THE INFLUENCE OF MINERAL FERTILIZATION

ON GRASSLAND LEAFHOPPER ASSOCIATIONS

BY

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ABSTRACT

NPK fertilizers were applied singly and in combination to an area
of natural grassland in the spring of 1978 and 1979. The levels of nitrogen
(total and soluble) were measured for a variety of plant tissues in both
1978 and 1979. In addition, levels of phosphorus, potassium, amino acids
and water content were measured in 1979.

Auchenorrhyncha were sampled weekly in 1978 and 1979. The abundance
and distribution of leafhoppers are discussed with reference to the biotic,
chemical and physical characteristics of the fertilized grass. Total leaf-
hopper abundance was best explained using an index of food quality and plant
architecture. A food quality index was based on the ratio of the levels of
favourable amino acids (amino acids deemed to favour insect growth and develop-
ment) and unfavourable amino acids (amino acids unfavourable to insect growth
and development) in the food. An index of plant architecture was calculated
as the product of plant height and biomass data.

Analyses of the abundance of individual species with the effects of NPK
fertilizers showed that different species of leafhopper were associated with
different nitrogen levels in the plants. Laboratory feeding and ovipositional
trials confirmed that performance was greatest at a particular plant nitrogen
level and that performance decreased when plant nitrogen levels were higher
or lower than this level.

An examination of Auchenorrhyncha host plant relationships confirmed
that in the majority of species, host associations are weakly developed or
totally absent, and that these species were associated with a plant nitrogen
level. A general theory proposing maintenance of an oligophagous habit
within grassland leafhoppers is presented.

Finally insect pest outbreaks in relation to plant nitrogen
levels as controlled by artificial fertilizers is discussed.

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SECTION I - GENERAL INTRODUCTION

1.1. Introduction

The population and general ecology of the grassland Auchenorrhyncha

(leafhoppers, froghoppers, etc.) have received a considerable amount

of attention.   This is not altogether surprising as they often form

the dominant insect fauna of calcareous (Whittaker 1969; Morris 1971)

and acidic (Waloff & Solomon 1973; Waloff 1974, 1975, 1980; Hill 1976;

Lawton & McNeill 1979) grasslands.

Although many species are important vectors of plant diseases,

in Great Britain they are not considered as serious agricultural pests.

There is little doubt, however, that they do have a marked effect on

the productivity of their host (Henderson & Clements 1977; Hill 1976;

Andrzejewska 1967).   In other parts of the world, for example, North

America (Weigert 1964), Asia (Sogawa 1973) and Southern Africa

(Metcalfe 1969; Rose 1974) Auchenorrhyncha are regarded as serious pests

of forage and crop plants.   Auchenorrhyncha nutritional behaviour has

been most studied whilst attempting to find a population control for

the rice plant and leafhoppers, Nilaparvata lugens (Stål) and

Nephotettix cincticeps (Uhler) (Pathak 1969; Sogawa 1973).   Port's

(1978) extensive survey on 53 species of Auchenorrhyncha gained insight

into the nature of the probing and feeding behaviour characteristic of

leafhoppers.   The extensive studies on the feeding biology of aphids

by a number of authors has relevance to leafhopper feeding (e.g. see

literature review of Hill 1976).

A number of authors have highlighted several aspects of the bio-

nomics and ecology of the Auchenorrhyncha at Silwood Park (Rothschild

1962, 1966; May 1971, 1975; Tay 1972; Solomon 1973; Waloff & Solomon

1973; Becker 1975; Hill 1976; Thompson 1977; Port 1978).   Much of this

work has been reviewed by Waloff (1980). The feeding and oviposition-al behaviour of the tree inhabiting Typhlocybinae have been extensively studied by Claridge & Reynolds (1972), Claridge et al. (1977), Claridge & Wilson (1978).

Recently Hill (1976) investigated the importance of the nutritional value of the host plant in a population of leafhoppers living on a relatively pure stand of Holcus mollis (L.). He argued that the quality of the food (as measured by available nitrogen) was a major influence in maintaining the observed insect patterns. Soluble nitrogen levels increased for very short periods during the growing and seed setting physiology of the grass and the phenology of the insects was closely cued to the phenology of the grass. Consequently McNeill & Southwood (1978) and Lawton & McNeill (1979) have shown that the leafhopper structure can be better explained by considering the mode of feeding of the species; phloem feeders being closely linked to soluble nitrogen levels, mesophyll feeders closely linked to levels of leaf total nitrogen, and xylem feeders maintaining a fairly constant population level independent of plant nitrogen levels. Hill (1976), McNeill (unpublished) and Broodbank (1980) have found high levels of individual amino acids to be important in determining the structure of the leafhopper community on Holcus mollis.

Other factors are also known to influence the structure and abundance of phytophagous communities (Lawton & McNeill 1979). In the grammivorous leafhoppers important factors must include area and plant architecture, natural enemies, and size of the area colonized by grass (i.e. patch size). Architecture and natural enemies will be considered in more detail later but the number of species colonizing an island has not been studied.

1.2 Species lists, Life histories and Host associations

The common species regularly breeding on the trial area, their
life histories and the host plants that they have been commonly assoc-
iated with are shown in Table 1.1. Life history data for those species
regularly breeding but occurring in low numbers has been taken from
Waloff & Solomon (1973). Host plant associations of the common species
has been extracted from papers by Le Quesne (1960, 1965, 1969), Waloff
& Solomon (1973) and Port (1978). Twenty six species of leafhopper,
i.e. 19 species of Cicadellidae, 5 of Delphacidae and 2 of Cercopidae,
bred each year within the experimental area.

In addition it is possible that Mocydia crocea (Herrich-Schaeffer),
Streptanus aemulans (Kirsch-baum) and Criomorphus albomarginatus (Curtis)
were also breeding in the area as they were taken very occasionally in
a number of samples. Thus it is probable that the total complex com-
prised twenty nine species.

Other non-grassland species that were frequently taken in the
samples were Cercopis vulnerata (Illiger)(Cercopidae), Graphocephala
coccinae (Forster) and Cixius pilosus (Olivier) (Cicadellidae) and
Conomelus anceps (Germar) (Delphacidae).

The two other population studies on acidic grassland (Waloff &
Solomon 1973; Hill 1976) recorded 63 and 16 species respectively. Hill's
relatively pure stand of Holcus mollis was structurally less diverse
than Waloff & Solomon's, and the experimental area. Waloff & Solomon
(1973) also noted that their method of sampling (sweep-net) may have
underestimated the number of species present so that their species list
may be even larger. On calcareous grassland, Whittaker (1969) recorded
33 species in an area of great botanical and structural diversity, and
Morris (1971) recorded a total complex of 45 species from grazed and

Table 1.1. Auchenorrhyncha species breeding within the study area; voltinism, hibernation stage, common host plant and mode of feeding. (P = Phloem; X = Xylem; V = Parenchyma; ** this study)

Regularly breeding on grass 1978-1980	No.annual generations	Hibernation stage	Common host on Acidic Soils	* Mode of feeding P	X	V	Authority
(1) Cercopidae							
Neophilaenus lineatus (L.)	1	Egg	Holcus spp., D.glomerata		+		**
Philaenus spumarius (L.)	1	Egg	Holcus spp., D.glomerata	–	+	–	Weigert 1964
(2) Cicadellidae							
Aphrodes albifrons (L.)	1(?)	Egg	Holcus spp., D.glomerata		?		
A.bicinctus (Schrank)	?	Egg	Holcus spp., D.glomerata		?		
Artheldeus pascuellus (Fall.)	2	Egg	Agrostis tenuis	+	–	–	**
Balclutha punctata (Thunberg)		Adult	Deschampsia flexuosa	+	–	–	
Diplocolenus abdominalis (Fab.)	1	Egg	Holcus spp.	+	–	–	Hill 1976
Doratura stylata (Boheman)	1	Egg	Agrostis tenuis, Festuca rubra		?		
Elymana sulphurella (Zetterstedt)	1	Egg	Holcus spp.	+	–	–	Hill 1976
Adarrus ocillaris (Fallen)	2	Egg	Holcus spp.	+	–	–	Hill 1976
Eucelis incisus (Kirschbaum)	2	Nymph	Festuca pratensis	+	+	–	Port 1978, **
E.lineolatus (Brulle)	2	Nymph	Festuca pratensis	+	+	–	**
Graphocraerus ventralis (Fall.)	1	Egg	?	–	–	+	**
Macrosteles laevis (Ribaut)	2	Egg	Agrostis tenuis	+	–	–	
M.sexnotatus (Fallen)	2	Egg	?	+	–	–	Port 1978

Table 1.1. continued.

Regularly breeding on Grass 1978-1980	No.annual generations	Hibernation stage	Common host on Acidic soil	* Mode of feeding P	X	V	Authority
(2) Cicadellidae							
Macustus grisescens (Zetterstedt)	2	Egg	Holcus spp.		?		
Mocydiopsis parvicauda (Ribaut)	1	Adult	?		?		
Psammotettix confinis (Dahlbom)	2	Egg	Agrostis tenuis	+	–	–	Solomon 1973
Recilia coronifera (Marshall)	1	Egg	Holcus spp.	+	–	–	Hill 1976
Streptanus sordidus (Zetterstedt)	2	Egg	Agrostis tenuis		?		
Zyginidia scutellaris (Herrich-Schaeffer)	numerous	Adult	Dactylis glomerata, Holcus spp.	–	–	+	Hill 1976 Port 1978
(3) Delphacidae							
Ribautodelphax angulosa (Ribaut)	2	Nymph			?		
Struebingianella dalei(Scott)	2	Nymph	Agrostis tenuis		?		
Dicranotropis hamata (Boheman)	1	Nymph	Holcus spp.	+	–	–	Hill 1976, **
Javesella pellucida (Fab.)	2	Nymph	?	+	+	–	Nuorteva 1962, **
Stenocranus minutus (Fab.)	1	Adult	Dactylis glomerata	+	–	–	**

16.

Key   P = Phloem; X = Xylem; V = Parenchyma.   ** = this study

ungrazed grassland. Waloff & Solomon (1973) compared the Auchenorrhyncha

fauna of acidic and calcareous grassland and formed the conclusion that

a different species assemblage generally occurred on each of the sampling

sites. Whittaker's (1969) most abundant species was Stenocranus

minutus which formed 48 and 43% of the total fauna in two consecutive

years. At Silwood this species invaded some sown plots and was by far

the most dominant species living on Dactylis glomerata (Section V).

Turrutus socialis (Flor.) formed 44 and 28% of Morris' (1971) total

collections, but is absent at Silwood (Waloff & Solomon 1973 , this study)

The life histories of the Auchenorrhyncha are interesting. In

general, the Cicadellidae overwinter in the egg stage and Delphacidae as

nymphs (Waloff & Solomon 1973). The two groups reach peak abundance

at different times so that 'waves of succession of abundance' are con-

structed (Waloff & Solomon 1973). The newly hatched larvae pass through

a series of five instars before the emergence of the adults which may be

macropterous or brachypterous (Waloff 1973). Two major groups of

parasites, the Dryinidae (Hymenoptera) and Pipunculidae (Diptera) are

known to parasitise nymphal leafhoppers. Waloff (1975) found that para-

sitism of Delphacidae by Dryinidae was greatest in the spring, as the

parasite involved, Dicondylus bicolor (Haliday) aestivates in the over-

wintering nymphs and emerges in the spring. In contrast, Hill (1976)

recorded very low levels of Dryinid parasites in Dicranotropis hamata

in spring. Waloff (1975) also found that cicadellid parasitism in the

spring generation was due primarily to Dryinidae, whilst the second

generation was parasitised mainly by Pipunculidae. Hill (1976) noted

that the Pipunculidae were largely responsible for parasitism in both

generations.

The major mortality factor of nymphs and adult Auchenorrhyncha can

be largely attributed to predation by Nabidae, Araneae, Acarina and

Opilïones (Rothschild 1966; Tay 1972; Solomon 1973; Becker 1975 and

Waloff 1980). Waloff (1980) has very recently reviewed these results

and concluded that spiders become the most important predator after

mid-July, 72.9% of the total spiders belonging to the Linyphiidae

family. The effect of this predation is density dependent and could

lead to population stability.

From life table analysis of the common species at Silwood, Waloff

& Thompson (1980) concluded that the key factor (Varley et al.' 1973)

was (k_o+k_1) i.e. the greatest population mortality could be due to

either low fecundity levels and/or high rates of egg mortality. In

five out of the six species chosen for detailed study, differences

between the average fecundity and egg mortality could not be distinguished.

In Adarrus ocellaris, however, egg mortality was considered the key

factor. Hill (1976) and Southwood & McNeill (1978) noted that the size

of second generation Dicranotropis hamata was dependent on the quality

of the food obtained by ovipositing females of the first generation.

In years when D.hamata adult emergence coincided with high nitrogen

levels in Holcus mollis, the second generation was large, whereas if

D.hamata emerged out of phase with high nitrogen levels in the grass,

the size of the second generation was small. Differences in ovipositional

behaviour between D.hamata (lays clutches of eggs in stems) and

A.ocellaris (lays eggs singly on a leaf blade) (Thompson 1977) may also

account for some of the observed variances between the species. It is

also probable that both regulatory mechanisms do exist. Egg parasites

namely Anagrus spp. (Mymaridae) have been shown to parasitise eggs

from a number of leafhopper species (Rothschild 1966; Tay 1972;

Moratorio 1977 and Waloff 1980), however the size and effect of the

field population is unknown. Obviously in the light of Waloff &

Thompson's (1980) study, further work is necessary to distinguish between

these two effects.

1.3 Grass phenology and Auchenorrhyncha feeding patterns

All Auchenorrhyncha are phytophagous, feeding on the cell contents and plant sap of a range of plants. Port (1978) recently tabulated known records of tissues probed by leafhoppers. In general the majority of species at Silwood are phloem feeders, some are exclusively xylem feeders, a few feed on both phloem and xylem, and a few feed on cell sap contents (Table 1.1).

Many grassland Auchenorrhyncha are oligophagous - there are relatively few examples of monophagy and polyphagy amongst them. Whitcomb et al. (1973) who surveyed the plant-host associations of grassland cicadellids in North America, concluded that species were confined to a single grass genus or tribe and suggested that the patterns of seasonal rhythmicity shown by both insect and plant may be responsible for maintaining specificity amongst the oligophagous species. At Silwood, Waloff & Solomon (1973) noted that with very few exceptions, leafhopper-host plant associations were not very strong, the commoner leafhoppers being found on a number of grass species. In contrast, studies on arboreal Typhlocybinae (Claridge & Reynolds 1972; Claridge et al. 1977; Claridge & Wilson 1978) show that quite strong host associations do exist.

The phenology of different grass species can be different (see Roy & Peacock 1972). Indeed it is this fact which often helps the farmer to decide which grass species to mix into his pasture. The NIAB Handbooks readily available to agriculturalists (Anon 1) list species of grass, their approximate growing season and approximate time of seeding. Varieties of the same species may set seed at intervals of up to one month difference. The spring nutrient flushing observed by Hill (1976) and McNeill & Southwood (1978) for H.mollis is an indication of the onset of new growth, known to

be determined by climate (temperature in U.K.) (Beddows 1968). It is interesting that H.mollis flowers approximately 3 weeks after Holcus lanatus, and everything being equal, the summer nutrient flush associated with seed filling should be temporally separated in the two Holcus species. Hill (1976) and McNeill & Southwood (1978) maintain that the seasonal rhythmicity of the nutrient flushes is a primary force in determining the leafhopper assemblage on H.mollis. I will return to this point in Sections III and V.

At Silwood the major grass species in the natural meadows is a Holcus sp./Agrostis tenuis (Sibth.)/Festuca rubra (L.)/Anthoxanthum odoratum (L.) complex. Although the varieties are unknown and the genetic pool is likely to be large so that flowering and seed setting may extend for periods greater than those recorded in NIAB Handbook 16 (Anon 1), flowering times are distinct between the major species. Anthoxanthum odoratum flowers as early as April in some years (Hubbard 1976); Agrostis tenuis June to August; Festuca rubra May to July; Holcus mollis June to August and H.lanatus May to August. It would seem probable that some of the leafhopper species would take advantage of the different grass phenologies and 'actively' search for those grasses with a higher food quality (c.f. Gibson 1976a) selection favouring the successful species who are then able to increase fecundity levels. I will return to this theme later in Section V.

The aims of this study are five fold. The following section is an examination of the influence of mineral fertilizers on the physical and chemical properties of a natural grassland. Section III is an attempt to determine what effects are then passed on to the leafhopper assemblage and to distinguish those that promote and/or depress population build up. Section IV examines more closely the effect of increased nitrogenous fertilizers on a selection of individual leafhopper species &

the ways that they cope with an increased food supply, and then

measures how their biology is geared to perform in relation to this.

In Section V, a re-examination of the host association data, and the

performance of an individual species when feeding on a number of

gramineae, is presented.

SECTION II

2.1. Introduction

It is impossible to alter the nutrient levels of the plant with artificial fertilizers without altering the physical, chemical and biological properties in the soil. In the temperate climates of the world, the quantity and quality of plant nutrients may be consequences of differences in storage, fluxes from other parts of the plant and the rate of turnover by soil microorganisms (Chapin et al. 1980). In the present study, we are concerned with the quality of the plant as food for herbivores and hence it is appropriate to start by examining the effects of fertilizers upon the plant itself and plant community.

Much is known about the uptake and role of mineral nutrients in the physiology of the plant. At an ecological level most routine nutrient trials attempt to quantify some or all of the following responses on the part of the plant:-

1. Growth in relation to a range of nutrient regimes.

2. Tolerance of deficiency or excess of nutrients.

3. Competitive effects of other species and individuals upon the mineral nutrition of the experimental plants.

Natural populations of plants are usually well adapted to the soils on which they grow (Bradshaw 1969) so that nutrient dificiencies are not always apparent. Individual plants may not show symptoms of toxicity or deficiency but may often respond to nutrient addition.

A vast literature exists on the results of experiments using culture techniques and small pots, the interpretation of which into field practice is very difficult. The major advantage of such studies is that factors other than soil nutrient status can be held relatively constant. A comprehensive account of culture solutions and related

techniques is given by Hewitt (1960).

2.2. Experimental design

The study was carried out at the Imperial College at Silwood Park,
Ascot, Berkshire. The study area was on Elm slope beside those studies
of Hill (1976) and Waloff and Thompson (1980).

The vegetation was a Holcus mollis/H.lanatus dominated natural
meadow, the other major grasses were Agrostis tenuis, Festuca rubra,
Anthoxanthum odoratum and scattered patches of Poa pratensis and
Dactylis glomerata. Dicotyledinous plants such as Rumex acetosa,
Urtica dioica, Stellaris media and Cirsium arvense were present at low
numbers (Appendix I).

The experimental area was divided into plots each $25m^2$ (5m x 5m)
except the N.P.K. "Growmore" + lime plot which was 10m x 10m and to each
of these areas was allocated one of the treatments listed in Table 2.1.
The treatments were allocated by random numbers and all were unreplicated.
In 1979 two further plots were added (5m x 5m) to increase the upper
range of nutrient treatments (Appendix II). A single application of
fertilizer was given each spring in 1978 and 1979.

Samples of H.lanatus were cut at ground level in the experimental
area at weekly intervals and placed into a freeze drier within 10 minutes.
After drying the samples were sorted into leaf, stem and flowers, ground
in a ball mill, and stored in airtight containers for chemical analysis.

Plant biomass was estimated for each of the trial plots by clipping
and removing all the above ground living material from one 10 x 10 cm.
quadrat (randomly positioned) at intervals of 10 days. This material
was weighed fresh and then dried at an oven temperature of 80° C for
24 hrs and reweighed to give a dry weight standing crop estimate.
It would have been desirable to take a greater number of samples
but the small size of the available plots meant that only minimal

Table 2.1 . Fertilizer treatments on experimental area.

Treatment	Applied as	Rate kg/ha
Control		
Nitrogen (N)	Ammonium nitrate	100, 300, 600
		900, 1200
Phosphorus (P)	Superphosphate	448
Potassium (K)	Potassium sulphate	560
N + P	Ammonium nitrate	300
	Superphosphate	560
N + K	Ammonium nitrate	300
	Potassium sulphate	560
N + P + K	Growmore 7:7:7	672
Lime	Calcium carbonate	1254
N + P + K Lime	Growmore 7:7:7	672
	Calcium carbonate	1254

sampling of the vegetation could take place without excessive des-
truction of the vegetation as a habitat for the insects.

Pasture height was determined every 10 days by measuring the
height of the vegetation against a graduated 1m ruler at five random
areas in each plot.

The plant species present were recorded in June of 1978 and 1979,
but the methods of detection differed in both years.   In 1978 $1m^2$
quadrat, dissected with string every 10cm, was placed randomly at 2
sites in each plot.   The plant species that touched a steel pin stuck
into the ground where the string intersected were recorded.   In addition,
some plant species occurred at very low density and the abundance of
these were estimated visually.   In 1979, a visual method was used to
determine the plant species present.   This entailed noting the plant
species present and their approximate abundance in a randomly placed
$0.5m^2$ quadrat at four sites on each plot.   All identifications were
from Hubbard (1976) and Sikula (1978).

Peak flowering times of the major grass species were estimated
every 10 days by counting the number of flower heads in three $0.25m^2$
randomly positioned quadrats.

2.3   Chemical analysis of grass

Nitrogen was chosen as an indicator of insect food quality because
of its fundamental importance to herbivores (Section III) and its ease of
measurement in plant material.   Leaf total and soluble nitrogen content
was used as the measure of food quality for chewing and cell sap feeding
insects.   Differences in stem soluble nitrogen levels gave an indication
of nutrient transport through the phloem, as the stem consists largely
of structural tissues with a low level of soluble nitrogen.

In 1979, estimates were also made of leaf total phosphorus and
potassium, and leaf soluble amino acid levels.   Amino acid analyses
were carried out on material taken at nine sampling occasions in

conjunction with material collected for soluble nitrogen.

All chemical analyses used standard techniques (Chapman 1976) and are given in Appendix III.

RESULTS

2.4.1 Grass phenology

A list of the plant species occurring on the individual plots in 1978 and 1979 is given in Appendix I. In general, five grasses form the bulk of the biomass present. These, together with relative abundance and the approximate flowering times (in 1979) are listed in Table 2.2. The relative abundance of the five most dominant grass species when measured for the experimental area showed quite large differences between the 2 sampling years. A.tenuis and H.mollis increased in abundance relative to A.odoratum and H.lanatus. F.rubra remained at a similar level in both years. The differences in abundance could be a result of fertilizer addition altering the competitiveness of the major grasses. An alternative explanation is that the differences in abundance are due to the different samp-ling methods used. Unfortunately, with only 2 years field data it is impossible to favour one explanation.

Each species flowered over a 3-4 week period but at different times during the summer. The dates of maximum flowering (when 50% flowers had emerged) spread from mid-June for A.odoratum to mid-July for H.mollis. The spread of flowering may be important to grassland insects which are capable of feeding and utilizing the increased level of food quality during the seed filling stage which takes place approximately 3 weeks after flowering.

2.4.2 Biomass

In general biomass increased with an increased rate of N fert-ilizer (Fig.2.1). No detectable difference between the biomass

Table 2.2   Percentage abundance, flowering times, and time of

peak flower emergence of the 5 most common grass

species on the experimental area.

Species	% abundance		Flowering duration	Peak flowering
	1978	1979		
Anthoxanthum odoratum	13	6	31/5 – 21/6	8 – 14/6
Agrostis tenuis	28	36	21/6 – 13/7	28/6
Festuca rubra	5	5	21/6 – 13/7	28/6
Holcus lanatus	22	12	28/6 – 2/8	6/7
Holcus mollis	25	36	6/7 – 20/7	13/7

Fig.2.1. The influence of nitrogenous fertilizer on the mean plant

biomass. ●—● 0 KgN/ha, ▲—▲ 600 KgN/ha, O—O 1050 KgN/ha.
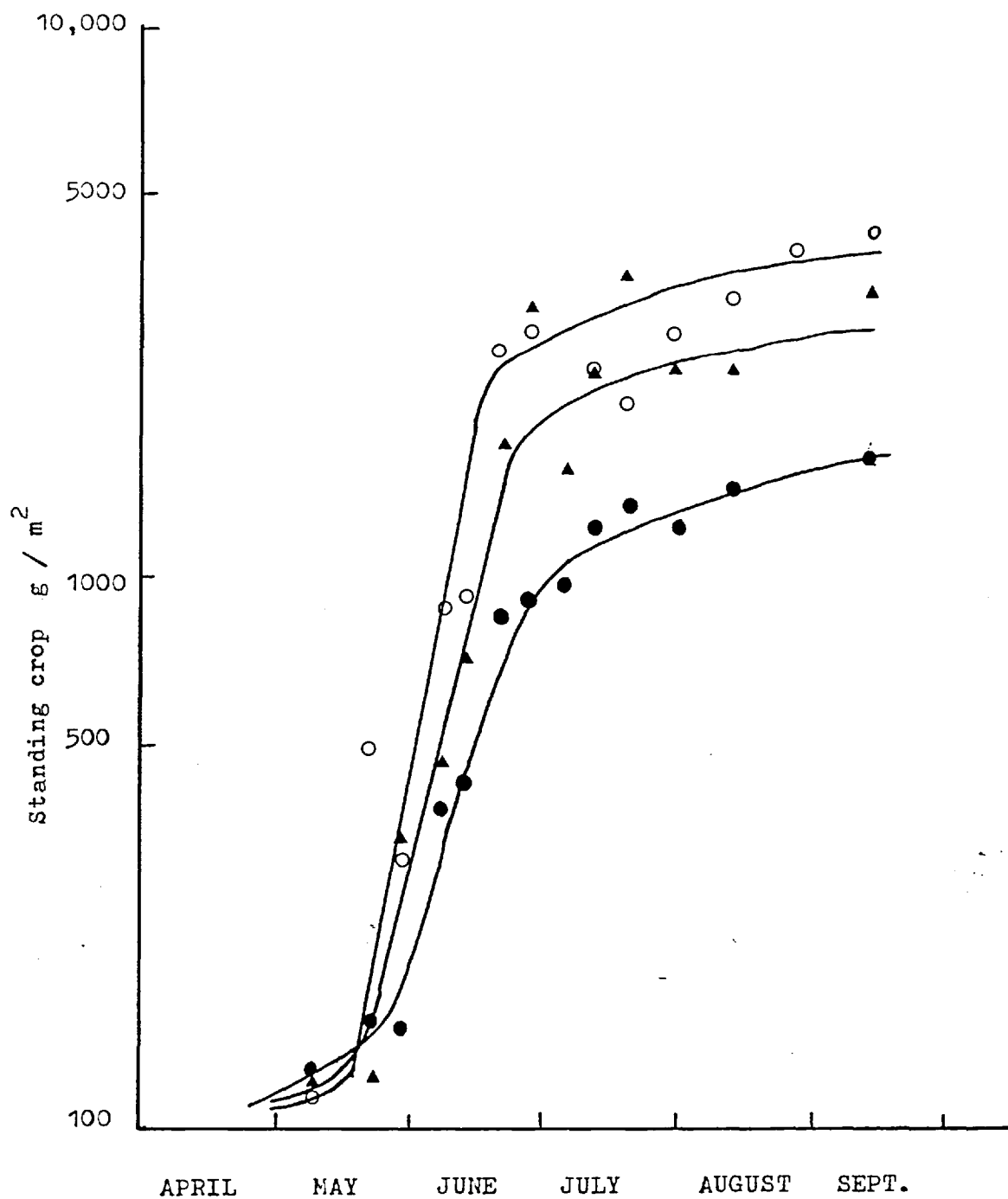
estimates was apparent between plots receiving 900 and 1200 KgN/ha

(Appendix IV) so these have been meaned in Fig.2.1. The growing

period, measured as the asymptote of the peaks, does not appear to

differ for plots receiving different rates of N fertilizer so that

increases in biomass are due to a faster growth rate over a set period.

The shape of the curve is characterised by a rapid increase in late

May to mid-June and then a longer period when rapid growth slows down

and appears to stop.

2.4.3 Pasture height

Figure 2.2 shows the pasture height (cm above ground) during the

growing season in 1979. There were no significant differences in the

average height between fertilized and unfertilized plots (Appendix V).

2.4.4 Nitrogen levels

The seasonal pattern of the leaf total nitrogen levels (Fig.2.3)

in 1978 and 1979 is similar to that of H.mollis described by Hill

(1976) and McNeill & Southwood (1979) (Appendix VI). A rapid decrease

in spring is followed by a summer low and a rapid increase at the time

of the autumn flush.

The effects of mineral fertilization are very clear. As the rate

of N applied to the soil in spring increases so does the leaf total

nitrogen levels in a linear fashion (Fig.2.4). The mean leaf total

nitrogen level for the 4 summer months (July to September) was sig-

nificantly higher in 1979 than 1978 only on the plot not fertilized

(1978 mean 16.37 mg N/gm dry weight; 1979 mean 23.36 mg N/gm dry weight;

$P < 0.01$). The effect of the fertilizer was to reduce the interyear

variability of leaf total nitrogen levels by raising the nitrogen levels

to a higher level, dependant on the quantity of N fertilizer added.

This is interesting as it suggests that the quantity of N available

each year is dependant on the turnover rate during the late autumn,

Fig.2.2. Mean pasture height on experimental area in 1979.
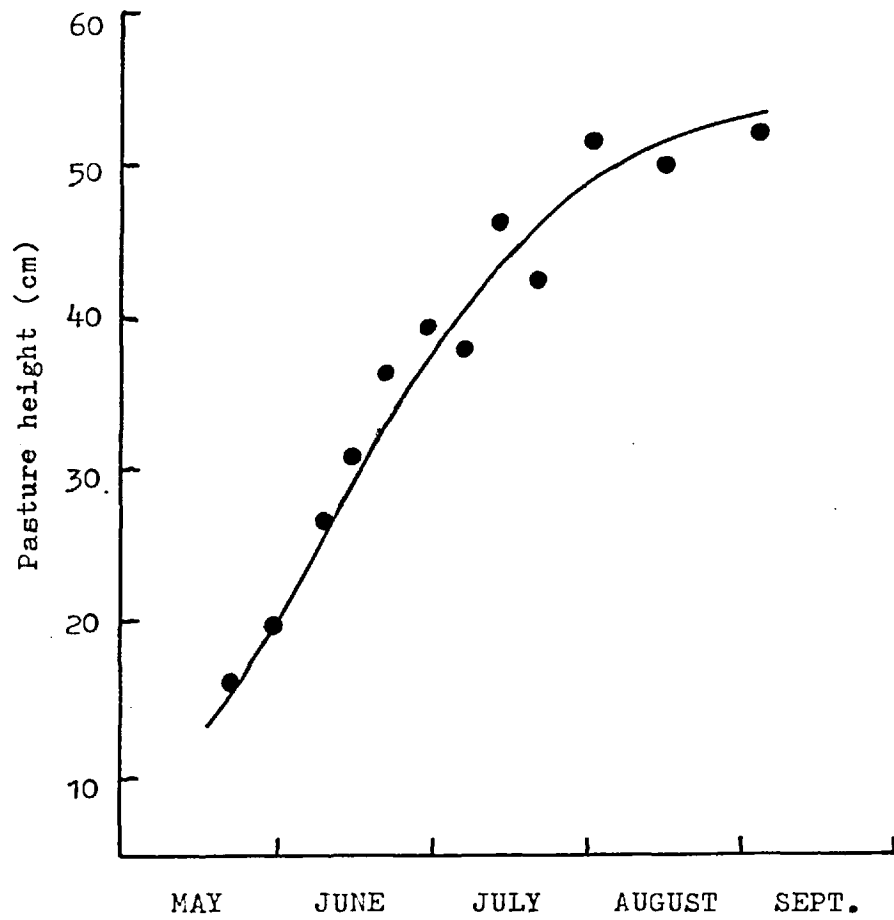
Fig.2.3. Mean leaf total nitrogen, O---O 1978,

●——● 1979, in <u>Holcus</u> <u>lanatus</u> on

experimental area (mg N/gm dry weight).
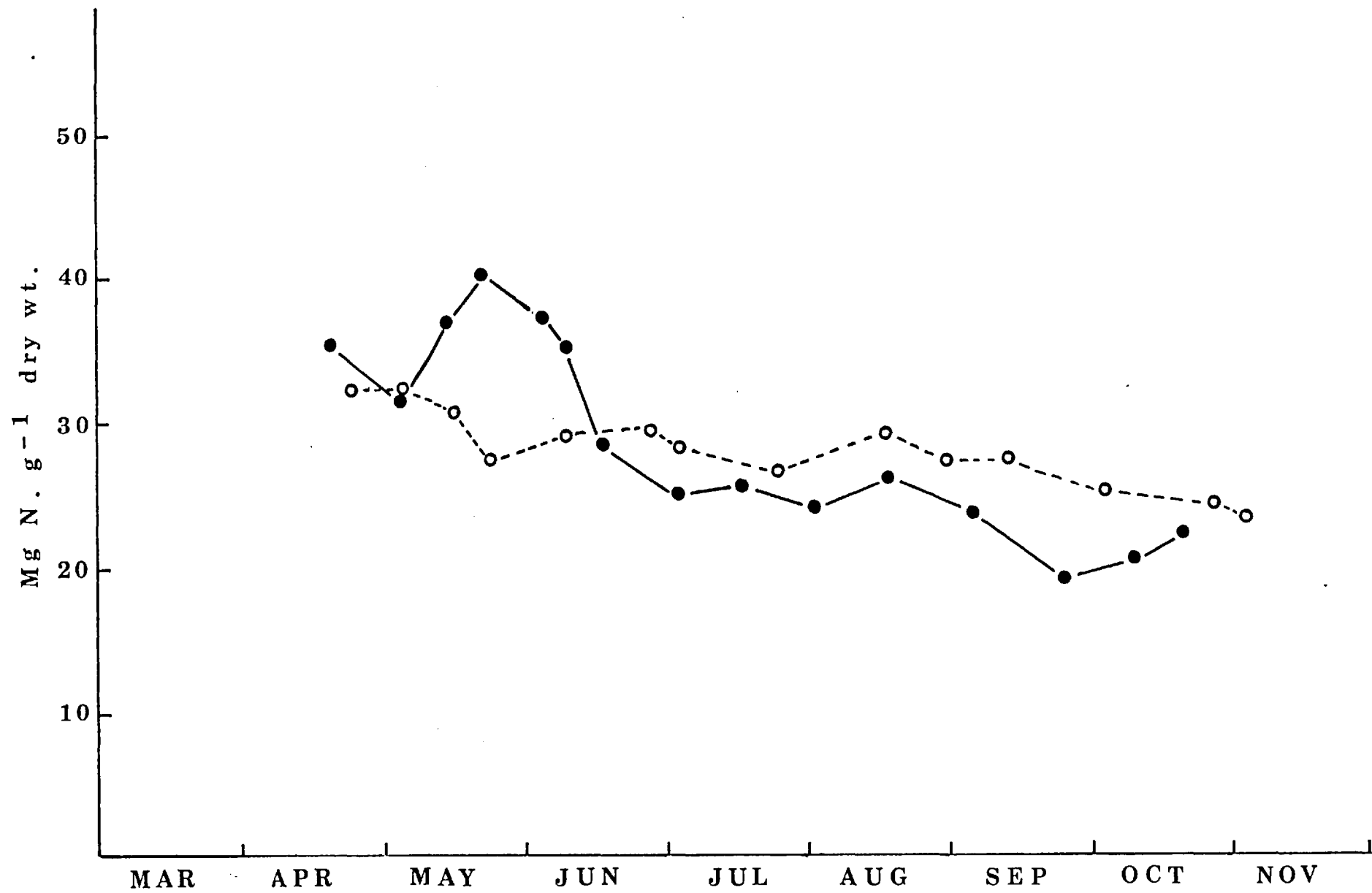
Fig.2.4. The influence of nitrogen fertilizer

on the mean total nitrogen levels in

Holcus lanatus .

O —— O   1978   Y = 0.02X + 21.42

● —— ●   1979   Y = 0.01X + 25.34

p < 0.001

Fig.2.5 The influence of nitrogen in combination

with other nutrients on the leaf total

nitrogen levels in Holcus lanatus .

Like symbols denote not significantly

different at p = 0.01.

