of the variance was explained by the groups (c^2 = 0.863) and 100% of the cases were correctly classified i.e. there was complete separation of the groups (Fig.6). A high degree of separation was also indicated by a small Lambda value of 0.136 (Table 6). The characteristics contributing most to the separation of the groups were the length of the cauda, the length of the siphunculi and the length of the femur.

The standardised coefficients were not very heterogeneous, suggesting some of the differences can only be attributed to differences in size.

5.2 THE INFLUENCE OF THE HOST PLANT ON THE MORPHOLOGY OF ALATE VIRGINOPARAE

5.2.1 A comparison of the morphology of alatae reared on wheat cv. Bouquet and wheat cv. Hobbit

A high proportion of the variance was explained by the groups (c^2 = 0.643) and 90.9% of the cases were correctly classified. The Wilks' Lambda value was significant (Table 7) but comparatively large, indicating poor separation of the groups. The standardised coefficients were heterogeneous in size and sign. The alatae reared on the two different host plants exhibited morphological differences, but some of these can be attributed to differences in size.

5.3 SUMMARY OF MORPHOMETRIC RESULTS

The morphological differences between aphids reared at 5°C and 10°C were small, being more prominent in alatae; the differences between the apterae appeared to be due to differences in size.

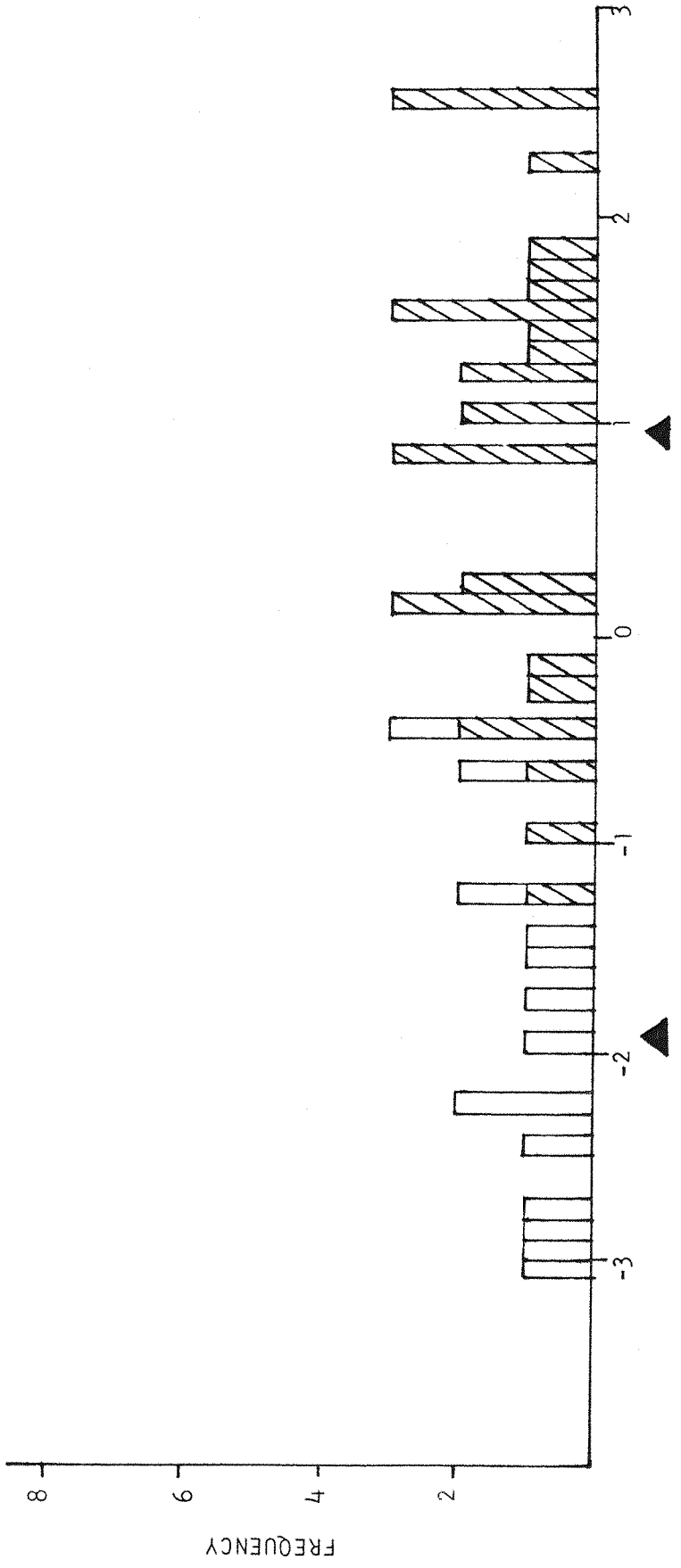
Both apterae and alatae exhibited marked differences in morphological characteristics when reared at low (5°C and 10°C) and high (20°C) temperatures. The influence of temperature produced

Table 7. Results of Canonical Discriminant Analysis of alate virginoparae reared on wheat cv. Bouquet and wheat cv. Hobbit under conditions of 20°C, 16h photoperiod. Standardised Coefficient is the Standardised Canonical Discriminant Function Coefficient.

Variables	Wilks' Lambda	Significance Levels	Standardised Coefficient
SIPHW	0.6506	$P < 0.001$	0.6204
FIFTH	0.5426	$P < 0.001$	0.8086
CAUDA	0.4313	$P < 0.001$	-0.7025
RHIN	0.3805	$P < 0.001$	-0.5384
TARTWO	0.3554	$P < 0.001$	0.3612

Fig.7. Canonical Discriminant Function Analysis on alatae virginoparae reared on wheat cv. Bouquet ▨ and wheat cv. Hobbit under conditions of 20°C and 16h photoperiod.

▲ = Group centroid



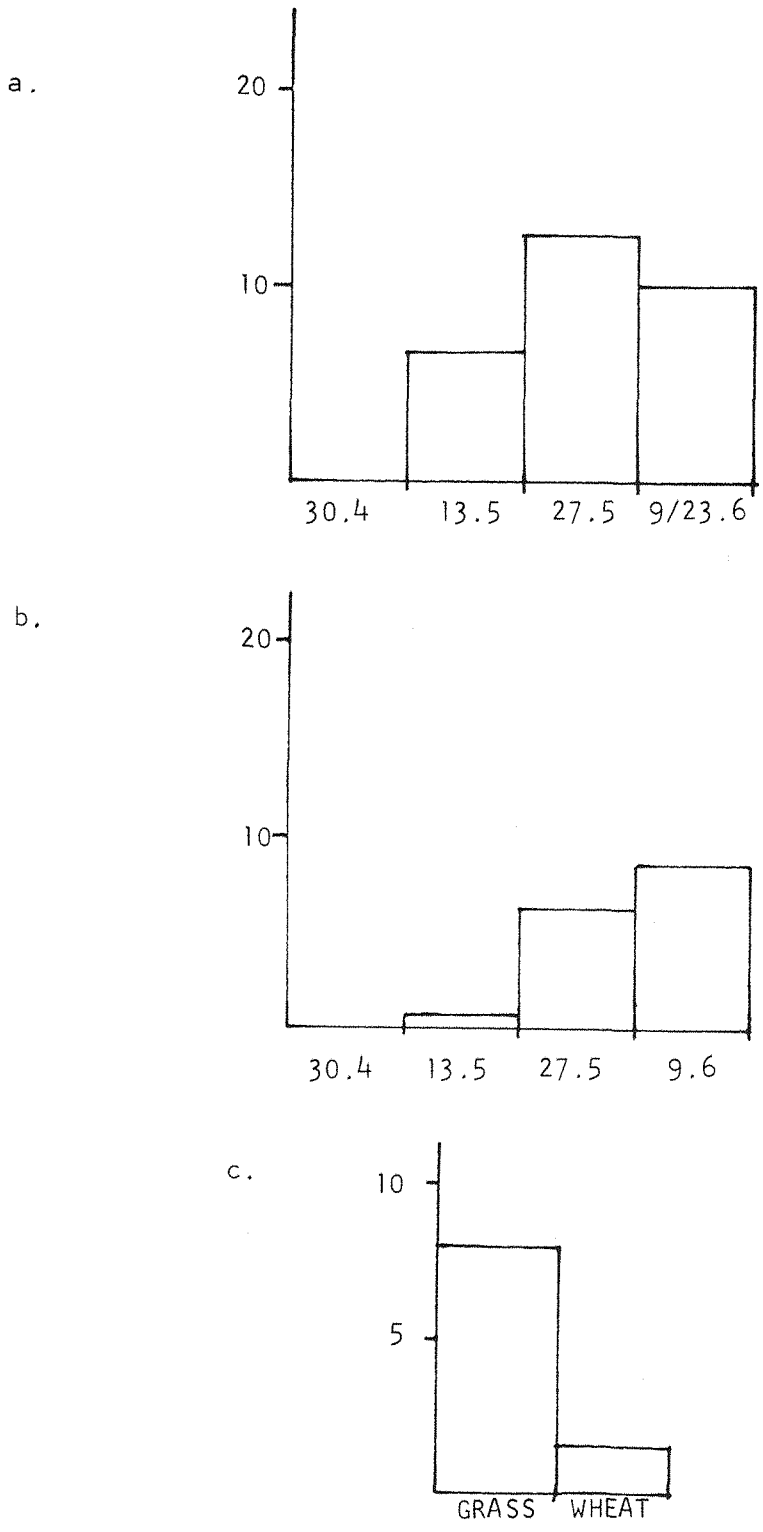


Fig.8. The proportions of red morphs found in samples taken from a field of a. L. perenne and b. wheat, c. a comparison between the proportions of red morphs found in grass and wheat.

distinct morphs. However temperature was not the only influencing factor. If this were the case then the variables contributing most to the axes (the variables with the largest standardised coefficients) would have been the same for all temperatures. However the length of the siphunculi was the only common variable.

The most obvious factor which could have contributed to morphometric differences was the rearing density of the aphids; however density has been shown to influence aphid size rather than morphological characteristics (Murdie 1969).

The host plant on which the aphids were reared had an influence on the shape of the aphids. The wheat cultivars used here are taxonomically similar; greater separation of groups would be expected between less related hosts.

5.4 COLOUR MORPHS

A larger proportion of red morphs was found on grassland than on wheat (Fig.8c). The relative numbers of coloured morphs found on the two host plants were significantly different (χ^2 = 32.95, d.f = 1, $P < 0.05$). The numbers of red morphs found, however, on grass and wheat were low.

The relative proportions of red morphs on grassland were not significantly different between sampling dates (χ^2 = 5.963, d.f = 3, $0.25 < P > 0.10$) (Fig.8a), whereas the proportion of red morphs increased through the season on wheat (χ^2 = 66.9, d.f = 3, $P < 0.005$) (Fig.8b).

DISCUSSION

The biology and pest status of cereal aphids has been the centre of a great deal of research for the last 15 years (see Carter, McLean, Watt and Dixon 1980; Vickerman and Wratten 1979) and yet some aphid morphs have either been inadequately described or undescribed so a study of morphometry would be useful (Vickerman and Wratten 1979).

A number of cereal aphid keys have been published but their use of multivariate analyses techniques are limited. The results from these

multivariate analyses suggest that not only is there a role for studies of differences between aphid morphs (Hand 1982) but also a study within aphid morphs. The apterae and alatae reared at different temperatures exhibited significantly different morphometric characters. This supports the view that there may be seasonal variation in the morphometry of aphid morphs (Hand 1982). A knowledge of how aphid morphology varies, with a morph, during the year is particularly important for aphids which are difficult to identify and separate from similar species or subspecies e.g. M. festucae sensu stricto, and M. festucae cerealium. The morphology of apterous and alate virginoparae has been shown here to vary according to the host plant on which the aphids were reared. Both temperature and host plant influence aphid morphometry. It would seem that the total variation possible within an aphid morph through the influence of seasonal variation in temperature and host plant is enormous. The present approach to aphid taxonomy may not be precise enough to distinguish between aphids derived from different host plants. Multivariate analysis techniques have obvious advantages under these conditions e.g. separation of aphids from suction trap catches (see Hand 1982).

The proportion of red aphids, from both wheat and L. perenne, was low. The difference in the proportion of red aphids on the two host plants suggests that colour may be a host plant effect, with more red aphids produced on L. perenne. The increase in the proportion of red aphids on wheat with time could be due to either a change in host plant condition or immigration from grass.

During field work (section 3.3) a variation in the colour of M. festucae cerealium was noted but not quantified. During the winter of 1981/82 (from November until April) the aphids on L. perenne were a dark olive green, but during April the aphids were a green-red colour and from May through the rest of summer the aphids were a bright yellow. On wheat the same pattern in colour changes was evident but the variation in colour was less marked. This type of seasonal colour variation has been recorded for the small willow aphid Aphis farinosa which ranges from dark blue-green to yellow according to the time of the year or

the temperature (Blackman 1974), and for Myzus persicae (Sulz.) which turns from green to yellow with an increase in temperature (Müller 1961). Despite these obvious and regular changes the function of aphid pigments is a mystery and the significance of seasonal colour changes within a species is an unsolved problem (Blackman 1974). The aphid pigments may not perform any particular function but are just a consequence of changing conditions. The variation in colour of M. festucae cerealium was probably due to seasonal variation expressed through changes in the host plant and/or temperature.

More information about colour variation in M. festucae cerealium is required as it has important implications for identification. Whilst multivariate techniques must in the future play an important role in cereal aphid identification, possibly through the establishment of a readily accessible taxonomic data base system of cereal aphid characters.

CHAPTER SIX

THE PRODUCTION AND REPRODUCTION OF APTEROUS AND ALATE VIRGINOPARAE

INTRODUCTION

A number of factors are known to influence the production of alatae; temperature and photoperiod (e.g. Johnson 1966), host plant (e.g. Sutherland 1969), host growth stage (e.g. Watt and Dixon 1981), but crowding is most often associated with wing polymorphism (e.g. Shaw 1970; Judge and Schaefers 1971). The interest in the crowding effect has been because of its interpretation as a mechanism by which aphids can leave an unsuitable environment. Many aphids colonize ephemeral herbaceous hosts during the summer. Apterae, which have a high reproductive potential (Wellings et al. 1980), multiply rapidly on these summer hosts and when they become unsuitable, alatae are produced which colonize more suitable hosts.

The unsuitability of the host and the subsequent production of alatae were thought to be caused by the aphid population overexploiting the food supply. However it was subsequently realized that aphids could produce alatae in response to aphid interaction through crowding, independent of the host's nutritional state (Schaefers 1972). Subsequent work has shown that host nutrition in relation to host plant condition including host growth stage can influence alate production (Schaefers 1972; Watt and Dixon 1981). The influence of aphid density has always remained an augmenting factor, however the response of aphids to produce alatae when crowded has been shown for R. padi (Dixon and Glen 1971), M. persicae (Awram 1968), Aphis craccivora (Johnson 1965), A. fabae (Shaw 1970), S. avenae (Watt and Dixon 1981) and Megoura viciae (Bukt.). (Lees 1967) among others, Schaefers and Judge (1971) have shown that the strawberry aphid C. fragaefolii produces more alatae when isolated than when they are crowded. They related this difference in response to the dispersal strategy of C. fragaefolii, which has a narrow host range and can best exploit its host plants by producing alatae when the growth stage of Fragaria verca is most suitable for further colonization. In view of this and other, earlier, work, Johnson (1966)

concluded that alate production can be the result of a combination of influencing factors and the view that the alate morph represents only an escape from a failing food supply can no longer be assumed to be valid throughout the Aphididae (Schaefers 1972).

It is generally believed that the phylogenetically primitive morphological condition of aphids was alate and sexual (Johnson 1966). Aphids have developed parthenogenesis and morphs which have enabled them to exploit more transient hosts. The extent to which the sexual condition (holocycly) is still retained varies between aphid species, but the cereal aphids M. dirhodum, S. avenae and R. padi are known to be able to maintain asexual populations throughout the year (anholocycly). Each morph produced in the life-cycle of an aphid has a specific function to perform. Associated with their different functional roles these morphs also exhibit different reproductive strategies (Dixon 1976). The reproductive strategies of the three alate morphs of R. padi were studied by Dixon (1976) but most workers have only compared the reproductive strategies of the apterous and alate virginoparae (Dixon and Wratten 1971; Taylor 1975; Wratten 1977). The virginoparae exploit the often ephemeral, actively growing herbaceous summer host plants. The apterous and alate morphs have different roles in the exploitation of this environment. Apterae are basically a unit with a high reproductive potential (Wellings et al. 1980) whilst alatae are important for dispersal, emigration and excape from natural enemies (Schaefers 1972). However alatae also show a great diversity in reproductive potential according to their predisposition to flight (Shaw 1973; Wellings et al. 1980; Walters and Leather unpublished; Dent unpublished).

The aim of the work reported in this chapter was to:

(I) Determine the influence of rearing density on alate induction for M. festucae cerealium reared on L. perenne.

(II) Determine the influence of rearing density on the weights of apterous and alate virginoparae.

(III) Compare the fecundity of apterous and alate virginoparae reared on L. perenne.