Leaf total nitrogen mg N/gm dry weight

Leaf total nitrogen mg N/gm dry weight

Treatment

Nitrogen Kg N/ha

34.
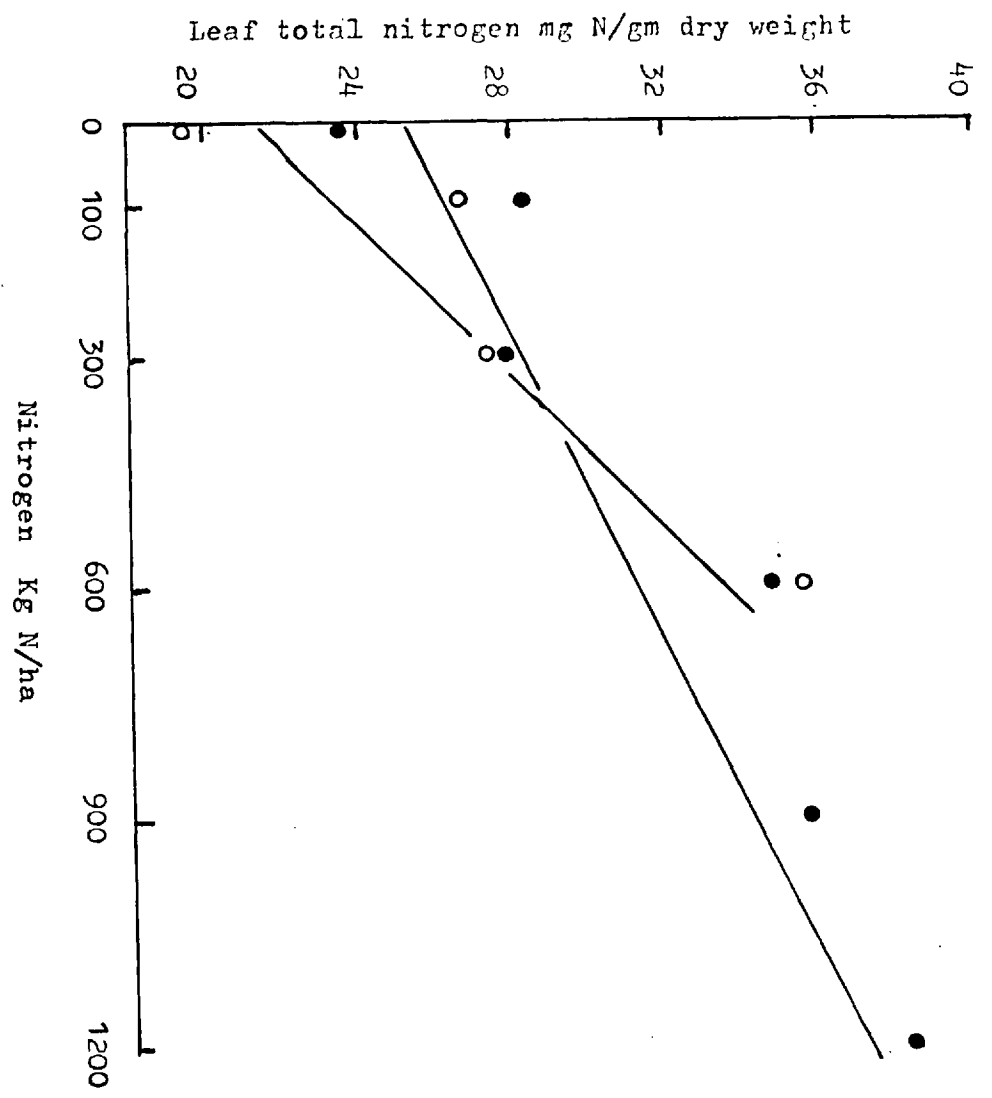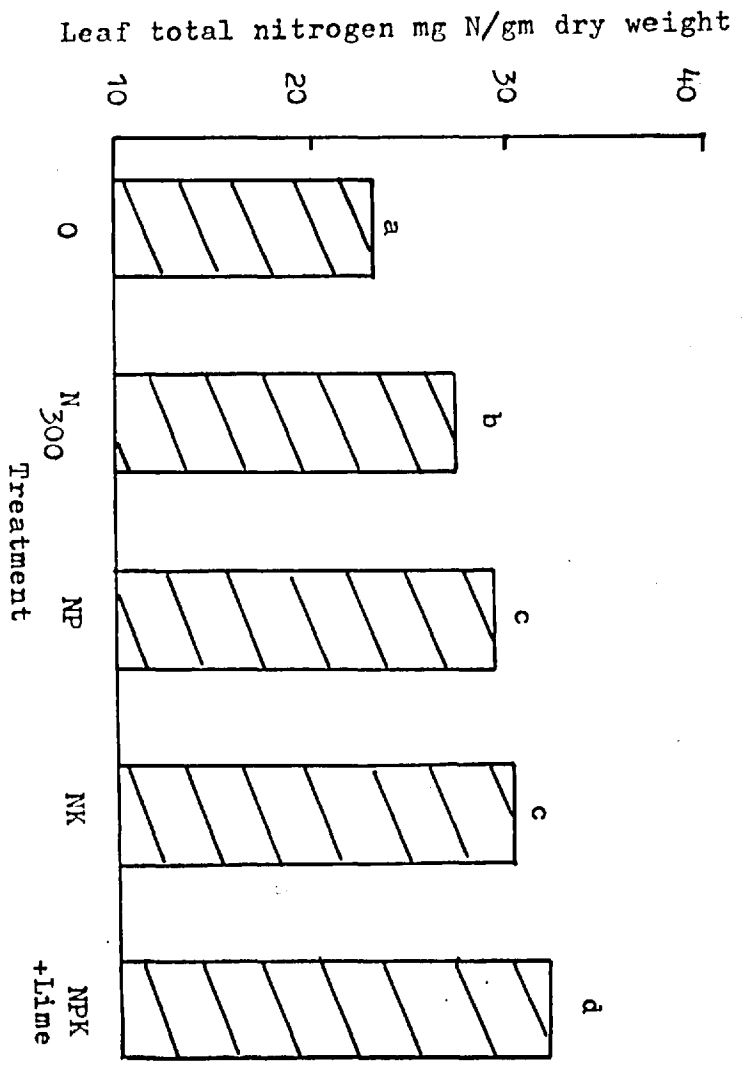
winter and early spring in the previous year. Probably all the N

available in the Silwood grassland ecosystem is that tied up in the

organic layer above the sandy soil (Bagshot Sands). Any nitrogen

(or nutrients in general) that escapes from the organic layer would

very quickly be leached from the soil and therefore not available

for the following year's growth. The effects of N fertilizers is to

replenish the N 'pool' available to growing herbage.

The effects of other nutrients in combination with N or alone on

the levels of leaf nitrogen are not so clear (Fig.2.5). The influence

of P and K, and PK are to significantly increase the level of leaf

total nitrogen. No significant differences were found between the

leaf nitrogen levels from control plots and plots treated with lime;

nor between the levels measured for material treated with NP and NK

fertilizer. A highly significant difference existed between the

levels of leaf nitrogen from plots treated with NP, NK, NPK and NPK+

lime, and the plot treated with the same rate of N. This is interest-

ing as the other nutrients in combination with N are having a syner-

gistic effect on the leaf N levels.

Leaf soluble nitrogen levels (Appendix VI; Fig.2.6) also followed

the characteristic pattern as described by Hill (1976) and McNeill &

Southwood (1978) for stem soluble nitrogen. An increase in spring

is due to metabolites being translocated to areas of new growth where

they are incorporated into leaf proteins. In the autumn (end of

August) there is also a gradual increase in leaf soluble nitrogen

levels associated with proteolysis in the old material prior to trans-

location to the roots and developing tillers.

The effects of N fertilizers on leaf soluble nitrogen levels are

shown in Fig.2.7. There is a highly significant relationship between

the amount of nitrogen applied and the leaf soluble nitrogen level.

Fig.2.6. Mean leaf soluble nitrogen levels

(O --- O 1978, ● —— ● 1979) in

Holcus lanatus on experimental area

(mg N/gm dry weight).
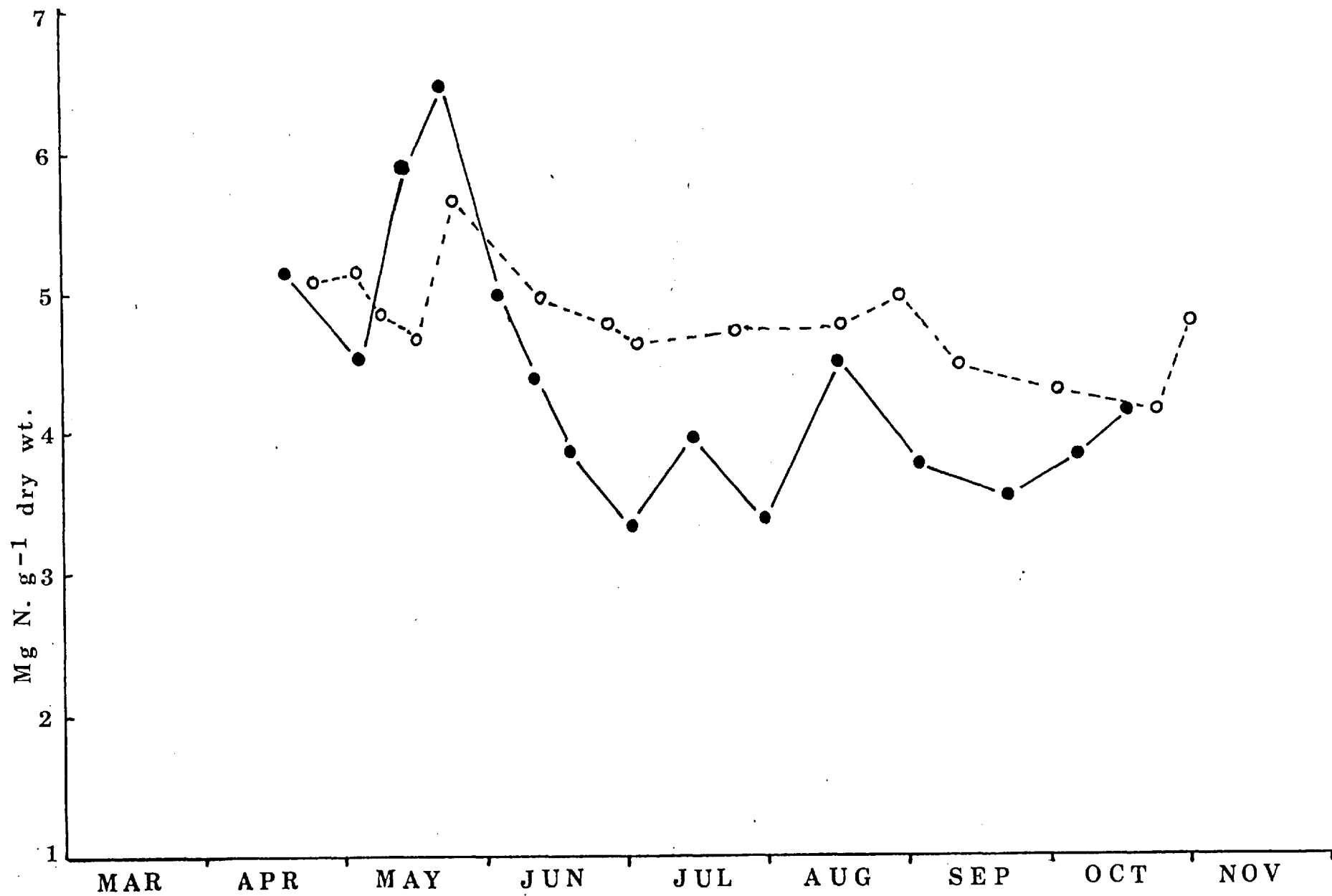
Fig.2.7. The influence of nitrogen fertilizer

on the leaf soluble nitrogen levels in

Holcus lanatus.

O ---- O 1978

● —— ● 1979

Y = 0.003X + 3.198. p<0.001   1978

Y = 0.004X + 3.037. p<0.001   1979

Fig.2.8. The influence of nitrogen in combination

with other nutrients on the leaf soluble

nitrogen levels.   Like symbols denote not

significantly different at p = 0.01.
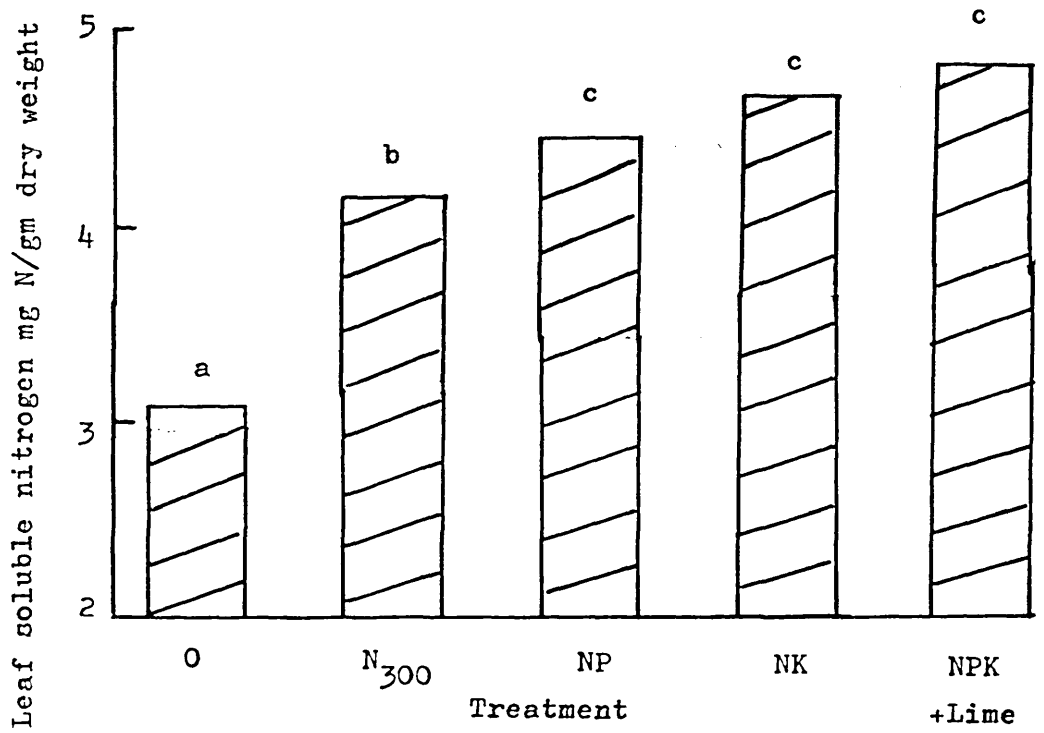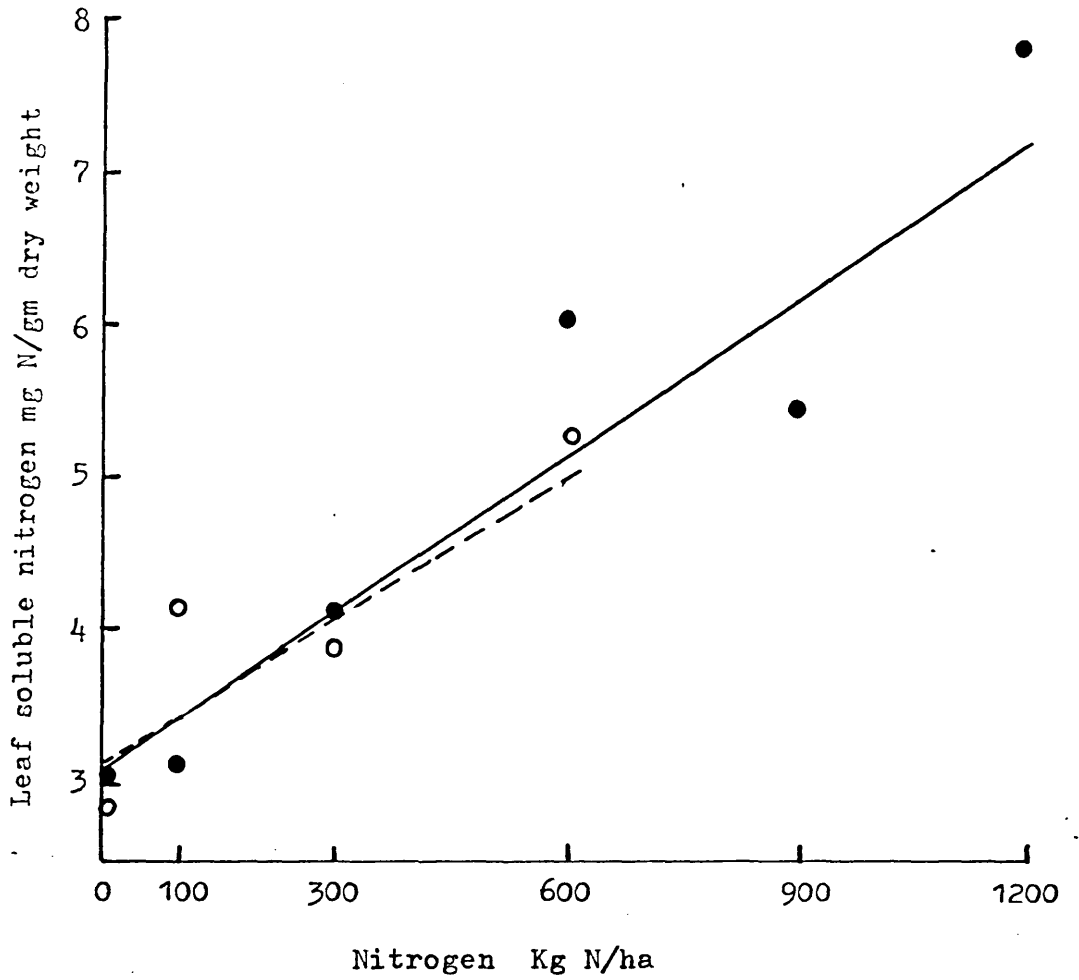
Inter-year differences, i.e. the differences between the slope of the curves for 1978 and 1979 are not significant. The addition of fertilizer saturates the plants environment to the extent that interyear variations become minimal in relation to the amount of N fertilizer added. The effect is to maintain a constantly higher level of leaf nitrogen than if fertilizer were not added.

The effects of the other nutrients either solely or in combination with N upon the leaf soluble nitrogen levels are very clear (Fig.2.8). No significant differences exist between the leaf soluble nitrogen levels on the untreated plots and these plots given the following treatments:- PK, P, K and lime. The soluble nitrogen levels on plots given NP fertilizer did not significantly differ from those on plots given NK fertilizer. Leaf soluble nitrogen levels from plots that had N at 300 Kg/ha do not differ significantly from plots with NP and NK fertilizer. Further, leaf soluble nitrogen levels from plots NPK, NPK + lime and N_{300} were not statistically different. These results indicate that the leaf soluble nitrogen levels are governed solely by the N given to the plant and that no synergistic influences of the other major elements could be detected.

Stem soluble nitrogen levels (Appendix VI, Fig.2.9) are also greatly influenced by the quantity of N added to the soil (Fig.2.9(b)). A significant positive relationship exists between quantity of N added to soil and the stem soluble nitrogen levels in the plant. It may be possible that a plateau is reached after 600 kg N/ha. Most stem material is non photosynthetic and its function is to hold the leaves and inflorescence erect so that most of the soluble nitrogen within the stem is in a transit stage, the quantity represents the phloem flow.

The effects of the other major nutrients influencing stem soluble nitrogen levels are interesting (Fig.2.10). Treatments P, K, PK do

Fig.2.9. Mean stem soluble nitrogen levels

(O---O 1978, ● —— ● 1979) in

Holcus lanatus on experimental area
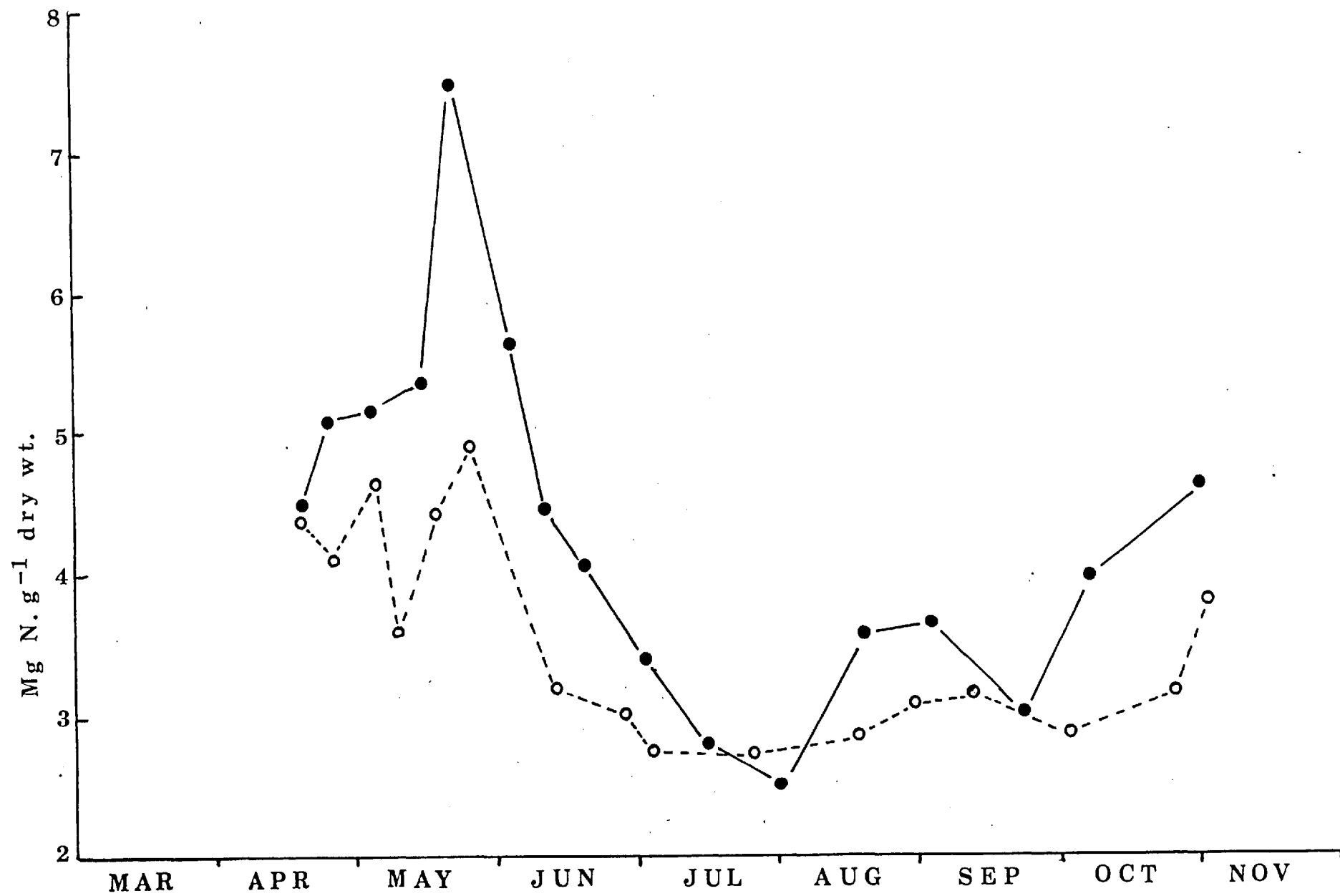
(mg N/gm dry weight).

Fig.2.9b. The influence of nitrogen fertilizer

on stem soluble nitrogen levels in

Holcus lanatus (mg N/gm dry weight)

0 --- 0 1978

● —— ● 1979

$Y = 0.002X + 3.544.$ $p<0.05$ 1979

$Y = 0.008X + 2.510.$ $p<0.001$ 1978

Fig.2.10. The influence of nitrogen in combination

with other nutrients on the stem soluble

nitrogen levels.   Like symbols denote not

significantly different at $p = 0.01$.

Stem soluble nitrogen mg N/gm dry weight
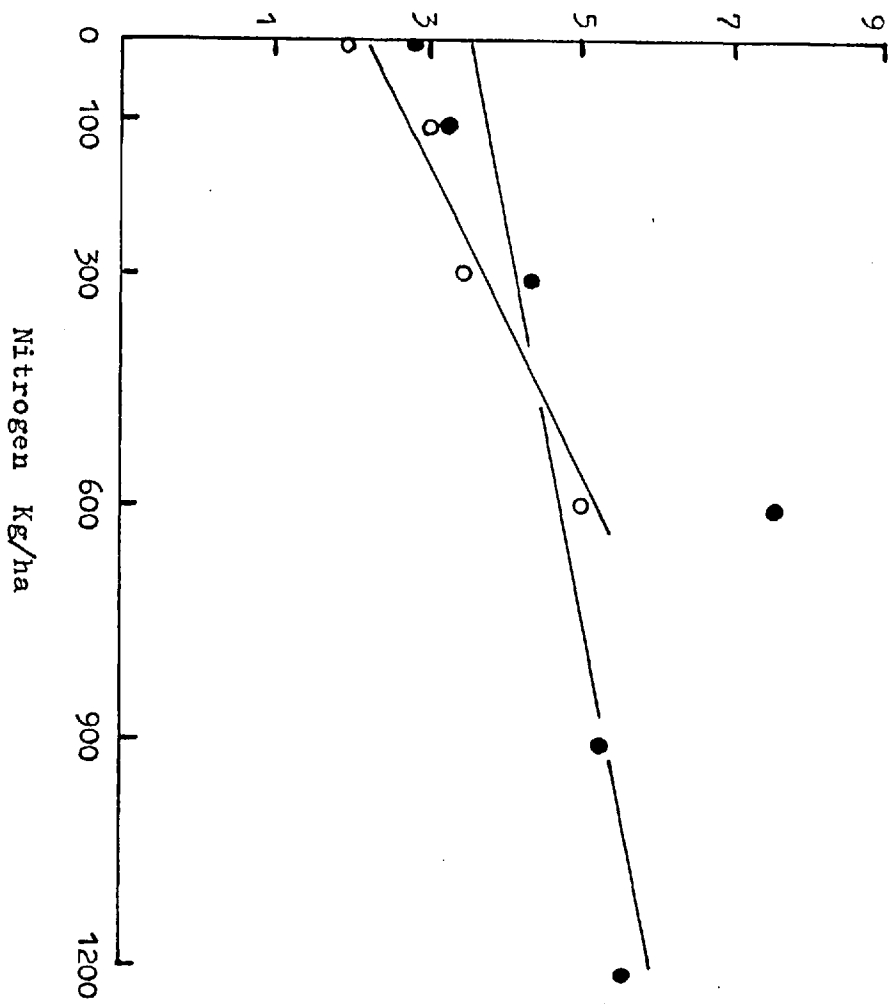
Treatment

Stem soluble nitrogen mg N/gm dry weight

Nitrogen Kg/ha

44.
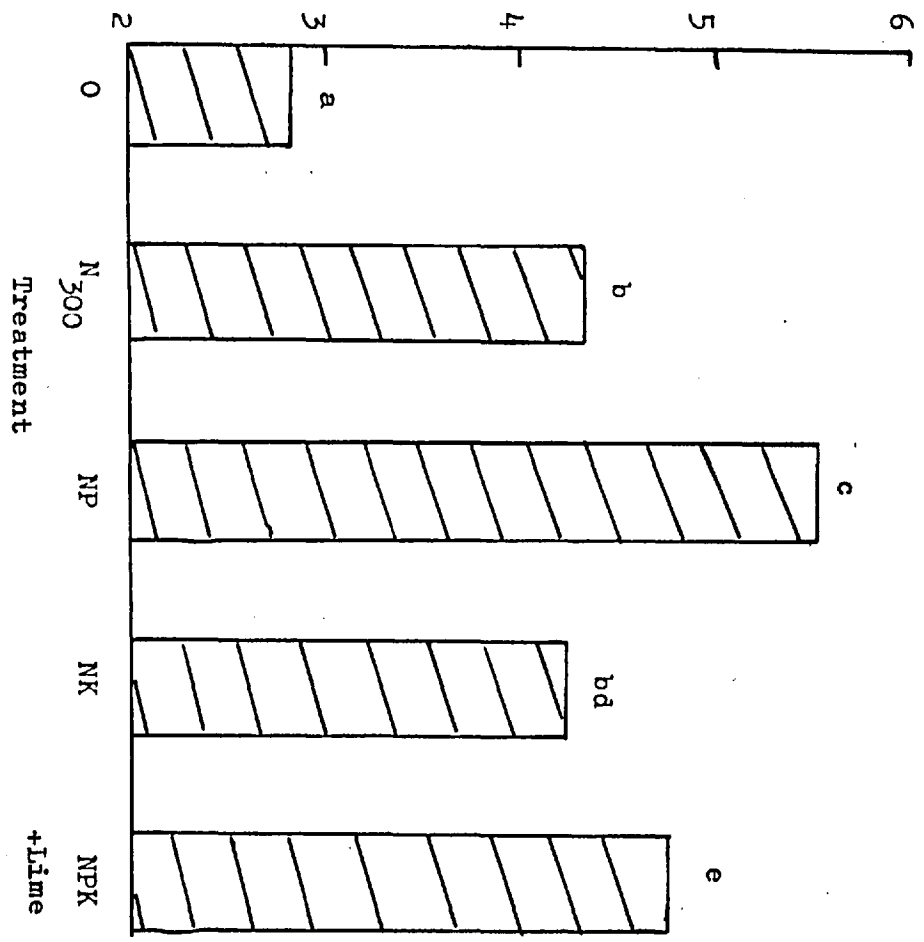
not differ significantly from control treatment. A significant difference exists between the treatments NP and NK and also between lime treatment and control. Fig.(2.11) shows the relationship between N applied to the soil and the duration of the flow of nitrogen to the leaves. Although the data are not good because of the size of the intervals between successive sampling dates, a positive relationship exists. That is, as the quantity of N fertilizer added to the soil increases so does the duration of the spring nitrogen flow. Fig.(2.12) depicts the positive relationship between the amount of N fertilizer added to the soil and the peak concentration of stem soluble nitrogen in the spring flush.

The levels of the other macronutrients also follow a similar seasonal pattern to that of nitrogen (Appendices VII and VIII). Two large peaks are associated with the spring and autumn growth periods respectively. The overall levels of leaf potassium and phosphorus $(\bar{x}$ K=1.94% dry weight, $\bar{x}$ P=0.23% dry weight) are typical of the levels found in many plants (e.g. Chapman 1976).

2.4.5 Potassium levels

In general, the level of potassium in the leaf blade is dependent on the quantity of nutrient added to the soil. K applied to the soil increased the potassium levels in the leaf (Fig.2.13). The levels of leaf potassium in other treatments all vary significantly from the levels in the control plots except those for treatment lime and for treatment NP. N_{300} has leaf potassium levels below that of the control plot suggesting that the levels have been depressed. The levels of leaf potassium in PK treatment do not differ significantly from the effect of K alone, all other treatments with potassium differ significantly from each other.

Fig.2.11   The influence of nitrogen fertilizer on

the duration of the nitrogen flow to the

leaves in Holcus lanatus.

0 --- 0   1979

● —— ●   1978

Y = 0.032X + 30.714.   p<0.001   1979

Y = 0.009X + 29.350.   p<0.001   1978

Fig.2.12   The influence of nitrogen fertilizer on

the peak stem nitrogen levels in Holcus

lanatus.

0 --- 0   1978

● —— ●   1979

Y = 0.006X + 4.022.   p<0.001   1979

Y = 0.006X + 6.625.   p<0.001   1978

47.
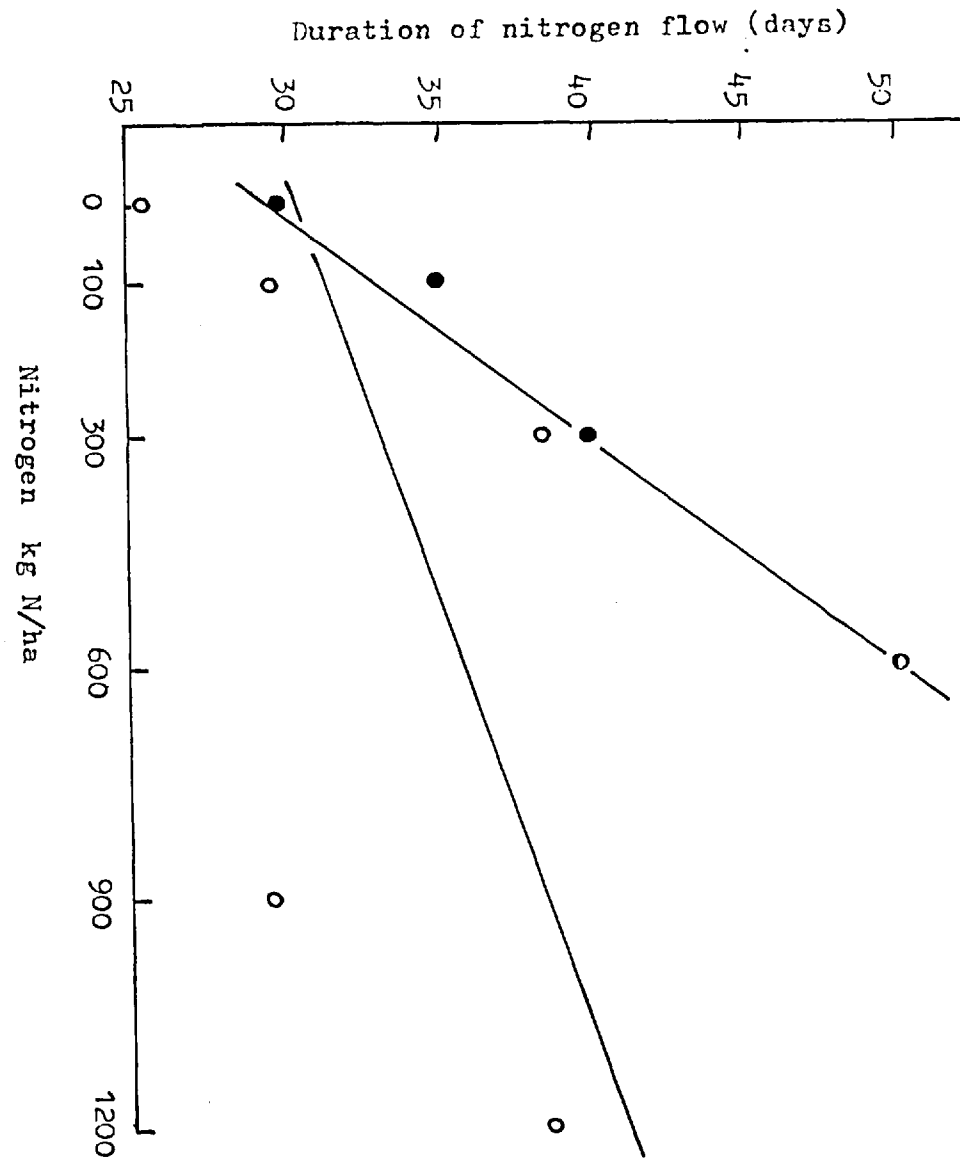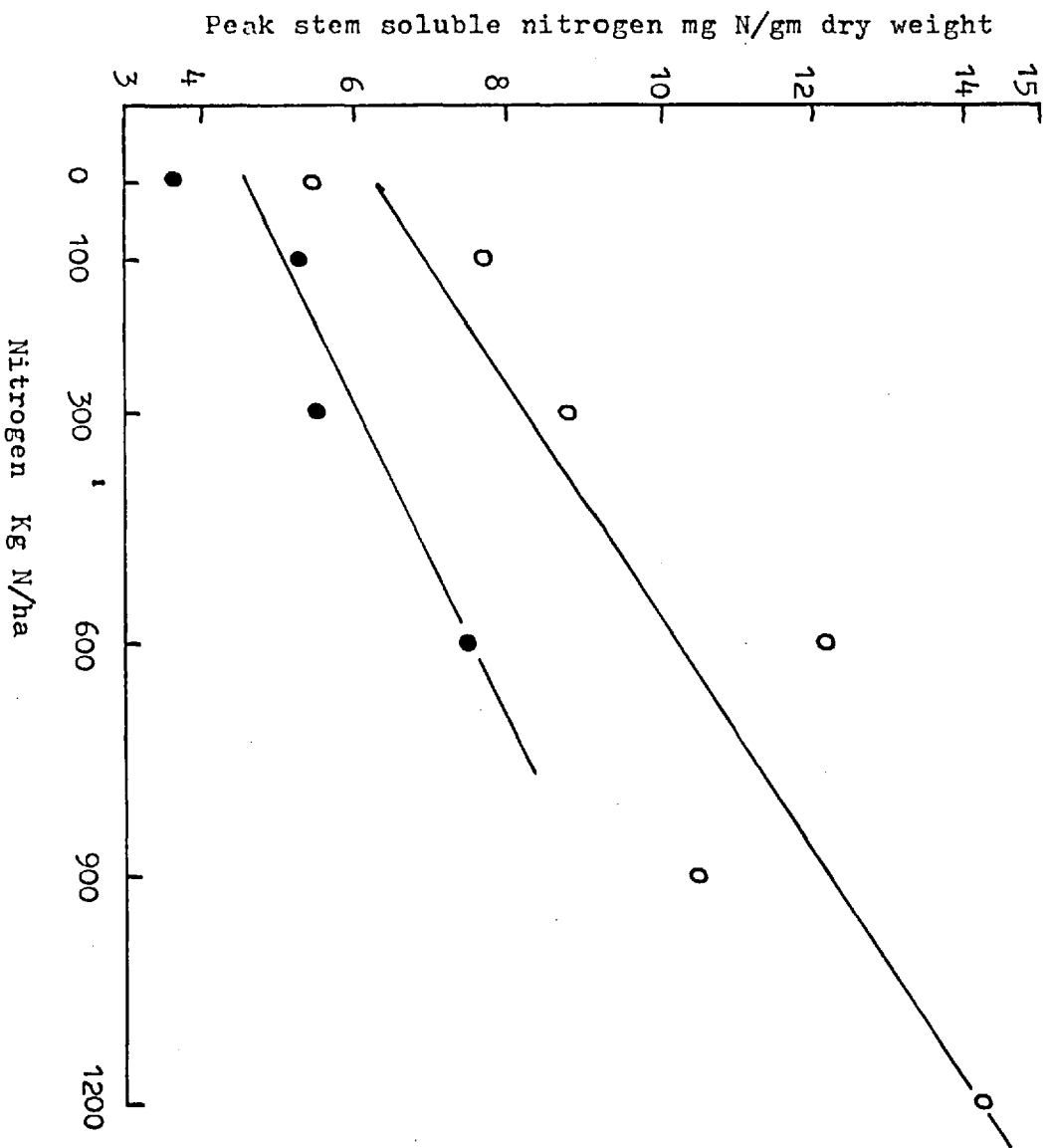
2.4.6 Phosphorus levels

Leaf phosphorus levels are also dependent on the quantity of P

added to the soil (Fig.2.14).   Leaf phosphorus levels from plots

receiving P treatments were significantly higher than the leaf phos-

phorus levels from plots not receiving P.   There were no differences

between the phosphorus levels in the leaves of grass taken from N

treated plots although in some cases (for example N_{1200} and N_{900})

the leaf phosphorus levels did differ significantly from the control

plots.

2.4.7 Amino acids

Fig.2.15 shows the seasonal pattern of leaf soluble amino acids.

Levels are highest in the spring and autumn during the major growth

periods.   It is very probable that a further small peak associated

with mobilization of protein into the developing seeds occurs in the

summer (Broodbank 1980).

Most of the soluble N fraction in the leaf can be attributed to

amino acid levels.   A highly significant relationship between soluble

N levels and soluble amino acid levels in the leaf exists (Fig.2.16).

The other soluble nitrogenous components are likely to be soluble

proteins, constituents unidentified with the amino acid analyser

(Beevers 1976).

The levels of individual amino acids in the leaf generally followed

the levels of total amino acids, i.e. an increase in the spring and

autumn growth period (Appendix IX).   Amide (Asparagine and glutamine

not separated in the analyses), threonine, alanine and γ-aminobutyric

acid together formed over 80% of the total content.   Valine, methionine

leucine, isoleucine, tyrosine, histidine, β-phenylalanine, arginine

and lysine together usually formed less than 10% of the total amount.

These can generally be described as the protein amino acids, being used

Fig.2.13. The influence of potassium in combination on the mean
leaf potassium levels in 1979. Like symbols denote
not significantly different at p = 0.01.
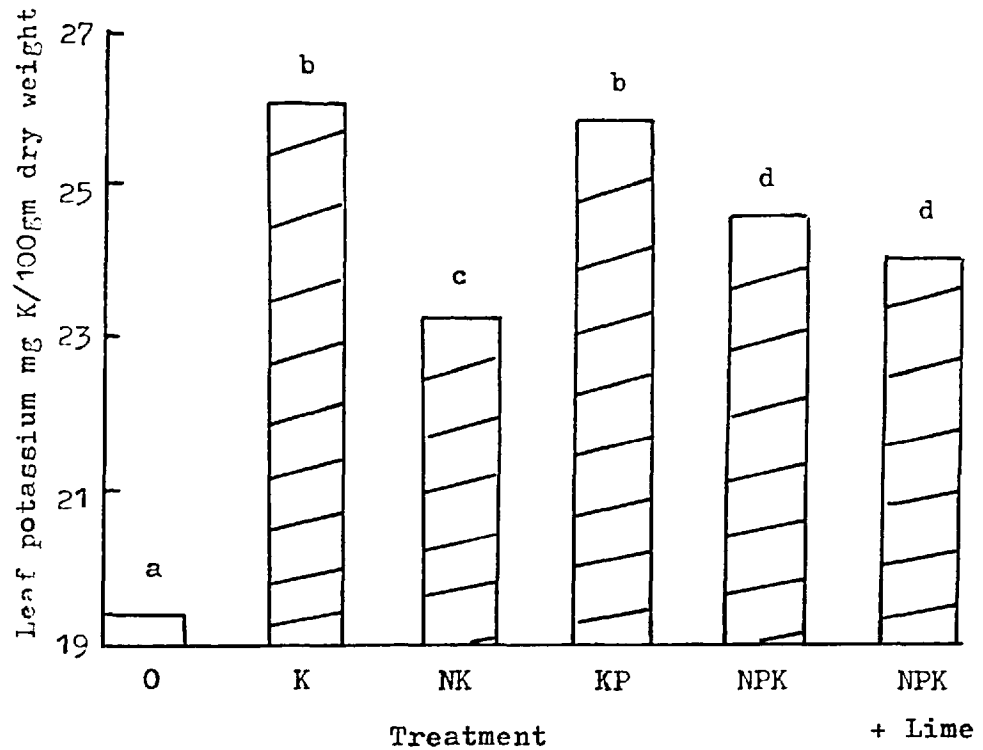
Fig.2.14. The influence of phosphorus in combination on the mean
leaf phosphorus levels in 1979. Like symbols denote not
significantly different at p = 0.01.
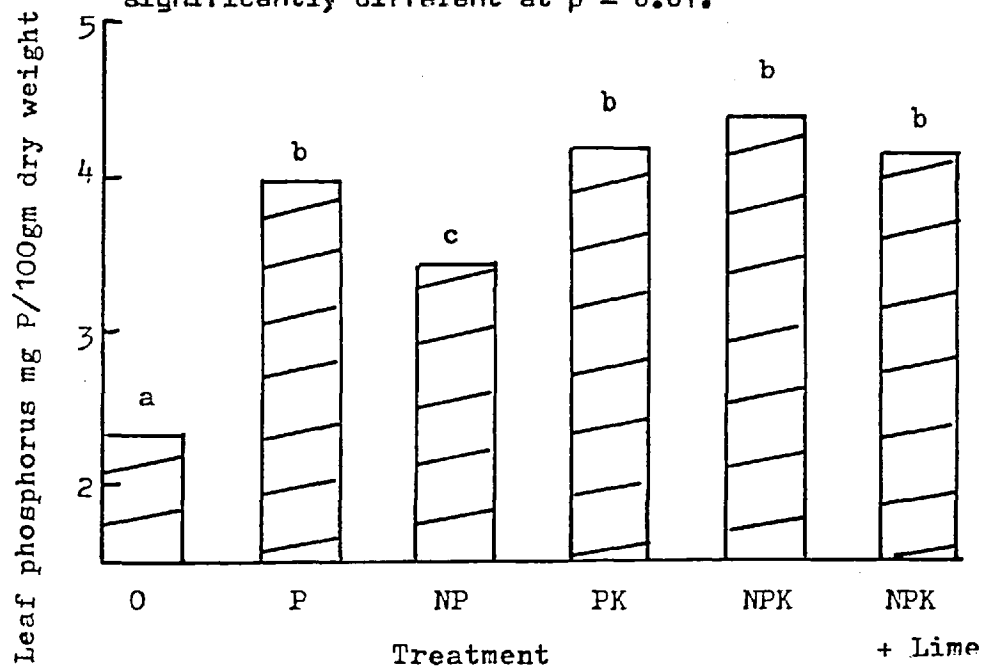
Fig.2.15 The mean seasonal leaf soluble amino

acid levels in Holcus lanatus on

experimental area in 1979.

Fig.2.16 The relationship between leaf soluble

nitrogen levels and leaf soluble amino

acid levels in Holcus lanatus in 1979.

$Y = -1.71 + 1.79X$, $r^2 = 70.3$, $p < 0.001$,

$n = 126$.
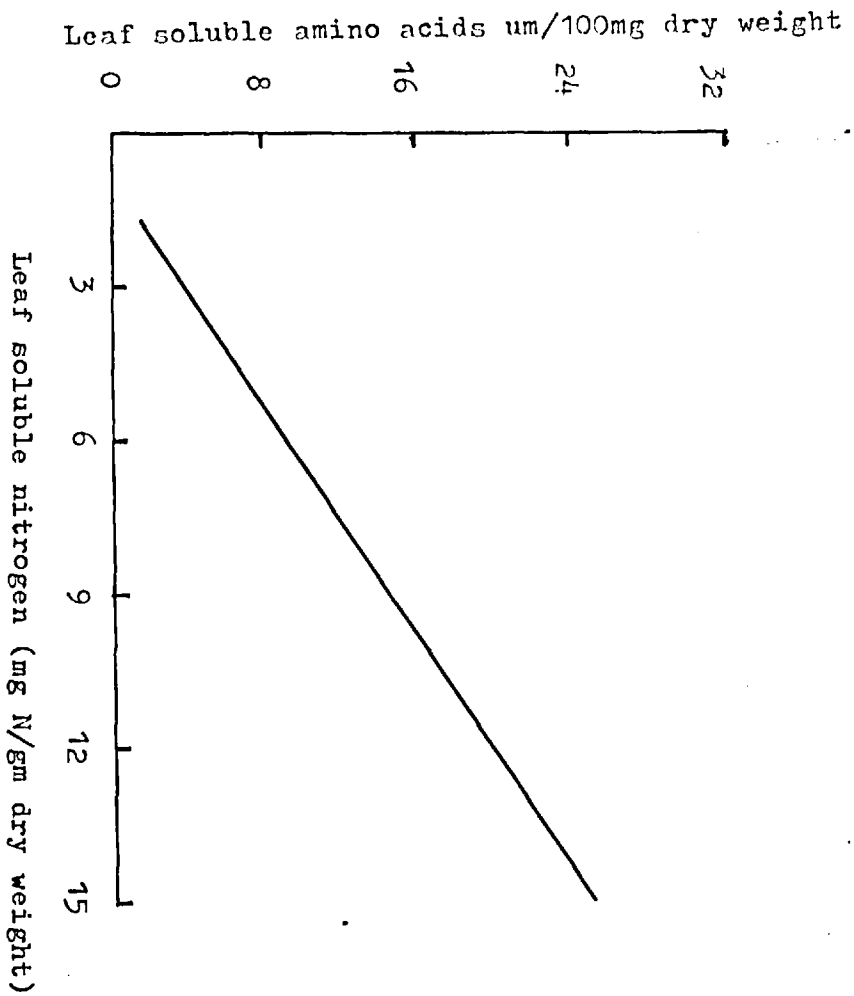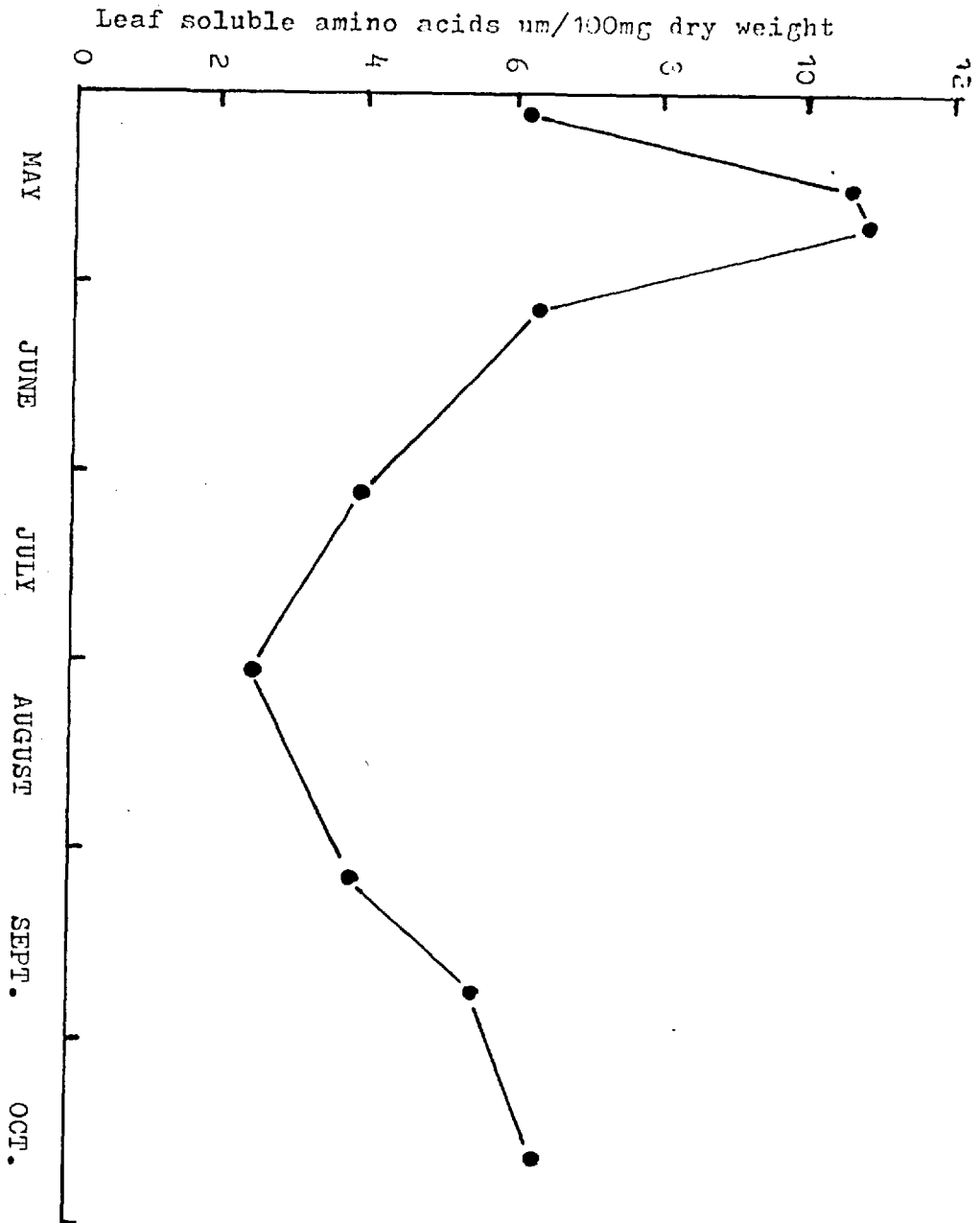
and replenished as required by the leaf cells. L Dopa (3-4 Dihydroxy-phenyl-L-alanine) levels were quite variable but generally they were highest in the spring and then decreased to extremely low, almost undectable levels during the summer. In the autumn the levels of L Dopa again increased. L Dopa has been found in large concentrations in seeds and is thought to be a defence against seed predators (e.g. Janzen 1973; Rehr et al. 1973).

The proportional levels of individual amino acids followed two patterns of seasonal distribution represented by Aspartic acid (Fig.2.17(a)) and γ aminobutyric acid (Fig.2.17(b)). The shape of the graphs can be most easily described as consisting of two peaks associated with the spring and autumn growth periods but with differences in the summer levels. The amino acids that followed the pattern of aspartic acid (Table 2.3, Group I) have sharp,well defined spring and autumn peaks with levels rapidly decreasing and then increasing from a summer low. By contrast, the amino acids that follow the pattern of γ aminobutyric acid (Table 2.3, Group II) have equally sharp spring and autumn peaks but the summer levels remain relatively high. Group I (and histidine from Group II) is essentially the protein amino acids, equivalent to Groups I and III in Table 2.4.

Fig.2.18 shows the relationship between total leaf soluble amino acids (summed over 9 consecutive sampling dates) and N fertilizer. The levels of total leaf soluble amino acids increase with increasing amounts of N fertilizer.

Although N treatment had the effect of boosting the levels of all the individual amino acids (Appendix IX) some were clearly boosted more than others (Table 2.4). Those in Group I were increased by N fertilizer; Group II amino acids remained proportionally unchanged; and Group III amino acids decreased proportionally with N fertilizer. In Group III, Leucine and β phenyl-alanine were significantly decreased

2.17 Patterns of leaf soluble amino acids in

Holcus lanatus

(a) Amide

(b) γ Aminobutyric acid

(a)

(b)
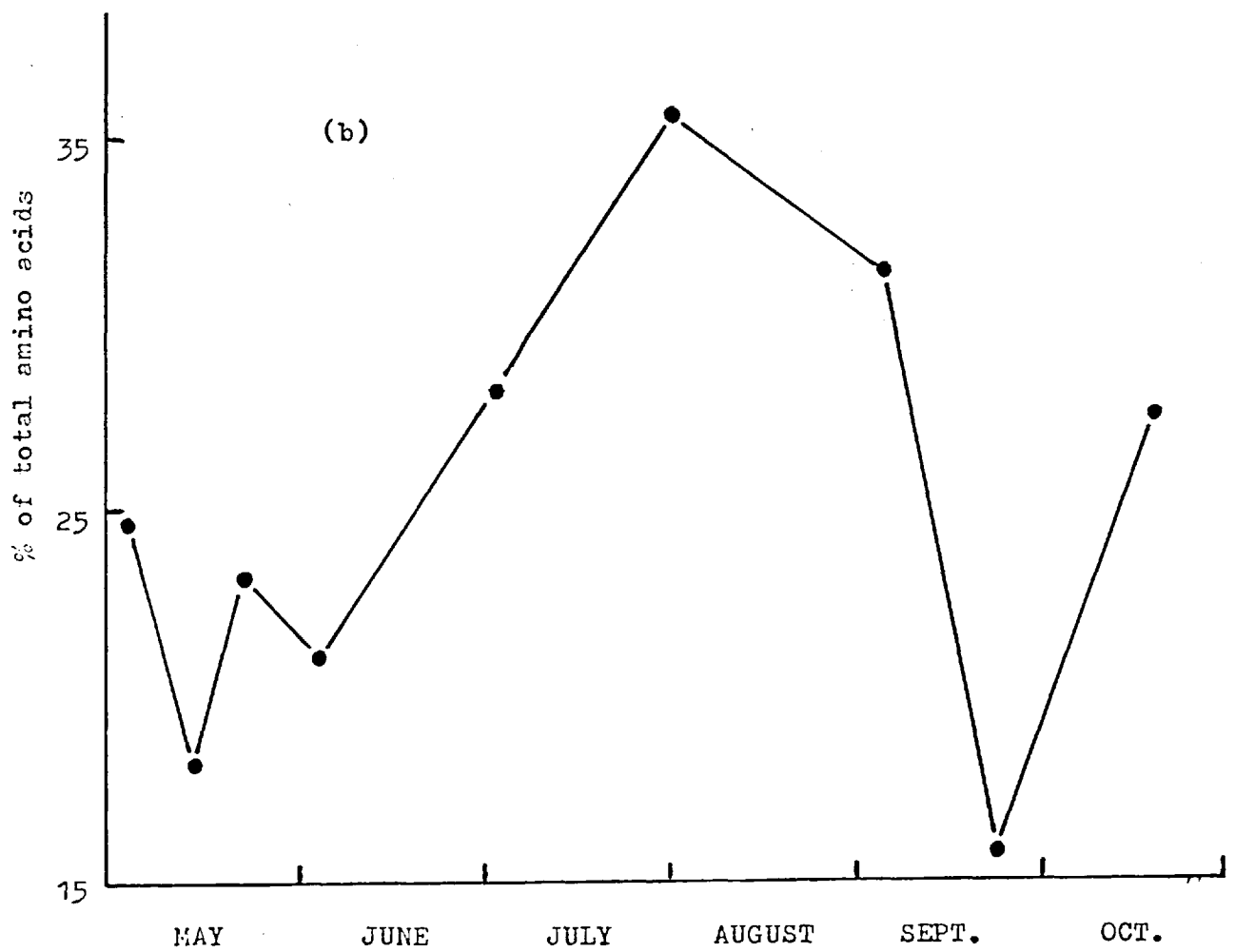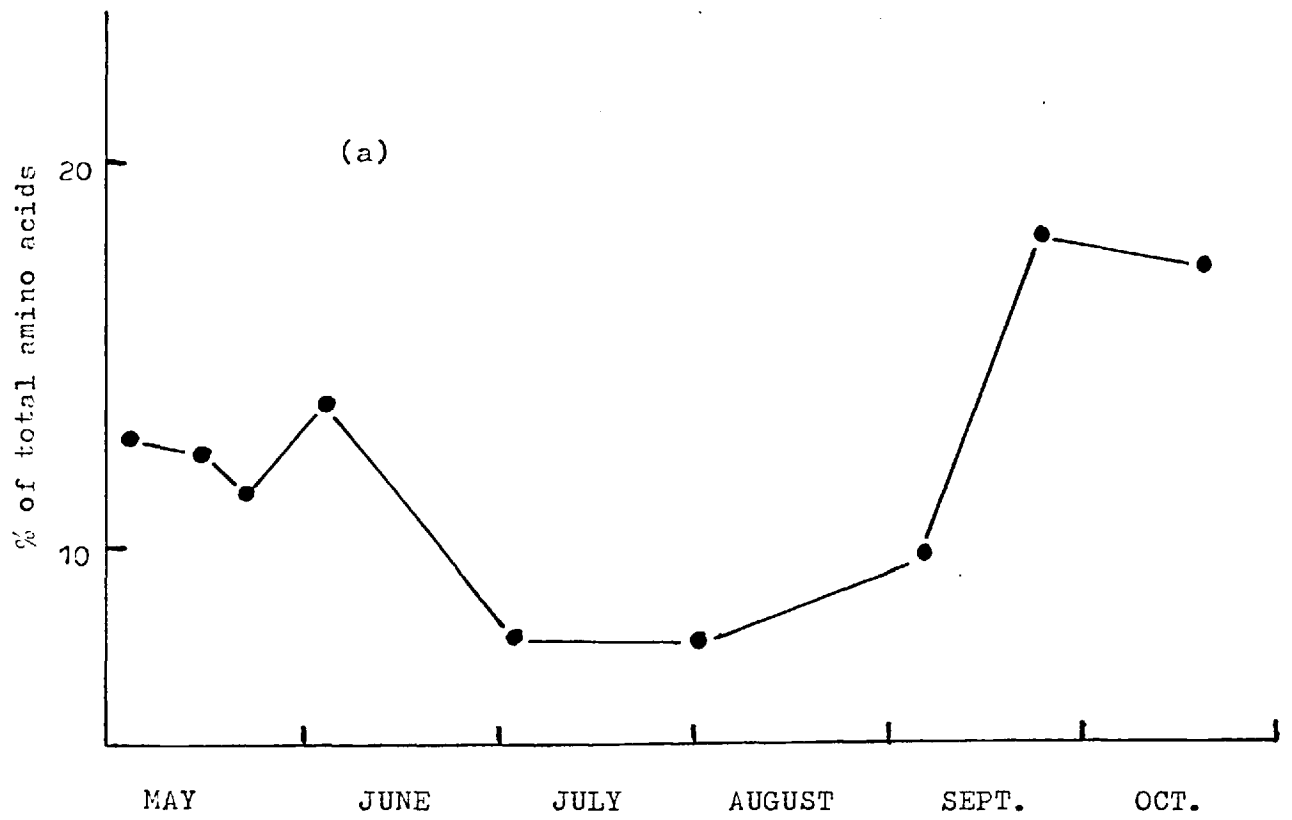
Table 2.3   Grouping of amino acids according to seasonal

proportional abundance.

	Group I	Group II
	Aspartic acid	Histidine
	Glutamic acid	Glycine
	Amide	Alanine
	Threonine	γ Aminobutryric acid
	Proline	L Dopa
	Tyrosine	
	β Phenylalanine	
	Lysine	
	Leucine	
	Isoleucine	
	Arginine	
	Methionine	
	Valine	

Fig.2.18. The influence of nitrogen fertilizer on the mean
leaf soluble amino acid levels in Holcus lanatus
in 1979.
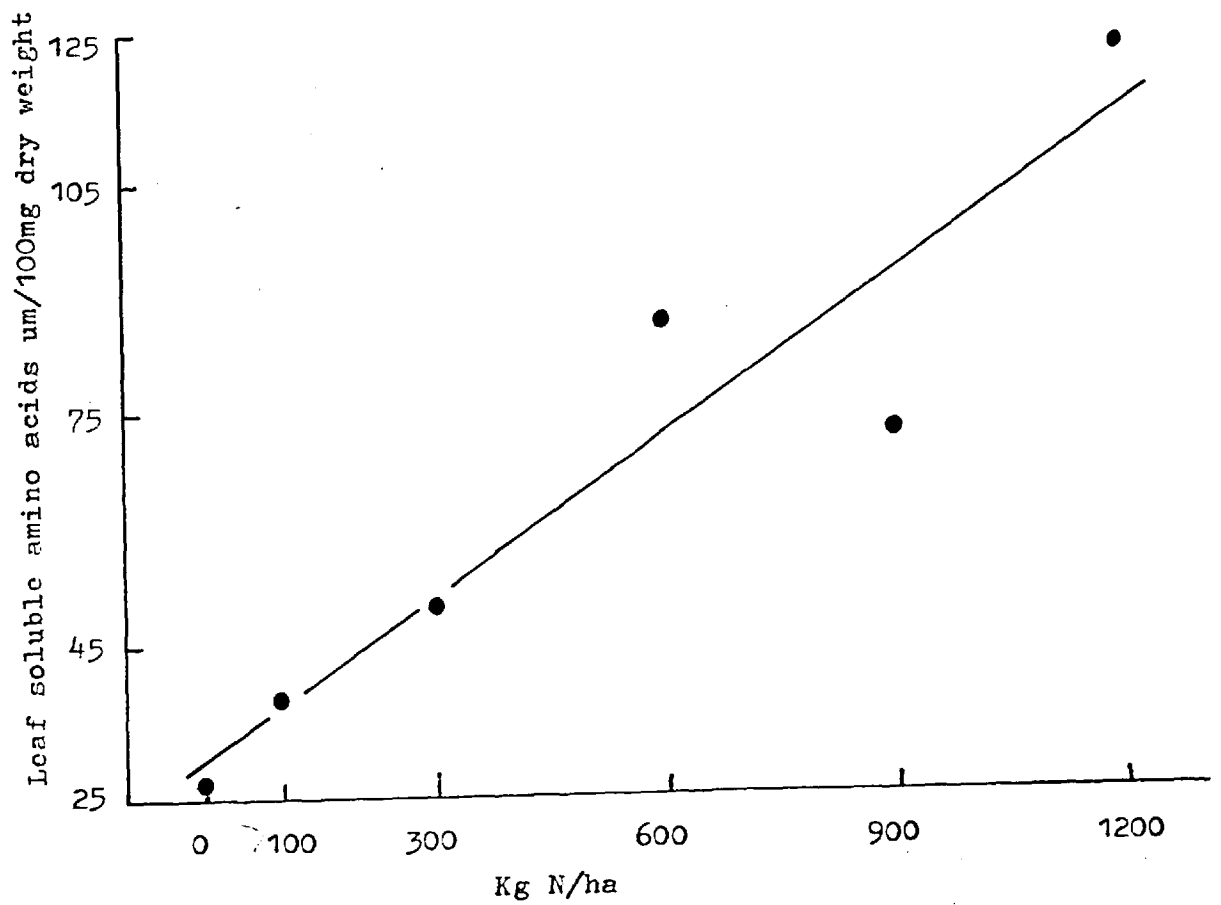
Table 2.4   The effect of nitrogenous fertilizer on the
             proportion of the total leaf soluble amino acids

Group I

                                        Glutamic acid

        Increase with nitrogen   Amide

                                        Threonine

Group II

                                        Aspartic acid

                                        Proline

                                        Valine

                                        Methionine

                                        Isoleucine

        No effect   L Dopa

                                        Tyrosine

                                        Histidine

                                        Lysine

                                        Arginine

Group III

                                        γ Aminobutyric acid

                                        Alanine

        Decrease with nitrogen   Glycine

                                        Leucine ?

                                        β Phenylalanine ?

but both contributed to a very small proportion of the total amino acids present (i.e. $\sim$2.5% and $\sim$0.6% respectively). These amino acids in Groups I, II (less L Dopa), and Leucine and β phenylalanine in Group III, are the amino acids primarily involved in or associated with protein metabolism. Glycine and alanine in Group III are not involved in protein metabolism and have been shown to be affected primarily by light (Larsen 1980). γ amino butyric acid is a known precursor to a number of plant chemical defences and it has been shown to be correlated with a decrease in insect performance by van Emden (1973).

Discussion

The usual effects recorded by agriculturalists researching the effects of fertilizers on grasslands have been shown in this study. Plant production increased with the addition of fertilizers. Species composition altered as the fertilizers affect the plant's competitiveness by adding nutrients to the soil.

From a phytophagous insect's viewpoint however, the system has been radically altered. Nitrogen usually maintained at low levels for most of the year or restricted to narrow windows in time during the plant's growth period, has become more abundant and for longer periods in time. The importance of insect synchrony with its host has been reduced because the duration of N flow to the leaves has increased. This allows the insects a margin of error in emergence timing before development and fecundity rates are depressed (see Section IV).

The results of analyses of total leaf nitrogen levels show similar fluctuations in both years, namely a rapid decline in spring and a rapid increase at the time of the autumn flush. The spring flush was about 3 weeks earlier in 1978 than 1979 and the peak leaf

nitrogen level during the spring flush was higher in 1979. These differences probably reflect differences in temperature during the period responsible for the initiation of growth. In 1978, leaf total nitrogen was very low during the autumn growth period because nitrogen analysis was done on the old grass material. The new growth of grass started in early September but none of this material was included in the analysis. In 1979, grass samples collected on 12/10 and 19/10 included material from the new autumn growth.

The increase in the stem soluble nitrogen levels in the spring is associated with degradation of leaf proteins into soluble amino acids and their subsequent translocation (Thomas et al.1973). In the autumn, there is an increase in the levels of soluble nitrogen in the old grass as a result of leaf proteolysis followed by trans-location of nutrients to the new grass. A small increase in the autumn nitrogen levels in new grass is a reflection of the rapid incorporation of the amino acids into leaf proteins (Thomas et al. 1973).

The results of the amino acid analysis show that there is a dramatic increase in the levels of amino acids during the spring and autumn, when the soluble nitrogen levels are high. Hill (1976) calculated that the amino acids accounted for 75.7% and 16.5% of the soluble nitrogen on the 1st of May and 6th of June 1975 respect-ively. From these figures it is clear that in the estimation of soluble nitrogen, sources of nitrogen other than amino acids were included in the analysis.

Tracer methods have demonstrated the concept of families of amino acids which have arisen from certain head compounds which are widespread, irrespective of the plant order involved (Fowden 1967) Fig.2.19. Oaks & Bidwell (1970) and Huffaker & Peterson (1974)
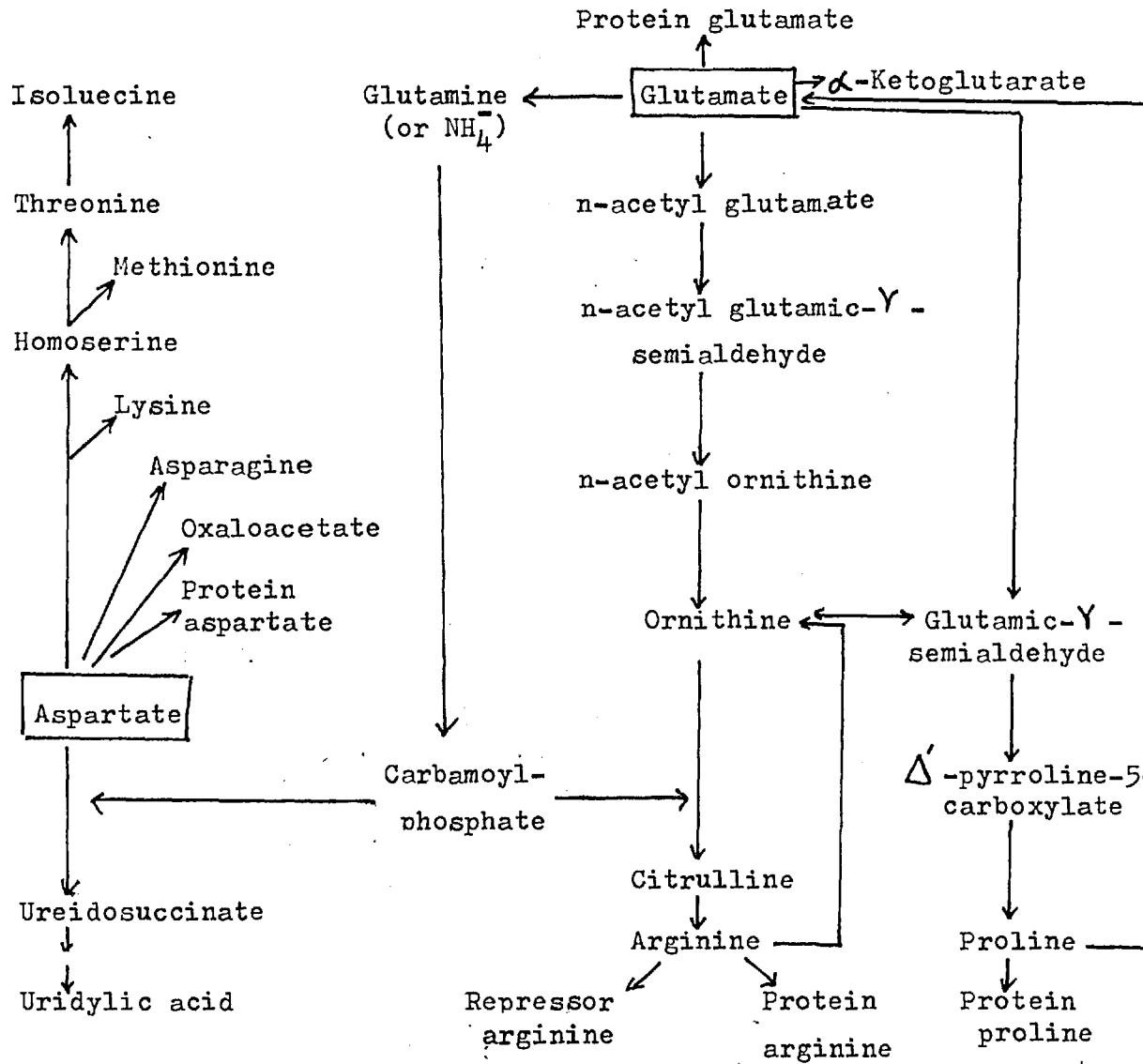
Protein glutamate

Isoluecine   Glutamine ← Glutamate ← α-Ketoglutarate
(or NH$_4^-$)

Threonine

n-acetyl glutamate

Methionine

Homoserine

n-acetyl glutamic-γ-
semialdehyde

Lysine

Asparagine

n-acetyl ornithine

Oxaloacetate

Protein
aspartate

Ornithine ⇄ Glutamic-γ-
semialdehyde

Aspartate

Carbamoyl-
phosphate

Δ'-pyrroline-5-
carboxylate

Ureidosuccinate

Citrulline

Uridylic acid

Arginine

Proline

Repressor
arginine

Protein
arginine

Protein
proline

60.

have presented evidence to show that amino acid metabolites are divided into pools within plant cells.   It is of interest that the amide levels show the most rapid acceleration and decline of all the individual amino acids so it is possible that this complex is concerned with the flow of metabolites.   Amide is a complex of asparagine and glutamine, the amide forms of aspartate and glutamate, two of the most important head compounds.   It is conceivable that amide is being translocated primarily as aspartate and glutamate and that these compounds are metabolised into amino acids as the plant demands (e.g. Oaks & Bidwell, 1970).

The effects of fertilizer are relatively short lived. Although levels of nitrogen and amino acids remain higher in leaves on fertilized than unfertilized plants, the effect of the fertilizer is to ' increase the levels during the flow periods.   The seasonal fluctuations are still maintained being related to the times of nutrient mobilization within the plant.

Individual amino acids can be grouped as to whether they are influenced by the nitrogen level in the plant (Table 2.4).   This is important to sucking insects if the levels of unfavourable amino acids (e.g. γ amino butyric acid to Myzus persicae (van Emden 1973)) proportionally increases.   Alternatively, if the levels of the favourable amino acids decrease relative to the proportion of unfavourable amino acids, development may also be reduced.   This theme will be developed further in the next section after analyses of the insect population data have been completed.

SECTION III –

INSECT POPULATION STUDIES

3.1 Introduction

Rarely are field trials undertaken with the sole purpose of testing the effects of fertilizers on insect pests. It is more usual to monitor infestations after they have occurred. For this and other reasons (e.g. host plant age differences (Kennedy et al. 1950; Van Emden 1969; Coley 1980), lack of reliable plant nutrient data, etc) the recorded effects of fertilizers on insect populations are variable (Jones 1977).

In a recent review, Jones (1977) concluded that 'in most pest-crop situations, nitrogenous fertilizers increase the number of pests, probably because nitrogen increases the food supply'. He provides a comprehensive list of the effects of nutrients in the laboratory and field on insect, mites and other pests. This should be consulted together with earlier reviews by Tandon (1973) and a Commonwealth Soil Bureau Handbook (Anon 2 (1976)). Table 1 summarizes Jones' list of the effects of nutrients on insects, mites and nematode populations.

Table 3.1   The number of citations of the effects of N, P, and K, on plants susceptible to a range of insect, mite and nematode pests (Jones 1977, Table 8).

Source	N			P			K		
	+*	0	–	+	0	–	+	0	–
Tandon	15	5	0	2	4	1	0	2	3
Anon	13	2	3	1	0	3	3	2	2
Others**	12	4	5	3	4	0	4	3	2
Totals	40	11	8	6	8	4	7	7	7

 * + numbers increased, 0 unaffected, – decreased

** mostly experiments with plants in sand or other cultures

McNeill & Southwood (1978) recently highlighted one of the major

problems of being an insect herbivore - how to obtain an adequate

level of nitrogen from a source originally low. They maintained that

if N was in low supply,growth and reproduction of phytophagous insects

should be influenced by the quality and quantity of available N.

Insects should have evolved mechanisms to increase the availability of

nitrogen to them at times when low levels were present in the plant.

The plants in turn should have utilized the non-availability of

nitrogen as a defence mechanism in the plant-insect evolutionary arms

race (Feeny 1976; Rhoades & Cates 1976).

Growth and reproduction of many insects have been positively

correlated with plant nitrogen levels and levels of total amino acids.

For example, Hemiptera (Mittler 1958; Dixon 1970, 1973; Sogawa 1971;

Van Emden 1972, 1973; Parry 1974; Hill 1976; Carter & Cole 1977;

Webb & Moran 1978; Reader 1980), Heteroptera (McNeill 1971, 1973;

Gibson 1976a) Lepidoptera (Feeny 1968, 1976; Scriber 1978; Scriber &

Feeny 1979; Schroeder 1976, 1977; Wint 1979; Riggell 1980), Orthoptera

(Smith & Northcott 1951; White 1976, 1978), Coleoptera (Strong & Wang

1977; Fox & Macauley 1977).

In many cases, however, gross nitrogen and total amino acid

levels do not tell the full story. A sucking insect is only interest-

ed in that soluble part of the total nitrogen that is being translocated.

A chewing insect cannot take advantage of high nitrogen levels if

nitrogen is protected by toxins or bound to tannin when the cell is

disrupted (Feeny 1968). Levels of available nitrogen and amino acids

may differ considerably from estimates of total and soluble nitrogen

(e.g. Wint 1979).

Evidence is accumulating to suggest that subtle changes in amino

acid composition may act as trigger cues to phytophagous insects well

before any changes in the levels of total amino acids are detected.

For example, Van Emden (1973) found that growth rates and fecundity

of Myzus persicae and Brevicoryne brassicae were positively correlated

with the levels of amide (glutamine + asparagine) in the leaves.

Other amino acids positively correlated with aphid performance

included threonine and glutamic acid for B.brassicae and methionine

and leucine for M.persicae (Van Emden 1973). He also found a number

of amino acids negatively correlated with aphid performance e.g.

phenylalanine and glycine for B.brassicae and Υ-Aminobutyric acid,

tyrosine and proline for M.persicae.   Sogawa (1971a)and Cheng &

Pathak (1972) linked fecundity levels in the rice leafhoppers,

Nilaparvata lugens and Nephottetix virescens, to the total amino

acid levels in the plants.   The main amino acid implicated (Sogawa

(1971b); Campampang et al. 1974) was asparigine - one of the con-

stituents of amide.   Harrewijn (1978) linked low population develop-

ment in Myzus persicae to a reduced amide concentration and noted

that low N fertilization reduces the overall amino acid content of the

leaves.   Low methionine content increased aphid restlessness and low

levels of pre-alates were recorded on plants with a high proline

content and a low amount of tyrosine, the latter known to stimulate

wing development in M.persicae (Harrewijn 1976).   Parry (1974)

suggested that population build-up and rapid decline of Elatobium

abietinum (Walker) on Sitka spruce needles was related to a high level

of essential amino acids (when temperature was not limiting) and a

rapid decline in the level of total essential amino acids, a view

recently modified by Carter and Cole (1977), who suggested that the

trigger to alate production may be due to subtle changes in amino

acid ratios during the time of the spring flush.