RESULTS

6.1 THE INFLUENCE OF REARING DENSITY ON ALATE PRODUCTION

6.1.1 A comparison of the proportion of alatae produced between two generations reared at different densities

The number of alatae produced was considered in relation to the rearing density. The starting density was the aphid density at the start of the experiment, and the finishing density the density after nymphal mortality.

The proportion of alatae produced as a function of the starting number of nymphs (starting density) was 23.2% and 17.4% for generation 1 and generation 2 respectively (Table 1a), i.e. the generation where mothers were isolated and the nymphs crowded produced a larger number of alatae than the generation where the mothers were crowded. The numbers of alatae produced in the two generations were significantly different ($\chi^2 = 5.584$, d.f = 1, $P < 0.05$).

The proportion of alatae produced as a function of the final number of nymphs (finishing density) was 25.61% and 20.62% for gen.1 and gen.2 respectively (Table 1b). The relative numbers of alatae produced were not significantly different ($\chi^2 = 3.098$, d.f = 1, $0.05 < P > 0.10$), although the proportion of alatae was greater for generation 1 than generation 2. The difference between the proportion of alatae produced had decreased because the numbers of alatae were the same but the decrease in the total number of nymphs due to mortality, was greater for generation 1 than for generation 2, i.e. the first generation suffered 9.5% mortality whilst being reared under crowded conditions compared with 15.6% mortality in the second generation (Table 1b).

6.1.2 The proportion of alatae produced in relation to rearing density

There was no significant correlation between the proportion of alatae produced and rearing density for starting and finishing densities of generations 1 and 2.

There was, for both generations, a significant correlation between the proportion of mothers which produced alate nymphs and rearing

Table 1. The total proportion of alatae produced in relation to (a) starting and (b) finishing aphid density for generation 1 and 2. Generation 1 aphids; the mothers were reared in isolation and the nymphs were crowded. Generation 2; both the mothers and the nymphs were crowded.

(a) STARTING DENSITY

Generation	No. nymphs	No. alatae	% alatae
1	893	207	23.2
2	759	132	17.4

(b) FINISHING DENSITY

Generation	No. nymphs	No. alatae	% alatae
1	808	207	25.6
2	640	132	20.6

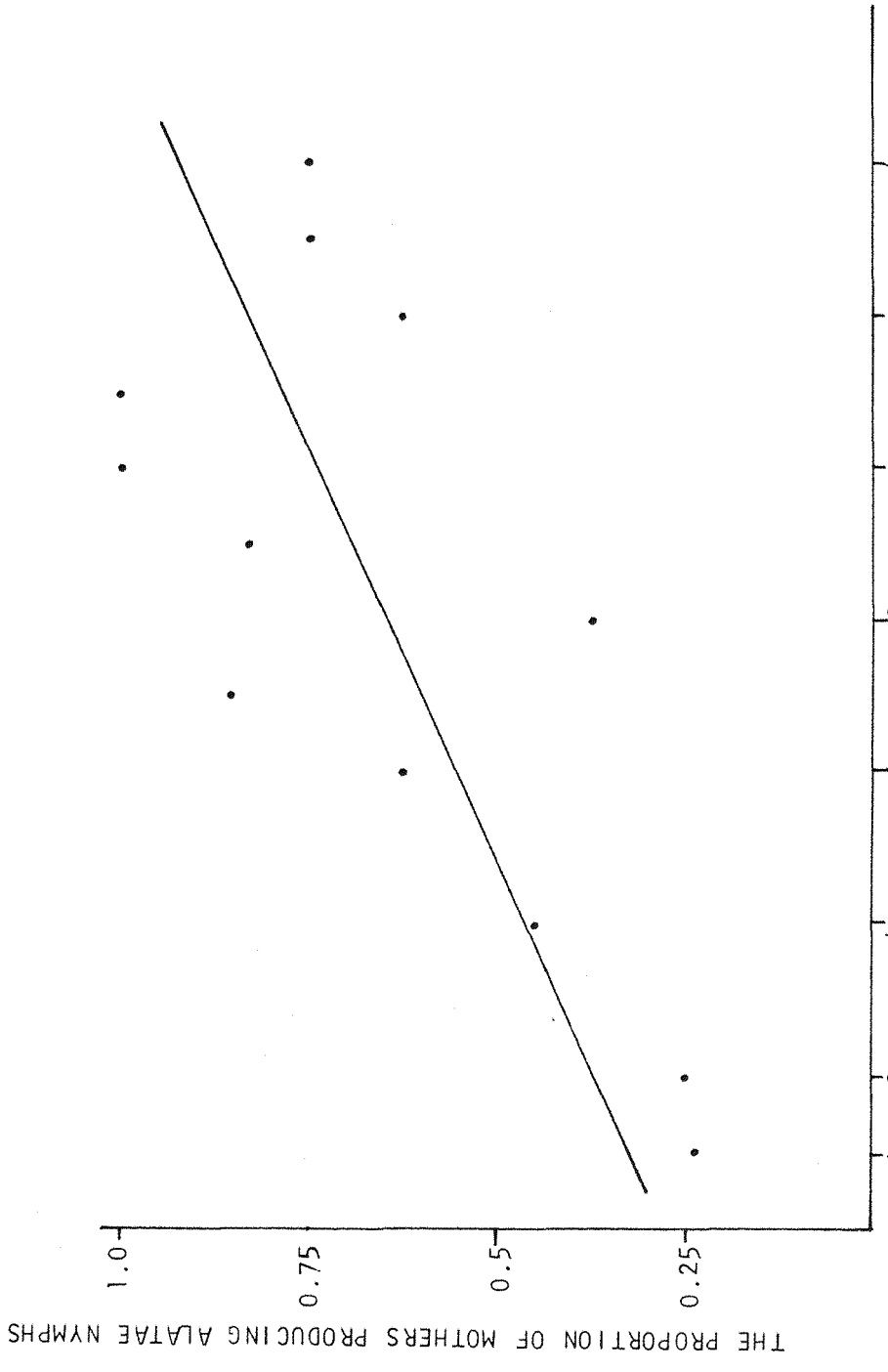


Fig.1 The relationship between the proportion of mothers which produce alate nymphs (when the mothers had been reared in isolation) and rearing density of the nymphs. $r = 0.7116$; d.f = 1,11; $y = 0.282 + 0.045x$. Density class is the number of nymphs per 0.45 cm^2 of leaf surface.

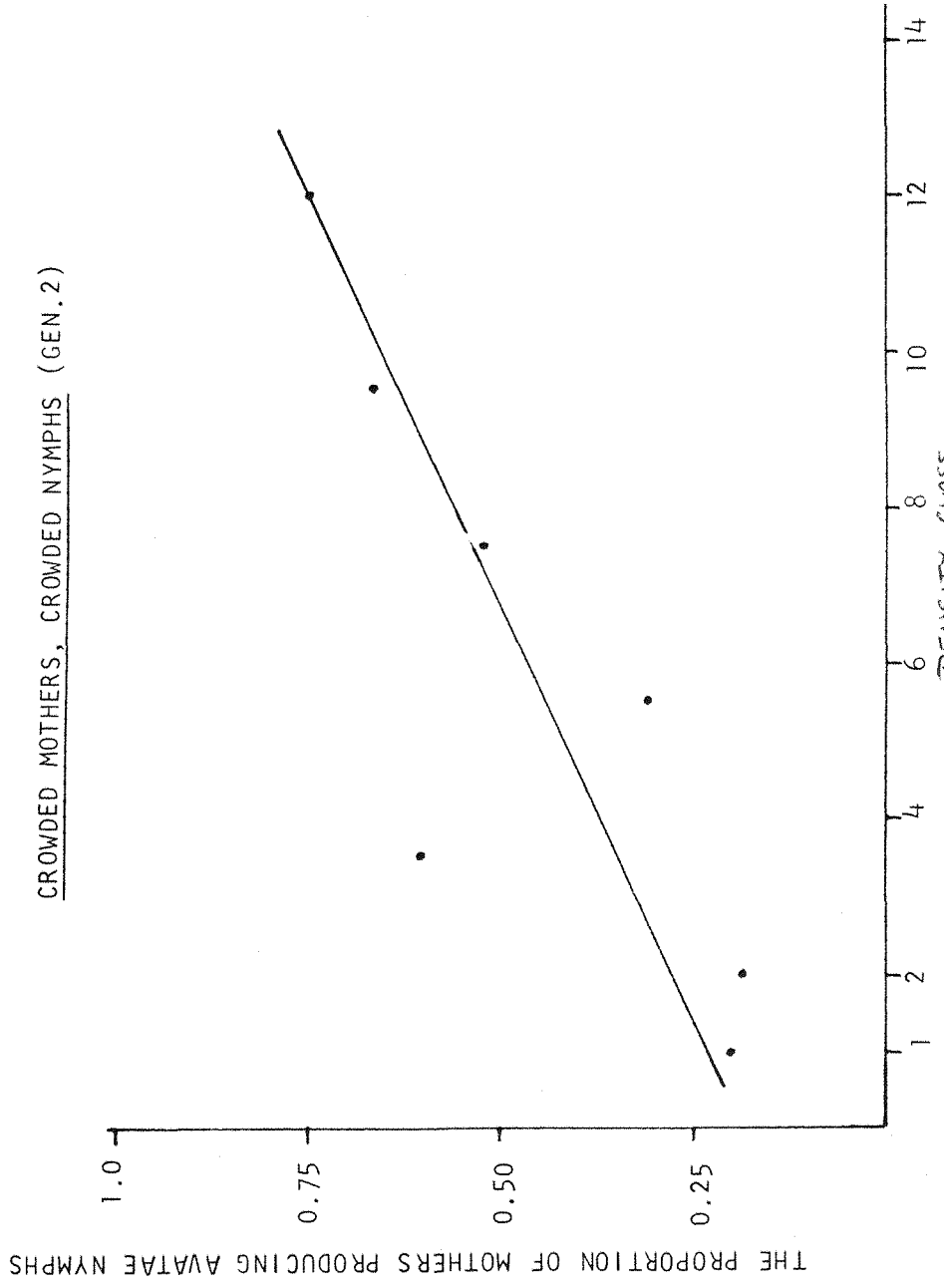


Fig.2. The relationship between the proportion of mothers which produce alate nymphs (when the mothers have been crowded) and rearing density of the nymphs. $r = 0.8443$; d.f = $1_2 5$; $y = 0.1836 + 0.0476x$. Density class is the number of nymphs per 0.45 cm^2 of leaf surface.

density (Figs.1 and 2). However despite the use of this method of analysis by Johnson (1966) the relationships here were invalid. Firstly the number of mothers in each density class was low; density classes were combined if numbers of mothers were low, which may have produced a bias in the results. Secondly the number of nymphs produced by each mother would influence the proportion of mothers having alatae nymphs. i.e. the proportion of nymphs which are alatae was known for each density class. The minimum numbers of nymphs required to show this proportion can be determined by claculating the reciprocal of the proportion. If the number of nymphs in each density class was less than the reciprocal of the proportion, then the proportion of mothers which produced alatae was an artefact of the low number of nymphs which each mother had produced. With these recalculations for the influence of the number of nymphs per mother on the proportions of mothers producing alatae, the subsequent analyses (which ignored those points that had too few nymphs) with density class gave correlations which were not significant. For gen.1, $y = 0.553 + 0.0219x$, $r = 0.406$, d.f = 8, NS at $P = 0.05$ and for gen.2, $y = 0.334 + 0.030x$, $r = 0.635$, d.f = 4, NS at $P = 0.05$.

6.2 THE INFLUENCE OF REARING DENSITY ON APTEROUS AND ALATE WEIGHT

6.2.1 A comparison of weights between apterous and alate virginoparae

The apterae were heavier than alatae when reared under similar conditions of crowding except for aphids reared at density class 8 in gen.2; however, the difference in weights were not significant (Tables 2a and 2b). There were significant differences between apterous and alate weights for only 3 density classes in gen.1. and one density class in gen.2. There were no consistent differences between apterous and alate weights with density class for gen.1, but for aphids reared in gen.2. there were no differences in apterous and alate weights for all density classes except density class 2. Density influences the difference in weight between apterous and alate more in gen.2 than gen.1.

Table 2a. A comparison between the weights of adult apterae and alatae for different rearing densities. The adult aphids were the first generation reared under crowded conditions; Gen.1.

Density Class	Mean Weight Apterae (mg)	Standard error	Mean Weight Alatae (mg)	Standard error	F-value	D.F.	Probability	Significance
12	0.512	0.018	0.459	0.019	3.69	1,48	0.060	NS
10	0.592	0.032	0.513	0.026	3.06	1,48	0.086	NS
8	0.600	0.018	0.523	0.023	6.72	1,48	0.012	S
6	0.681	0.023	0.595	0.025	5.83	1,47	0.019	S
4	0.826	0.029	0.791	0.024	0.66	1,48	0.418	NS
2	0.967	0.023	0.830	0.025	7.79	1,33	0.008	S
1	0.882	0.044	0.841	0.029	0.24	1,19	0.625	NS

Table 2b A comparison between the weights of adult apterae and alatae for different rearing densities. The adult aphids were the second generation of nymphs reared under crowded conditions, i.e. their mothers were also crowded.

Density Class	Mean Weight Apterae (mg)	Standard error	Mean Weight Alatae (mg)	Standard error	F-value	D.F.	Probability	Significance
12	0.416	0.026	0.359	0.031	1.88	1,36	0.178	NS
10	0.391	0.013	0.398	0.019	0.08	1,38	0.774	NS
8	0.410	0.019	0.462	0.030	2.06	1,36	0.159	NS
6	0.412	0.018	0.376	0.019	1.82	1,40	0.184	NS
4	0.579	0.026	0.558	0.039	0.21	1,35	0.650	NS
2	0.765	0.032	0.505	0.033	11.72	1,23	0.002	S

(a) FIRST GENERATION APTERAE

DENSITY CLASS	12	10	8	6	4	1	2
MEAN WEIGHT (mg)	0.512	0.592	0.600	0.681	0.826	0.882	0.967

(b) FIRST GENERATION ALATAE

DENSITY CLASS	12	10	8	6	4	2	1
MEAN WEIGHT (mg)	0.459	0.513	0.523	0.595	0.791	0.830	0.841

(c) SECOND GENERATION APTERAE

DENSITY CLASS	10	8	6	12	4	2
MEAN WEIGHT (mg)	0.391	0.410	0.412	0.416	0.579	0.765

(d) SECOND GENERATION ALATAE

DENSITY CLASS	12	6	10	8	2	4
MEAN WEIGHT (mg)	0.359	0.376	0.398	0.462	0.505	0.558

Fig.3. Multiple range tests comparing mean weights of aphids reared at different densities. Each density class refers to the number of nymphs reared per 0.45 cm^2 of leaf surface. The generation number refers to the generation of aphids which have experienced crowded conditions. Any two means not underscored by the same line are significantly different at $P > 0.05$.

Table 3. The relationship between adult weight (y) and the density of nymphs (x). Generation 1 aphids, mothers were reared in isolation; generation 2, mothers were reared in crowded conditions.

Morph	Generation	Regression Line
Apterae	1	$y = 0.980 - 0.041x$ ($r = 0.722$, d.f = 191, $P < 0.01$)
Alatae	1	$y = 0.882 - 0.038x$ ($r = 0.756$, d.f = 109, $P < 0.01$)
Apterae	2	$y = 0.728 - 0.033x$ ($r = 0.655$, d.f - 121, $P < 0.01$)
Alatae	2	$y = 0.554 - 0.016x$ ($r = 0.358$, d.f = 96, $P < 0.01$)

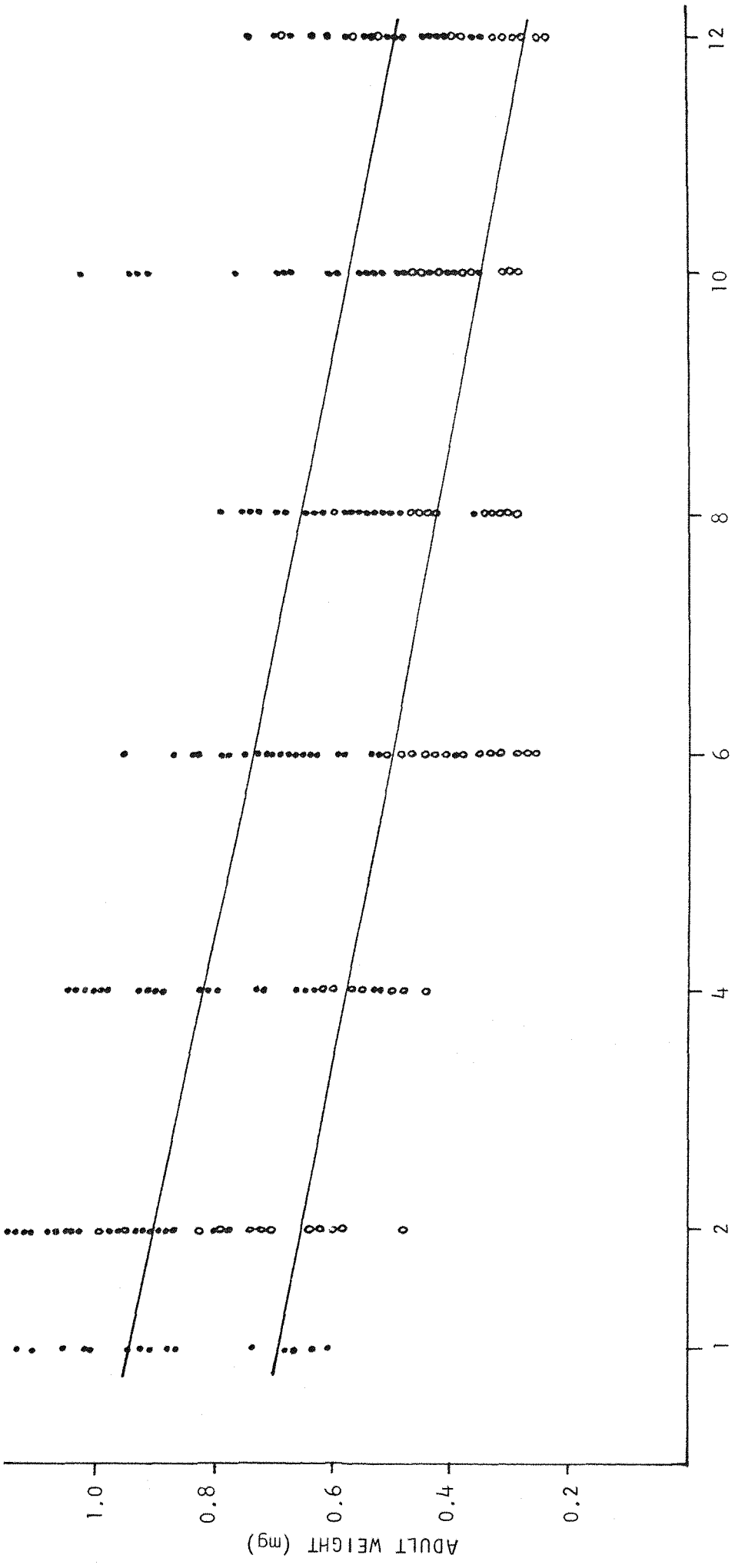


Fig.4. The relationship between rearing density (x) and adult weight (y) of apterae.
(•) First generation reared under crowded conditions, (o) their offspring. Density class refers to the number of nymphs reared per 0.45 cm^2 of leaf surface.