Hill (1976) noted a 34X difference in total essential amino acids

in *Holcus mollis* leaves between samples taken within 28 days of each other. The life histories of 5 species of Auchenorrhyncha were closely linked to the periods when levels of amino acids were high in the plant. McNeill & Southwood (1978) suggest that very low methionine levels in *Holcus mollis* in June may be responsible for alate production in the grassland aphid *Holcaphis holci*.

Broodbank (1980) measured amino acid levels in *Holcus mollis* and suggested that the important essential amino acids that showed the greatest rise and fall in concentration included amide and proline.

The ten amino acids generally regarded as being essential components of insect diets are arginine, histidine, iso-leucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine (House 1972). Retnakaran & Beck (1968) using the deletion technique on artificial diets, concluded that in *Acyrthosiphon pisum* (Harris) the absence of any of the ten essential amino acids plus cysteine resulted in up to 75% weight reduction of the first generation, reproduction also being impaired. Dadd & Krieger (1968) concluded that only methionine, histidine, iso-leucine and possibly lysine were essential for the growth of *M.persicae*, the remaining essential amino acids being provided by symbionts. Mittler (1970) found that omission of methionine and histidine from a synthetic diet reduced ingestion in *M.persicae* by 50% and 33% respectively. Artificial diets have been important in elucidating some of the finer points in aphid nutrition but as Van Emden *et al.* (1969) and Van Emden (1973) pointed out, it is impossible to alter the amino acid balance without upsetting other correlated factors like pH, etc.

In summary then, we are dealing with a complex problem of deciding what levels of individual amino acids in the plant are critical to provide a healthy insect diet. We know too little about the role of

gut symbionts and their effect of providing essential nutrients to the host. Different, closely related, insects often have different requirements of which we know very little. There are good indications to suggest that total levels of essential amino acids (and soluble nitrogen levels) do markedly affect the phytophagous insect community (e.g. Reader 1980). It is also very probable that individual amino acid proportions are responsible for the observed structuring of the herbivorous community. A great deal of the variance may be removed when a technique is found which enables plant sap to be readily and quickly taken for analysis rather than whole leaf extracts. Amide and methionine appear to be the most universally important individual amino acids to insect growth and fecundity and it is not unreasonable to assume that some individual amino acids may have a negative (or harmful) effect on insect performance. Unusual amino acids, as are often found in Compositae e.g. lugumes (Bell 1978; Janzen 1978) may also play a major role in plant defence, determining the phytophagous insect community able to live on those plants.

The only other study on the effects of mineral fertilizers on the grassland Auchenorrhyncha fauna showed that when NPK was applied at 640 Kg/ha the number of leafhoppers (Andrzjewska 1976b) and other phytophagous fauna (Andrzjewska 1976a) increased. Plant protein levels were increased on the fertilized areas relative to the unfertilized areas. An analogy between artificially raising the N levels with fertilizers and examining the spread of N levels over a number of years can be drawn. McNeill (pers.com.) has seven years data on the yearly levels of N and the Auchenorrhyncha on H.mollis. In general, years when plant N levels are high also have a higher biomass of Auchenorrhyncha and other herbivorous fauna.

The grassland Auchenorrhyncha are characterised by having great lability (Waloff 1980) both in time and space. Immigrations and emigrations occur frequently so that populations are very local. This lability and the absence or occurance of secondary compounds in low concentrations throughout the gramineae(e.g. Harborne & Williams 1976) would suggest that leafhoppers have great potential to find those areas where the food quality has been increased with fertilizer.

3.2 Sampling methods

Leafhoppers were sampled weekly with a DVac suction sampler (Southwood 1979). Random samples were taken at the same time of day (1400 hrs) and only when the grass was dry. Each sample consisted of a 1 minute suck from each plot, the area being sampled on each occasion was $0.1m^2$.

The sample was killed in 70% alcohol within 15 minutes of collection and all Auchenorrhyncha were removed and sorted to instar. All identifications were from Le Quesne (1960, 1965, 1969) but incorporate some recent revisions by Payne (1980).

While most of the adults could be identified relatively easily, some of the smaller instars were more difficult. Regular sampling within a defined area, together with rearing to adults of the young nymphs of some species collected in the field, enabled the nymphal stage of the common species to be identified.

3.3 Results

The number of Auchenorrhyncha caught on all sampling occasions in 1978 and 1979 are presented in Appendix .X. Altogether 4122 and 17,964 leafhoppers were captured in 1978 and 1979 respectively. The low numbers captured in 1978was probably a result of the dry summer of 1976 which severely depleted the resident populations. An alternative explanation is that the large number captured in 1979 is due to the

effect of fertilizers added in 1978, the populations in the second half of 1978 and 1979 having an increased food supply.

The population fluxes of the leafhopper fauna are shown in Fig. 3.1. A large population build up in the latter half of both years dominates the shape of the graphs.

Table 3.2 shows the changes in proportion of Delphacidae and Cicadellidae of the total leafhoppers captured. The majority of both the Delphacidae and Cicadellidae have two discrete generations such that both families show two peaks of abundance. Also both families are separated temporally from each other, although there is some overlap late in the season (Fig.3.2).

When the total leafhoppers captured are divided according to feeding types-phloem, mesophyll and xylem feeders - a different pattern can be seen (Table 3.3). Phloem feeders are the dominant group, mesophyll feeders make up a small but significant proportion of the total leafhoppers present, and xylem feeding leafhoppers are present in very low numbers for most of the year.

The seasonal patterns of the different feeding types are presented in Fig.3.3. Phloem feeders show the same patterns as shown by the total leafhoppers (Fig.3.1) simply because they form the bulk of the insects present. Mesophyll feeding leafhoppers show a slow population increase which peaks late in the year. Mesophyll feeders are dominated by Zyginidia scutellaris, a polyvoltine typhlocibine. Xylem feeding leafhoppers show a small population peak during mid summer.

The biomass of leafhoppers caught has been calculated from the average weight data in Appendix XI. No significant differences between individual weights in 1978 and 1979 were found, so the data were pooled. Further, no significant differences were found between the pooled individual weights and the weights for the same 5 species recorded by

Fig.3.1   Leafhopper population fluxes on

experimental area.

●   ● 1978

▼   ▼ 1979
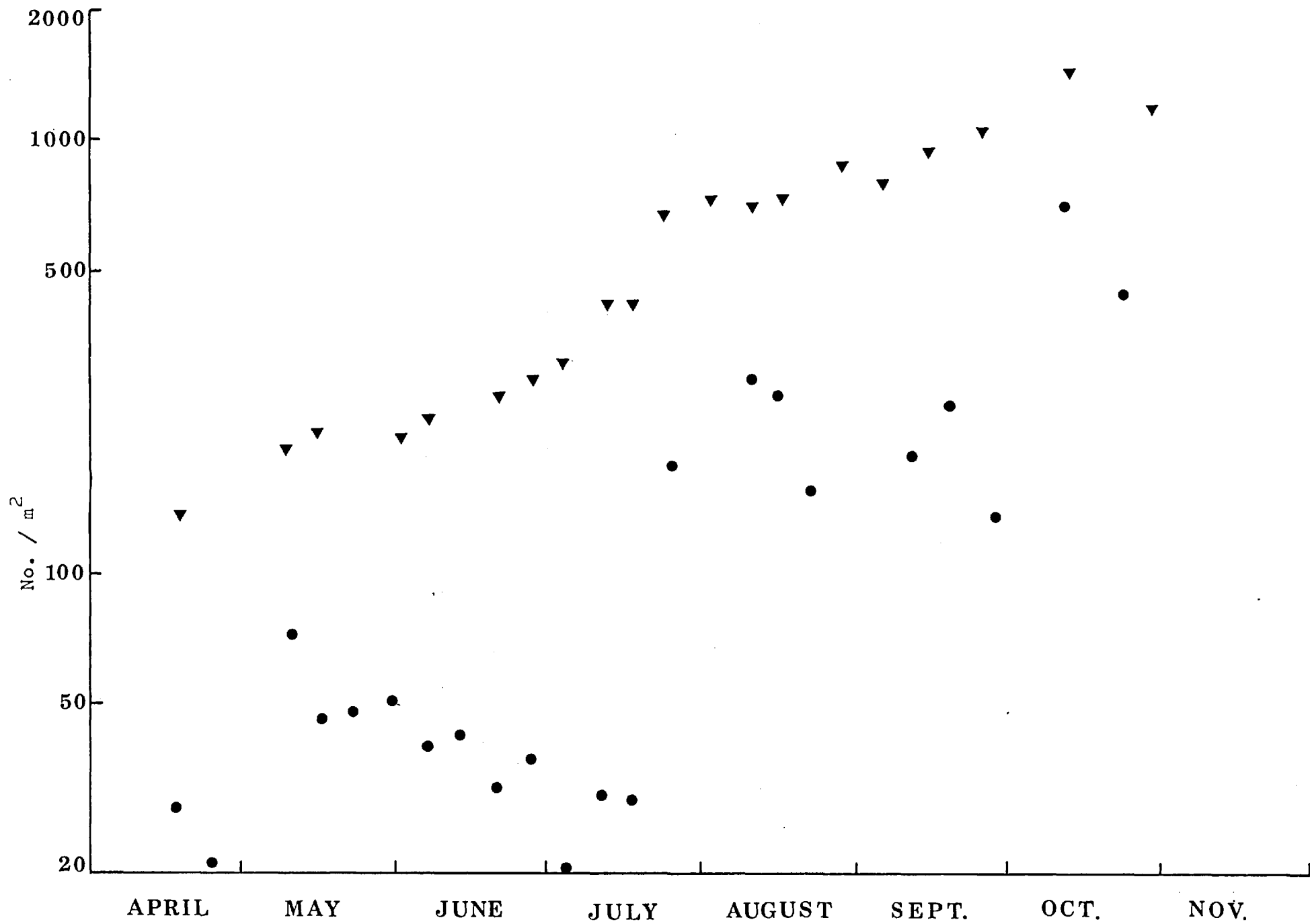
Table 3.2   Percentage of Delphacidae and Cicadellidae in total catch

1978			1979		
Date	Cicadellidae	Delphacidae	Date	Cicadellidae	Delphacidae
17.4	80.6	19.4	18.4	21.9	78.8
24.4	78.3	21.7	9.5	68.9	31.1
10.5	100.0	0	15.5	75.1	25.8
16.5	96.0	4.0	1.6	76.0	24.0
22.5	98.1	1.9	6.6	66.5	33.9
30.5	94.5	5.5	20.6	77.5	22.5
6.6	100.0	0	27.6	71.4	28.6
12.6	97.9	2.1	3.7	63.8	36.2
20.6	100.0	0	12.7	46.7	53.5
27.6	63.4	36.6	17.7	38.2	62.0
4.7	100.0	0	23.7	27.6	72.4
11.7	84.8	15.2	2.8	18.9	81.1
17.7	97.0	3.0	10.8	32.0	68.9
25.7	79.1	20.9	16.8	36.2	64.7
10.8	82.8	17.2	28.8	37.2	62.8
15.8	83.6	16.4	5.9	36.2	63.8
22.8	86.6	13.4	14.9	32.3	67.1
11.9	41.7	58.3	25.9	29.2	70.8
18.9	51.3	48.7	12.10	12.5	87.5
27.9	78.4	21.6	29.10	12.1	88.1
11.10	28.0	72.0			
23.10	17.4	82.5			

Fig. 3.2. The density of Delphacidae and Cicadellidae captured on the experimental area (o—o) Delphacidae (●--●) Cicadellidae.
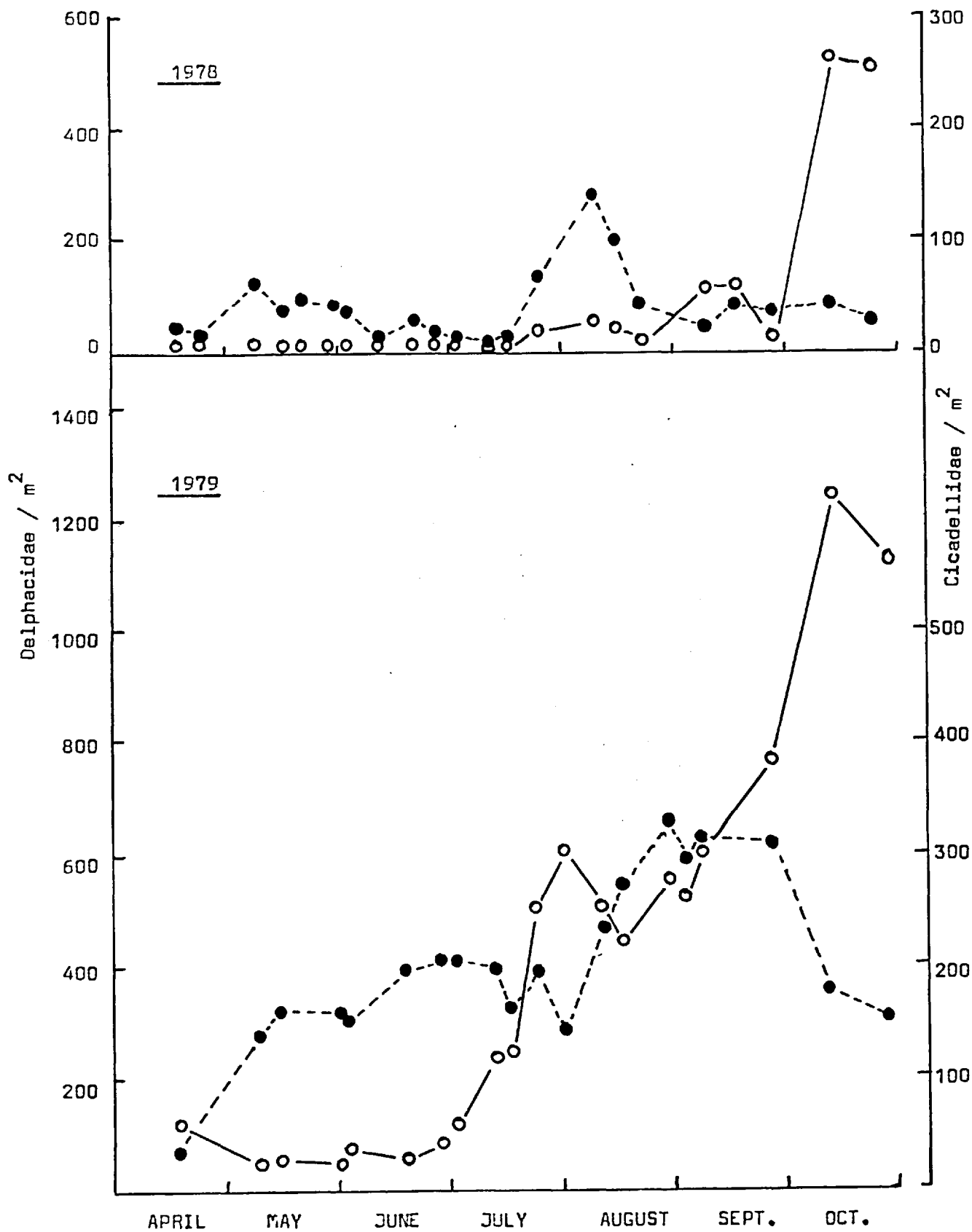
Table 3.3   The percentage of different feeding types captured in 1978 and 1979

	1978				1979		
Date	P^1	M^2	X^3	Date	P^1	M^2	X^3
17.4	86.5	5.3	8.2	18.4	85.8	13.7	0.5
24.4	85.3	14.7	0	9.5	94.6	5.4	0
10.5	91.6	7.3	0.1	15.5	93.7	6.3	0
16.5	91.6	8.4	0	1.6	90.4	6.0	3.6
22.5	96.7	1.6	1.6	6.6	92.7	4.6	2.8
30.5	93.9	6.1	0	20.6	87.1	9.7	3.1
6.6	100.0	0	0	27.6	91.7	7.5	0.8
12.6	88.1	11.9	0	3.7	82.9	14.0	3.1
20.6	92.4	7.6	0	12.7	81.1	16.8	2.2
27.6	77.4	22.6	0	17.7	84.0	15.6	0.4
4.7	65.5	34.5	0	23.7	92.3	7.4	0.3
11.7	20.6	79.4	0	2.8	92.1	7.8	0.1
17.7	46.3	53.7	0	10.8	88.4	11.6	0.
25.7	59.1	40.9	0	16.8	82.9	17.0	0.1
10.8	63.2	36.6	0.3	28.8	84.0	15.3	0.7
15.8	54.1	45.9	0	5.9	84.1	15.5	0.5
22.8	32.4	64.8	1.0	14.9	82.6	17.1	0.3
11.9	70.7	28.5	0.8	25.9	78.9	20.9	0.2
18.9	77.6	21.7	0.7	12.10	91.7	8.2	0.1
27.9	47.9	49.8	2.3	29.10	90.0	9.8	0.2
11.10	76.3	22.7	1.0				
23.10	88.3	10.7	1.0				

1   Phloem

2   Mesophyll

3   Xylem

Fig. 3.3. Phloem (O-O), Mesophyll (●-●), and Xylem (●·-●) feeder density

on experimental site.
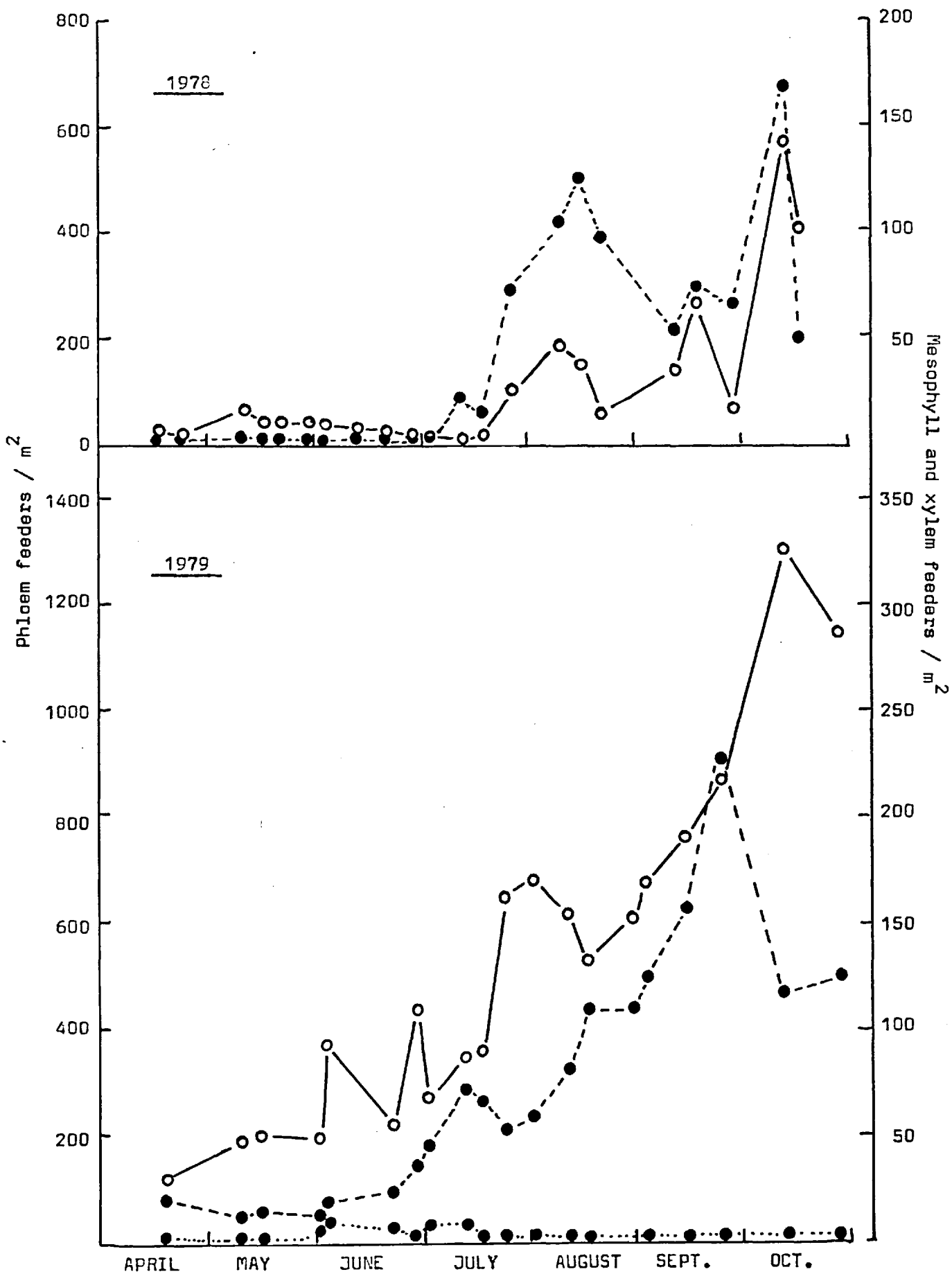
Hill (1976). His data were used to calculate biomass for these five species. Species which occurred in low numbers on the experimental area and for which no reliable weight data were obtained were asigned weights of a similar sized individual of a species of known weight. The error involved is likely to be small when consideration of their contribution to the total biomass is examined. Fig.3.4 shows the seasonal pattern of leafhopper biomass during 1978 and 1979.

The relative abundance of the ten most common species is shown in Table 3.4. Although Z.scutellaris was ranked first in abundance in 1978, it was reduced to third in 1979. Dicranotropis hamata population increased dramatically in 1979 to form 43% of the total catch. Other populations which increased in proportion in 1979 were Javesella pellucida, Adarrus ocellaris and Recilia coronifera. In contrast, Z.scutellaris, Aphrodes albifrons, Psammotettix conifinis and Mocydiopsis parvicauda populations all decreased in proportion in 1979. Elymana sulphurella and Diplocolenus abdominalis populations remained proportionally the same in both years.

3.3.1 Species diversity

A number of indices of diversity have been proposed and recently reviewed by Whittaker (1972), May (1975) and Pielou (1975). When dealing with insects, all attempt to quantify the relative complexity of communities, when the number of species of insects is small, diversity is low, reaching a minimum when all the insects are of the same species. When the number of different species of insects is large, diversity is high, reaching a maximum when each insect is of a different species.

Most indices are not independent of the size of the collection of species considered (Pielou 1966). The exception is Williams' diversity index α, which is independent of sample size but is only valid if the 'log species abundance on rank curves' (Southwood 1979) conform to the

Fig. 3.4. Auchenorryncha biomass on experimental site.
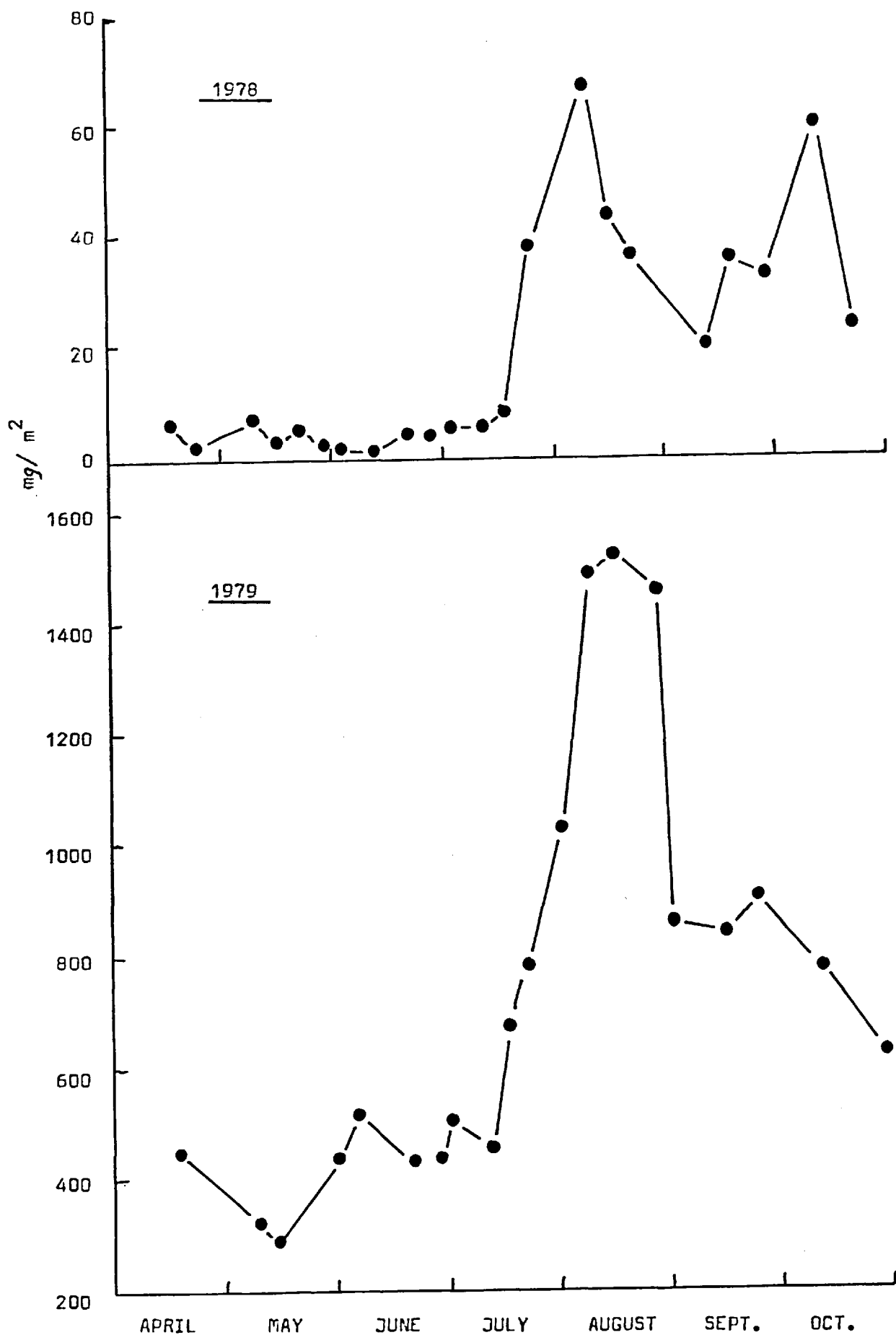
Table 3.4   Relative abundance of the 10 most common species
            breeding on the experimental area

Species	Relative abundance	
	1978	1979
Zyginidia scutellaris	28.3	11.3
Dicranotropis hamata	22.2	43.1
Javesella pellucida	19.2	23.1
Adarrus ocellaris	8.6	9.2
Aphrodes albifrons	4.4	0.6
Psammotettix conifinis	3.5	1.3
Mocydiopsis parvicauda	3.0	0.5
Recilia coronifera	2.9	4.6
Elymana sulphurella	2.9	2.8
Diplocolenus abdominalis	0.6	0.6
Others	4.4	2.7

log or log normal distribution (Williams 1964). The index is given
by

$$S = \alpha \, \log_e \, (1 + \frac{N}{\alpha})$$ (1)

where S is the number of species, N is the total number of individuals
and α can be conveniently read off from a nomograph (e.g. Southwood
1979).

For small sample sizes, however, α cannot be accurately read from
the nomograph. Margalef (1958) proposed an index such that

$$\alpha = \frac{S-1}{\log_2 N}$$ (2)

which was accurate for small sample sizes.

Both indices have been calculated for the experimental area (Fig.3.5).
Williams' diversity index α = 4.8 and 4.0 in 1978 and 1979 respectively,
whilst Margalef's index α = 2.66 and 2.26 in 1978 and 1979 respectively.
Both indices show that leafhopper species diversity decreased in 1979.
The total number of leafhopper species remained the same in both years,
but their proportional abundance altered such that the most abundant
species increased from 28% to 43% (Table 3.4). This effectively
decreased leafhopper diversity in 1979 by lowering the equitability of
the community.

Fig.3.6 shows the seasonal pattern of leafhopper diversity calcul-
ated for Control (unfertilized) and NPK + lime fertilized plots.
Diversity was lower on the fertilized plots. The total diversity for
the same plots has been calculated and is shown in Table 3.5. Diversity
has decreased in 1979 although the number of species is relatively
constant in both 1978 and 1979. The leafhopper diversity on the
fertilized plots is lower in both years.

Fig.3.5. Leafhopper species diversity on the experimental area.
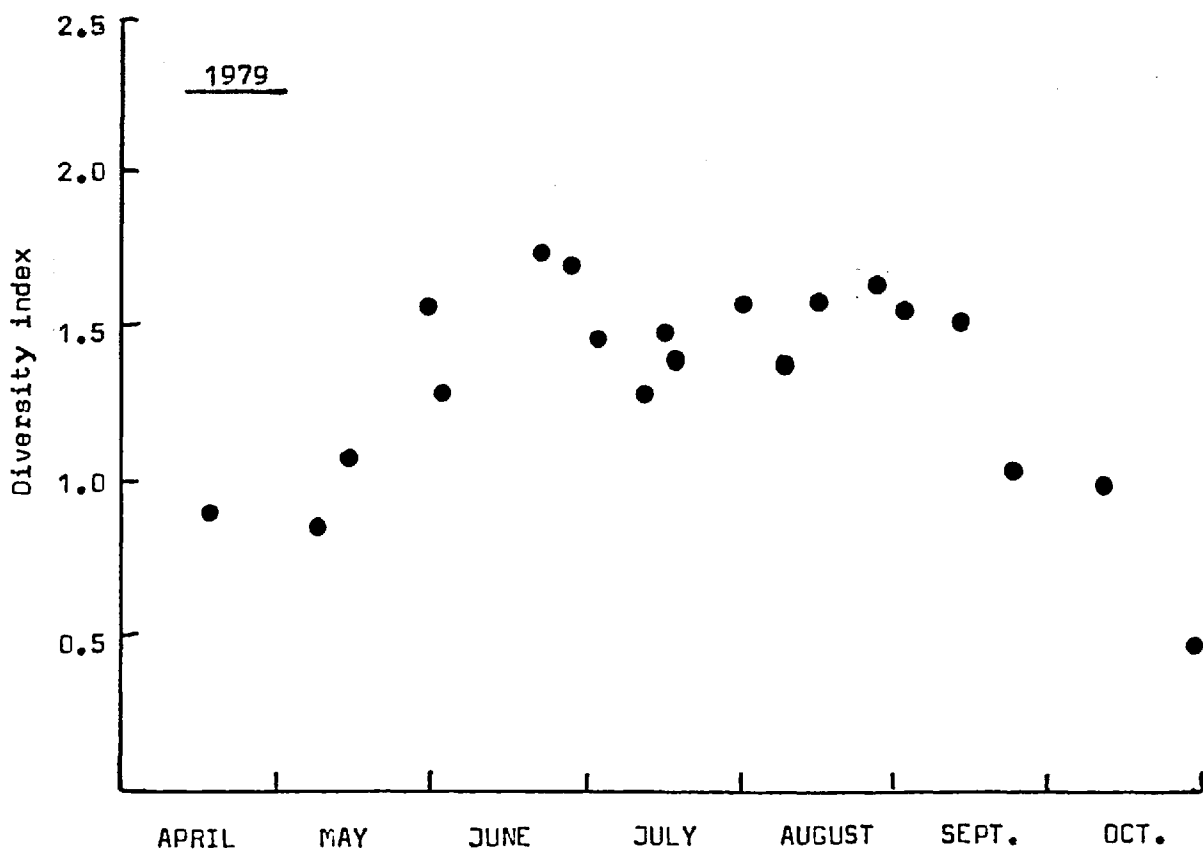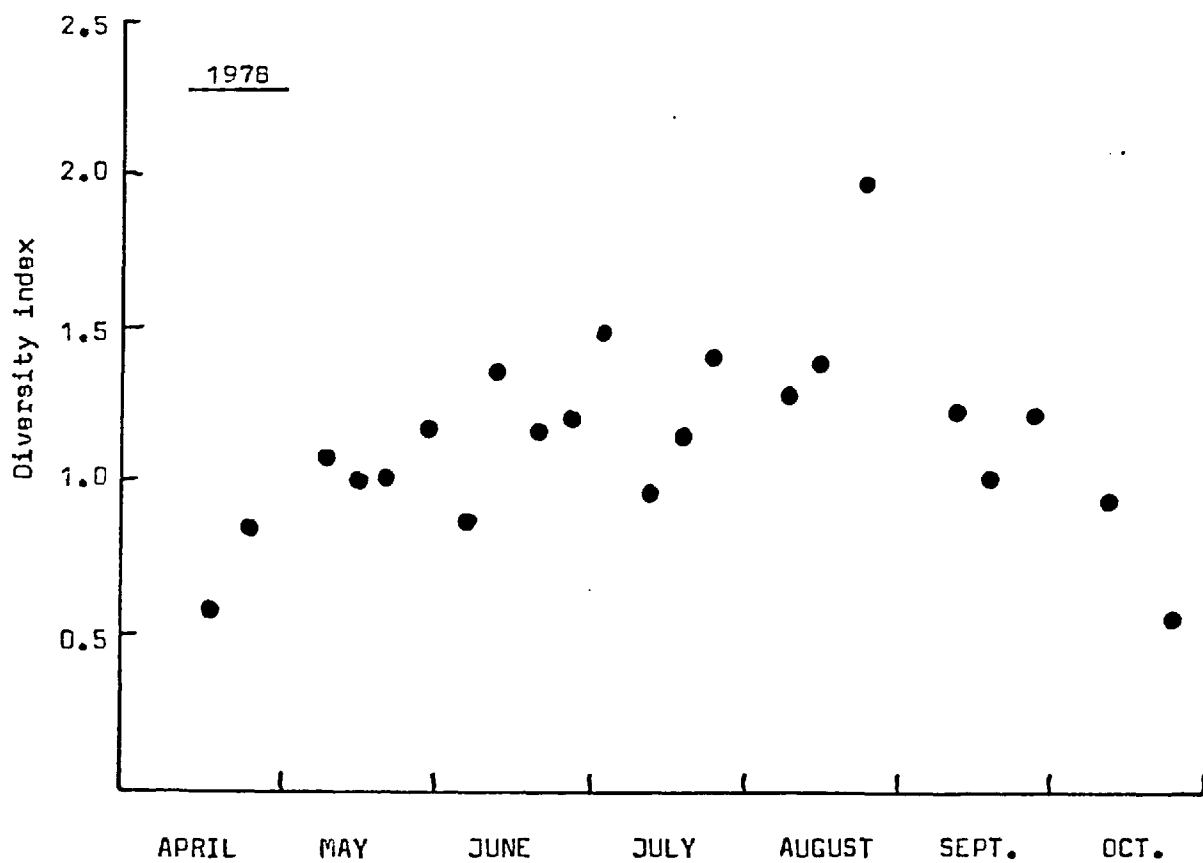
Fig. 3.6. Leafhopper species diversity on control (●)

and NPK+Lime fertilized (O) plots in 1979.
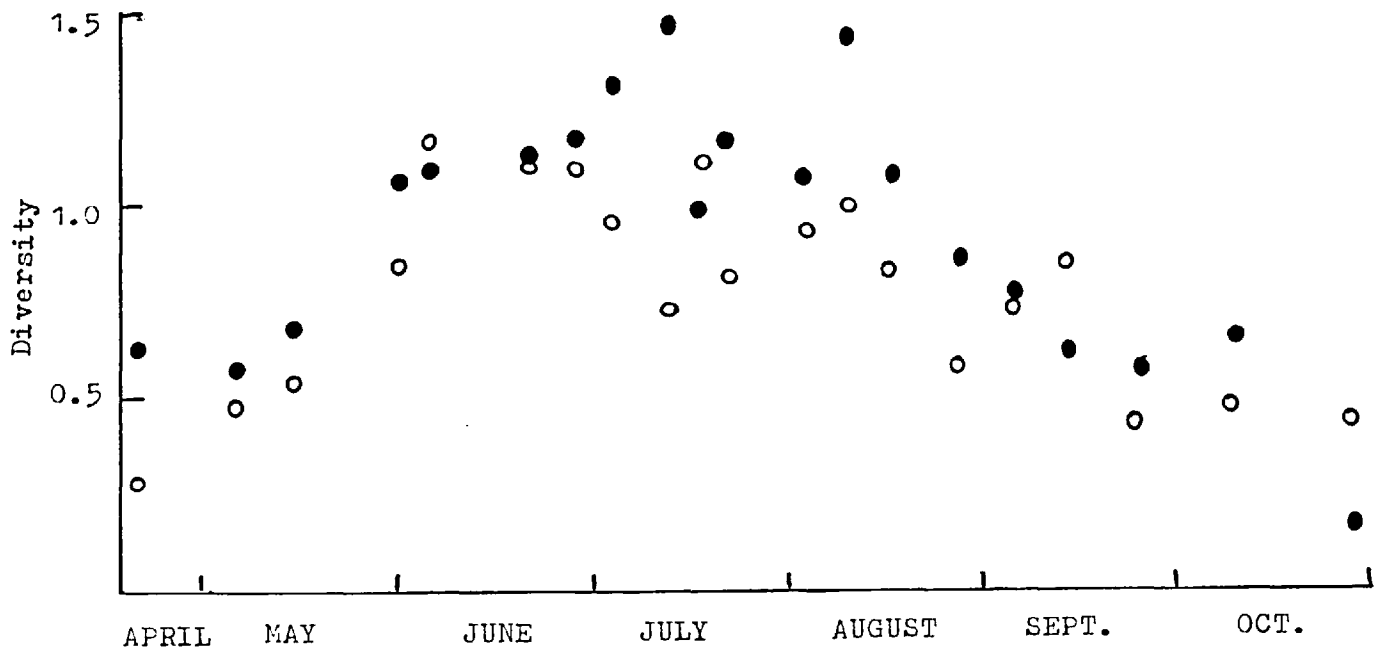
Fig. 3.7. The mean density of predators on the experimental

site in 1979. (O—O) Nabidae, (●—●) spiders.
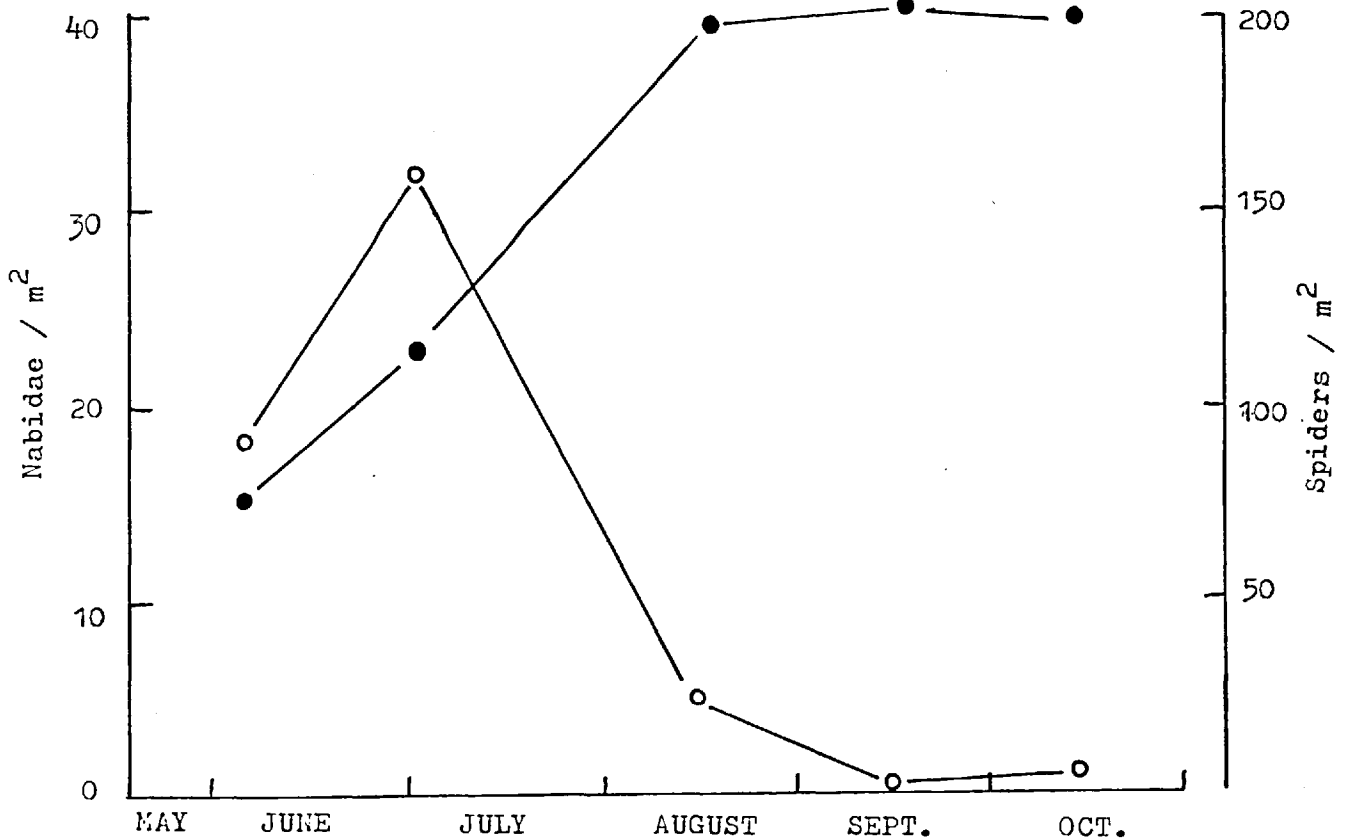
Table 3.5   Diversity indices calculated for unfertilized
            (control) and NPK fertilized plots.