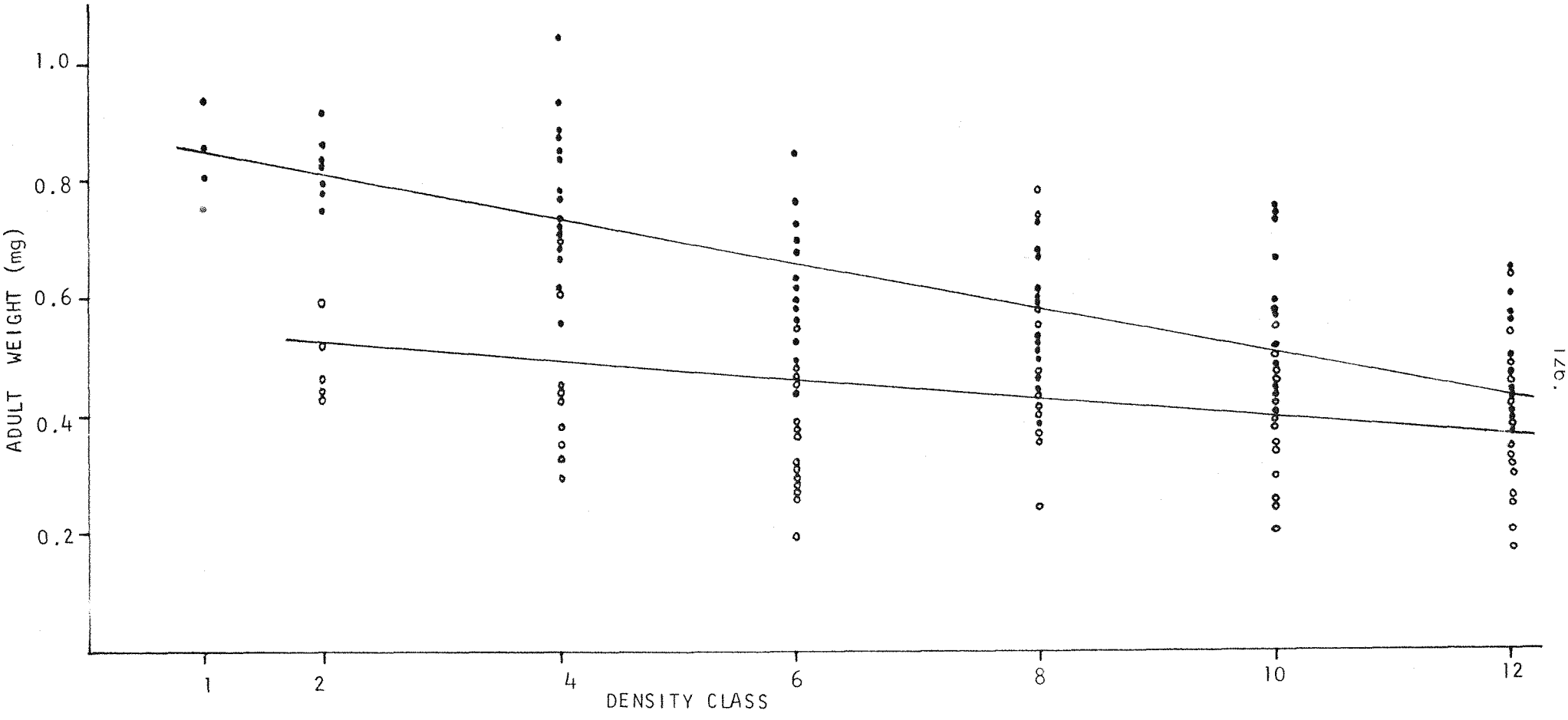


Fig.5. The relationship between rearing density (x) and adult weight (y) of alatae. (•) First generation reared under crowded conditions, (o) their offspring. Density class refers to the number of nymphs reared per 0.45 cm^2 of leaf surface.

6.2.2 The relationship between adult weight and rearing density

The weights of the aphids reared at different densities were found to be significantly different (Gen.1 apterae $F = 40.9$, d.f = 6,186, $P < 0.001$; Gen.2 apterae, $F = 38.8$, d.f = 5,117, $P < 0.001$; Gen.1 alatae, $F = 31.4$, d.f = 6,104, $P < 0.001$; gen.2. alatae, $F = 6.73$, d.f = 5,92, $P < 0.001$). For aphids reared in generation.1. there was a clear distinction between aphids reared in density classes 1, 2 and 4 compared with the other classes (Fig.3a & b). The aphids in the lower density classes were significantly heavier.

There was no clear division of aphid weights with density for aphids in generation 2. The heavier aphids were not necessarily associated with the lower density classes (Fig.3c and d) and there was much more overlap of the weight distribution between density classes.

The aphids of both generations exhibited a significantly negative relationship between adult weight (y) and rearing density (x) (Figs. 4 & 5; Table 3) i.e. as the rearing density increased the adult weight decreased.

A covariance analysis, with the generation as the covariate (Figs.4 & 5) showed the residual variances were heterogeneous, hence a comparison of the regression slopes and elevations could not be made.

6.3 A COMPARISON OF APTEROUS AND ALATE REPRODUCTION

The adult weights of the alatae were not normally distributed (K-S $Z = 1.611$, $P = 0.011$) but were significantly less than the adult weight of the apterae ($Z = -2.136$, $P = 0.032$). This difference must be taken into account when comparing apterous and alate reproduction (Dixon and Wratten 1971; Wratten 1977). Apterae produced a significantly larger number of nymphs than alatae over 7 days ($t = 6.01$, d.f = 91.9, $P < 0.001$), 10 days ($t = 7.52$, d.f = 90.6, $P < 0.001$). 15 days ($t = 8.13$, d.f = 91.93, $P < 0.001$) (Table 4). The difference between the mean number of nymphs produced by apterae and alatae increased with time e.g. the difference at 7 days = 4.02 nymphs but at 20 days the difference = 11.03 nymphs.

Table 4. The mean weights, and fecundities for the first 7 days, 10 days, 15 days and 20 days of apterae and alatae adult life. S.E. Standard error.

	Apterae		Alatae	
	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Adult weight (mg)	0.568	0.025	0.487	0.018
No. of nymphs, 7 days	16.40	0.552	12.38	0.377
No. of nymphs, 10 days	22.09	0.593	16.73	0.394
No. of nymphs, 15 days	29.88	0.693	23.06	0.474
No. of nymphs, 20 days	36.66	0.805	25.63	0.728

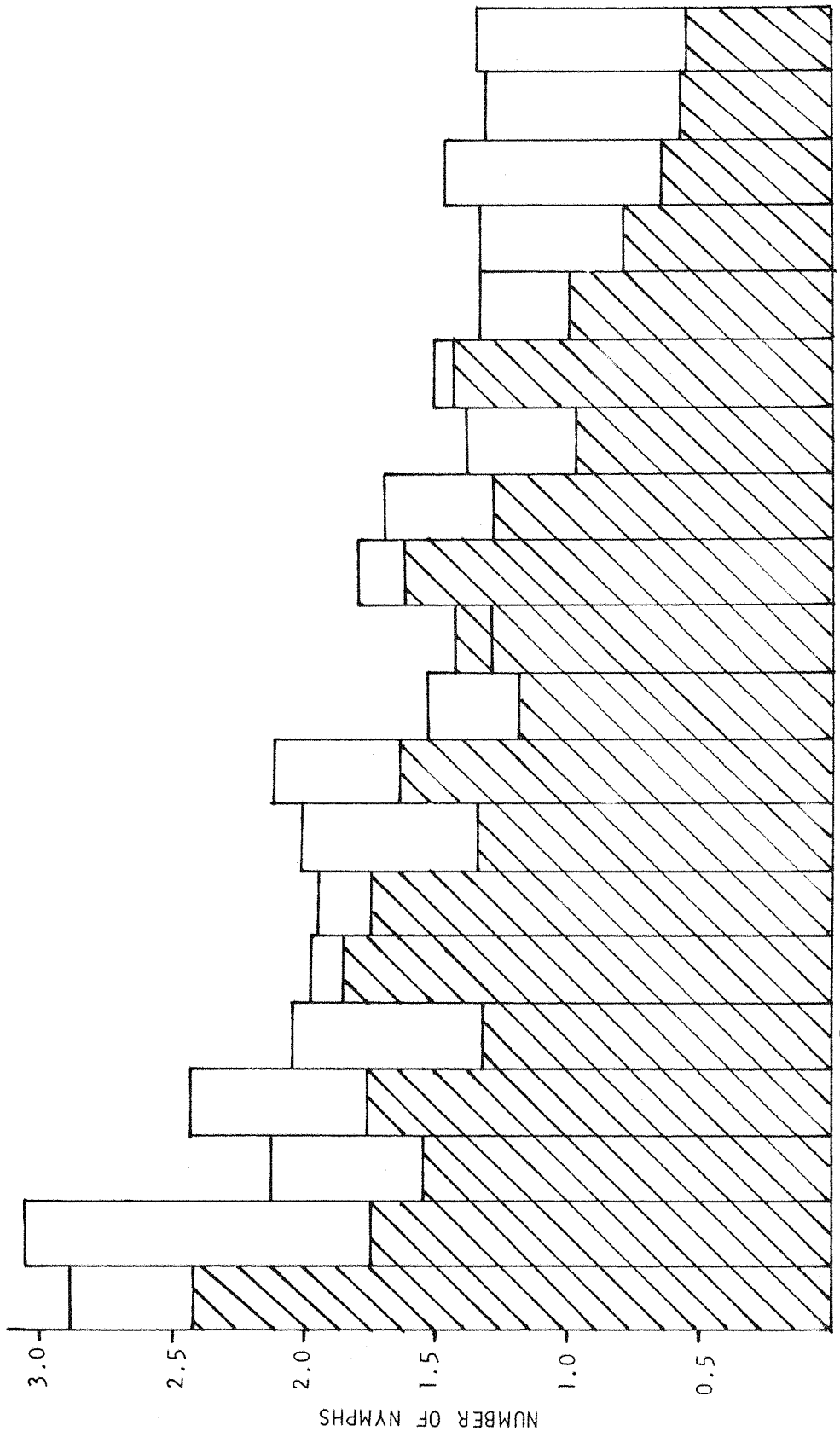


Fig.6. The mean daily fecundity of apterae □ and alatae ▨ of M. festucae

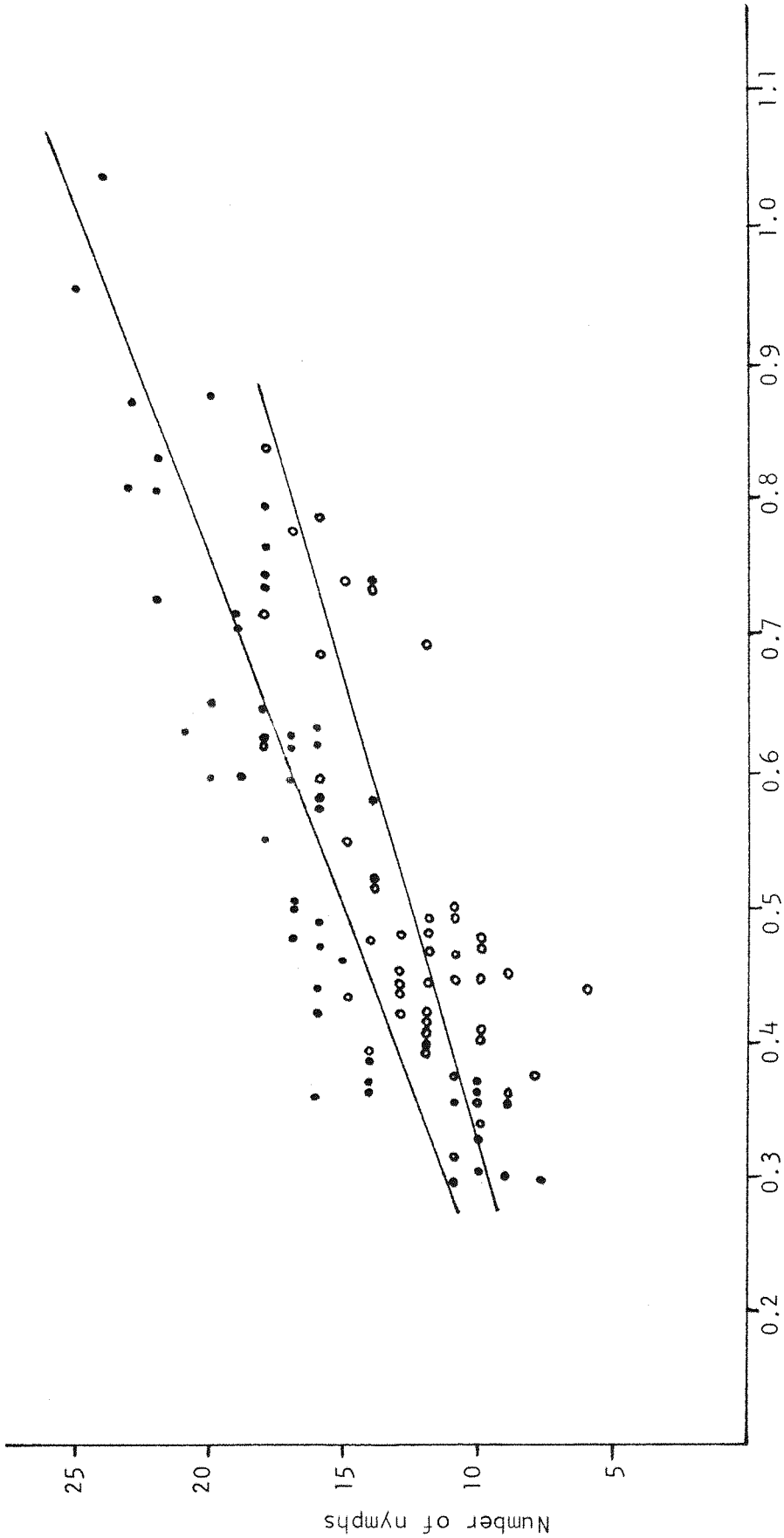


Fig.7 The relationship between adult weight (mg) and fecundity during the first 7 days of adult life for apterous (•) and alate (o) virginoparae.

The mean daily fecundity decreased from 3 nymphs to 1.5 nymphs over 20 days for apterae and from 2.5 nymphs to 0.5 nymphs for alatae. Both show a steady decline after an initial peak in reproduction. There was an increase in reproduction for alatae on the sixth and seventh day; however the difference was unlikely to be significant (Fig.6).

Heavier adults were more fecund than light ones (Fig.7). The correlation between fecundity and weight decreased in value with increased time for reproduction (Tables 5a and b). A covariance analysis to compare the relationship between fecundity and weight for apterae and alatae (Dixon & Wratten 1971) showed that the residual variances were heterogeneous ($F = 1.206$, $d.f = 52, 47$, $P = < 0.05$), therefore it was statistically invalid to compare the slopes and elevations. However the slopes were consistently steeper for apterae except at 20 days when the slopes were similar, but the intercept for apterae was higher (Tables 5a and 5b).

Table 5a. The relationship between adult weight (x) and the number of offspring (y) produced during the first 7 days, 10 days, 15 days and 20 days of adult life of apterae.

No. of nymphs in 7 days	$y = 5.574 + 19.062x$
	$r = 0.869$, d.f = 52, $P < 0.01$
No. of nymphs in 10 days	$y = 10.737 + 19.981X$
	$r = 0.848$, d.f = 52, $P < 0.01$
No. of nymphs in 15 days	$y = 17.87 + 21.14X$
	$r = 0.768$, d.f = 52, $P < 0.01$
No. of nymphs in 20 days	$y = 25.83 + 19.06X$
	$r = 0.596$, d.f = 52, $P < 0.01$

Table 5b. The relationship between adult weight (x) and the number of offspring (y) produced during the first 7 days, 10 days, 15 days and 20 days of adult life of alatae.

No. of nymphs in 7 days	$y = 5.177 + 14.78X$
	$r = 0.724$, d.f = 47, $P < 0.01$
No. of nymphs in 10 days	$y = 9.963 + 13.88X$
	$r = 0.652$, d.f = 47, $P < 0.01$
No. of nymphs in 15 days	$y = 15.60 + 15.29X$
	$r = 0.597$, d.f = 47, $P < 0.01$
No. of nymphs in 20 days	$y = 16.30 + 19.13X$
	$r = 0.486$, d.f = 47, $P < 0.01$

DISCUSSION

The proportion of alatae produced by *M. festucae cerealium* on *L. perenne* was low compared with the proportion of alatae produced by other cereal aphids reared under similar densities on cereals (Dixon and Glen 1971; Watt and Dixon 1981) (Table 1). This suggests that crowding may be less important factor influencing alate induction in *M. festucae cerealium*, despite the fact that aphids are generally thought to produce alatae in response to crowding (Johnson 1965; Lees 1967; Awram 1968; Shaw 1970; Dixon and Glen 1971; Watt and Dixon 1981). The density of the aphid colony is an indication to the aphids, either indirectly through host plant nutrition or directly through interaction between aphids, of a future decline in host condition. Alatae are produced in anticipation of this decline, enabling dispersal to a more favourable environment.

Alatae of *M. festucae cerealium* were not produced in response to increased density. The same proportion of alatae were produced at low densities as there were at high densities, i.e. density independent production of alatae.

As aphid numbers increase on a host plant there is a corresponding increase in the numbers of migrating alatae (Dixon 1971). The host plants and/or the preferred growth stages of the cereal aphids *S. avenae* and *M. dirhodum* are temporary habitats distributed heterogeneously in space and time, e.g. ears of cereals for *S. avenae*. Consequently there is a risk associated with dispersal; a large proportion of alatae will not successfully colonize preferred host plants. For this reason alatae virginoparae are produced at the onset of adverse conditions, at which time the risk associated with dispersal and unsuccessful host selection is outweighed by the necessity to leave an unsuitable host.

The host plants and preferred growth stages of *M. festucae cerealium* are, in contrast to those of *S. avenae* temporally and spatially abundant. Spatially: grassland constitutes a minimum 40% of all agricultural land in the south central and east of England and a minimum of 70% in the west of England and Wales (Fig.8). Grasses are also abundant on embankments and verges and adjacent to hedgerows.

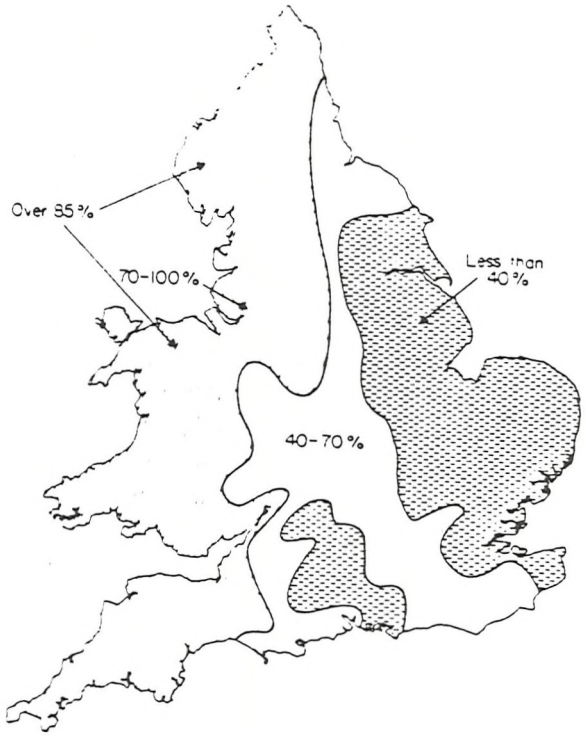


Fig.8 The proportion of agricultural land in grass (including rough grazing with sole rights) in England and Wales. From June 1971 census. (Grassland Research Institute) (Holmes 1980)

Cereals can also be colonized by M. festucae cerealium, so there are no shortage of host plants. Temporally, cereals may not always be at a suitable growth stage for colonization, but like M. dirhodum, M. festucae cerealium is a leaf feeder and is probably less affected by growth stage than an ear feeder like S. avenae (Watt 1979). However, in contrast to cereals, grass swards provide an almost continuous dynamic environment of suitable and preferred feeding sties, i.e. a grass sward consists of actively growing and established tillers each with emerging, mature and senescing leaves. At most times during the year grasses are suitable for colonization by alatae of M. festucae cerealium; the only exceptions would be shortly after a sward had been cut.

Because of the dense and dynamic structure of a grass sward, and because apterae of M. festucae cerealium can readily disperse by walking from centres of high population density there is little 'need' for a density dependent production of alatae. Instead alatae are produced in low numbers enabling a low level dispersal of alatae to colonize other areas of the grass sward, perhaps in the manner of trivial flights made by the sycamore aphid (Dixon 1969).

Work on the density relations of aphids has mostly concerned the induction of alatae; the influence of aphid size in relation to density has rarely been studied. Crowding influenced the size of A. pisum (Murdie 1969) and the increase in density of M. festucae cerealium, although not influencing alate production, did decrease the weight of both apterae and alatae. Alatae of M. festucae cerealium appeared to be less affected by overcrowding, with their weights being affected relatively less than apterae. Murdie (1969) attributed this in A. pisum to there being a survival value in producing large and presumably fitter dispersive stages.

Large aphids of M. festucae cerealium were more fecund than small aphids; this is also true for A. fabae (Dixon and Wratten 1971; Taylor 1975), R. padi (Dixon 1971, 1976). M. dirhodum (Wratten 1977) and S. avenae (Wratten 1977; Watt 1979).

The apterae were consistently heavier than alatae, making a

comparison of reproduction difficult. Alatae of A. fabae, S. avenae and M. dirhodum all have a lower fecundity than apterae of comparable weight (Dixon and Wratten 1971; Wratten 1977). The difference in reproductive rate has been attributed to the maintenance of wing muscles which compete for nitrogen with embryogenesis (Wratten 1977). The breakdown of wing muscles has been shown to coincide with an increase in alate reproduction in A. fabae (Taylor 1975), however this has not been substantiated for any other aphid. As Dixon (1973) states, 'when the wing muscles constitute 13% of the aphid's weight, it is unlikely that the degenerating muscles can supply more than a small proportion of material needed for the developing embryos. Alatae have a relatively large thorax so that the proportion of the body weight represented by the reproductive organs in alatae is lower than that in apterae, resulting in a lower reproductive rate on a weight for weight basis (Wratten 1977).

The long reproductive delay of alate exules in R. padi (Dixon 1976) was not evident in the alatae of M. festucae cerealium. Alate exules of R. padi are produced late in the season in response to density and have an initial low reproductive rate which allows more time to seek out the few remaining hosts (Dixon 1976). The strategy of M. festucae cerealium (in contrast to R. padi) could be to produce continuously low numbers of alatae which have a short reproductive delay (similar to the apterae) and can readily disperse and reproduce making maximum use of a readily abundant summer host which nevertheless exhibits, local rapidly-changing differences in suitability.

CHAPTER SEVEN

APHID PERFORMANCE IN RELATION TO TEMPERATURE

INTRODUCTION

Weather affects the physiology and behaviour of insects. Day-length has important effects on an insect's endocrine system; this can modify the effect of other abiotic factors on the survival, development time and reproduction of an insect (Varley, Gradwell and Hassell 1973).

Temperature and photoperiod effects on cereal aphids have been studied as an influence on morph determination (e.g. Dixon and Glen 1971). However because of the importance of predicting cereal aphid outbreaks the influence of weather and hence temperature on aphids has attracted interest (Sparrow 1974; Dean 1974; Vickerman 1977). The influence of temperature is important because it has a marked effect on the rate of aphid increase (Carter et al. 1981). Dean (1974) showed that temperature affected survival, development time and fecundity of M. dirhodum, R. padi and S. avenae. A study by Hill (1971) examined the influence of temperature on the development time and fecundity of M. festucae cerealium. M. festucae cerealium was able to reproduce at temperatures below 6°C and as a consequence has been labelled a cold-hardy species. Subsequent work however has suggested that M. festucae cerealium may not be as cold adapted as other cereal aphids (Williams pers.comm.).

Warm winter and early spring weather causes an increase in the numbers of M. festucae cerealium present in spring on cereals (Vickerman 1977). When there were few air frost days during the winter and high mean temperatures during April (mean = 10°C) the populations of overwintering aphids were high, and subsequently in April there were large numbers of M. festucae cerealium on cereals (Vickerman 1977).

The influence of temperature and photoperiod on the induction of alate virginoparae has been investigated for A. craccivora (Johnson 1966), C. fragaefolii (Schaefers and Judge 1971) and A. pisum (Kenton 1955). However only the study by Kenton (1955) considered alate production below temperatures of 15°C. Low temperatures and short

photoperiods are normally associated with the production of sexuals in the autumn. For an anholocyclic aphid like M. festucae cerealium there could be distinct advantages in producing alatae in response to low temperatures and short photoperiods. R. padi is more fecund on P. pratense at low temperatures than on other grasses (Leather and Dixon 1982), similarly M. festucae cerealium may be more fecund on certain grasses at low temperatures thus alatae may be produced in the autumn to disperse to preferred winter hosts. The fecundity of aphids on these hosts will be influenced directly by abiotic factors (Dean 1974) and indirectly by an intrinsically programmed reproductive potential (Wellings et al. 1980). The ovariole number (a measure of reproductive potential) of the heteroecious aphids M. dirhodum and R. padi varies both between and within generations. This in marked contrast to the autoecious aphids Drepanosiphum acerinum (Wlk.), D. platanoidis, Eucallipterus tiliae (L.) and Euceraphis punctipennis (ZeH.) for which the ovariole number was almost constant (Wellings et al. 1980). The changes in the ovariole number and hence the reproductive potential of heteroecious aphids (both between and within generations) are programmed and anticipate predictable seasonal changes in habitat quality (Wellings et al. 1980).

Although recently much work has been carried out on the implications of ovariole number for aphid life history strategies (Wellings et al. 1980; Dixon and Dharma 1980a and 1980b; Ward, Wellings and Dixon 1983a and 1983b) there has been no study of the influence of seasonal variation in ovariole number of an anholocyclic aphid.

The aims of this work are to:

(i) determine how temperature/photoperiod influence the nymphal development time, adult weight and fecundity of apterous virginoparae

(ii) compare the daily fecundity of apterous and alate virginoparae reared at $10^{o}C$

(iii) determine whether temperature influences alate induction when both the mothers and nymphs are reared in isolation

(iv) determine the variation in ovariole number of apterous and alate virginoparae reared under different temperatures/photoperiod.

RESULTS

7.1 THE INFLUENCE OF TEMPERATURE/PHOTOPERIOD ON NYMPHAL DEVELOPMENT TIME, ADULT WEIGHT AND REPRODUCTION OF APTEROUS VIRGINOPARAE

Aphids reared at 10°C, 13°C, 15°C and 20°C exhibited differences in development time, adult weight and 7-day fecundity. The aphids reared at the higher temperatures had shorter development times, lower adult weights and higher 7-day fecundities than aphids reared at lower temperatures (Fig.1). The development times were all significantly different from one another at $P < 0.001$. The weights of adults reared at 10°C and 13°C, 13°C and 15°C were not significantly different at $P > 0.05$ ($t = 0.37$, $d.f = 38.7$, $P = 0.712$; $t = 1.63$, $d.f = 30.5$, $P = 0.112$ respectively). The 7-day fecundities of apterae reared at 15°C and 20°C were not significantly different at $P > 0.05$ ($t = 0.38$, $d.f = 54$, $P = 0.703$) (Fig.1). Regression and correlation analyses of development time, weight and 7-day fecundity with temperature were all significant at $P < 0.01$. Development time and weight were negatively correlated with temperature (Figs.2 and 3) whilst 7-day fecundity was positively correlated (Fig.4).

7.2 A COMPARISON OF APTEROUS AND ALATE DEVELOPMENT TIMES, WEIGHTS AND REPRODUCTION AT 10°C

The development times of apterae and alatae were not significantly different at $P = 0.943$ ($t = 0.07$, $d.f = 48$) (Table 1). The weights of the alatae were significantly less than that of the apterae ($t = 2.82$, $d.f = 28.8$, $P < 0.05$); this difference was perhaps reflected in the aphid fecundities. Apterae had significantly higher fecundities than alatae ($P < 0.001$) in the first 7 days ($t = 4.53$), 10 days ($t = 4.81$), 15 days ($t = 6.30$) and 20 days ($t = 6.95$) from adult moult. At each interval large aphids gave birth to more nymphs than small aphids (Tables 2 and 3). The relationships were significant for apterae (7-day $F = 27.1$; 10-day $F = 36.9$; 15-day $F = 27.8$; 20-day $F = 12.8$; $d.f$ 2 1,36, $P < 0.05$) but were not significant for alatae (7-day $F = 0.59$; 10-day $F = 0.29$; 15-day $F = 1.27$; 20-day $F = 1.82$;

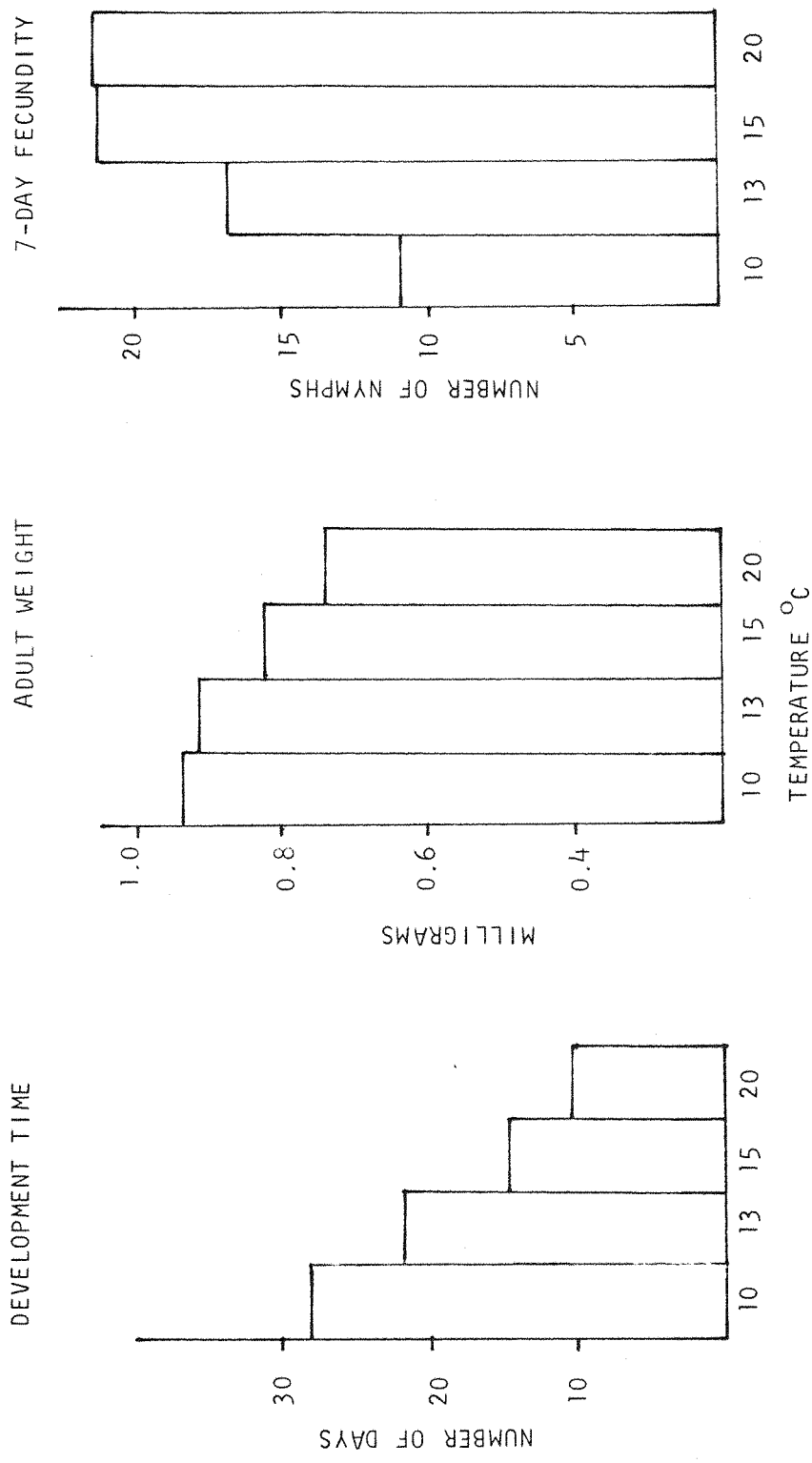


Fig.1 Histograms of mean development time, adult weight and number of nymphs produced in the first 7 days of adult life for apterae reared at 10°C, 13°C, 15°C and 20°C. Sample size at each temperature were 3♂, 19, 28, 28 for 10°C, 13°C, 15°C and 20°C respectively.