	S	N	Margalef's α	William's α'
1978				
Unfertilized	17	125	2.29	5.2
NPK fertilized	16	323	1.79	3.5
1979				
Unfertilized	17	638	1.71	3.2
NPK fertilized	17	2982	1.38	2.3

3.3.2 Parasitism

In 1979 adults and late instar nymphs of the most common Auchen-orrhyncha were dissected to determine percentage parasitism in the population. The parasitoids were classified to order and no attempt was made to classify them further. Details of the biology and life histories of Auchenorrhyncha parasitoids in acidic grasslands are given by Waloff (1974, 1975, 1980) and Benson (1975). The only two groups found in the experimental area were Pipunculidae (Diptera) and Dryinidae (Hymenoptera).

The number of parasitoids and the percentage parasitism for the common leafhopper species are shown in Table 3.6. A low level of parasitism existed on the experimental area with levels below 20%. Pipunculidae accounted for the majority of the individuals parasitised. It is of interest that although only two species of Delphacidae were examined, all 3 individuals out of a total of 265 examined were para-sitised with Dryinidae larvae.

3.3.3 Effects of predators

In 1979, the numbers of nabids and spiders were estimated from the D.Vac samples. These 2 groups form the bulk of the predators preying upon leafhopper populations (Section I). The major nabid species in-volved was Nabis flavomarginatus (Scholtz). The majority of spiders belonged to the family Linyphidae. No attempt was made to identify spiders below a family level and all specimens have been grouped as 'spiders/m^2'.

The number of predators/m^2 captured on the experimental area in 1979 are shown in Fig.3.7. Nabidae populations peak early in late June/early July. Spider populations increased from a low level in June and reached a plateau in mid August when the leafhopper biomass reached its greatest level.

Table 3.6   Parasitism of Nymphs and Adults

Species			No.Examined	Pipunculidae	Dryinidae	% Parasitism
D.hamata	generation	(1)	142	0	0	0
		(2)	31	0	2	6.5
J.pellucida		(1)	70	0	0	0
		(2)	22	0	1	4.5
Z.scutellaris			91	0	0	0
M.laevis			40	0	4	10
A.ocellaris		(1)	157	18	0	11.5
		(2)	219	40	3	19.6
D.abdominalis			63	4	0	6.3
E.sulphurella			132	8	1	6.8
P.conifinis		(1)	123	23	1	19.5
		(2)	10	0	0	0
R.coronifera			57	0	0	0
E.incisus		(1)	88	7	4	12.5
		(2)	9	0	0	0
M.parvicauda			39	3	0	7.7

Other potential predators must include members of the Carabidae
and Staphylinidae, but these were taken in very low numbers for most
of the year, probably as a result of the sampling efficiency of the
D.Vac. (Thornhill 1979).

Hymenopterous ants (Myrmica scabrinodis Nyl.) were seen carrying
leafhoppers to their nests. Ant abundance was similar to the pattern
shown by nabid abundance, peak numbers $(37.1/m^2)$ occuring on 3.7.79
and the population remaining at a low level after this date.

3.3.4 Analysis of Field Sampling Data with reference to Fertilizer Application

In Section 2 it was shown that the levels of plant nutrients could
be manipulated by the addition of artificial fertilizers to the soil.
If an element is limiting the size of the leafhopper population resident
in an area, a positive response to increasing the food quality should
become apparent. Food quality is defined here in its broadest sense
as a measure of the general excellence of the food. It takes into
account presence and/or absence of particular elements, their relative
proportions in the overall diet, and the fact that what is a 'good'
quality diet for one insect may not be an 'adequate' diet for another
insect. It is important to remember that a 'good' quality diet is
only a relative measure e.g. catastrophic, poor, good, very good,
excellent.

A gross measure that food quality has been increased with fertilizer
addition has already been seen in that the year after fertilizers were
first applied, there were four times as many leafhoppers present in the
study area. Appendix X show the mean number of leafhoppers present
on plots given different treatments in 1978 and 1979 respectively.

Nitrogen

Plots that received N fertilizer had significantly more leaf-hoppers present than plots not fertilized with a N dressing (Table 3.7). Further, delphacids were present in significantly greater numbers on the N fertilized plots, whilst the cicadellids tended to be more abundant on those plots not receiving N fertilizer.

Figs.3.8 and 3.9 show the relationship between the mean number of leafhoppers within a feeding type (phloem, mesophyll & xylem) and the mean nitrogen content of the plants. There is a general linear relationship between leaf soluble N levels and the size of the phloem feeding population (Fig.3.8). Mesophyll feeders exhibit different patterns in the two sampling years (Fig.3.9) which suggests other factors in conjunction with leaf total N levels may be responsible for the size of the populations.

The variation in seasonal fluctuations of insects and nitrogen levels is compounded when dealing with means of both types of parameters. In some cases the results are obscured by the large differences assoc-iated with the seasonal fluctuation of both insects and plant N levels. It is appropriate therefore to examine the times when insects reach maximum abundance in the field and then to examine the plant N levels corresponding to this time. Adult Z.scutellaris reach maximum abundance on those plots with leaf nitrogen levels approximating 20 mgN/gm dry weight (Fig.3.10). The range of the nitrogen level that permits the highest population of adult Z.scutellaris is quite small with variations in nitrogen on either side of this level resulting in drastically reduced populations.

Adult D.hamata, the most abundant phloem feeder in 1979 reached maximum abundance on those plots with leaf soluble nitrogen levels around 4 mg N/gm dry wgt. (Fig.3.11). The shape of the relationship

Table 3.7   Mean leafhoppers/m^2 with and without N fertilizer

| | Treatment | | |
	$\overset{+}{N}^1$	$\overline{N}^2$	Significance[3]
1978			
Total leafhoppers	161	106	P<0.001
Delphacidae	83	22	P<0.001
Cicadellidae	41	37	NS
1979			
Total leafhoppers	638	542	P<0.001
Delphacidae	456	307	P<0.001
Cicadellidae	182	235	P<0.001

1. plots with N fertilizer

2. plots without N fertilizer

3. 2 way ANOVA with column contrasts

Fig. 3.8   Mean abundance of phloem feeders
            associated with mean leaf nitrogen
            levels in 1978 (O) and 1979 (●).

Fig.3.9   Mean abundance of mesophyll feeders
            associated with mean leaf total
            nitrogen levels in 1978 (O) and
            1979 (●).

Leaf soluble nitrogen (mg N/gm dry weight)

Leaf total nitrogen (mg N/gm dry weight)
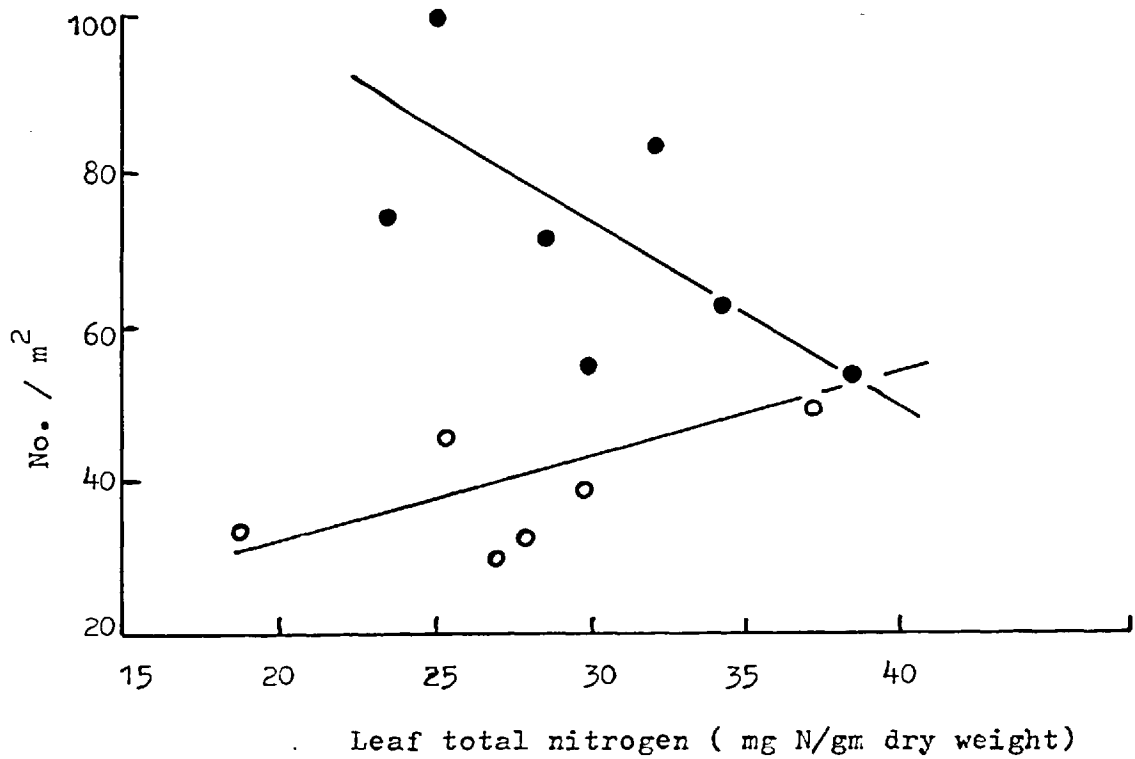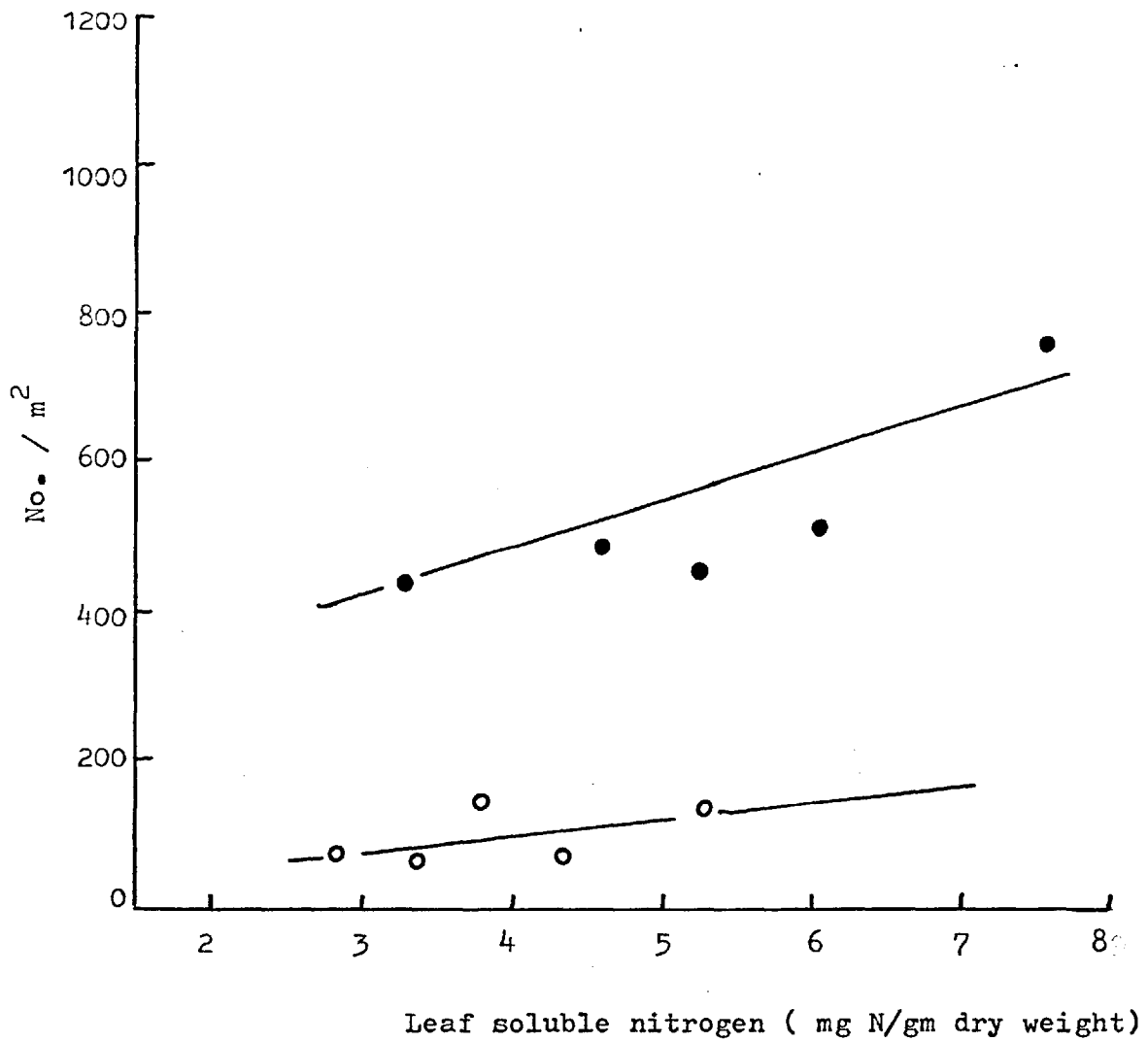
Fig. 3.10. Peak adult _Z. scutellaris_ abundance associated
with leaf total nitrogen levels.
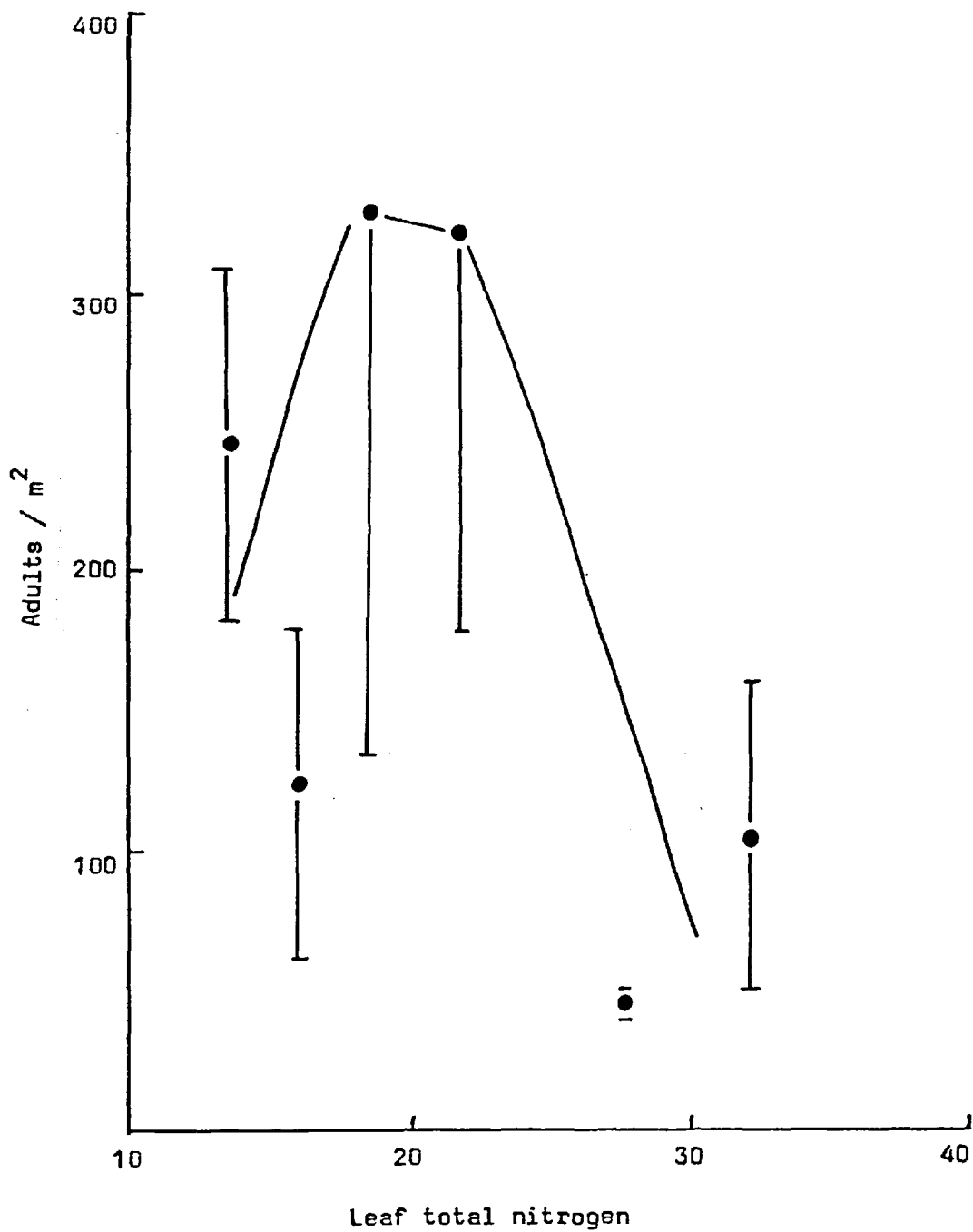
is similar to that shown by Fig.3.10 and is characterised by a rela-
tively sharp peak around a certain nitrogen level in the plant,
deviations from this level resulting in a lower level of adult abun-
dance.

Adult J.pellucida increase their abundance with increasing levels
of leaf nitrogen (Fig.3.12) in a way similar to that shown by total
phloem feeders (see Fig.3.9). It is also apparent that this species
was not present in the field as adults during times of extremely high
leaf N levels so that the graph may only represent the ascending
portion of the peak. Very low nitrogen levels, and very high nitrogen
levels, theoretically should support very low levels of insects, such that
a curvilinear relationship similar to that shown by D.hamata will be
seen. It is interesting to speculate at this stage that J.pellucida
must have a much wider band of leaf nitrogen levels that it is assoc-
iated with, than both D.hamata and Z.scutellaris.

Fig.3.13 shows the relationship between peak adult abundance and
soluble nitrogen levels in the grass during peak abundance of first
generation A.ocellaris in 1979. A.ocellaris reaches maximum abundance
on those areas with a leaf nitrogen level below that of both D.hamata
and J.pellucida.

The number of first instar nymphs related to the leaf nitrogen
levels during the previous adult generation is shown in Fig.3.14 for
A.ocellaris. A greater number of nymphs/female emerged on those plots
which had the greatest adult abundance (Fig.3.13). It is unfortunate
that it was not possible to determine fecundity and egg mortality in the
field as differences in both these factors could account for the differ-
ences shown in Fig.3.14. In Section IV, ovipositional rates for
reproducing females in constant environment conditions, suggested that
leaf nitrogen levels can markedly affect ovipositional performance so

Fig.3.11   Peak abundance of adult <u>D.hamata</u> assoc-
            iated with leaf soluble nitrogen levels.

Fig.3.12   Peak abundance of adult <u>J.pellucida</u> assoc-
            iated with leaf soluble nitrogen levels.

Soluble nitrogen levels (mg N / gm dry weight)

Soluble nitrogen levels (mg N / gm dry weight)
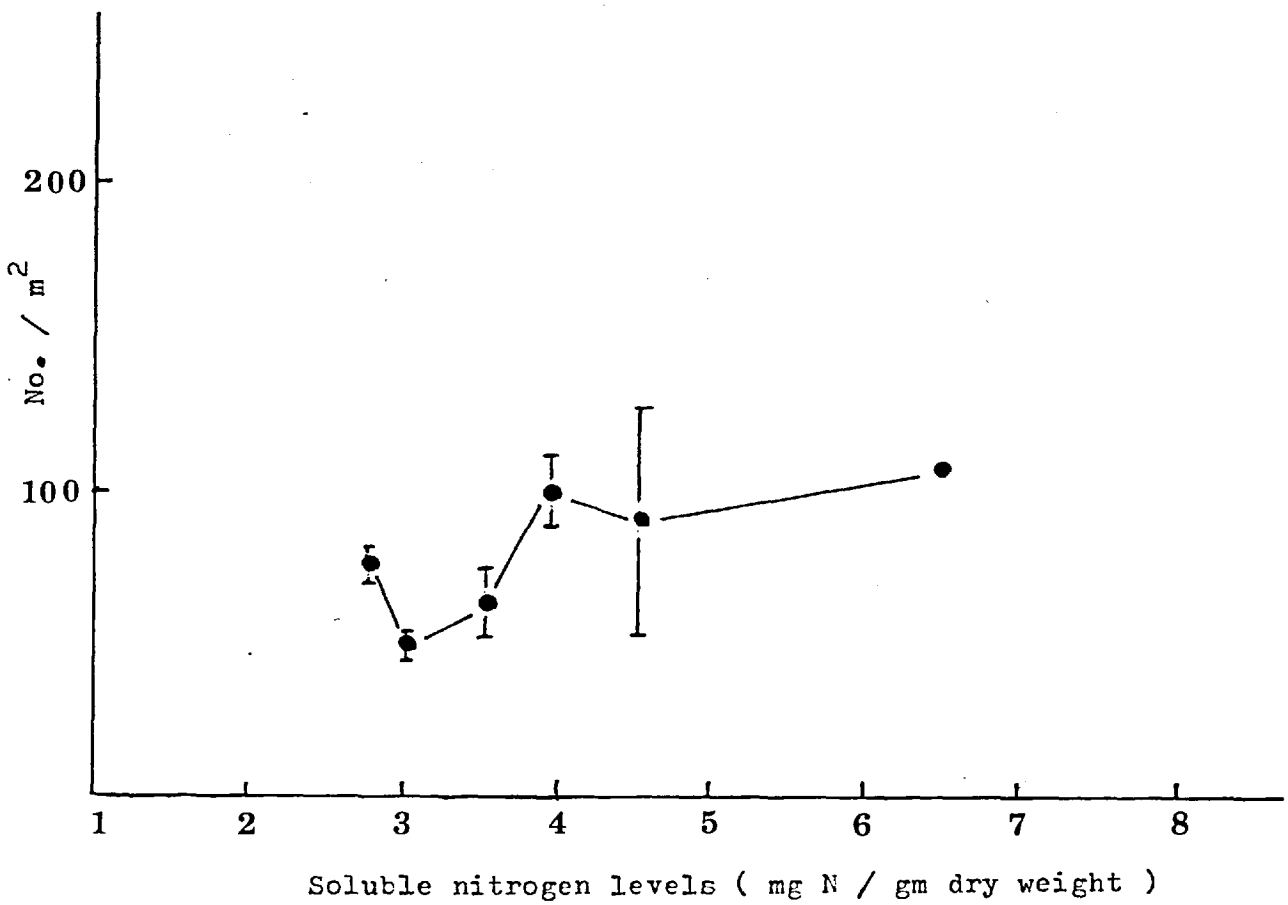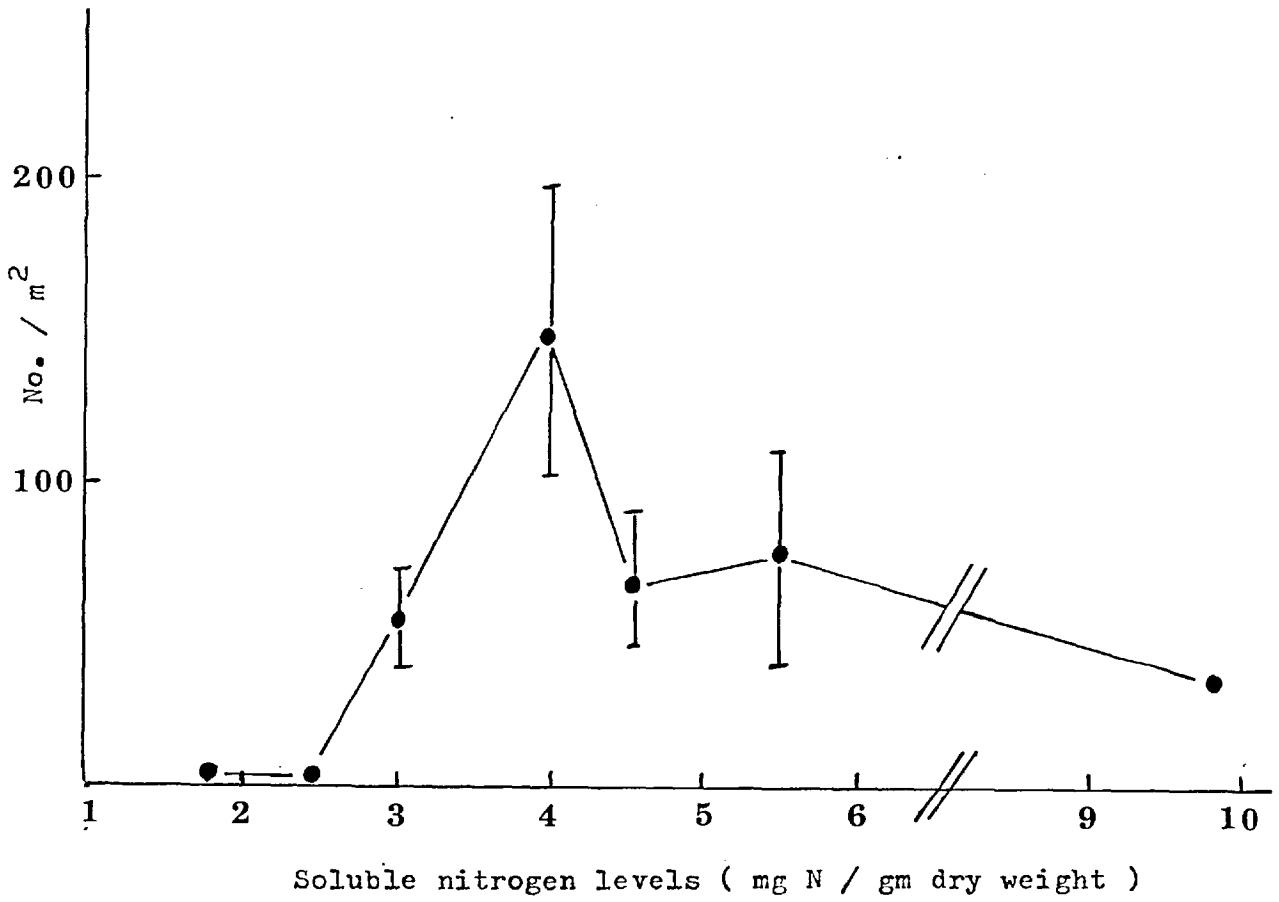
Fig.3.13   Peak abundance of adult A.ocellaris
           associated with leaf soluble nitrogen
           levels.

Fig.3.14   The number of nymphs/female A.ocellaris
           associated with leaf soluble nitrogen
           levels during adult flight period.

$Adults / m^2$

Leaf   soluble   N

$Nymphs / ♀♀$

Leaf   soluble   N
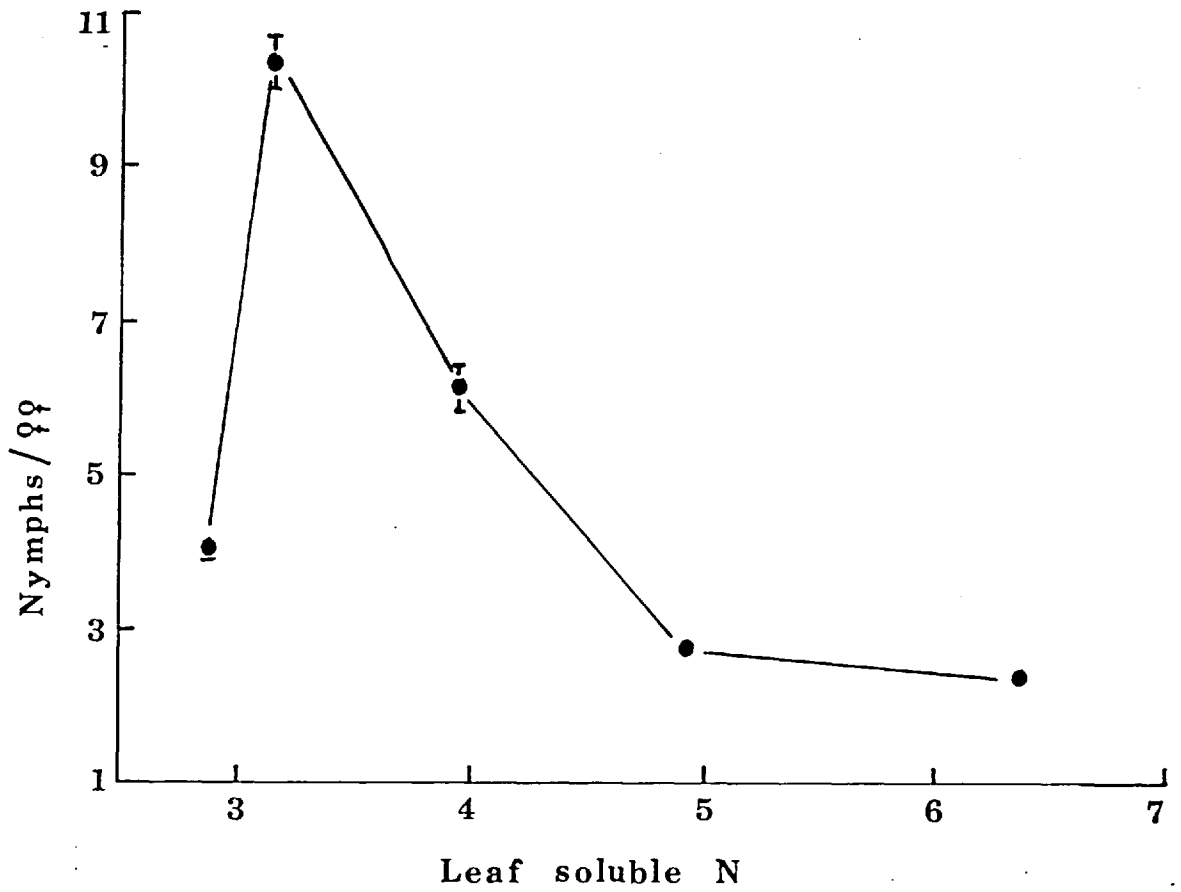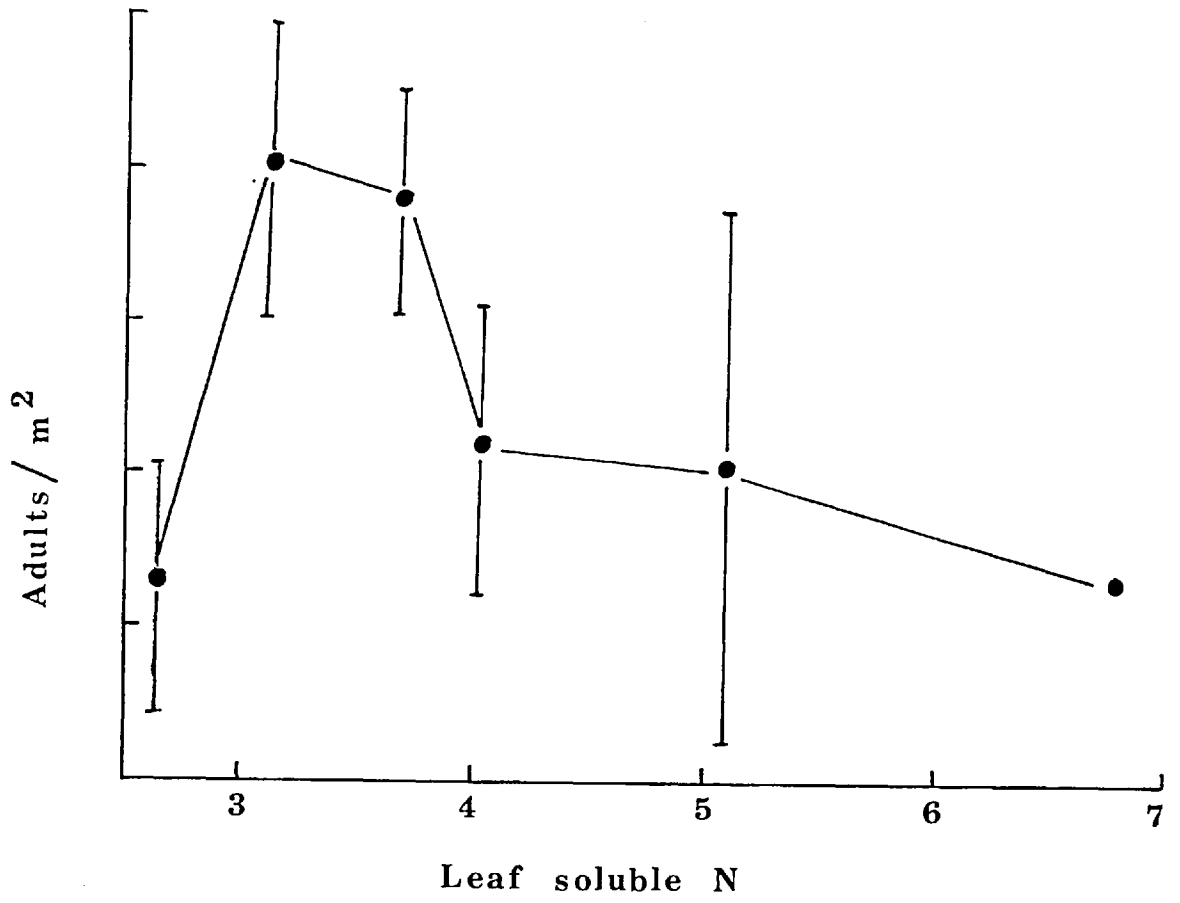
the shape of Fig.3.14 is probably representative of the increase in

female fecundity rather than differences in egg mortality.

3.3.4.2 Potassium

In 1979, data are available with which to interpret the influence

of potassium levels on the leafhopper populations. Fig.3.15-3.17

show the numbers of total leafhoppers, phloem, mesophyll and xylem

feeders associated with a particular potassium level in the leaf. In

general, the patterns of total leafhoppers, phloem and mesophyll

feeders show a bimodal distribution. Xylem feeders exist at low pop-

ulation levels irrespective of the levels of leaf potassium (over the

range recorded). Phloem feeders, because they exist in the greatest

proportion, determine the shape of the curve for total leafhoppers.

It is interesting that both phloem and mesophyll feeders show more

or less the same pattern, and both peak at approximately similar

potassium leaf levels.

Fig.3.18 shows the relationship between leaf K levels and the

insect families. Delphacids exhibit a bimodal distribution whilst

the cicadellids have a linear relationship, although there is a ten-

dency to increase in abundance with an increase in leaf potassium

levels.

Interpretation of the leaf potassium data when adult Z.scutellaris,

D.hamata, J.pellucida and A.ocellaris are at maximum abundance is shown

in Figs.3.19-3.22. All leafhopper species attain maximum abundance

on those plots with leaf potassium levels approximating 22 mgK/gm dry

wgt. The shape of the graphs are similar in many respects to the shape

of the graphs showing leaf nitrogen levels during peak adult abundance

(see Figs.3.10-3.13). This is not surprising as both macronutrients

are closely linked, any increase in the level of one results in an

increase in the other. It is most probable that the leafhoppers are

Fig.3.15   The abundance of leafhoppers associated
           with leaf potassium levels.

Fig.3.16   The abundance of phloem feeders associated
           with leaf potassium levels.

Leaf K mg K / gm dry wgt.

Leaf K mg K / gm dry wgt.
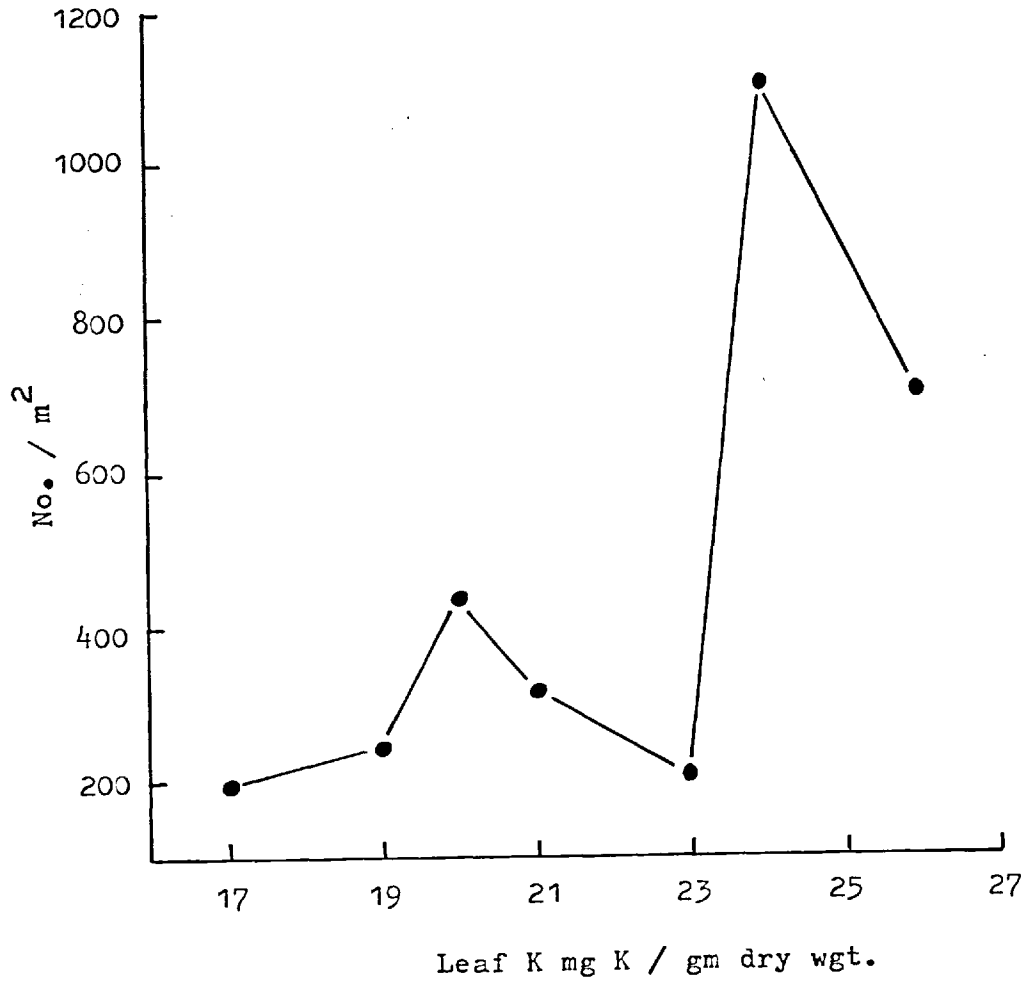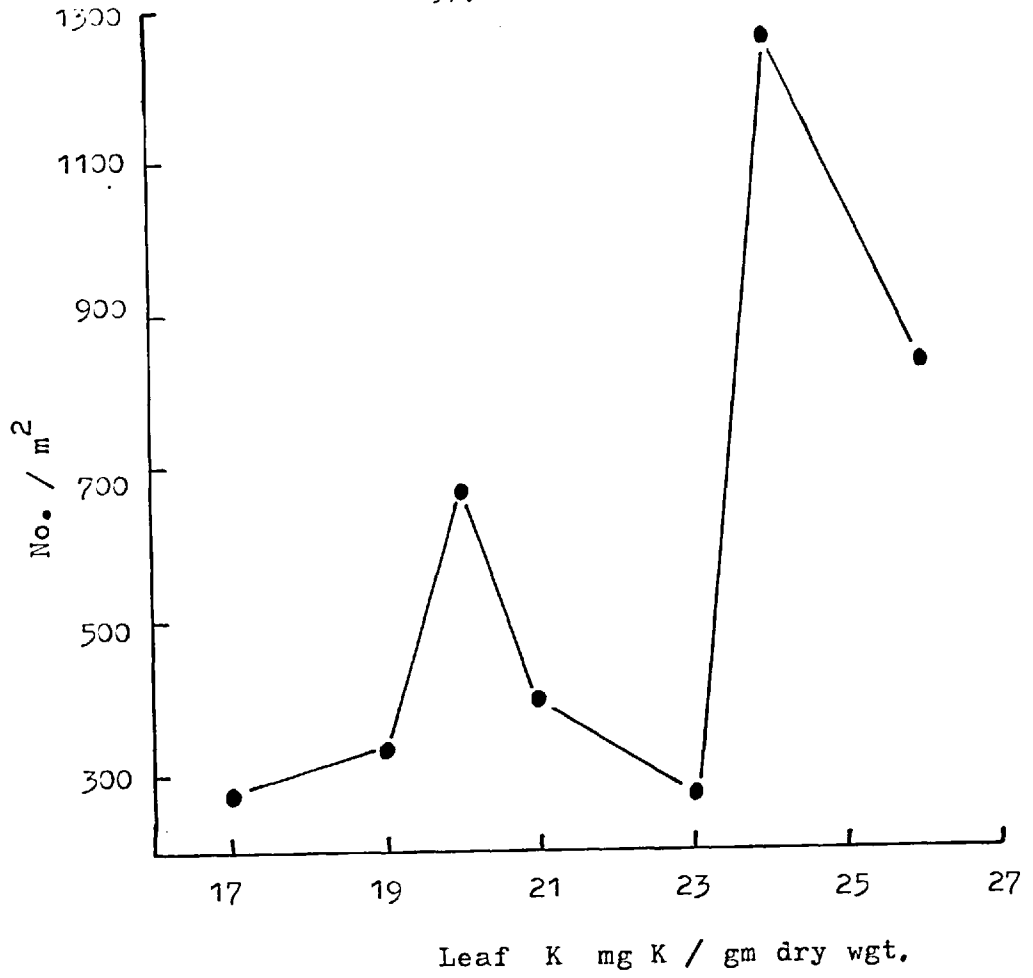
Fig.3.17   The abundance of mesophyll (O) and xylem
           (●) feeders associated with leaf potassium
           levels.

Fig.3.18   The abundance of Delphacidae (O) and
           Cicadellidae (●) associated with leaf
           potassium levels.

Leaf K mg K / gm dry wgt.

Leaf K mg K / gm dry wgt.
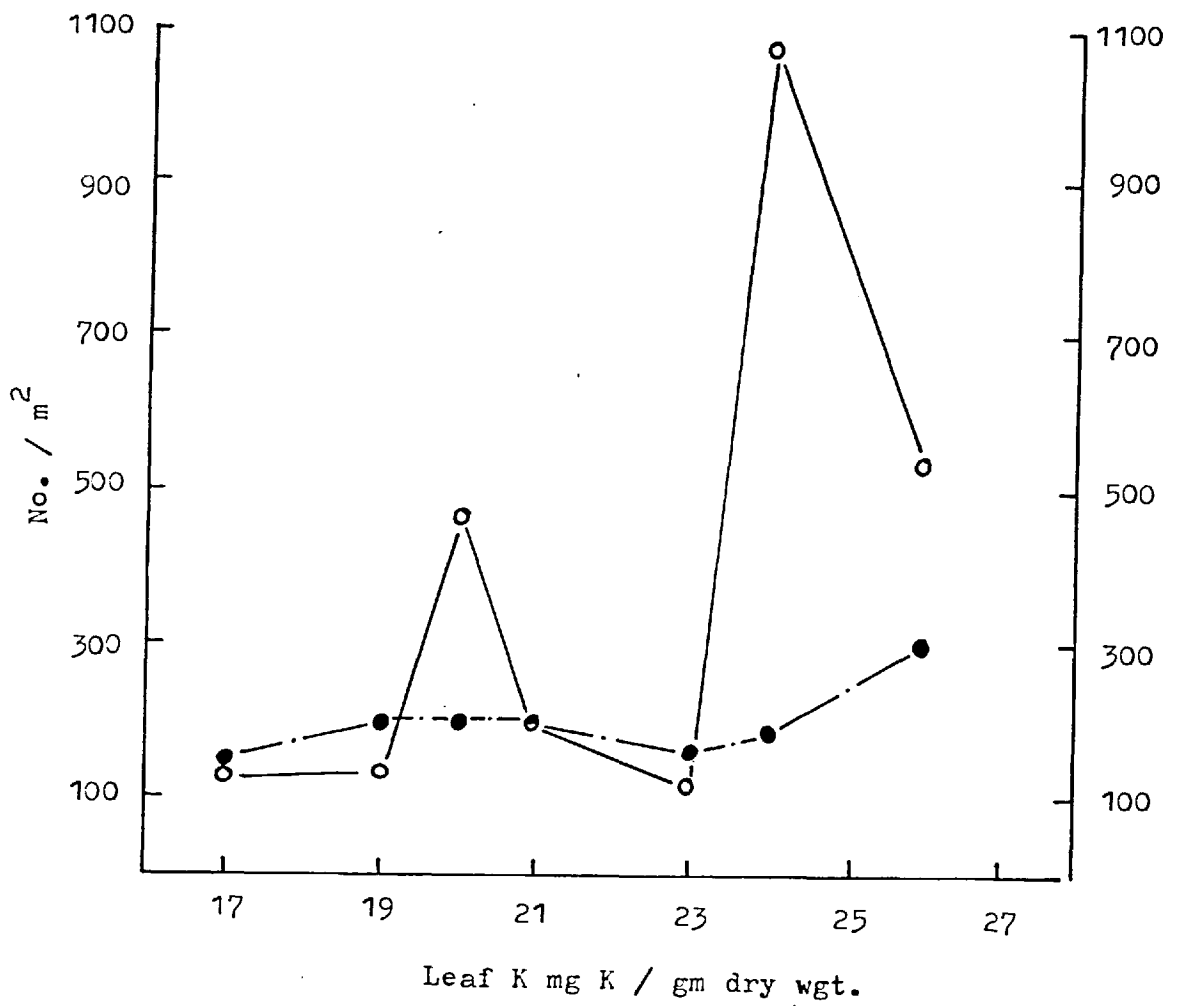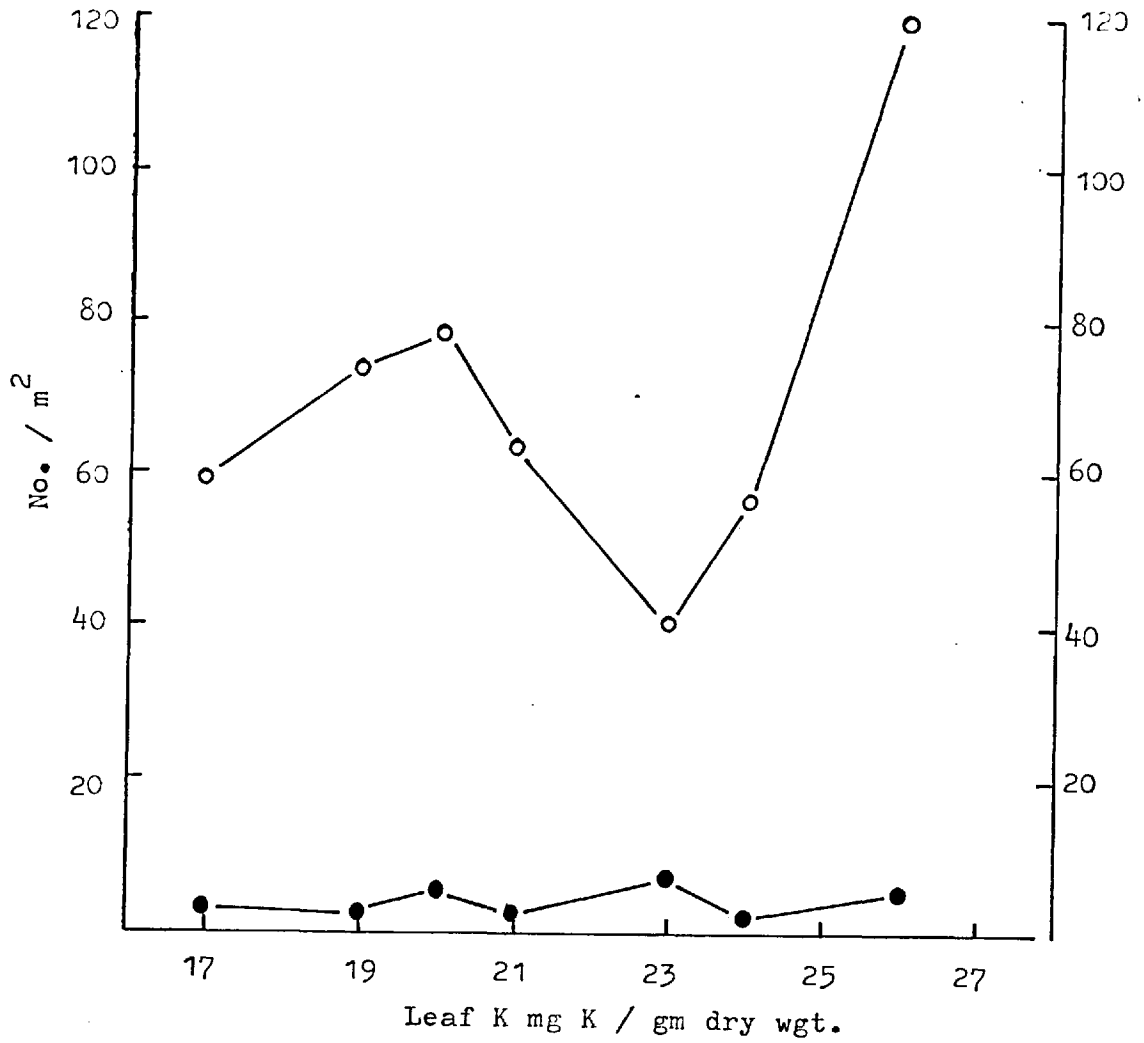
Fig.3.19   Peak adult Z.scutellaris abundance assoc-
           iated with leaf potassium levels.

Fig.3.20   Peak adult D.hamata abundance associated
           with leaf potassium levels.

No. / m^2

Leaf K (mg K / gm dry wgt.)

No. / m^2

Leaf K (mg K / gm dry wgt.)
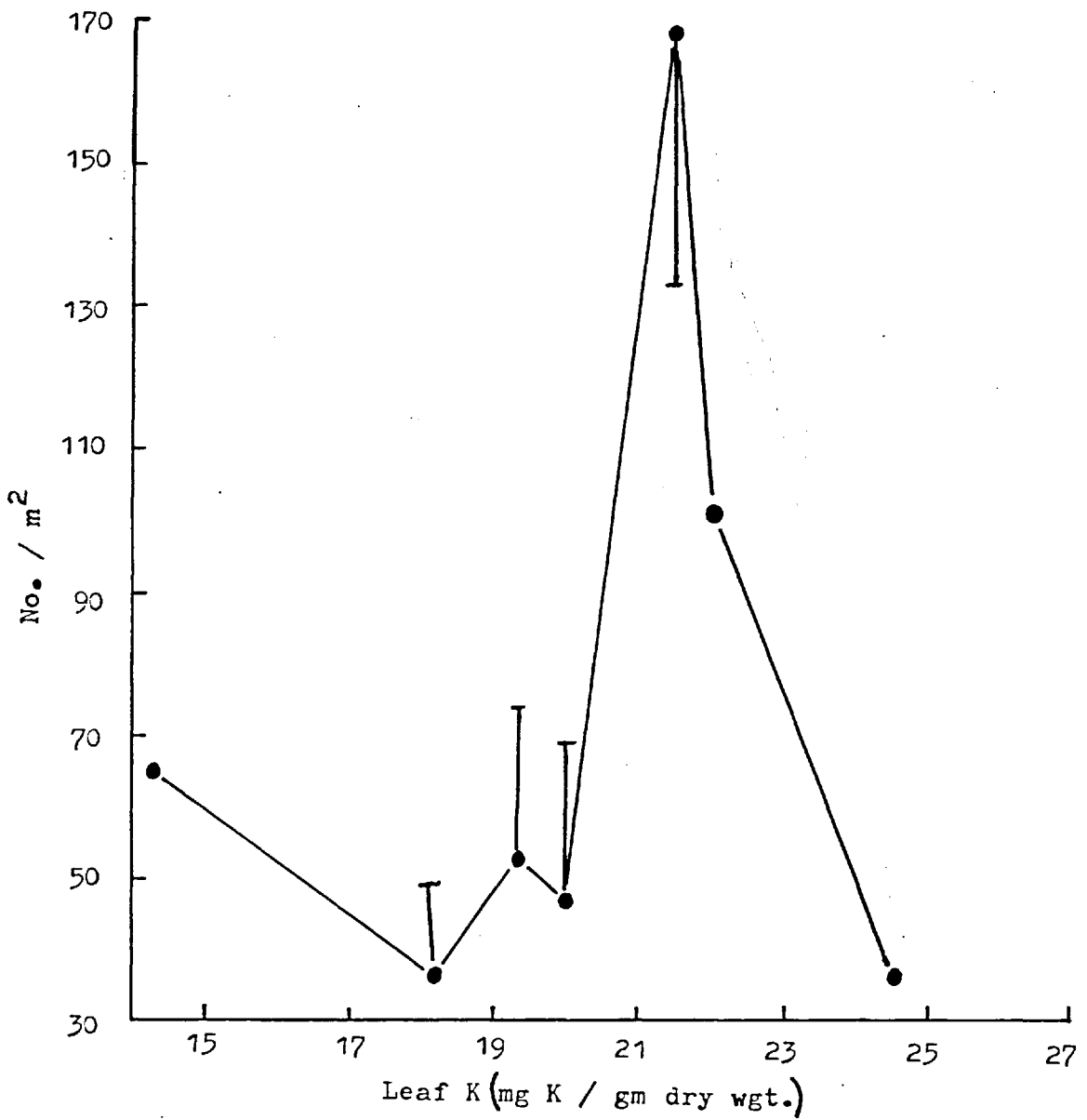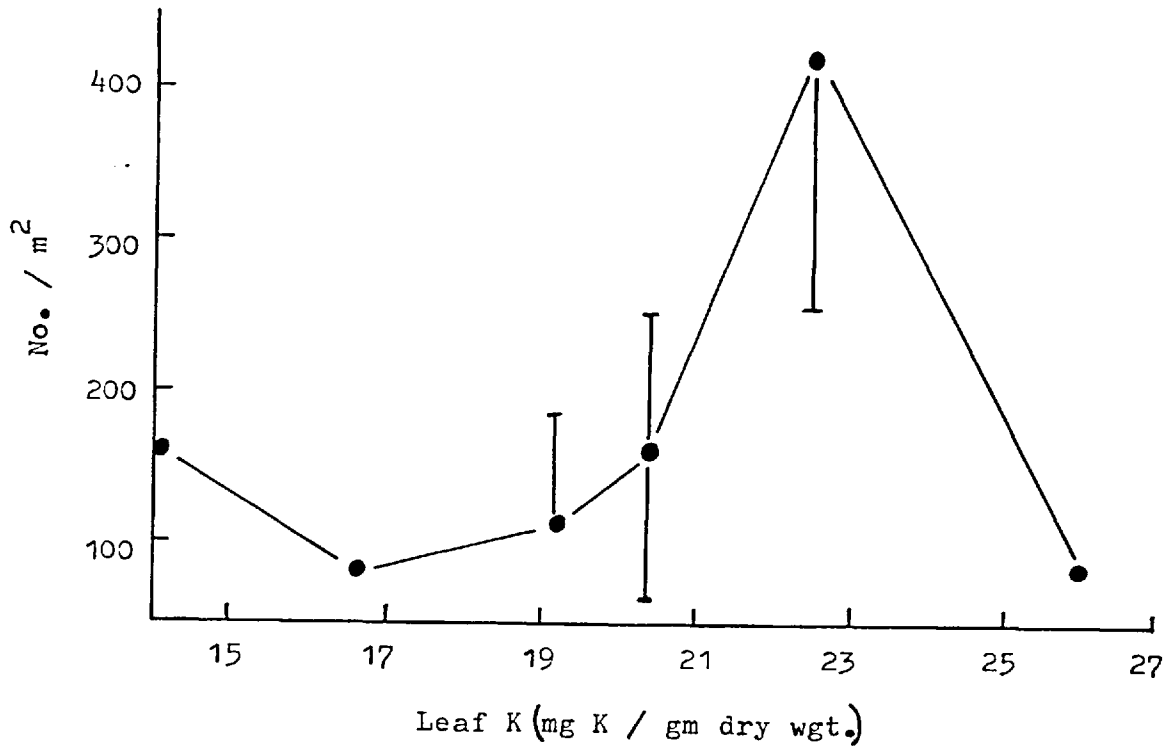
Fig.3.21　Peak adult *J.pellucida* abundance assoc-
iated with leaf potassium levels.

Fig.3.22　Peak adult *A.ocellaris* abundance associated
with leaf potassium levels.

Leaf potassium   (mg K / gm dry weight)

Leaf potassium   (mg K / gm dry weight)
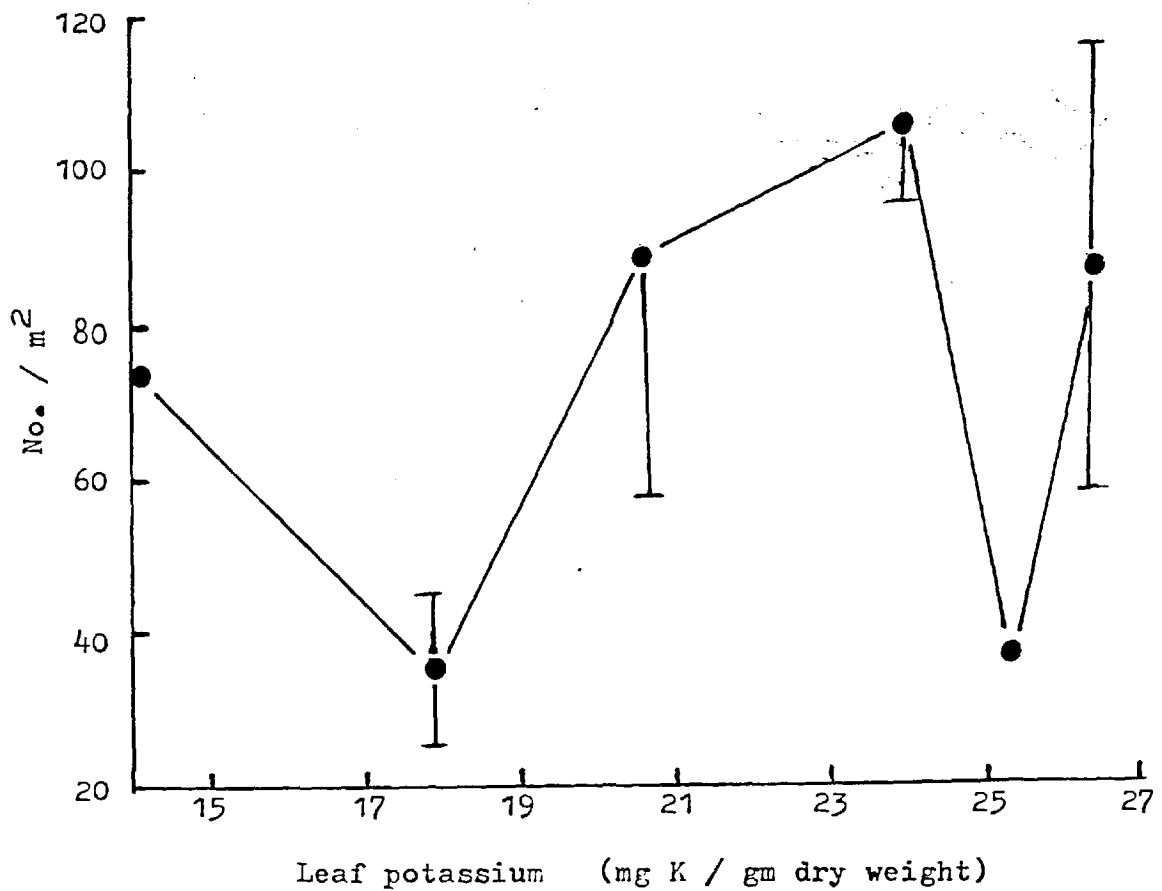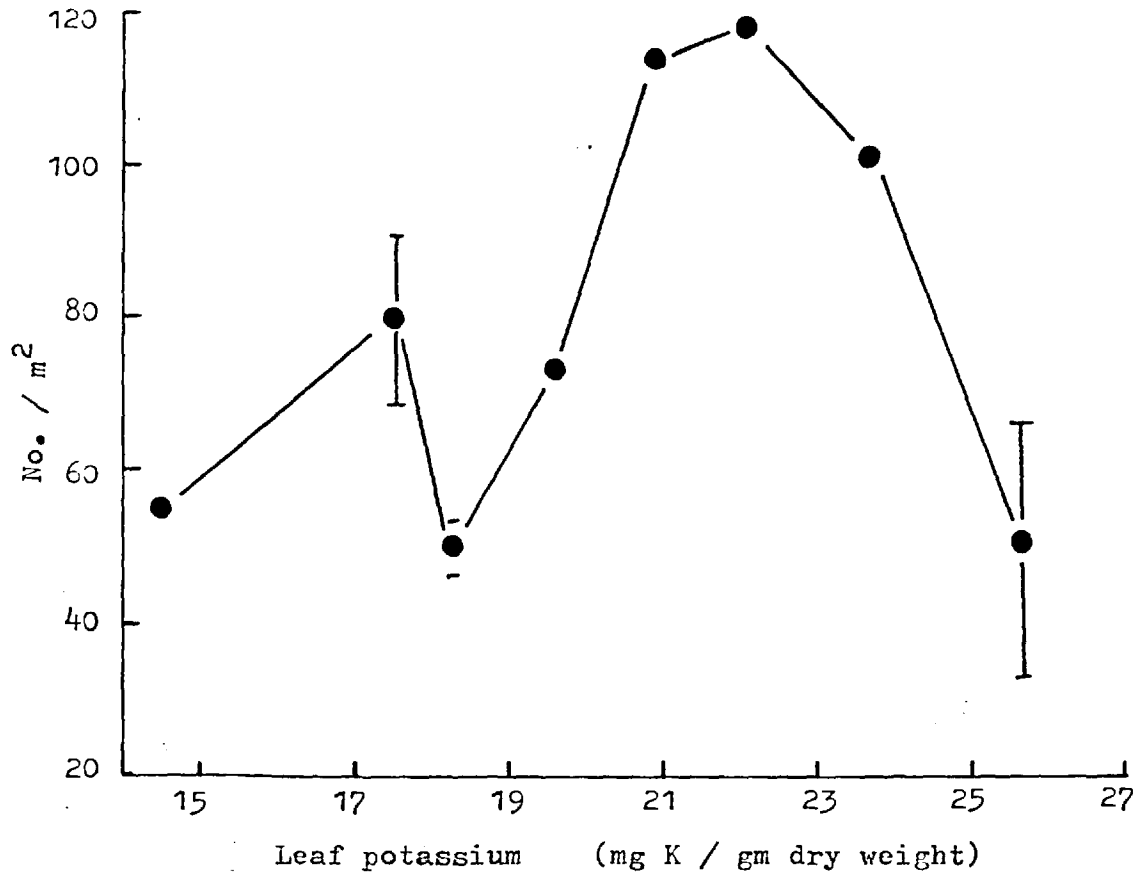
responding to an overall increase in food quality, and the nutrients

that are measured are then only an index of food quality.

Phosphorus

Figs.3.23 and 3.24 show the number of leafhoppers and, Delphacidae

and Cicadellidae associated with leaf phosphorus levels in 1979. Total

leafhoppers/m^2 and delphacids/m^2 exhibited a linear relationship, abun-

dance increased as the levels of phosphorus in the leaf increased.

Cicadellids, although showing a positive linear relationship with leaf

phosphorus levels, remained relatively unaffected by the levels of leaf

phosphorus.

When leafhoppers were divided into feeding types, phloem feeders

were the most affected by increased leaf phosphorus levels (Fig.3.25).

They increased in abundance to a maximum point at 4.2 mg P/gm dry wgt.

It is possible that low leaf phosphorus levels restrict the abundance

of mesophyll feeders, as leaf phosphorus levels greater than 2.8 mg P/

gm dry wgt supported a similar population size. Xylem feeders remained

at low levels over the range of leaf phosphorus levels measured and

showed no obvious patterns of distribution according to leaf phosphorus

levels.

Interpretation of the leaf phosphorus data when adult Z.scutellaris,

D.hamata, J.pellucida and A.ocellaris are at maximum abundance in the

field is shown in Figs.3.26-3.29. Z.scutellaris and J.pellucida attain

maximum abundance on those plots with leaf phosphorus levels at 3.5 mgP/

gm dry wgt.and 2.7 mg P/gm dry wgt.respectively and then decrease in

abundance on those plots with higher leaf phosphorus levels. A.ocellaris

remained at relatively the same level of abundance over the range of leaf

phosphorus levels examined although at higher levels, e.g. 5.3 mg P/gm

dry wgt., there may have been a tendency to increase. D.hamata increased

its abundance as leaf phosphorus levels increased. It is unfortunate

Fig.3.23   The abundance of leafhoppers associated
            with mean leaf phosphorus levels.

Fig.3.24   The abundance of Delphacidae (●─●) and
            Cicadellidae (O─O) associated with mean
            leaf phosphorus levels.

leaf phosphorus levels (mg P/ gm dry weight)

Leaf phosphorus levels (mg P/ gm dry weight)
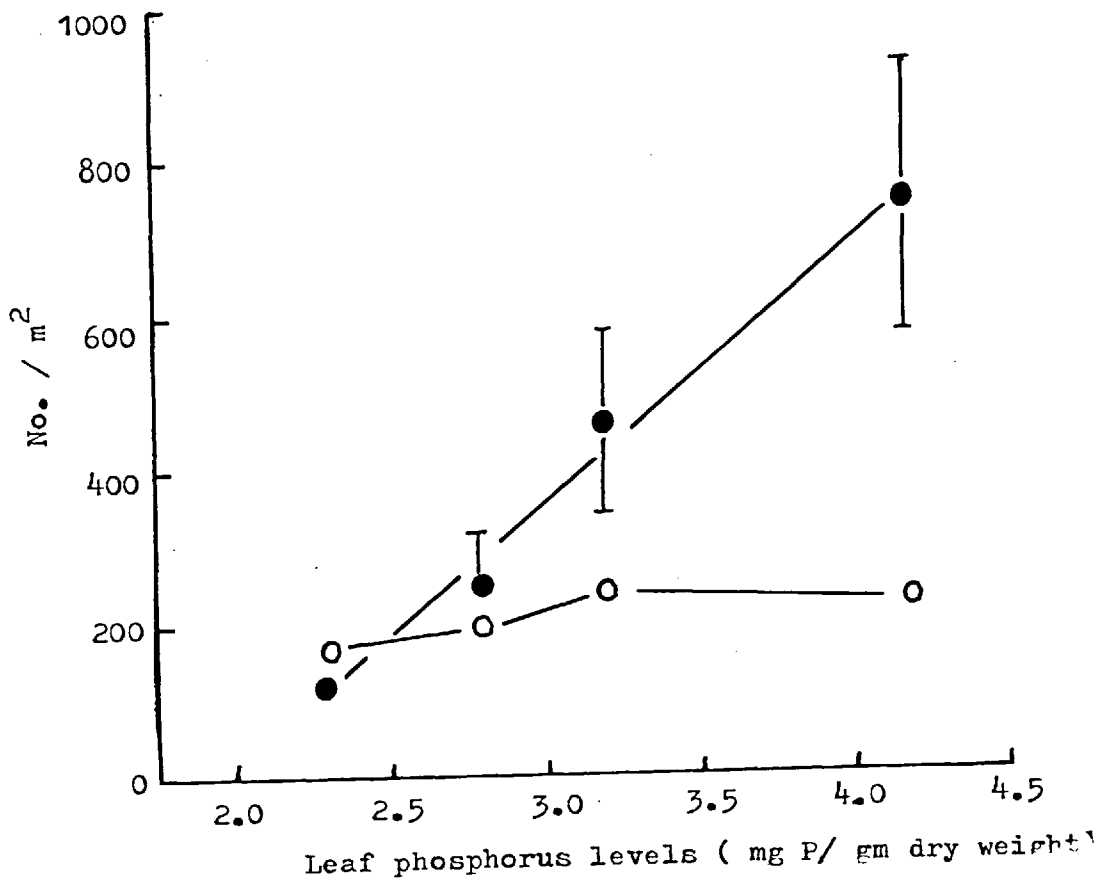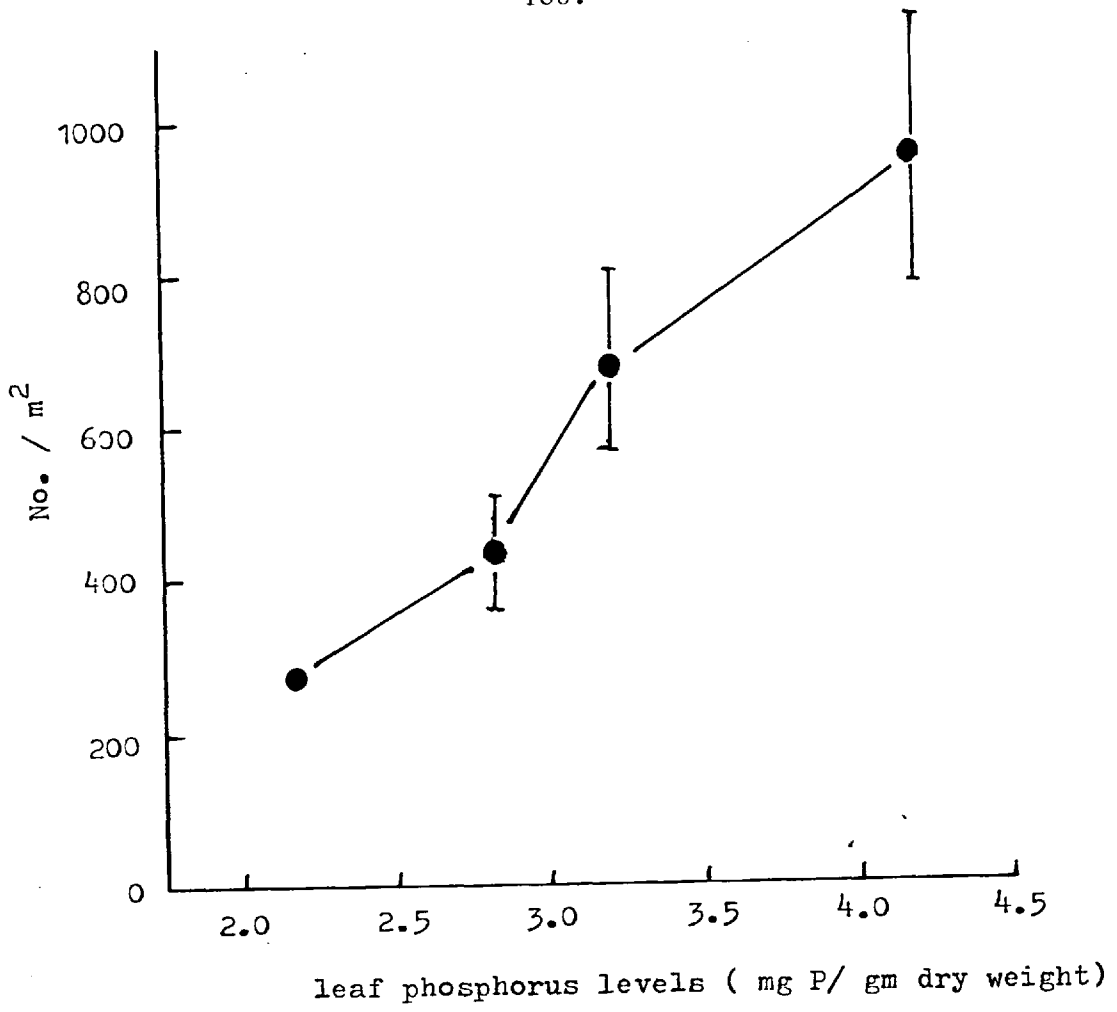
Fig.3.25. Phloem (O-O), Mesophyll (●-●), and Xylem (●--●)

feeder density associated with leaf phosphorus

levels.