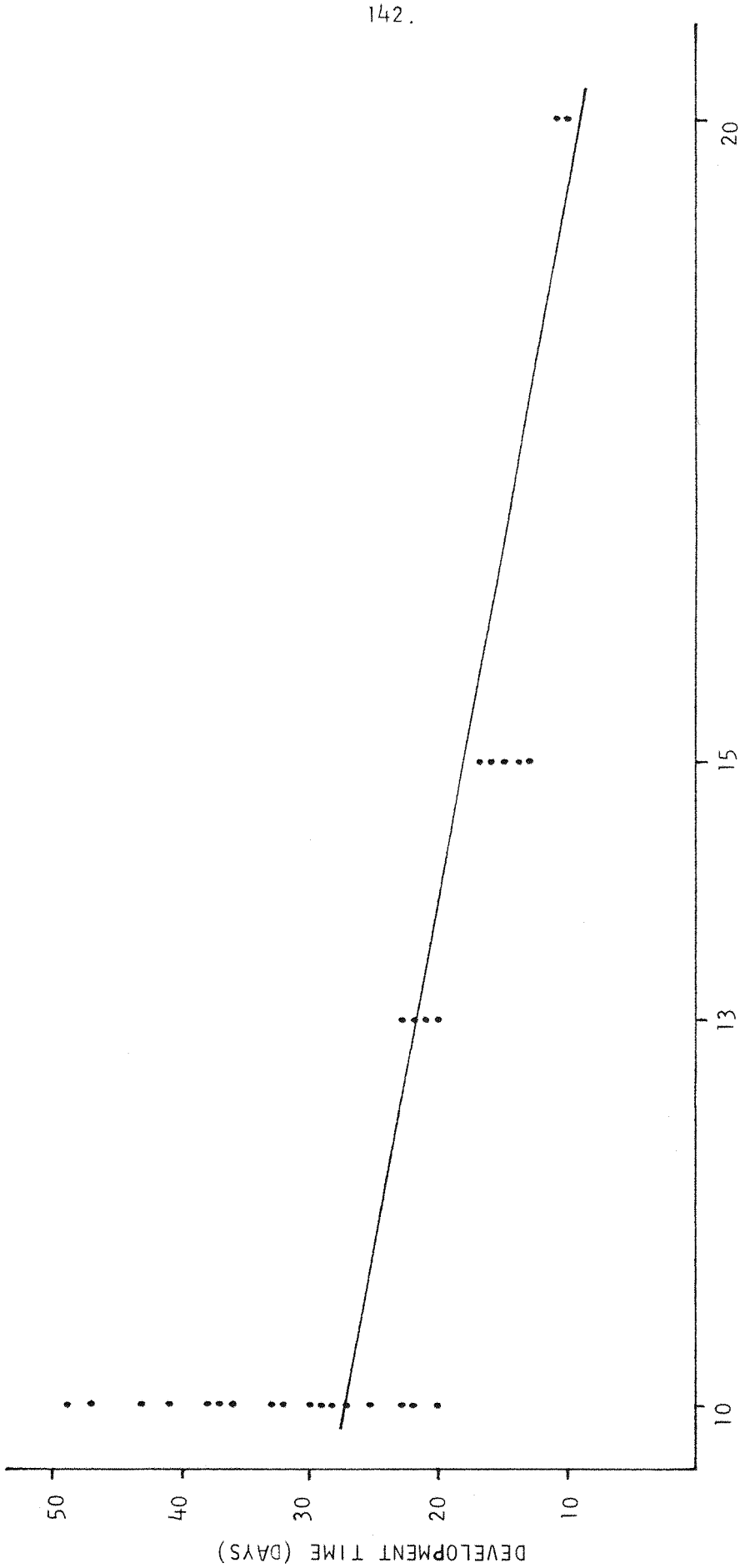


Fig.2 The relationship between development time of apterous aphids and rearing temperature.
r = -0.797, P<0.01, d.f = 111, y = 45.21 + -1.819x, F = 194.2

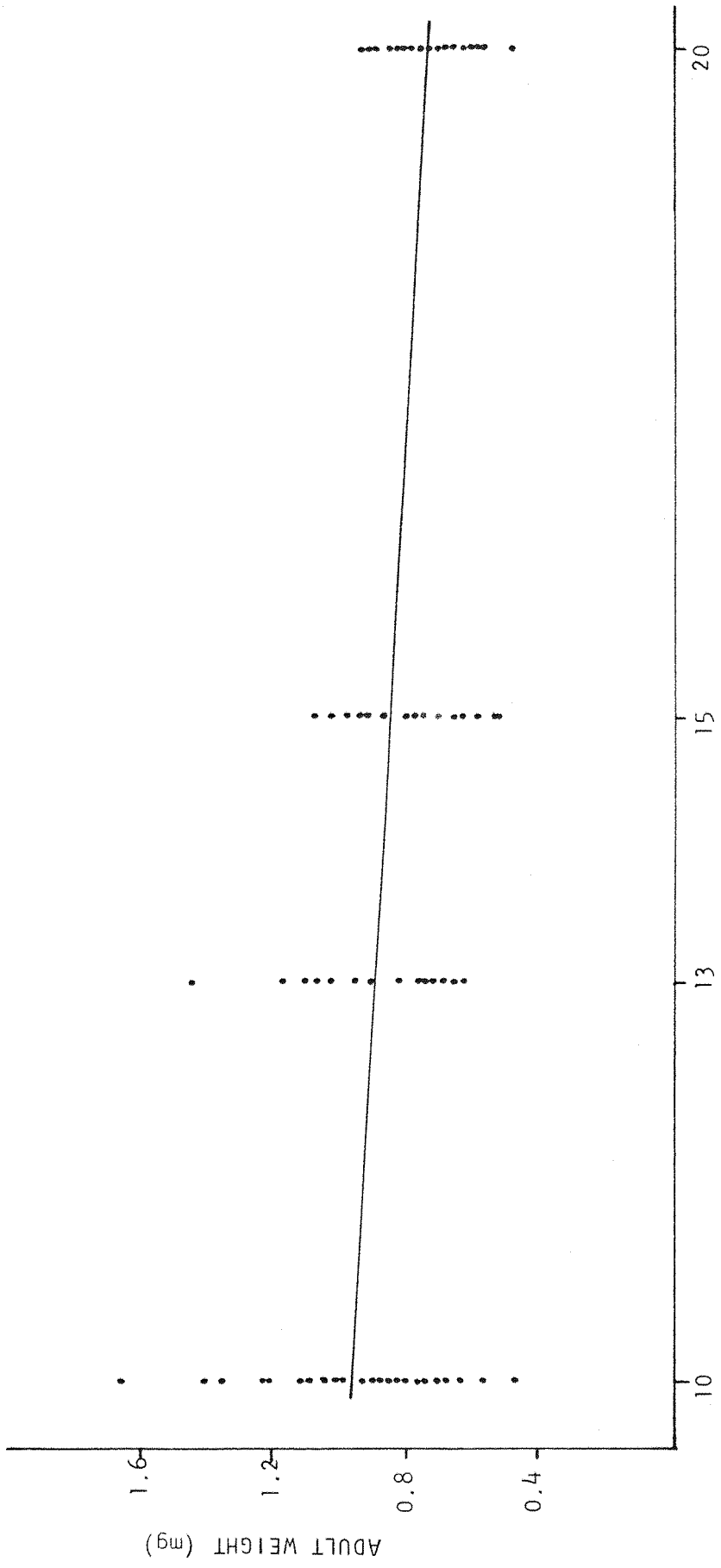


Fig.3 The relationship between adult weight of apterae and rearing temperature.
$r = -0.394$, $P < 0.01$, d.f = 111, $y = 1.150 + -0.0207x$, $F = 20.45$

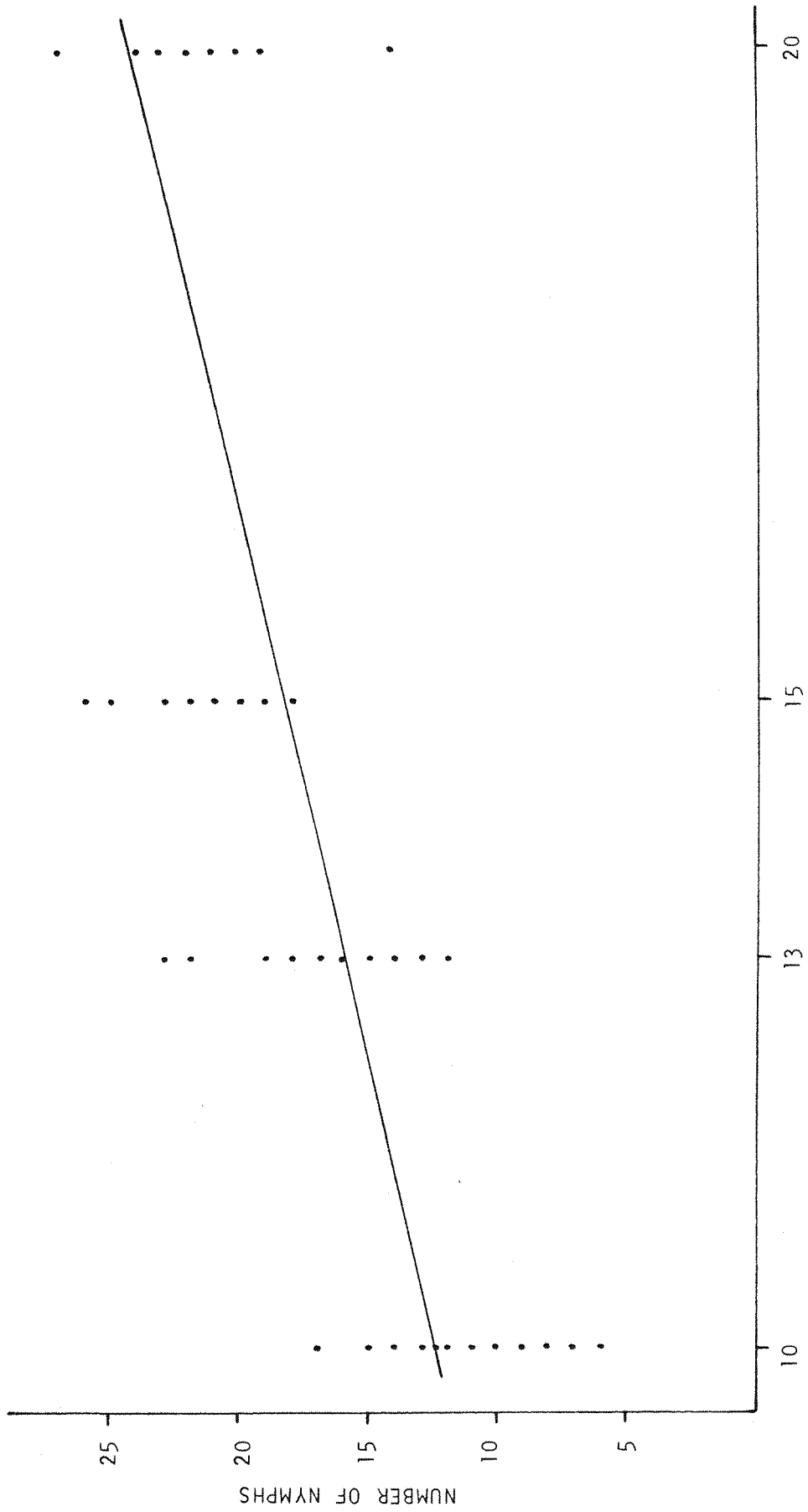


Fig.4 The relationship between the number nymphs produced in seven days and temperature.
$r = 0.775$, $P < 0.01$, d.f = 111, $y = 1.791 + 1.07x$, $F = 167.6$

Table 1. The mean development times, weights and fecundities of apterae and alatae. S.E.: standard error.

	Apterae		Alatae	
	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Development time (days)	28.76	1.340	28.58	1.170
Adult weight (mg)	0.930	0.037	0.771	0.043
No. nymphs in 7 days	10.92	0.437	7.916	0.499
No. nymphs in 10 days	14.71	0.546	10.250	0.750
No. nymphs in 15 days	20.05	0.815	12.833	0.805
No. nymphs in 20 days	25.26	1.006	15.000	1.080

d.f = 1,10, $P > 0.05$). The relationships for apterae are all significant but the amount of variation explained by the regression decreases with an increase in reproductive time.

Apterae reared at 10°C produced 12.5% of their nymphs on the first day of adult life and 50% of them in 9 days compared with alatae which produced 19.2% of their nymphs on the first day and 50% in 7 days. The daily fecundity of the apterae gradually decreased over the 20 days whilst the reproduction of alatae was very irregular (Fig.5).

7.3 THE INFLUENCE OF TEMPERATURE/PHOTOPERIOD ON MORPH DETERMINATION

The relative proportions of aphids which were alate at 20°C and 10°C were significantly different at $P < 0.005$ ($\chi^2 = 8.40$, d.f = 1). A larger proportion of alatae was produced when reared at 10°C than at 20°C (both mothers and nymphs were isolated, so there was no density effect) (Fig.6).

7.4 THE INFLUENCE OF TEMPERATURE/PHOTOPERIOD ON THE OVARIOLE NUMBER OF APTEROUS AND ALATE VIRGINOPARAE

The ovariole number of apterae and alatae was not significantly different at P = 0.05 for (i) apterae reared at 20°C, 15°C and 10°C, (ii) alatae reared at 20°C, 15°C and 10°C and (iii) apterae and alatae reared at each temperature. The modal ovariole number in each case was 10 (Fig.7). Hence temperature did not affect the distribution of ovariole number in M. festucae cerealium, and the range in ovariole number was very small.

Figure 8 shows the frequency distribution of the number of large embryos (LEN) of aphids reared at the three temperatures. The distribution of LEN within an aphid is dependent upon morph, temperature, age and weight. Age and weight were not controlled for (since weight does not influence ovariole number (Wellings, Leather and Dixon 1980) and as long as very old individuals are avoided, the ovariole number can be determined irrespective of aphid age). Analysis of LEN showed

Table 2. The relationship between the number of offspring (y) produced during the first 7 days, 10 days, 15 days and 20 days of adult life and adult weight (x)

No. of nymphs in 7 days	$y = 3.811 + 76201x$
	$r = 0.6550$, d.f = 1,36, $P < 0.001$
No. of nymphs in 10 days	$y = 5.060 + 10.343x$
	$r = 0.7119$, d.f = 1,36, $P < 0.001$
No. of nymphs in 15 days	$y = 6.701 + 14.310x$
	$r = 0.6603$, d.f = 1,36, $P < 0.001$
No. of nymphs in 20 days	$y = 12.436 + 13.748x$
	$r = 0.5135$, d.f = 1,36, $P < 0.01$

Table 3. The relationship between the number offspring (y) produced during the first 7 days, 10 days, 15 days and 20 days of adult life, and adult weight (x), NS, not significant

No. of nymphs in 7 days	$y = 5.811 + 2.730x$
	$r = 0.2373$, d.f = 1,10, NS
No. of nymphs in 10 days	$y = 7.996 + 2.921x$
	$r = 0.1691$, d.f = 1,10, NS
No. of nymphs in 15 days	$y = 8.015 + 6.248x$
	$r = 0.3366$, d.f = 1,10, NS
No. of nymphs in 20 days	$y = 0.7469 + 9.765x$
	$r = 0.3924$, d.f = 1,10, NS

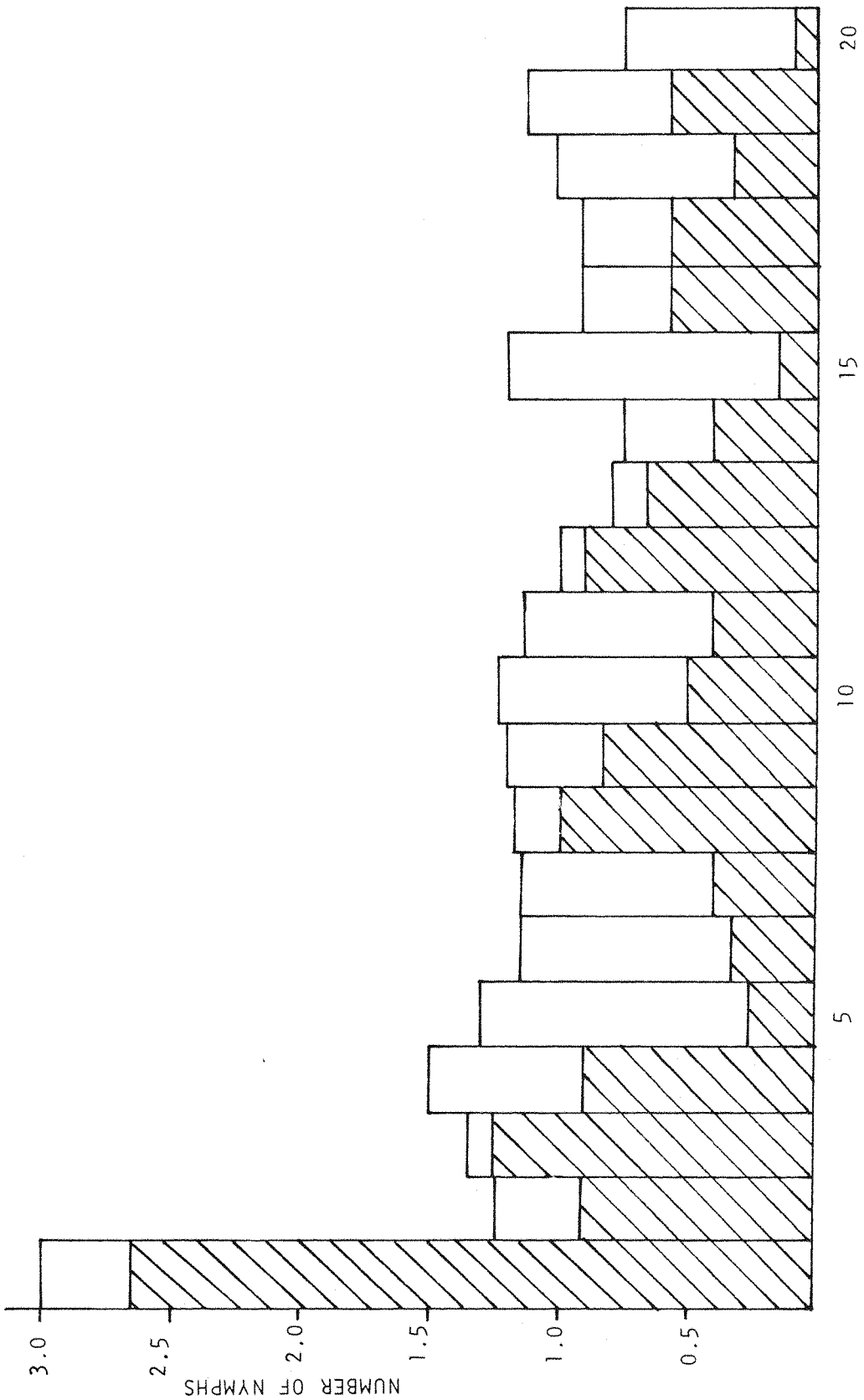


Fig.5 The mean daily fecundity of apterae □ and alatae ▨ reared at 10°C $13\frac{1}{2}$ hours photoperiod

Fig.6 The percentage of alate nymphs produced from isolated mothers on Lolium perenne cv. Cropper: the nymphs were also isolated. Numbers in brackets are the sample sizes.

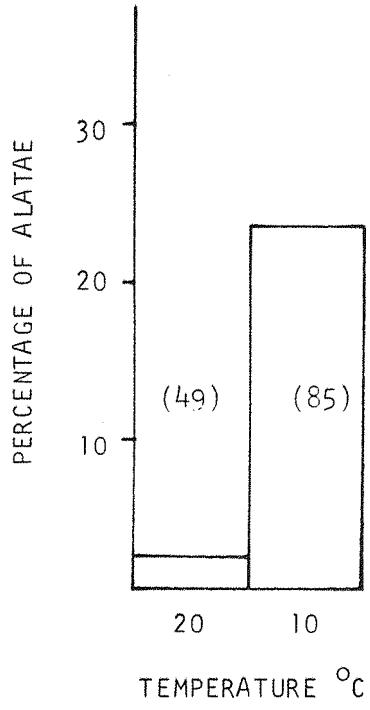
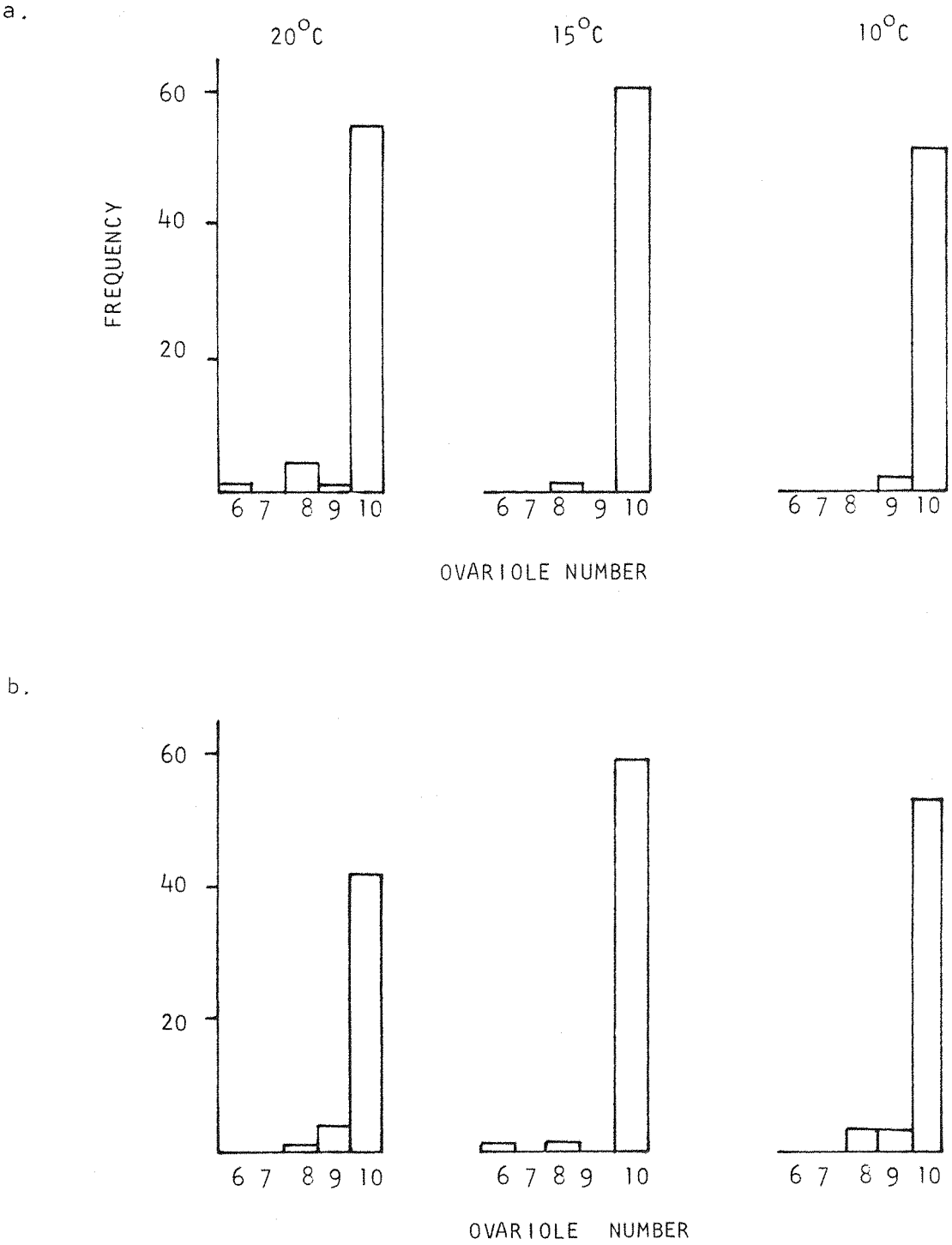


Fig.7 The frequency distribution of ovariole number for (a) apterae and (b) alatae reared at 20°C, 15°C and 10°C.



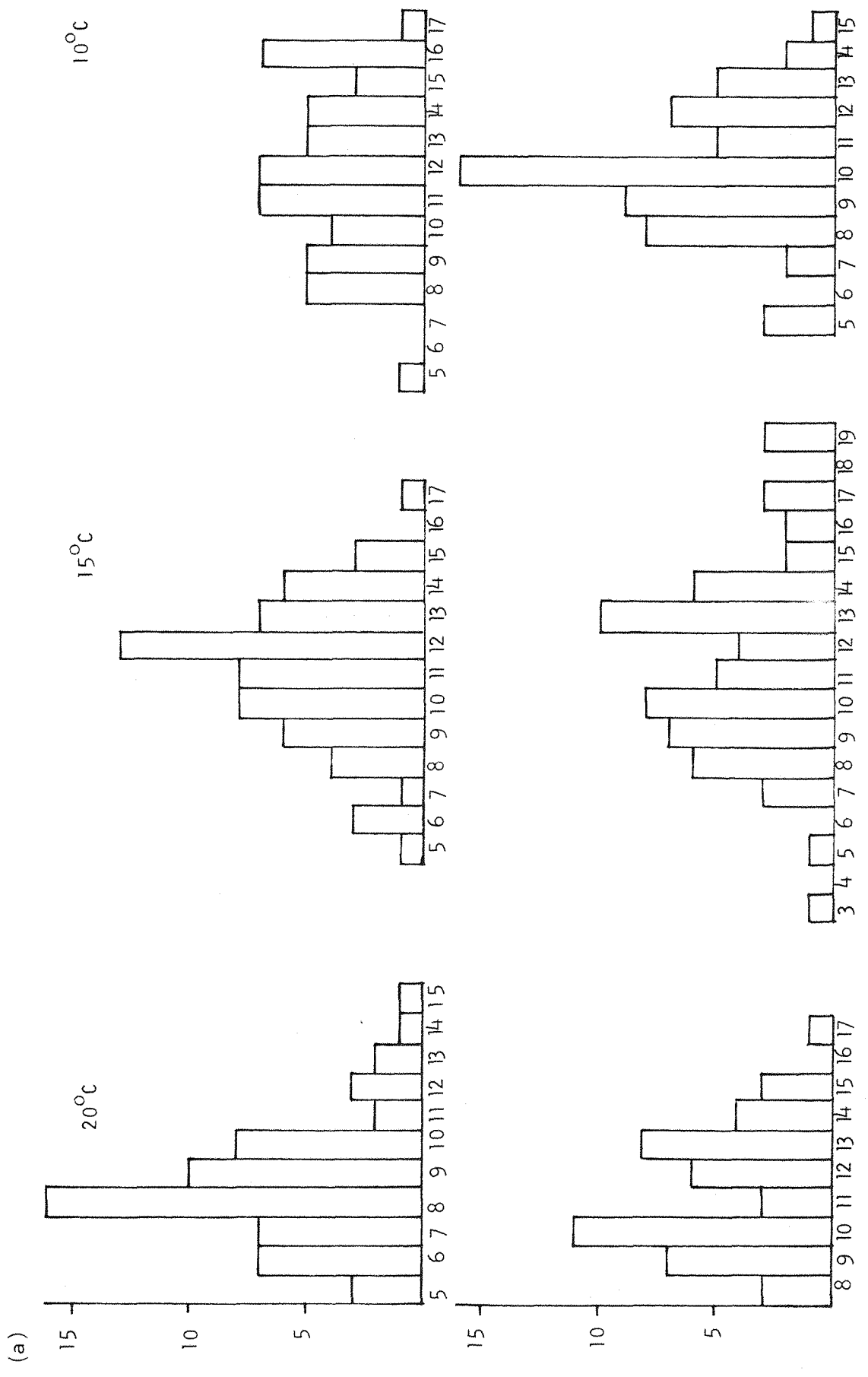


Fig.8 The frequency distribution of the large embryo number of (a) apterae and (b) alatae reared at 20°C, 15°C and 10°C.

the means to be significantly different at $P < 0.05$ with apterae and alatae reared at 15°C having the highest mean numbers. However since the age and weight of the aphids were not controlled any conclusions drawn from this data can only be tentative.

DISCUSSION

The reproductive performance of M. festucae cerealium at 10°C and 22.8°C was investigated by Hill (1971). Despite the poor control of temperature the values obtained by Hill for the development times were similar to those obtained in this study (Table 4). However the daily fecundity of aphids at 10°C (over similar reproductive times) was higher for both apterae and alatae in this study (for apterae a daily fecundity of 1.29 ± 0.05 nymphs compared with 0.96 nymphs (Hill 1971); for alatae a daily fecundity of 1.10 ± 0.05 nymphs compared with 0.42 nymphs (Hill 1971). The values obtained here and by Hill (1971) for the development times and fecundity of M. festucae cerealium were less than values obtained for other cereal aphids reared at similar temperatures (Dean 1974). At 10°C the development times of M. dirhodum, R. padi and S. avenae were almost half that for M. festucae cerealium (Table 4), whilst the fecundities of the other cereal aphids were consistently higher at all temperatures that those of M. festucae cerealium. A characteristic of the population dynamics of M. festucae cerealium is the early population increase in spring when temperatures are low. This is in contrast to the other cereal aphids which do not increase in numbers until June or July. Therefore it would be expected for M. festucae cerealium to show an enhanced response to low temperatures relative to the other cereal aphids. However this was not substantiated here. A long development time provides a longer time over which mortality can act, therefore a longer development time at low temperatures could only be compensated for if the chances of survival at such temperatures was high. During winter M. festucae cerealium is the only cereal aphid commonly found on non-crop Gramineae, and large numbers have been found overwintering on mature crop grasses

Table 4. A comparison of nymphal development times for apterous virginoparae reared at different temperatures from three separate studies.

REFERENCE	Dean (1974)						Present study			Hill (1971)	
HOST PLANT	barley		barley		barley		*L. perenne*			oat	
APHID SPECIES	*M. dirhodum*		*R. padi*		*S. avenae*		*M. festucae cerealium*			*M. festucae cerealium*	
TEMPERATURE °C	DAYS	S.E.	DAYS	S.E.	DAYS	S.E.	TEMP. °C	DAYS	S.E.	TEMP. °C	DAYS	S.E.
10	14.7	± 0.16	14.7	± 0.15	16.8	± 0.23	10	28.0	± 1.38	10.2	24.7	-
12.5	11.7	± 0.15	-		12.8	± 0.23	13	21.7	± 0.21	-	-	-
15	9.5	± 0.12	9.3	± 0.11	10.8	± 0.19	15	14.8	± 0.23	-	-	-
20	7.8	± 0.06	6.1	± 0.07	8.8	± 0.12	20	10.3	± 0.08	22.8	9.0	-

(Hand 1982). The overwinter survival of M. festucae cerealium may therefore be high and although its fecundity may be relatively low at spring temperatures, the large numbers of M. festucae cerealium overwintering may compensate for this. Subsequently populations of M. festucae cerealium increase in spring and are particularly large when there have been mild winters (see Vickerman 1977).

A reproductive threshold was calculated from the 7-day fecundity and temperature regression (Fig.4). The extrapolated value was -1.6°C i.e. reproduction was possible for M. festucae cerealium at temperatures above -1.6°C. However little significance can be attributed to this value since the regression was derived from only 4 temperatures; also one of the major hazards of extrapolating is that the regression line of the population means may actually be curved to an extent which is small within the limits of the sample but becomes more pronounced beyond these limits (Snedecor and Cochran 1978); this would be particularly true of a regression with so few x values.

More alatae were produced from isolated mothers at 10°C than at 20°C. Alate virginoparae are normally produced to allow dispersal from an unfavourable environment but alate induction at low temperatures suggests an alternative strategy. When mean spring temperatures are high (e.g. 10°C) this may induce alate production. The alatae can then disperse to other areas within a sward and so avoid concentrations of aphids which could seriously damage the host plant (in the manner of trivial flights made by the sycamore aphid within a tree canopy; Dixon 1969). Alternatively alatae could be produced in autumn to disperse to other grass hosts, e.g. hedgerow grasses (Hand 1982) to maximise the chance of overwintering survival. However this is mainly conjecture as there is no information on flight threshold temperatures for M. festucae cerealium which would be a critical factor influencing take-off and subsequent dispersal.

Alate M. festucae cerealium produce a larger proportion of their total number of nymphs on their first day of life than apterae (at 10°C, 12.4% and 19.2%; at 20°C, 7.8% and 8.9% for apterae and alatae respectively). There are two possible reasons for this, (1) it is an

advantage to produce many offspring quickly as this is an effective way of achieving a high rate of increase (Dixon and Wratten 1971), (11) alate survival may be low, i.e. wings are a disadvantage in wet weather, water can pin down an alata and cause mortality; this would be particularly important during spring and autumn, and hence it would be advantageous for an alate to produce as many nymphs as soon as possible in adult life to maximize its chances of reproductive success.