Leaf phosphorus levels (mg P / gm dry weight)
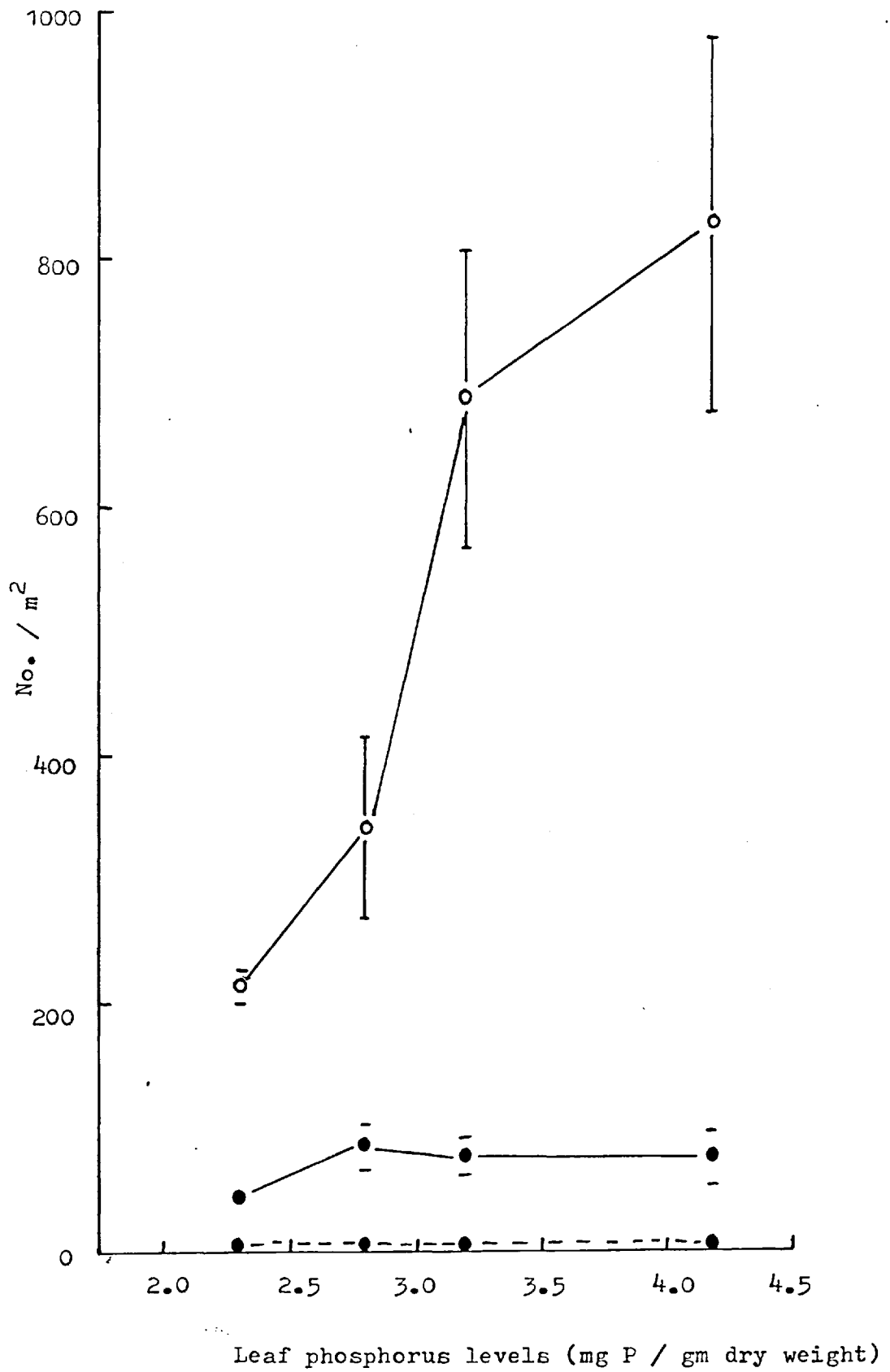
Fig.3.26   Peak adult Z.scutellaris abundance
           associated with leaf phosphorus
           levels.

Fig.3.17   Peak adult A.ocellaris abundance
           associated with leaf phosphorus
           levels.

Leaf phosphorus levels   (mg P / gm dry weight)

Leaf phosphorus levels   (mg P / gm dry weight)
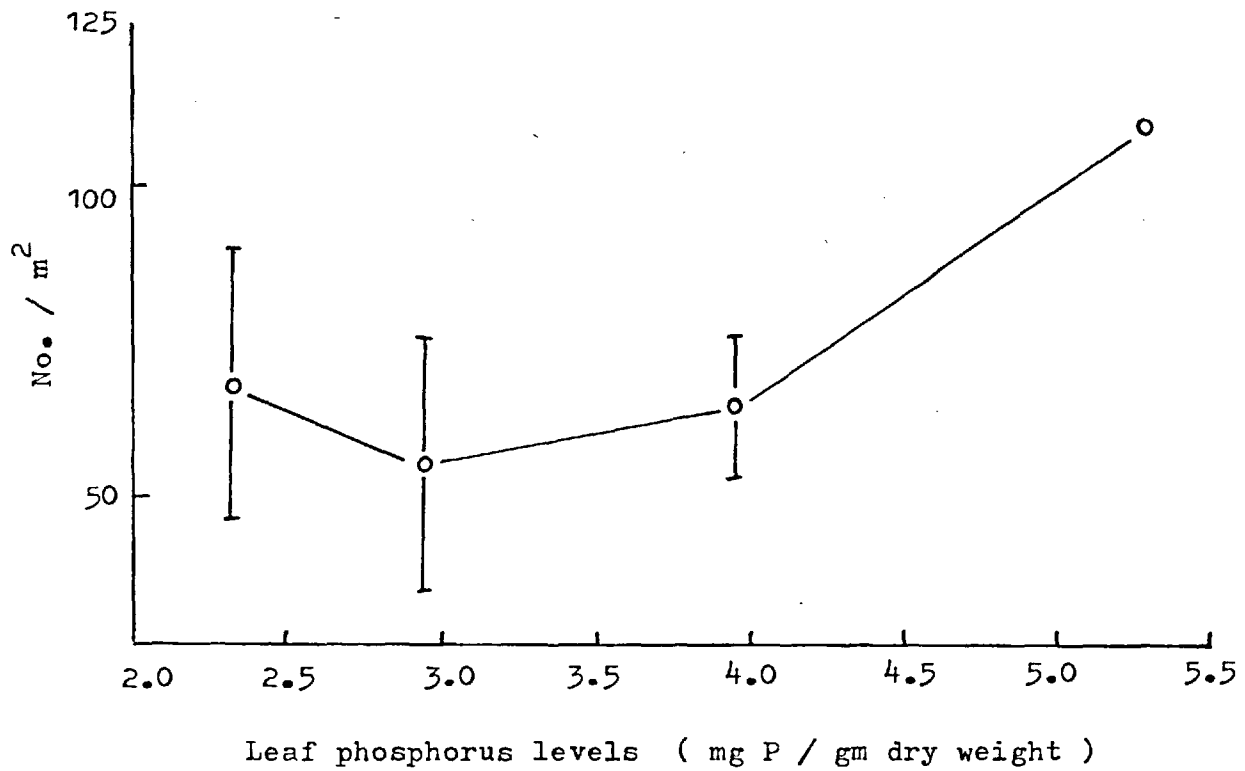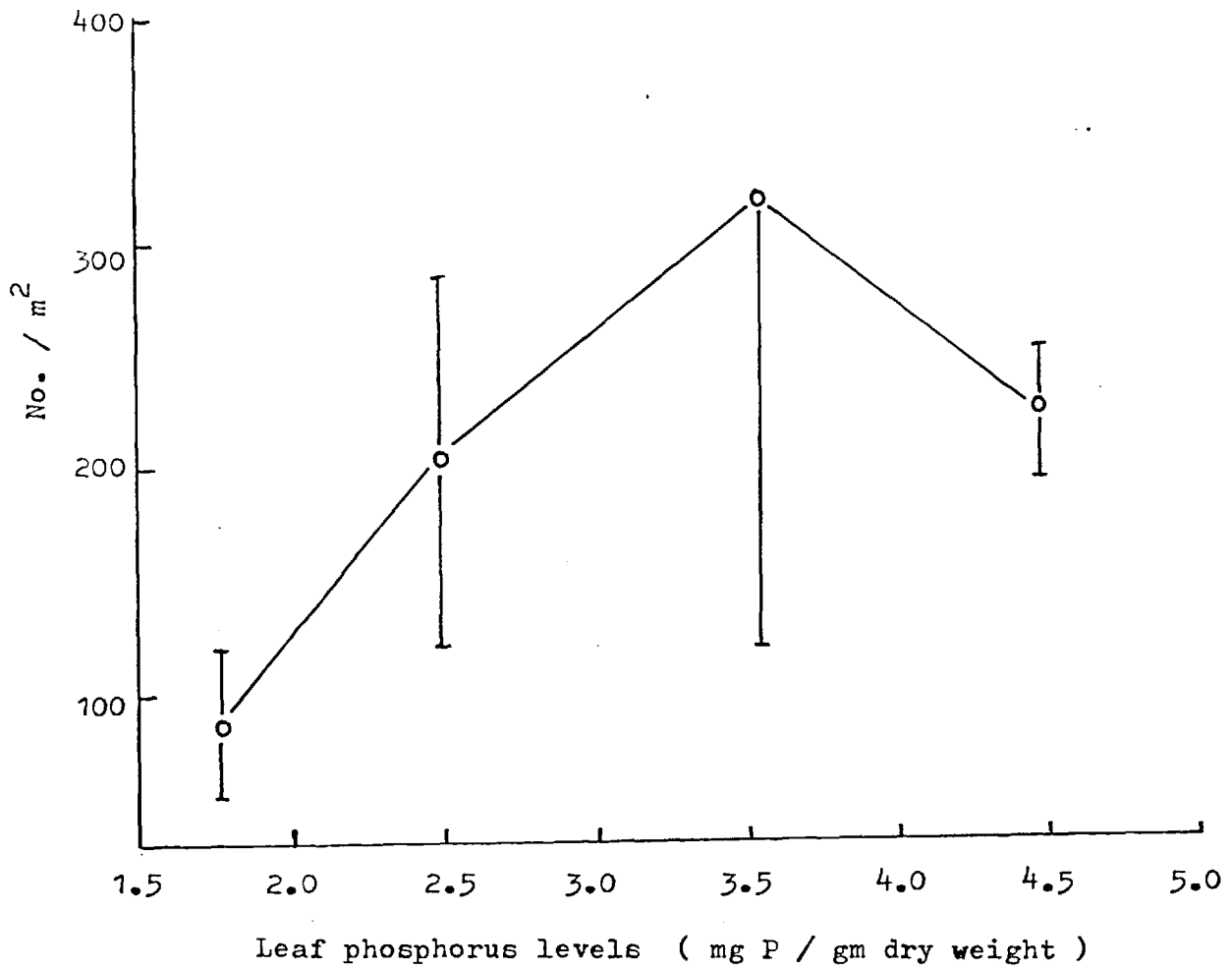
Fig.3.28   Peak adult *J.pellucida* abundance
           associated with leaf phosphorus
           levels.

Fig.3.29   Peak adult *D.hamata* abundance
           associated with leaf phosphorus
           levels.

Leaf phosphorus levels   (mg P / gm dry weight)

Leaf phosphorus levels   (mg P / gm dry weight)
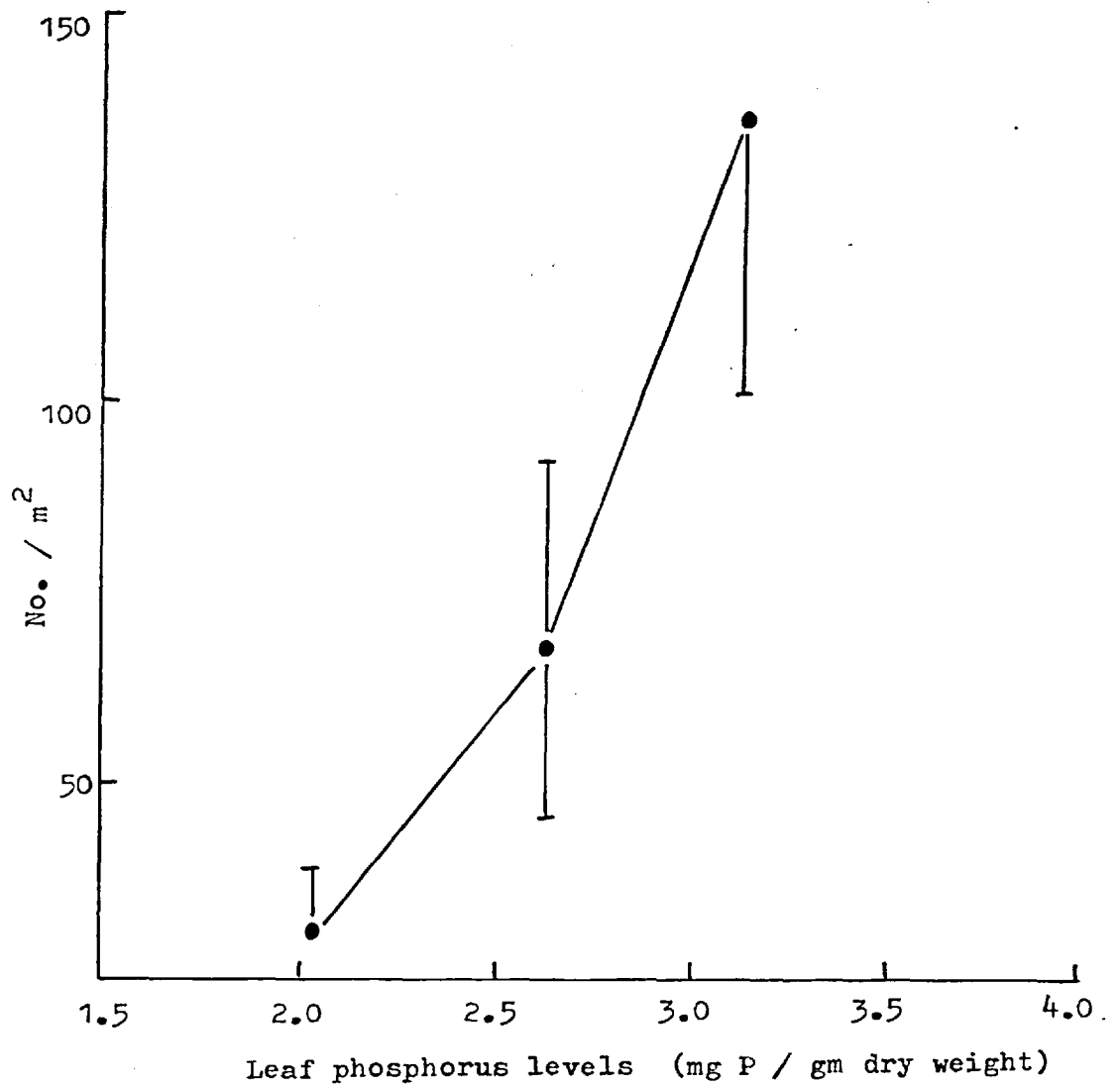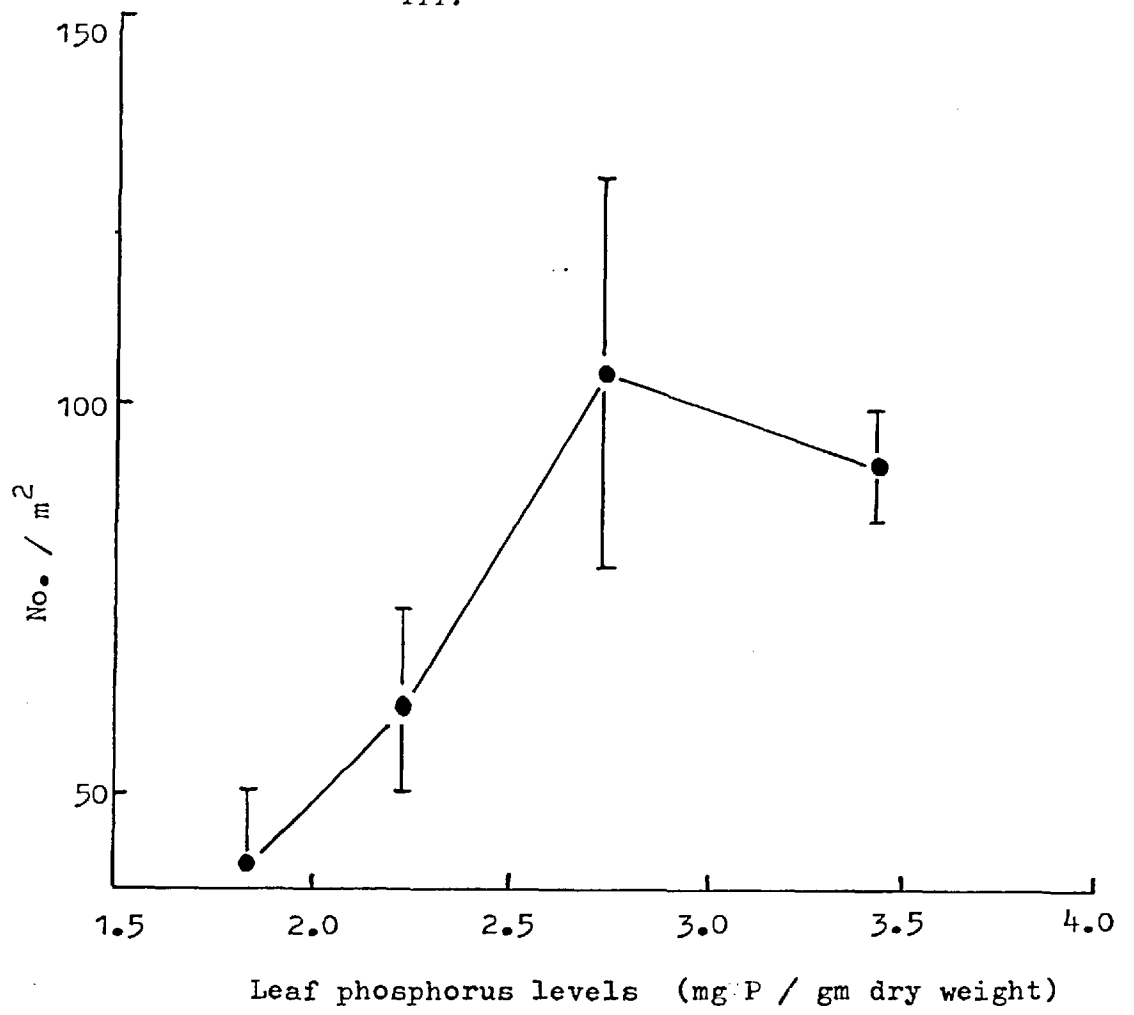
that D.hamata adults were absent in the field when higher levels of leaf phosphorus were available.

The levels of leaf nitrogen appear to be a more sensitive measure of leafhopper abundance than the levels of phosphorus and potassium. However, levels of nitrogen give no indication of the subtle dietary requirements of insects, therefore it was decided to examine the leaf soluble amino acids in the grass.

3.3.4.4 Amino acids

In 1979, data are available with which to examine associations between leafhoppers and leaf soluble amino acids (Figs.3.30-3.32). Early in the season, (including the spring growth period and part of early summer i.e. < mid July), there is no significant relationship between leaf soluble amino acid levels and the abundance of leafhoppers. After mid-July when first generation delphacids have emerged (D.hamata and J.pellucida mainly) there is a curvilinear relationship between the numbers of leafhoppers (in particular the Delphacidae) and leaf soluble amino acid levels. The Cicadellidae show the inverse relationship with higher populations existing on low leaf soluble amino acid levels. At amino acid levels above 6μm/100 mg dry wgt, the number of cicadellids remained fairly constant.

Two curves can be drawn through the data showing the number of phloem feeding leafhoppers and the levels of leaf soluble amino acids (Fig.3.33) in a way similar to Fig.3.30 which showed the number of leafhoppers associated with leaf soluble amino acid levels. Before mid-July when relatively low numbers of phloem feeders were present but leaf soluble amino acid levels ranged from 2-23 μm/100 mg dry wgt, no relationship was found (Fig.33). After mid-July when phloem feeder population increased (due to hatching of first generation nymphs) the relationship is curvilinear i.e. as the levels of leaf soluble amino

Fig.3.30. Density   of leafhoppers associated with leaf soluble amino acids.

(● prior to 3/7/79)

Leaf soluble amino acids μm / 100mg
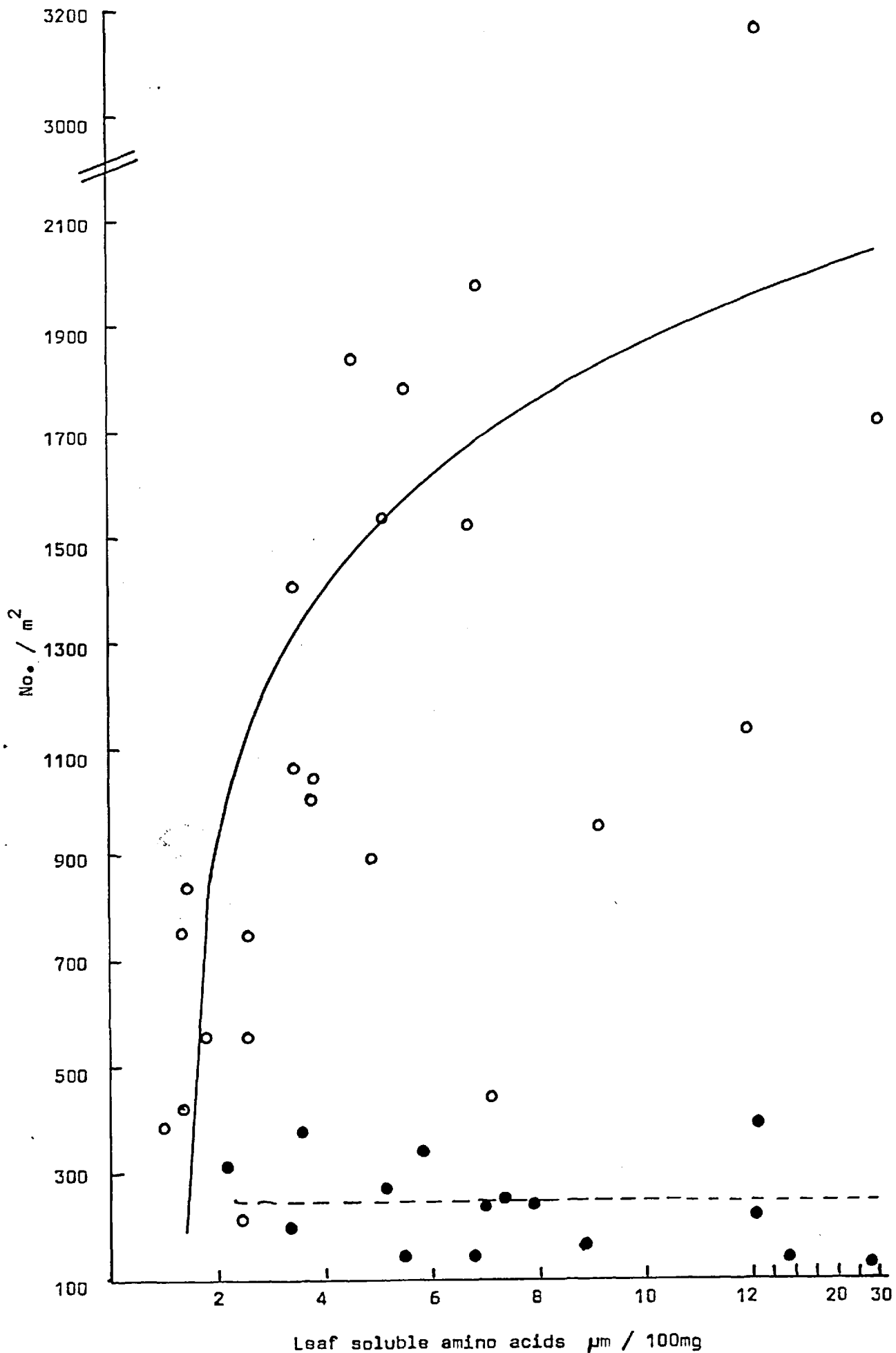
Fig.3.31. The abundance of Delphacidae associated with leaf soluble amino acids   (● Prior to 3/7/79)
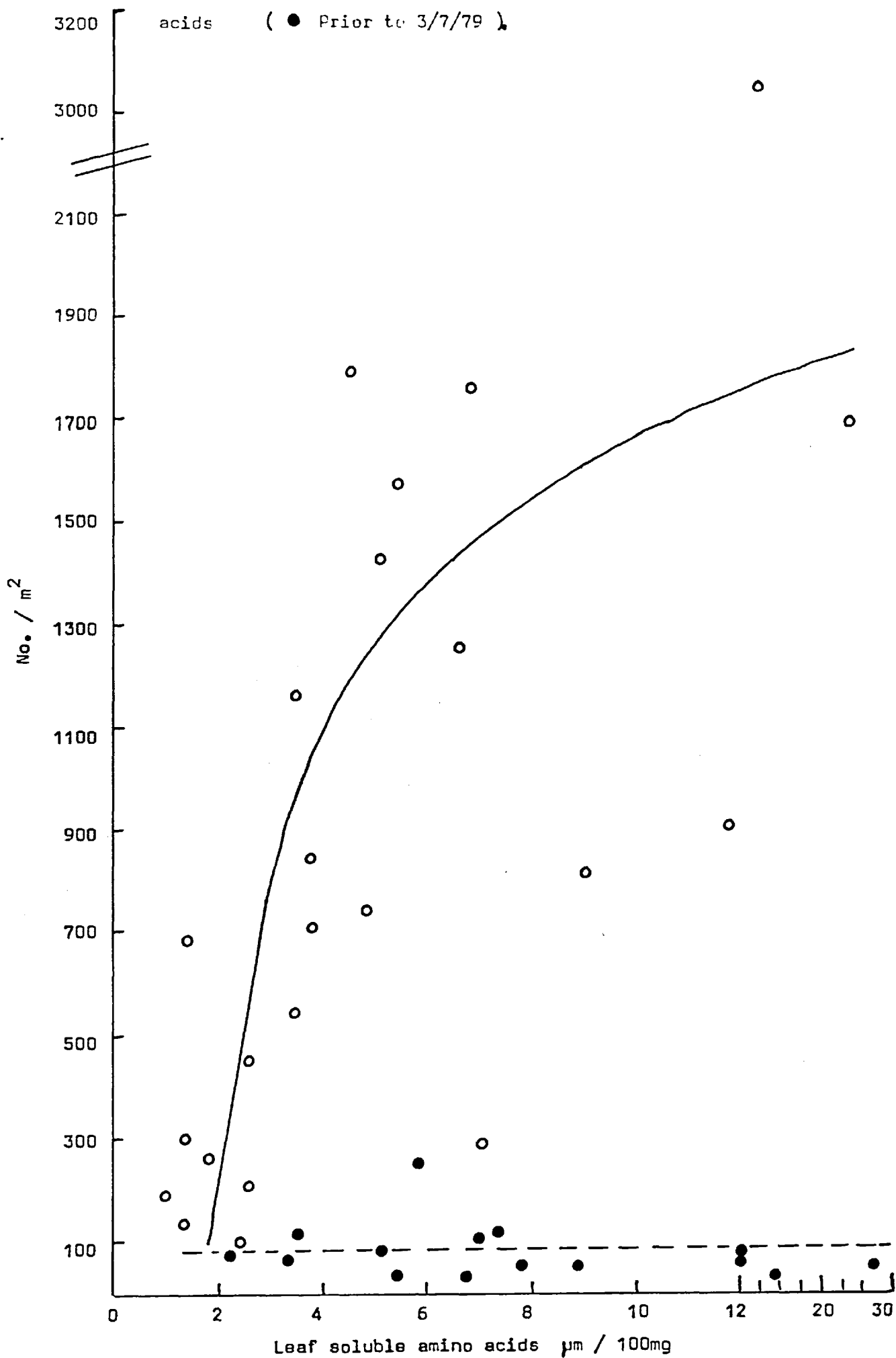
Fig.3.32. The abundance of Cicadellidae associated with leaf

soluble amino acids.

Leaf soluble amino acids μm / 100mg
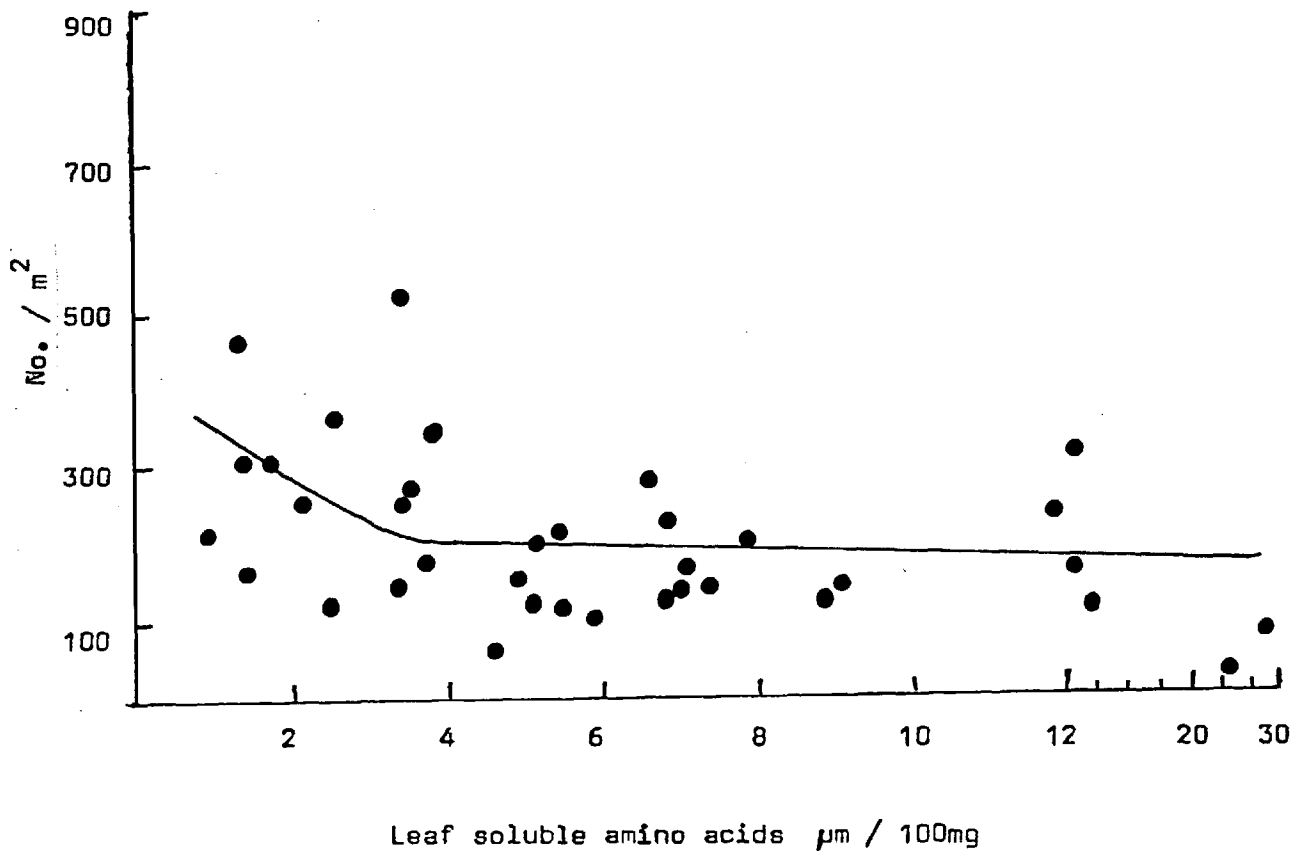
Fig.3.33. The abundance of phloem feeders associated with leaf
soluble amino acids. (o) Prior to 3/7/79.

Leaf soluble amino acids ug / 100mg
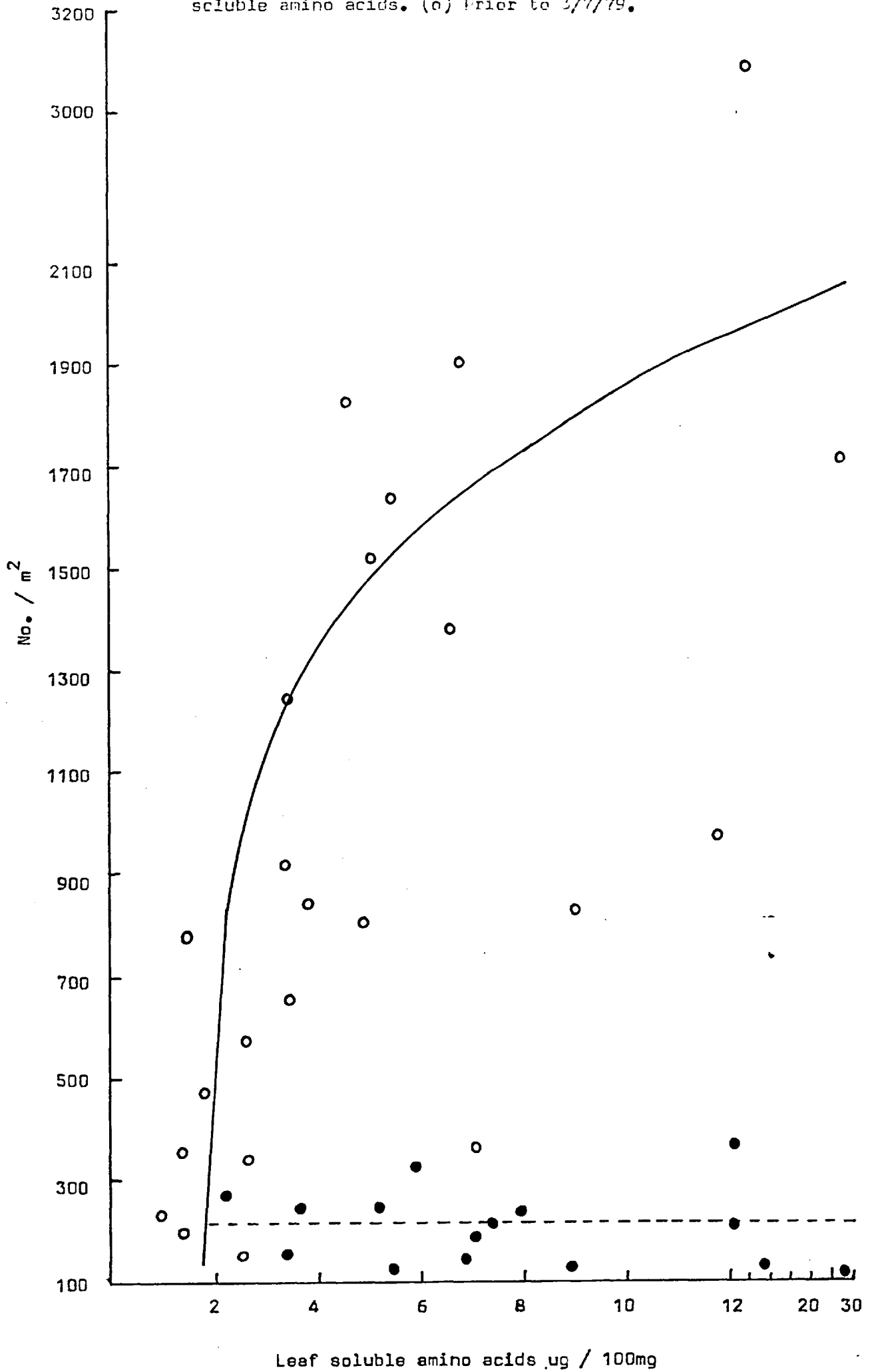
acids increased, the numbers of phloem feeding leafhoppers increased
but at a decreasing rate. At high population densities, the relation-
ship starts to break down as factors other than leaf soluble amino
acid levels disrupt the relationship.

The relationship between the number of mesophyll feeders and the
leaf soluble amino acid levels (Fig.3.34) in many way follows the
same pattern as the number of cicadellids and leaf soluble amino acid
levels (Fig.3.32). As the levels of leaf soluble amino acids increased,
the number of mesophyll feeders decreased such that higher numbers of
mesophyll feeders were present when leaf amino acid levels were below
4.0 μm/100 mg dry wgt. The only 2 amino acid levels measured above
16 μm/100 mg dry wgt both supported no mesophyll feeders, so that the
'quality' of the food to this species decreased as leaf soluble amino
acid levels increased above a "threshold".

The number of xylem feeders does not appear to be associated with
the levels of leaf soluble amino acids (Fig.3.35).

From Section II (Table 2.3) it was shown that individual amino
acids could be classified as belonging to 2 groups depending on the
type of pattern that they followed during the season (Fig.2.17).

Table 3.8 lists the amino acids according to this pattern. The
amino acids that occur at low constant levels throughout the year are
not included in this table. These amino acids are often essential for
insect survival (House 1965) but they remain at such low levels that
they have been removed from the following calculations.

The amino acids listed in Group I (Table 3.8) now represent the
actual and close relatives of the head compounds (Oaks & Bidwell 1974)
(Section II). Most have been shown to be positively correlated with
insect performance, and are essential for insect survival (Van Emden
1973). Group II amino acids include those known to be unfavourable to

Fig.3.34   The abundance of mesophyll feeders
            associated with leaf soluble amino
            acids.

Fig.3.35   The abundance of xylem feeders assoc-
            iated with leaf soluble amino acids.