There are two ways an aphid species can optimize its reproductive success in a predictable but variable environment. Firstly an aphid species could have a constant reproductive potential which provides an optimal reproductive strategy for all the changes each generation will encounter. Secondly an aphid species could have a programmed reproductive potential which differs for each generation according to the conditions which are encountered. The ovariole number of an aphid has been used as a measure of its reproductive potential (Wellings *et al.* 1980; Dixon and Dharma 1980a, 1980b; Ward, Wellings and Dixon 1983a and 1983b). The ovariole number of the autoecious aphids *D. acerinum*, *D. platanoides*, *E. tiliae* and *E. punctipennis* were constant whilst the ovariole numbers of two heteroecious aphids *M. dirhodum* and *R. padi* differed both within and between generations (Wellings *et al.* 1980). The difference in the two strategies for autoecious and heteroecious aphid species could be caused by the extent of the variation in the habitat quality experienced by the aphids. A constant ovariole number allows a certain flexibility in reproduction through size variation, but if the variation of the hosts is so extensive that the size variation is not sufficient then reproductive potential could be increased by a variable ovariole number. *M. festucae cerealium* is anholocyclic on grasses and like the autoecious tree aphids (Wellings *et al.* 1980) has a constant ovariole number. The grass habitat does not have predictable changes in growth, e.g. flowering, but *M. festucae cerealium* being a leaf feeder may not be affected by this unpredictability. Hence the variation experienced by *M. festucae cerealium* is probably small and could be accommodated by changes in aphid size.

CHAPTER EIGHT

DAMAGE ASSESSMENT

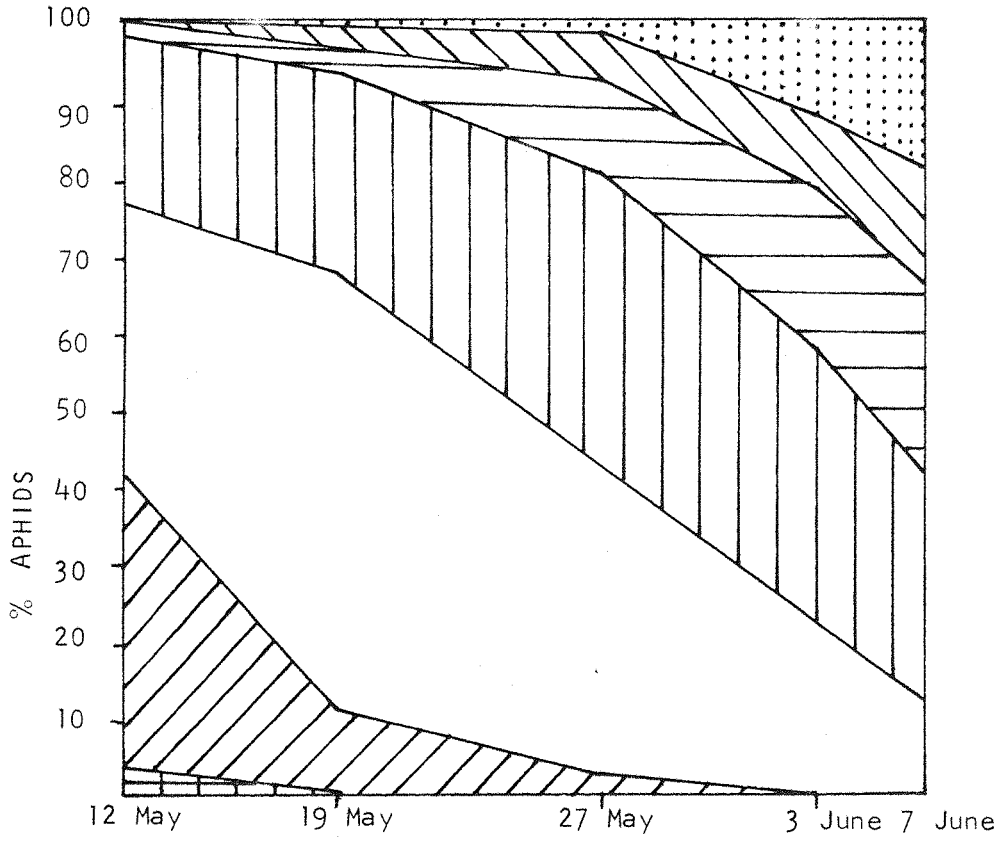
INTRODUCTION

M. festucae has caused direct damage to cereals and herbage seed crops (see Ch.1) whilst *M. festucae cerealium* has caused damage to grass crops (Vickerman 1978) and is thought to have the potential to cause damage to cereals. The numbers of *M. festucae cerealium* in cereals remain low and thus the effects on yield to date are probably negligible (Vickerman and Wratten 1979). However, should numbers of *M. festucae cerealium* ever reach outbreak proportions in cereals then the damage could be very severe (Massee 1936; Stroyan 1952; Janson 1959). The timing of *M. festucae cerealium* population increase was an important factor in the severity of the damage caused in 1935 and 1957 (Massee 1936; Janson 1959 respectively). The numbers of *M. festucae* reach maximum population levels between April and June (Theobald 1917; Massee 1936; Anon 1945; Anon 1950; Stroyan 1952; Gair 1953; Janson 1959; Vickerman 1976) which in cereals means that the aphids are most abundant on the plants from tillering (G.S. 20) to the beginning of grain formation (G.S. 43) (Kolbe and Linke 1974). The damage caused at this time would be stunted growth (Massee 1936) and/or a reduction in the number of grains per ear; a reduction of 1 grain per ear could reduce yield by 3% (Kolbe and Linke 1974).

Although *M. festucae cerealium* may cause direct damage to grasses and cereals, it may be more important as a vector of barley yellow dwarf virus (BYDV). *M. festucae cerealium* was identified as a carrier of BYDV by Plumb (1974) and, as 93% of all *L. perenne* cv. S.24 sampled between January and March 1966 in Britain contained the virus (Doodson 1967), *M. festucae cerealium* could be an important vector between grasses and cereals. Furthermore, yield loss due to BYDV is usually greater when early infection takes place (Vickerman and Wratten 1979); the early population increase of *M. festucae cerealium* may be particularly important in this context.

Fig.1 The feeding distribution of M. festucae cerealium on wheat.

▦ , leaf 1; ▨ , leaf 2; □ , leaf 3; ▥ , leaf 4; ▤ , leaf 5; ▧ , leaf 6; ⊡ , flag leaf.



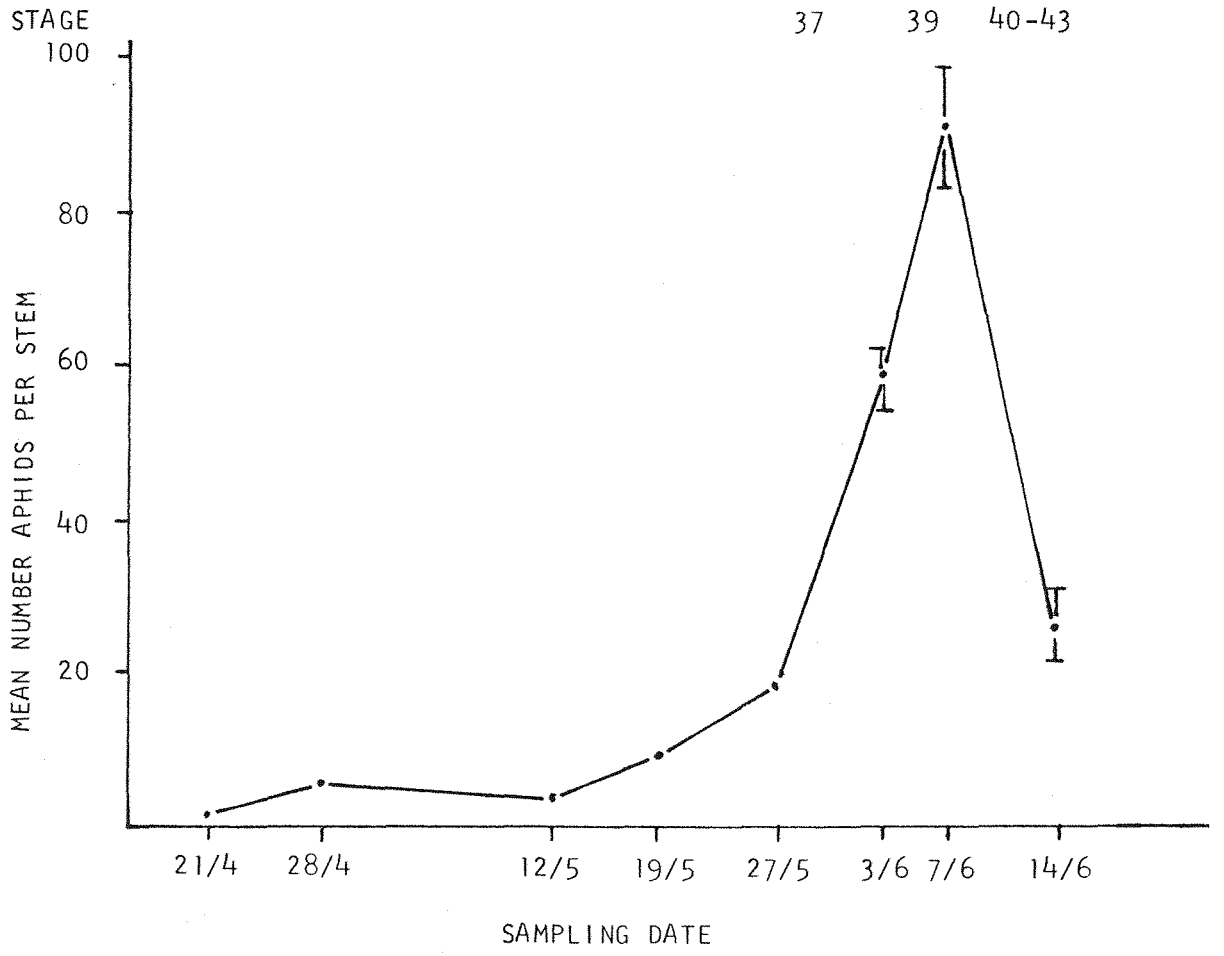


Fig.2 The mean total number of aphids (all instars and morph) per wheat stem. ⊤ = standard error. The standard errors for the other dates were too small for the graph and were from left to right; 0.25; 0.67; 0.47; 0.69; 1.38.

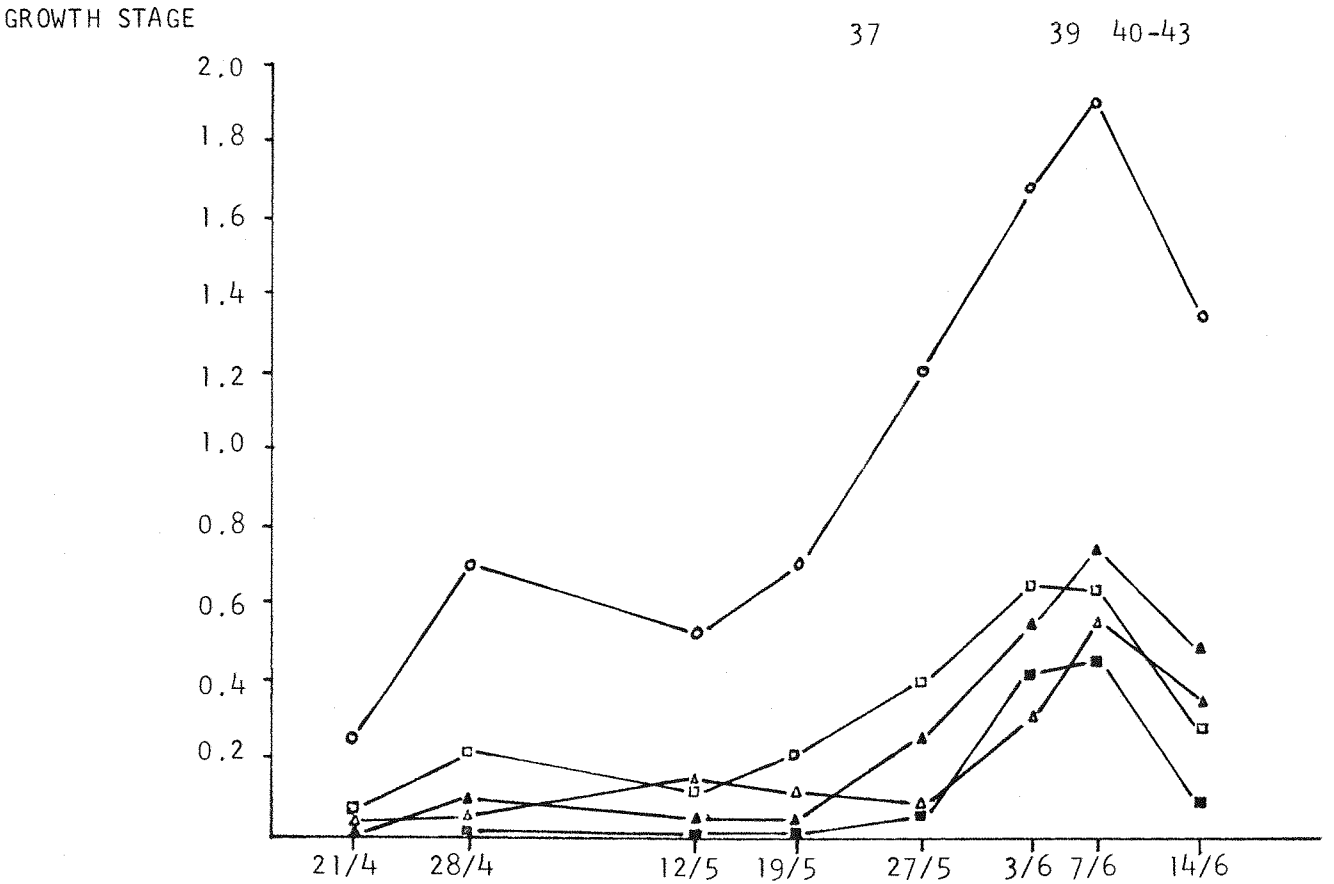


Fig.3 Numbers of M. festucae cerealium per stem (3 cage mean).
o, first-, second-, and third instar aphids; ▲, apteriform fourth-instar aphids; ▲, alatiform fourth-instar aphids; □, adult apterous aphids; ■, alate adult aphids.

M. festucae cerealium has important implications for grass and cereal yields because it is a virus vector and because it can cause direct damage. The effect of the direct damage on grassland and cereals has not yet been quantified and because of this an attempt at quantification was made here. The reasons for the lack of success in these experiments were given in Chapter Two; however, the work was such an integral part of the conceptual framework of the project that it warrants mention here. The feeding distribution and population data of M. festucae cerealium on wheat salvaged from the experiment and are included here.

RESULTS

The vertical distribution of the aphids on the wheat changed with the pattern of leaf growth (Fig.1), i.e. the aphids moved onto each new leaf as it unfolded. However, the lower leaves were more heavily infested until 7 June when all the leaves had unfolded and the distribution of the aphids was more even (Fig.1).

The peak aphid number per stem (90 per stem) was reached on 7 June at G.S. 40, i.e. start of booting. The population had markedly decreased by 14 June. Entomopthorales were very much in evidence and may have been responsible for the population decline (Fig.2).

Fourth instar alatae were being produced (albeit at low levels) from 21 April and reached their highest numbers on 7 June (Fig.3).

DISCUSSION

The results obtained here for the feeding distribution of M. festucae cerealium on fully-leaved wheat stems (7 June) were similar to those for the distribution of apterae on wheat in the laboratory (Ch.3), i.e. the aphids were fairly evenly distributed over all leaves with a tendency for higher numbers to occur on the lower leaves. In contrast to the feeding distribution of M. dirhodum which reflected the

senescence pattern of wheat leaves with all the aphids eventually feeding on the flag leaves (Wratten 1975), in the present experiments only the very lowest leaves were senescing during the time M. festucae cerealium was present and the upper leaves were actively growing, so the flag leaf was relatively under colonized.

Alatae were produced for the duration of the experiment (Fig.3) which is in contrast to M. dirhodum and S. avenae (Wratten 1975) which produced alatae only as aphid numbers increased. This again suggests (see Chs.3, 4, 6) that there is some unfavourable characteristic of wheat which subsequently induces alate production in M. festucae cerealium.

Rigoursly obtained yield-loss data for M. festucae cerealium on wheat and grass remain an urgent need; the unexpected outbreaks of M. dirhodum in Europe in 1979 highlighted the sparcity of yield-loss data for that species, for instance (only those of Wratten (1975) existed at the time). The lack of success of the grass yield experiment and the unsympathetic behaviour of the M.A.F.F. Experimental Husbandry Farm with respect to the wheat experiments prevented the acquisition of the data for this thesis.

Plate 1. The damage caused by M. festucae cerealium in the field cages. The peak population density was 90 per stem.

Plate 2. Dead wheat stems caused by a peak population density of 90 aphids/stem.

Plate 3. The wheat grown in the control cages.

Plate 4. Wheat taken from a cage infested with M. festucae cerealium (above) and a control cage (below).

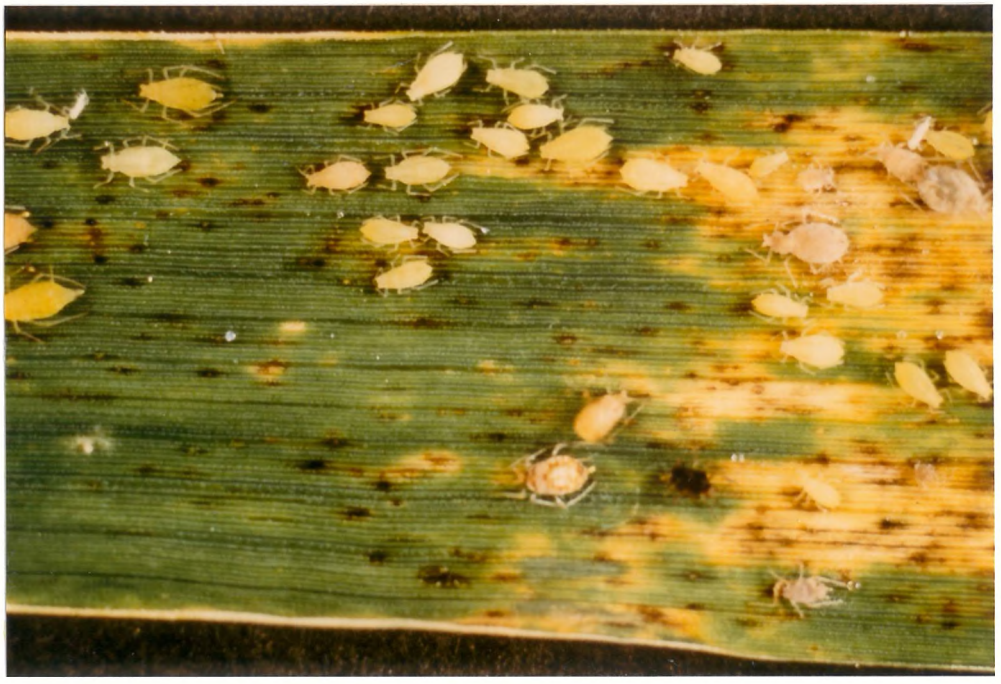


Plate 5. The yellowing and necrotic brown spots caused by M. festucae cerealium on the flag leaf of a wheat plant.

CHAPTER NINE

FINAL DISCUSSION

WHEAT/GRASS DIFFERENCES IN RELATION TO ALATE PRODUCTION STRATEGIES

The dual discrimination theory of aphid host plant selection (Kennedy and Booth 1951) proposes that the strength of an aphid's preference for a particular host depends upon a balance between the suitability of the plant's nutrition and flavour, the former comprising of amino acids, sugars etc. and the latter 'secondary' plant substances. For aphids, nutritional properties are more important within a plant than between plants, whilst flavour is important between plants; discrimination may be tolerance of or preference for, certain flavours (Kennedy and Booth 1951). Within a species, apterae contribute to a colony's growth but have little influence over the selection of appropriate host species, whereas alatae respond strongly to the characteristic flavour of host plants and thus have a greater role in finding and selection of host species (Edwards and Wratten 1980).

Alatae of M. festucae cerealium fly from wheat despite producing larger numbers of nymphs on this host than on any other. This flight response when considered in conjunction with the high alate production on wheat (both in the field and the laboratory) and the greater restlessness shown by alatae on wheat, suggested that there was some characteristic of this host which M. festucae cerealium finds unsuitable. Apterae, when confined to the host plant, are more fecund on wheat than on other hosts, which suggested that wheat is nutritionally acceptable but that the flavour of wheat may be responsible for the behaviour and induction of alatae. The response of M. festucae cerealium alatae to the flavour of wheat could be due to the aphids phylogenetic history. M. festucae cerealium is a subspecies of the grass aphid M. festucae which is restricted to grasses (Stroyan 1982) whilst M. festucae cerealium has a propensity towards colonizing cereals; presumably to do so it must be able to tolerate or actively prefer the flavour of wheat. Individuals tolerant of a secondary plant substance and

proliferating on a new host may become a race isolated from the original species and in this way a new host-restricted species could develop (van Emden 1978). M. festucae cerealium could be an example of such a phenomenon, but tolerance of a host may not be an 'all or nothing' response, but a gradual adaptation to the secondary plant substances. As van Emden (1978) pointed out, the literature suggests that once an insect has succeeded in dealing with secondary substances, their role in the plant-insect relationship is at an end, but, as can be seen in the case of M. festucae cerealium, the interaction of the behaviour of this aphid with the chemical composition of wheat persists throughout the plant-insect interaction (van Emden 1978). M. festucae cerealium may have developed a level of tolerance towards the flavour of wheat which allows it to exploit this resource but only to the extent that the flavour stimulates alate induction. The alatae may respond to the flavour through an enhanced willingness to fly. Van Emden (1978) suggested that some secondary substances may provide barriers to insect colonization whilst others, to which insects can adapt, provide 'flags' (nutritional or secondary substances which orientate insects during host selection) for the partitioning of plant production by herbivorous species. K-selected herbivores develop a tolerance of secondary substance 'barriers' whilst r-selected herbivores use the secondary substances as 'flags' for herbivore orientation. Cereal aphids occupy an intermediary position on the r-K continuum (Southwood and Comins 1976) and hence may be subject to 'flag' and 'barrier' types of secondary substances.

Secondary substances apart, there is evidence to suggest that M. festucae cerealium is more K-selected than other cereal aphids. It has a longer generation time and a lower fecundity than M. dirhodum, S. avenae and R. padi when reared on wheat at 20°C (Dean 1974). Although these two factors have little significance on their own, when considered in conjunction with habitat stability (Southwood 1977) differences in strategy become more apparent.

S. avenae prefers to colonize and exploit the ears of grasses: an ephemeral habitat (Watt and Dixon 1981). An ephemeral habitat is available and suitable for reproduction for only a short time and

although during this time it is highly favourable (Southwood 1977), subsequent generations of S. avenae are required to leave when the ears become overpopulated or the growth stage becomes unsuitable, i.e. since grass species flower at different times they are colonized sequentially depending on their development (Watt 1981). Grassland and cereals are abundant in summer but the time over which they are favourable for S. avenae is short; therefore interpatch distances (distances between suitable patches of grass ears) may be large. The exploitation of this type of ephemeral habitat is characteristic of an r-selected species (Southwood 1977). The ephemeral habitat of S. avenae is in contrast to the habitat of M. festucae cerealium; the latter like M. dirhodum, is a leaf feeder and hence is less subject to variation in host growth stage than is S. avenae (Watt 1979); also preferred feeding sites are abundant in grass swards. Grassland, in terms of preferred feeding sites, is a predictable habitat which has a relatively low variability of unfavourable periods both in terms of the length of time favourable and in the level of suitability. Grassland provides a large patch size with small interpatch distances. The interpatch distances for M. festucae cerealium are even smaller if cereals and hedgerow grasses are taken into account. The large patch size and small interpatch distances means that there is a high level of predictability in finding a new habitat and also the probability of the different habitats being favourable is high. This type of habitat, which remains suitable for reproduction for such a long time in relation to the aphids' generation time, has a high degree of stability (Southwood 1977). The longer an aphid colony can remain in the same area the greater expectancy of survival it can have since it has to devote fewer of its 'resources' to migration which has a relatively low survival probability. However there are distinct disadvantages associated with remaining in an area (a stable habitat) over a long period, namely the accumulation of natural enemies and making the environment unfavourable by overcrowding. Organisms adapted to these habitats and conditions exhibit particular characteristics; increased size, longevity, protection against natural enemies and low fecundity, i.e.they are K-selected organisms (Southwood 1977). M. festucae cerealium is an

aphid of a stable habitat and, compared with the cereal aphids R. padi, M. dirhodum and S. avenae, exhibits the more K-selected characteristics of a longer generation time and a lower fecundity.

HABITAT AND DENSITY DEPENDENT ALATE PRODUCTION

Another characteristic of K-selected species is a low level of dispersal; although it is difficult to gauge the relative extent of dispersal of a species it is possible to compare different dispersal strategies. The type of stimulus which induces movement from a host by a species is again dependent upon the type of habitat utilized by each species. The habitat will determine the necessity for either long migratory flights or trivial flights (Kennedy 1961). Migratory flights occur when the thresholds for stimuli, such as food or shelter are high, resulting in the aphid leaving the habitat, whilst trivial flight occurs when the thresholds for vegetative stimuli are low and the aphid as a consequence remains within its habitat (Dixon 1969). Migratory flights are likely to prove hazardous, resulting in a few animals successfully establishing themselves in other habitats (Dixon 1969; Southwood 1977). Hence the cereal aphids S. avenae and R. padi have a density dependent production of alatae (Watt and Dixon 1981; Dixon and Glen 1971 respectively) so that only when conditions are likely to be unfavourable will alatae be produced in large numbers and undertake hazardous migratory flights. This is a response to ephemeral habitats which can best be exploited by movement between hosts as suitable growth stages develop.

The stability of the grassland habitat (see above) enables a different dispersal strategy for M. festucae cerealium. Both migratory and trivial flights have little risk associated with them since grass is abundant in both time and space. Alatae are produced independently of density, apterae possibly dispersing within the sward if crowding occurs. Any alatae which are produced may undertake trivial flights to redistribute the aphids within the habitat, or migratory flights to colonize other habitats. Both have a lower risk associated with flight for M. festucae cerealium than for other cereal aphids. However, the

proportion of alatae produced when reared on wheat was much higher than when reared on L. perenne, probably, as explained above, due to the influence of secondary plant substances in wheat. The numbers of alatae produced on wheat may increase as a response to density (Hand 1982) but since a higher proportion of alatae are produced on wheat, the large number of alatae observed may just be a result of the population size. A large number of M. festucae cerealium alatae are caught in suction traps between midsummer and mid-July (Stroyan 1982) and it seems most likely that these are alatae migrating from wheat. However alatae were produced on L. perenne during early summer (field work) and then reared at 10°C in the laboratory, which suggested that alatae may be produced in response to spring or autumn temperatures, allowing migration to occur.

OVERWINTERING, SPRING POPULATIONS AND THE NATURAL ENEMY THEORY

During the laboratory experiments investigating the effects of low temperatures and from the overwintering field work, no sexual morphs were observed, although both apterae and alate virginoparae exhibited changes in morphometry. These changes in shape, observed under laboratory conditions, may reflect seasonal variation in the morphology of M. festucae cerealium. Different generations of the autoecious aphids M. viciae (Lees 1966) and D. platanoidis (Dixon 1974, 1975) have been shown to differ morphometrically even though, in the case of D. platanoidis the ovariole number was constant (Wellings et al. 1980). Likewise the ovariole number of M. festucae cerealium, although not constant exhibited a low frequency of numbers other than the modal value. The ovariole number of M. festucae cerealium was less variable than that of other cereal aphids and this may be an adaptation to a predictable and stable habitat, where any changes required in reproductive potential can be accommodated by changes in size.

The reproductive potential of M. festucae cerealium as expressed through ovariole number was not influenced by temperature unlike the fecundity. In addition the number of nymphs produced were less than that of other cereal aphids reared at the same temperatures (Dean 1974). This was particularly obvious at low temperatures where M. festucae cerealium was expected to perform relatively better than the other

cereal aphids, because of its capacity for population increase during spring. However during winter and especially during March and April, M. festucae cerealium is the most numerous cereal aphid in grassland and it was the only cereal aphid species which frequently increased in proportion in winter relative to other cereal aphids (Hand 1982). Because M. festucae cerealium is less fecund relative to other cereal aphids the population increase described by Hand (1982) could either mean that it has a higher fecundity at temperatures lower than those used in these experiments or that it has a higher survival of all instars than other cereal aphid species. However there is no evidence to support either of these ideas.

M. festucae cerealium is the most numerous cereal aphid overwintering on non-crop Gramineae and thus hedgerows are important as overwintering sites. Hedgerows are also important because they border other crops (Hand 1982). M. festucae cerealium is often not found in grass crops before March and this may be because the aphids move out of the hedgerows at this time (Hand 1982). Hedgerows, despite harbouring large numbers of natural enemies probably provide very good overwintering sites because of the larger amount of organic matter may provide more shelter from the weather. During the winter field work, aphids were rarely found feeding and most were on the walls of the clip cages. Many of the aphids which died were found with their stylets still inserted in the leaf, and as Parry (1979) remarked, any cold-hardening mechanism would be superfluous in an aphid overwintering in the feeding stage as the temperature at which the aphid froze would be dependent not on the ability of the insect to avoid freezing, but on the freezing properties of the gut contents. The aphids probably feed very little, only on occasions when temperatures are sufficiently high. Aphids would have no need to stay at their preferred feeding site but could move down the plant into the dead organic matter to gain protection from the weather (see Gair 1953). This could also be the reason why a larger number of M. festucae cerealium were found overwintering on more mature swards (Hand 1982). M. festucae is most abundant between April and June (Theobald 1917; Massee 1936; Anon 1945; Anon 1948/49; Stroyan 1952; Gair 1953; Janson 1959; Vickerman 1976). The early build up

of its numbers is thought to cause a corresponding increase in natural enemies (Vickerman 1977). Warm winters and springs can cause higher than average early spring populations of M. festucae cerealium. With this species as an abundant prey source, natural enemy populations may increase rapidly and large numbers may be present in the cereal fields when alatae of S. avenae arrive later in the summer (Vickerman 1977). This effect however may be very localized depending upon the abundance of good overwintering sites. There are indications that during years when there have been large populations of M. festucae cerealium in spring there have been no severe outbreaks of S. avenae (Vickerman 1977). M. festucae cerealium may have potential as an indicator species by which it is possible to predict other cereal aphid population levels. Vickerman (1977) described such a shceme and showed that the number of severe infestations of S. avenae decreased in cereals with the increase in severity of M. ascalonicus outbreaks in grass and weeds. A forecasting system using grassland indicator species has been successfully developed in Switzerland (Suter 1980) and M. festucae cerealium certainly has the potential for such a role, although more information concerning overwintering is required.

THE POTENTIAL DAMAGE AND CONTROL

The suggested role of M. festucae cerealium in integrated control strategies has been as a method of increasing the size of natural enemy populations so that they are sufficiently large to prevent major outbreaks of S. avenae. Numbers of M. festucae cerealium in cereal crops may be enhanced by undersowing the cereal with an annual ryegrass, thus providing an effective overwinter habitat. However there are two major problems with this strategy; firstly farmers are unlikely to increase their acreage of undersown cereals; secondly and perhaps more importantly M. festucae cerealium may build up in sufficient numbers in spring, overwhelm the influence of natural enemies (Southwood and Comins 1976) subsequently to damage both the undersown grass crop and the cereal crop. This potential is present because this species has

been known to damage both grass and cereal crops (see Ch.1 and Ch.8) severely and, despite the use of more aphid resistant cultivars, an outbreak as described could occur. There have been reports of severe outbreaks of M. festucae in cereals in 1935 (Massee 1936) and in 1957 (Janson 1959) and in grasses in 1945 (Anon 1945; Cameron 1945), 1949 (Anon 1950), 1957 (Janson 1959) and more recently 1974 (Vickerman 1978). As can be seen the majority of outbreaks are recorded between 1935 and 1957 and it is likely that changes in farming practices have prevented outbreaks of M. festucae cerealium more recently. There have been major changes in grassland management since the second world war. The area of temporary pasture has increased from 1.71 to 1.84 mha between 1944 and 1975 (Holmes 1980). Ley farming was developed during the war, which with strict rotation provided more control of pasture species composition, pests and diseases. The species composition of swards has changed so that now swards are often composed of a single species of ryegrass and a clover. This move away from long term pasture which had a highly varied plant composition to a more effectively controlled grass monoculture may have influenced the population dynamics of M. festucae cerealium. More importantly the metabolizable energy obtained from grassland for livestock has doubled between 1935 and 1972/73 (Holmes 1980). This increase is mostly due to an increase in fertilizer and an increase in the proportion of silage cut. The conservation of grass as silage has probably been the single most important factor influencing the population dynamics of M. festucae cerealium over the last 30 years. Silage production has become more efficient and up to 4/5 cuts can be made during a summer, both mechanically removing populations and leaving behind a habitat which for many weeks is hostile for the aphid. Cutting grassland has been used as a method of control for M. festucae cerealium in spring (Edwards and Heath 1964) and unwittingly further cutting has probably also prevented M. festucae cerealium re-establishing large populations throughout the summer. Perhaps the most important factors contributing to the absence of outbreaks of M. festucae cerealium in cereals have been: the reduction of undersown cereals and removal of 'weed grasses' with herbicides and the development of more aphid-resistant cereal cultivars (although none have been specifically developed against

M. festucae). However it still remains to be seen, how large a M. festucae cerealium population can cause significant yield loss in cereals.

FURTHER RESEARCH

There are two main areas which are obvious gaps in the knowledge of M. festucae cerealium, both having been studied here without success. Firstly, more needs to be known about the overwintering survival of M. festucae cerealium in grassland and in cereals, and the relative importance of these habitats for spring population levels. Secondly more information is required about the yield losses caused by M. festucae cerealium in grassland and cereals. With more information on grassland yield losses, a control strategy involving timing of the first spring cut, could be devised and implemented.

It would be interesting to extend the morphometric study of M. festucae cerealium on different host plants and extend it to try to determine whether alatae caught in suction traps are flying from wheat or grass. More work is required on the trivial and migratory flight behaviour of M. festucae cerealium to determine its role as a vector of BYDV between grass and wheat.

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