No. / m² vs Leaf soluble amino acids um / 100mg

No. / m² vs Leaf soluble amino acids um / 100mg
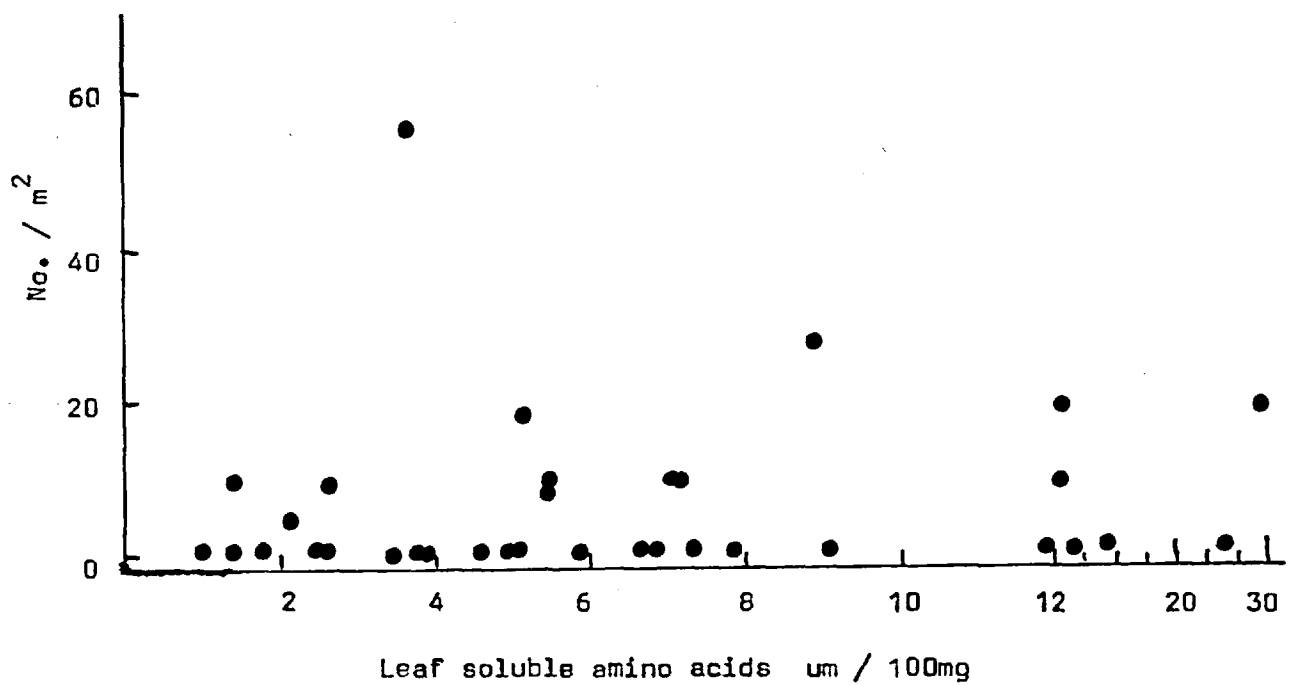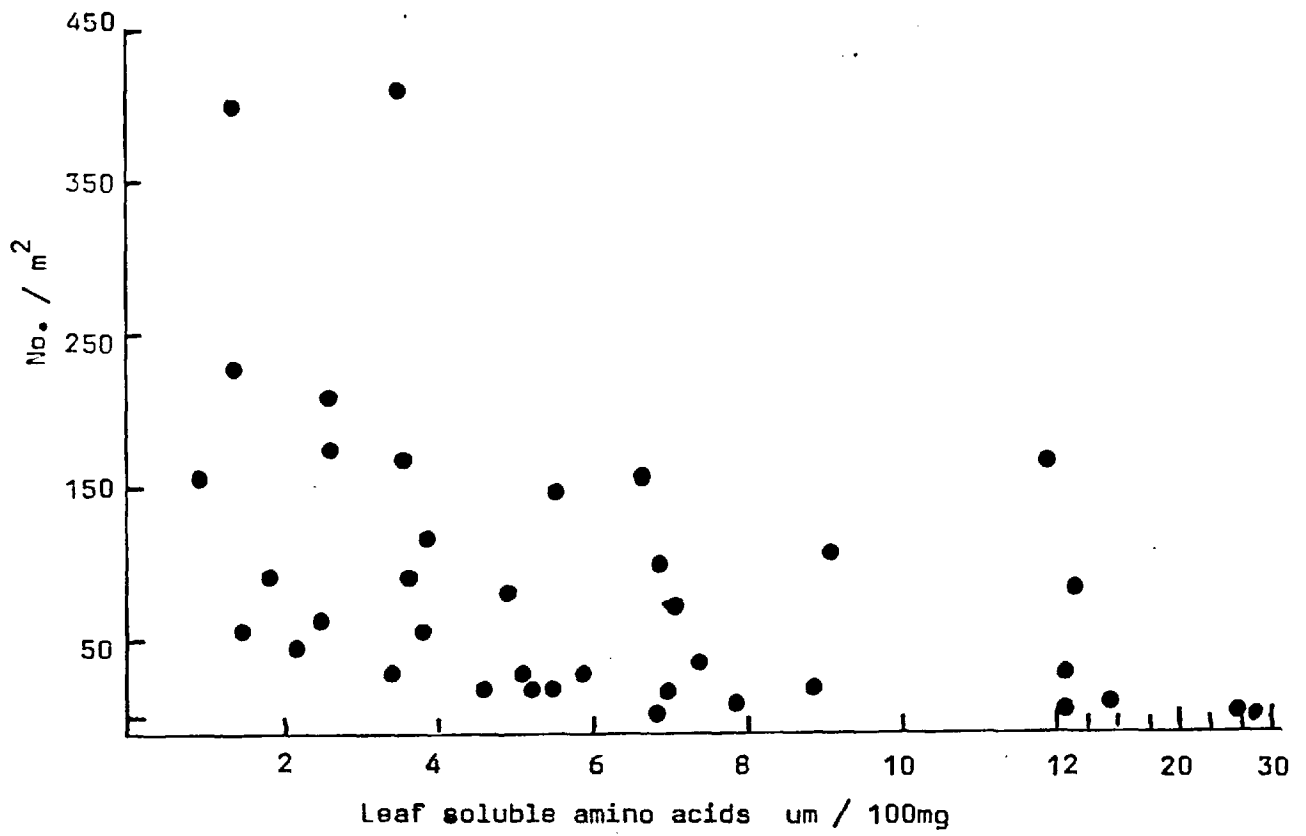
Table 3.8   An index of amino acid quality. Group I —
                 beneficial to insect performance; Group II —
                 adverse to insect performance.

Group I   Group II

Amide   Alanine
Threonine   Glycine
Proline   L Dopa
Aspartic acid   γ Aminobutyric acid
Glutamic acid

$$\text{Amino acid quality} = \log \frac{\Sigma \ \text{Group I}}{\Sigma \ \text{Group II}}$$

insect performance (i.e. γ amino butyric and L Dopa) and those that occur

in high concentrations, but for which no favourable attribute can be

shown e.g. Alanine (House 1965). Glycine has been included in this

group because it shows the same pattern as the other 3 amino acids and

is not generally regarded as being related to the N nutrition of the

plant (Larsen 1980).

Fig.3.36 shows a graph of the number of total leafhoppers associated

with the levels of the favourable amino acids (i.e. Group I, Table 3.7).

Interpretation of this graph requires a knowledge of the insects phen-

ology. Two regression lines can be fitted to this data, both with

significantly different slopes. Early in the season (i.e. before mid-

July) before hatching of second generation nymphs and when temperature

is likely to restrict flight activity, an increase in the levels of

favourable amino acids results in a small but positive increase in total

leafhoppers. After mid-July when second generation nymphs appear and

the summer temperatures are not restrictive, the relationship between

the levels of favourable amino acids and leafhopper abundance becomes

stronger, such that any small increase in the levels of favourable amino

acids results in a relatively large increase in leafhoppers.

Fig.3.36 can also be interpreted in another way. The levels of

unfavourable amino acids (Group II, Table 3.8) proportionally increase

during the summer, such that the quality of the total amino acids in the

food would be low.

A ratio between the levels of beneficial amino acids and non-beneficial

amino acids would give an index of amino acid quality (Table 3.8).

Fig.3.37 shows the relationship between an index of amino acid

quality and the abundance of leafhoppers in 1979. A curvilinear relation-

ship exists such that more leafhoppers are present on those plots with a

higher quality index. Towards the lower end of the index, below values

Fig.3.36   The abundance of leafhoppers associated
            with the sum of the favourable amino
            acids in 1979 (nm/100 mg dry weight)
            (●) prior to 3/7/79.
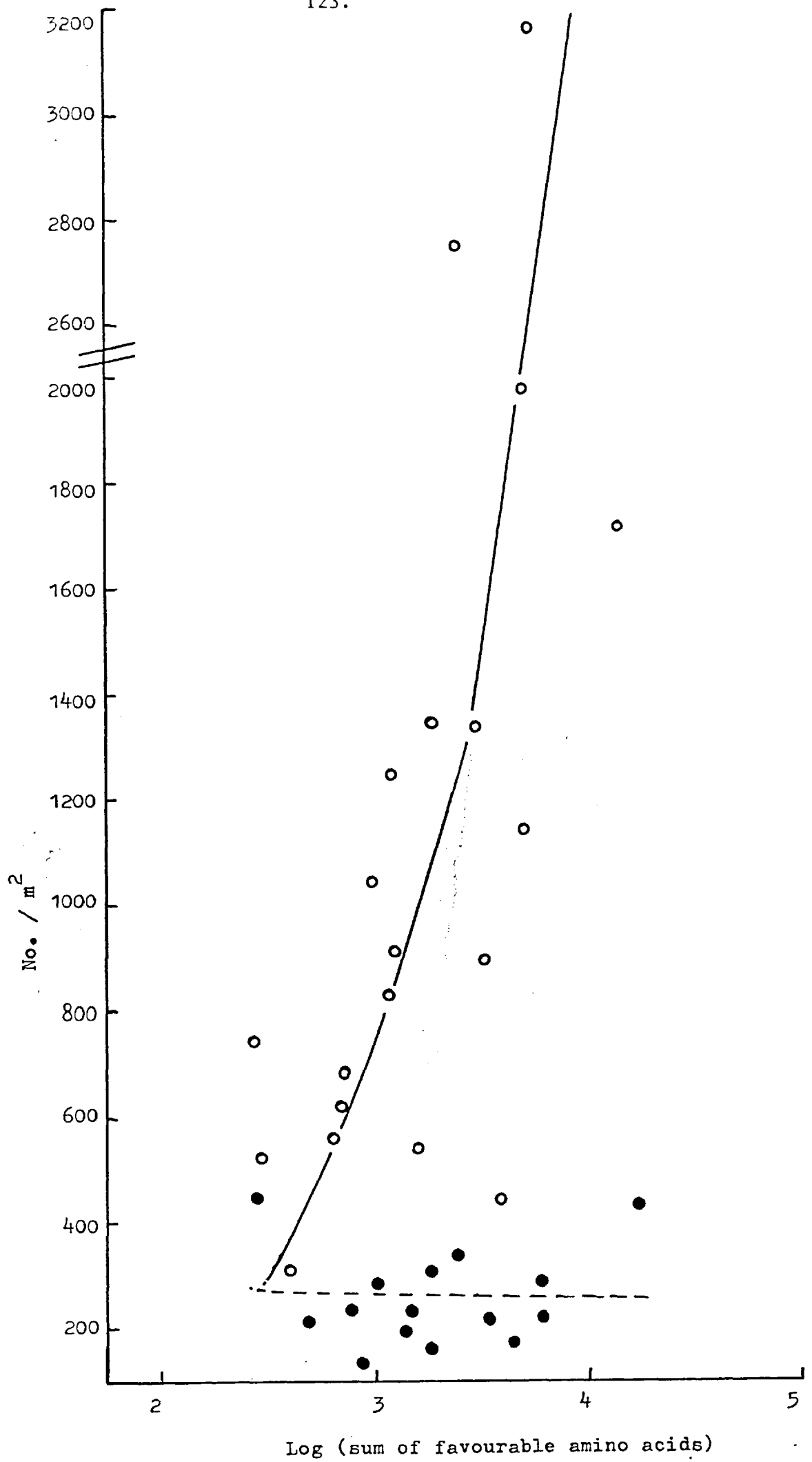
Fig. 3.37. The density of leafhoppers associated with amino
acid quality. (●) prior to 3/7/79.

No. / m^2

Amino acid quality index
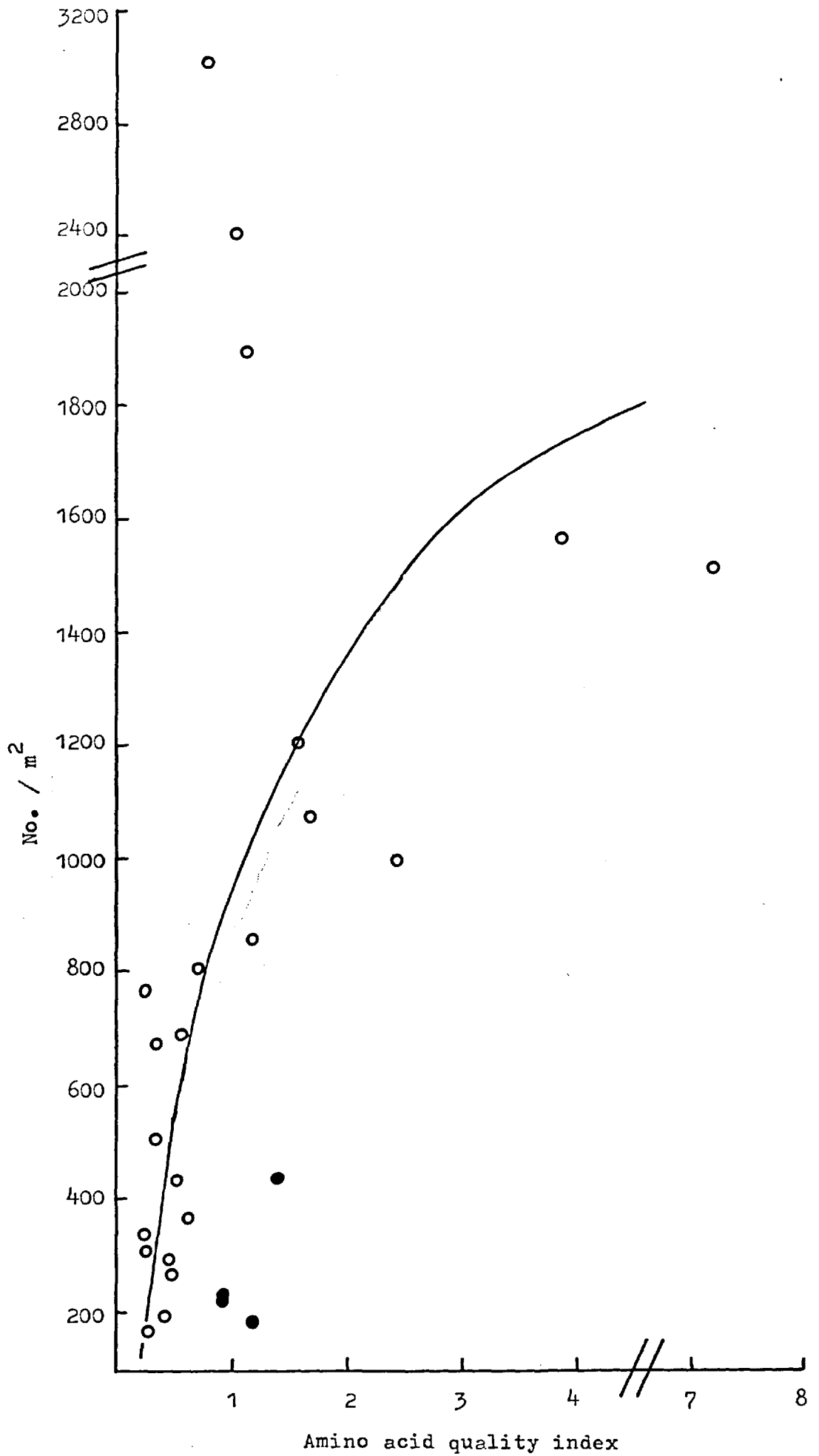
1 (i.e. when unfavourable amino acid levels increase relative to favourable amino acid levels), any small increase in the value of the index results in more leafhoppers being present. Above an index value 1, when favourable amino acids levels are greater than unfavourable amino acid levels, the curve relating insect abundance and amino acid quality begins to flatten out. At high levels of leafhopper abundance, factors other than amino acid quality become important in determining the observed leafhopper patterns.

Figs.3.38-3.40 show the number of leafhoppers belonging to different feeding types associated with the amino acid quality index for 1979. The number of phloem feeders (Fig.3.38) and mesophyll feeders (Fig.3.39) show the curvilinear relationship as discussed earlier for total leafhoppers (Fig.3.37). At an index value of greater than 2 the number of mesophyll feeders associated with amino acid quality decreases. This effect may be caused by the balance of available amino acids or by factors such as plant architecture, etc. (see later).

The numbers of xylem feeders (Fig.40) do not show any relationship with amino acid quality. This is contrary to the expected results. Most of the xylem nitrogen is in the form of amino acids (Beevers 1976). Horsefield (1977) has shown that it is possible to artificially increase total xylem amino acid levels, therefore it is possible that the xylem feeders in this system are responding to factors other than amino acid quality.

Fig.3.41 shows the relationship between peak adult D.hamata abundance and the amino acid quality index during peak abundance in 1979. At the lower end of the index, adult D.hamata are present in low numbers. Above a threshold value of 0.31, the number of D.hamata increase sharply and remain relatively constant.

Fig.3.38   The abundance of phloem feeders
           associated with amino acid quality
           in 1979.   (O) prior to 3/7/79.

Amino acid quality index
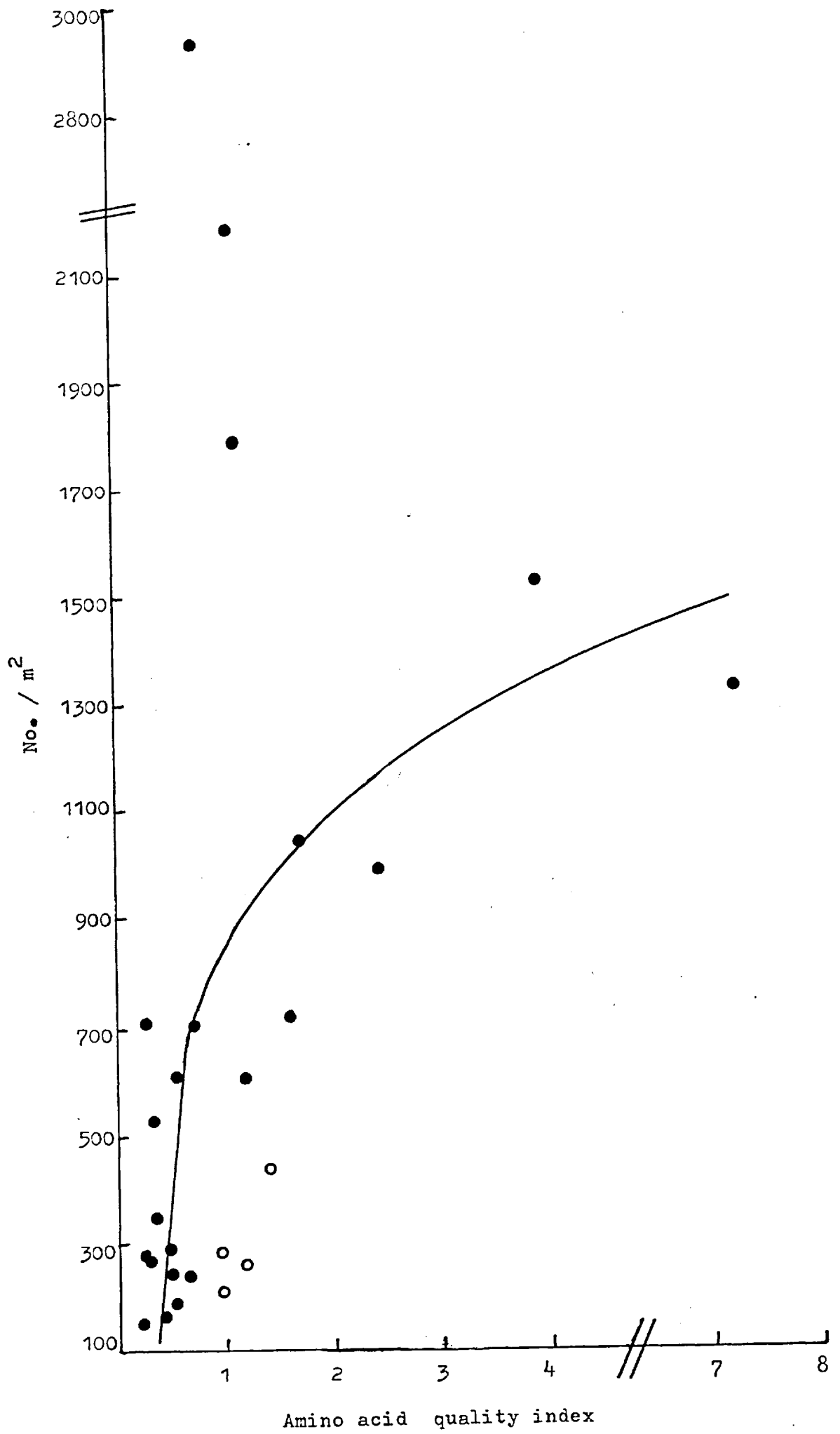
Fig.3.39   The abundance of mesophyll feeders
            associated with amino acid quality.
            (O) prior to 3/7/79.

Fig.3.40   The abundance of xylem feeders assoc-
            iated with amino acid quality.
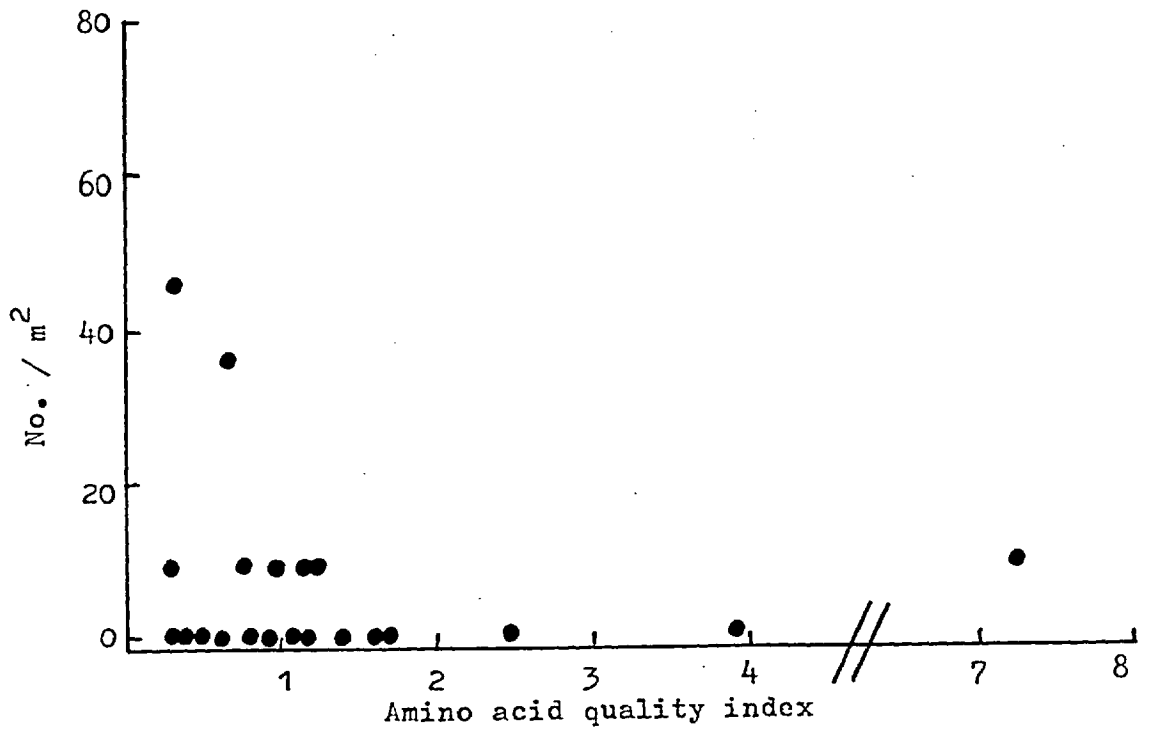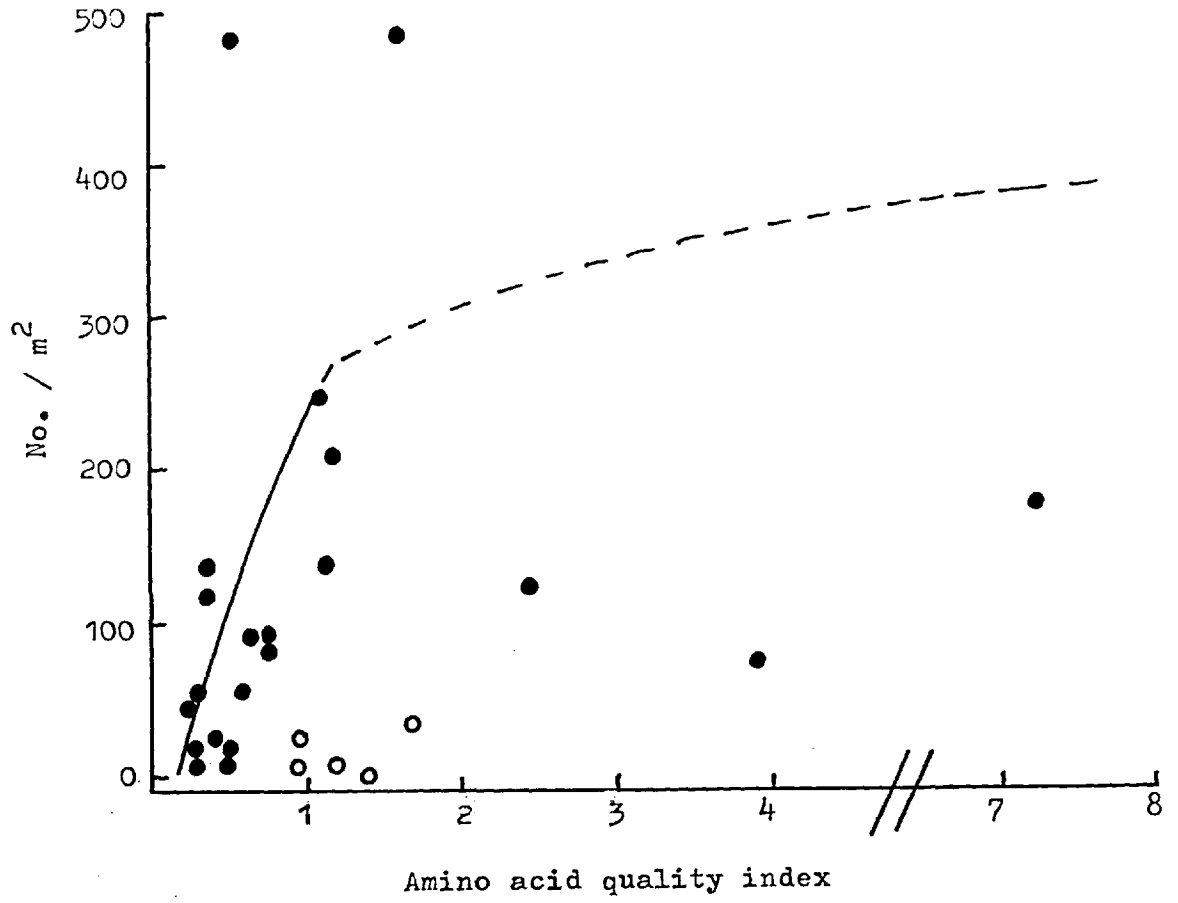
Fig.3.41   Peak abundance of adult <u>D.hamata</u> assoc-
   iated with amino acid quality index.

Fig.3.42   Peak abundance of adult <u>A.ocellaris</u>
           associated with amino acid quality index.
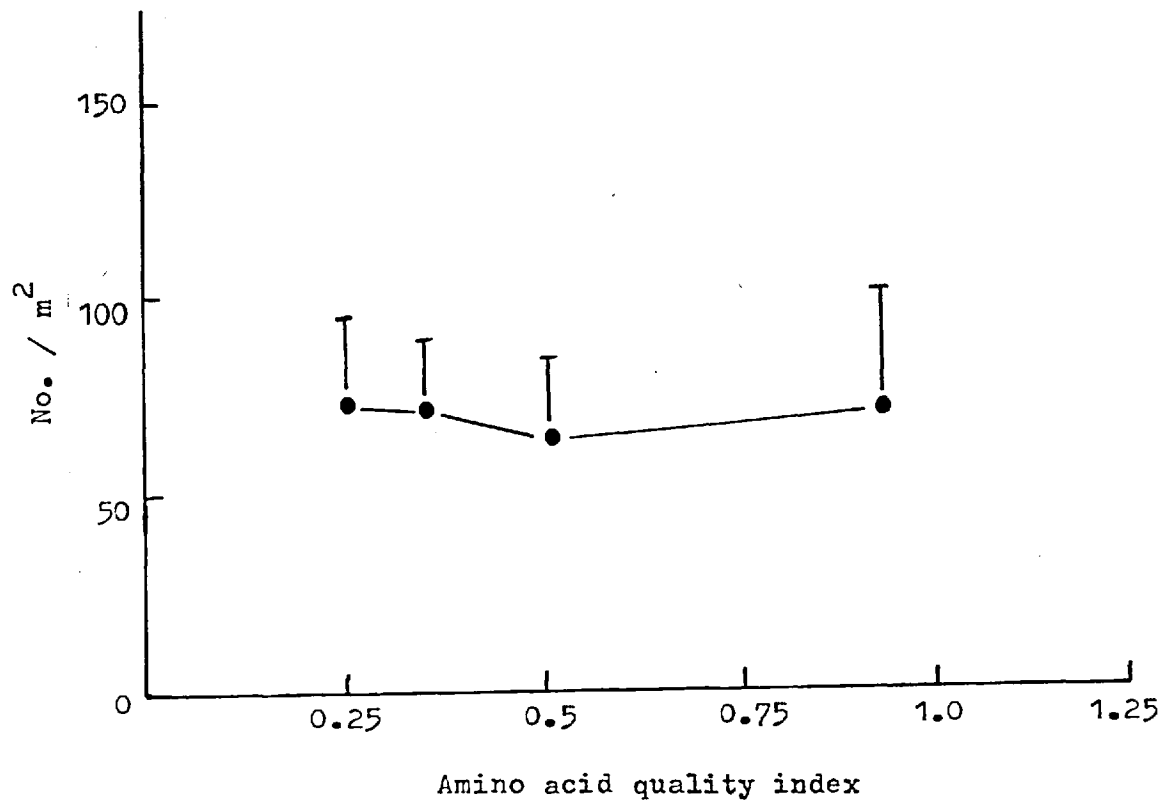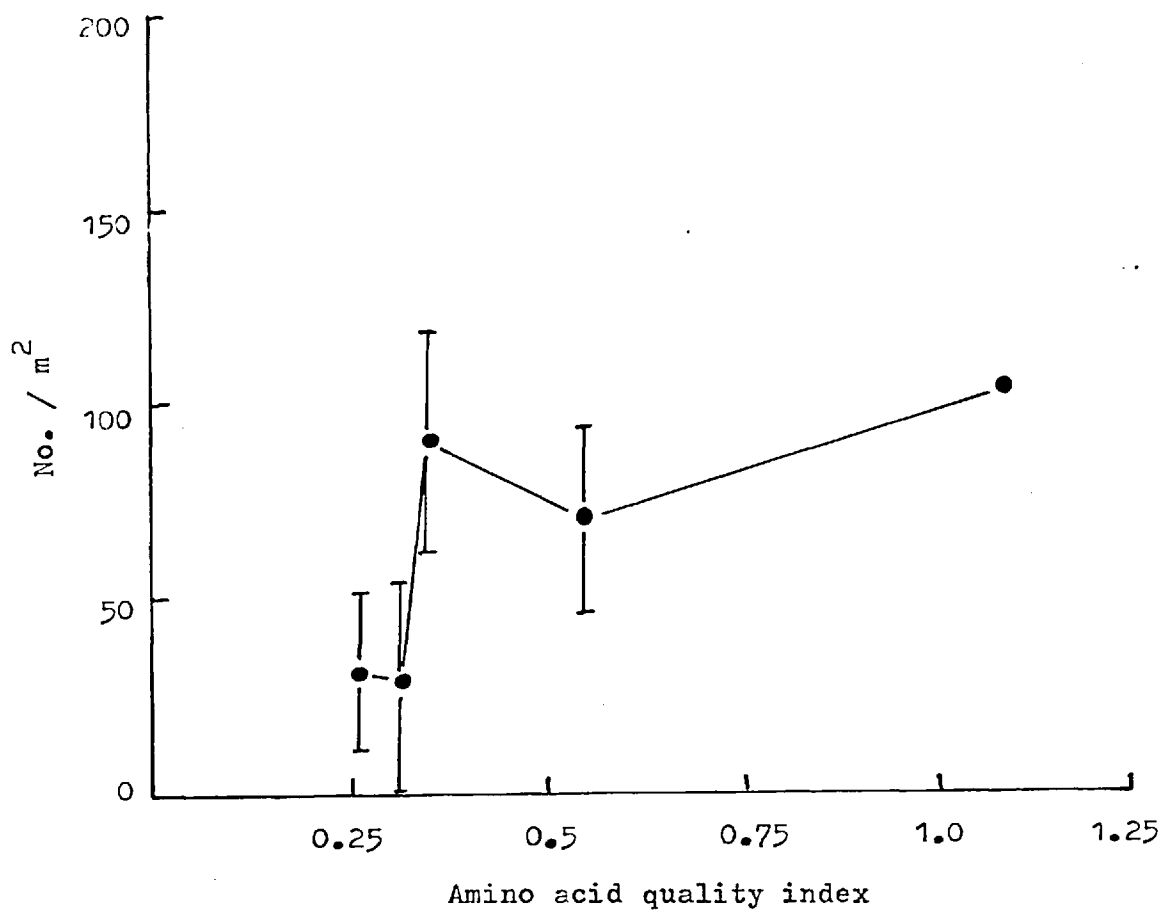
There is no relationship between peak adult D.hamata abundance
and levels of favourable and unfavourable amino acids during this time.
This reinforces the supposition that it is the ratio of favourable
to unfavourable amino acids that is responsible for the leafhopper
abundance. There is no advantage to D.hamata when levels of favour-
able amino acids are high if the levels of unfavourable amino acids
are also high. The advantage is apparent when the levels of favour-
able amino acids increase relative to the levels of unfavourable
amino acids.

Fig.3.42 shows the relationship between peak adult A.ocellaris
abundance and the amino acid quality during peak abundance for the
first generation in 1979. It is very possible that the lower thresh-
old has not been reached in 1979 since the shape of the graph is linear.
Different leafhopper species have different nutritional requirements
(see Section IV), thus the threshold levels are likely to differ
between species.

The number of nymphs/♀ A.ocellaris increased when the amino acid
quality during the previous generation adult ovipositional period
increased above an index value of 0.25 (Fig.43). It is interesting
to note that the curve drops away at index values approaching 1. This
must remain unexplained at this stage.

3.3.5 Plant Architecture

An index of plant architecture can be calculated from the data of
plant biomass (Appendix IV) and plant height (Appendix V), such that

$$\text{Plant architecture} = \log [\text{Biomass(Kg)} \times \text{Height (cm)}]$$

Fig.3.44-3.46 show the relationships between plant architecture
and leafhopper abundance in 1979. Above a certain population thresh-
old, plant architecture is responsible in determining the numbers of

Fig. 3.43. The number of nymphs / ♀ A.ocellaris associated
with amino acid quality.
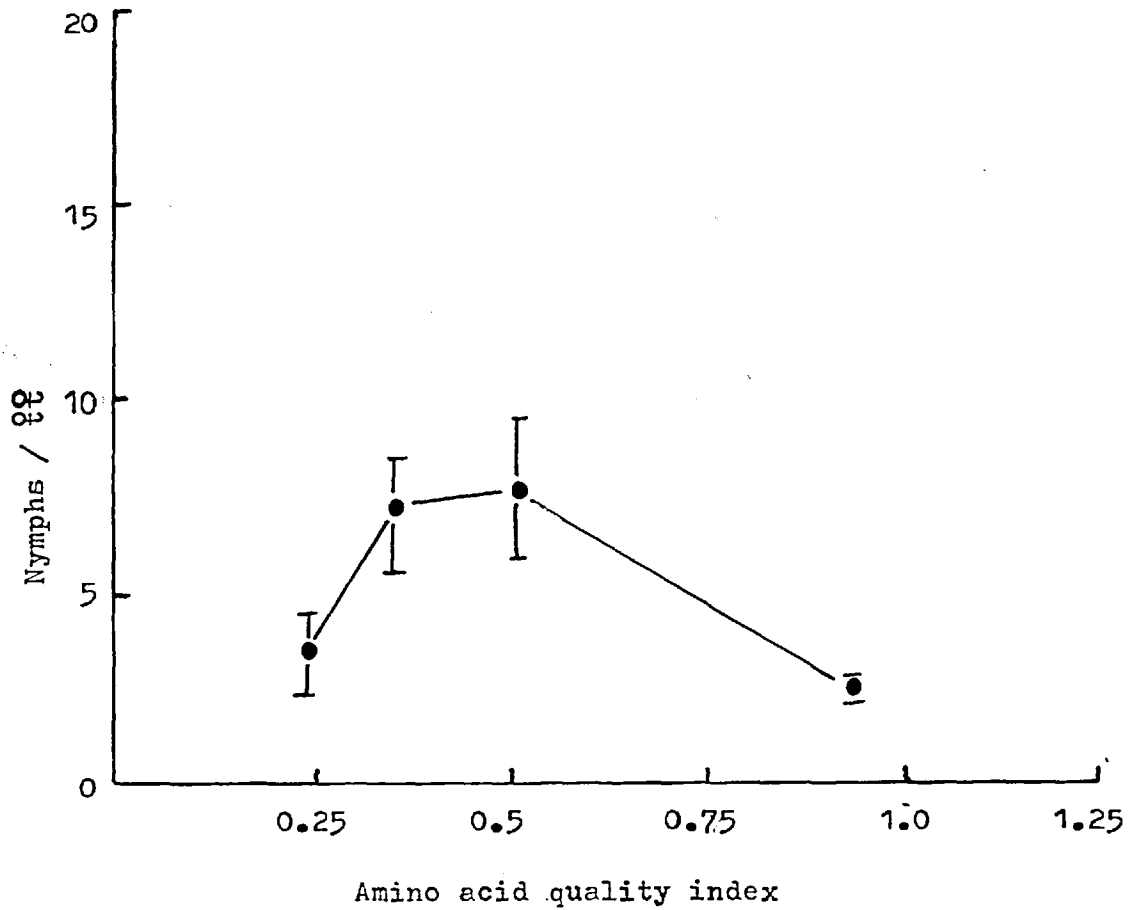
Fig.3.44   The abundance of leafhoppers assoc-
           iated with plant architecture.

Plant architecture index
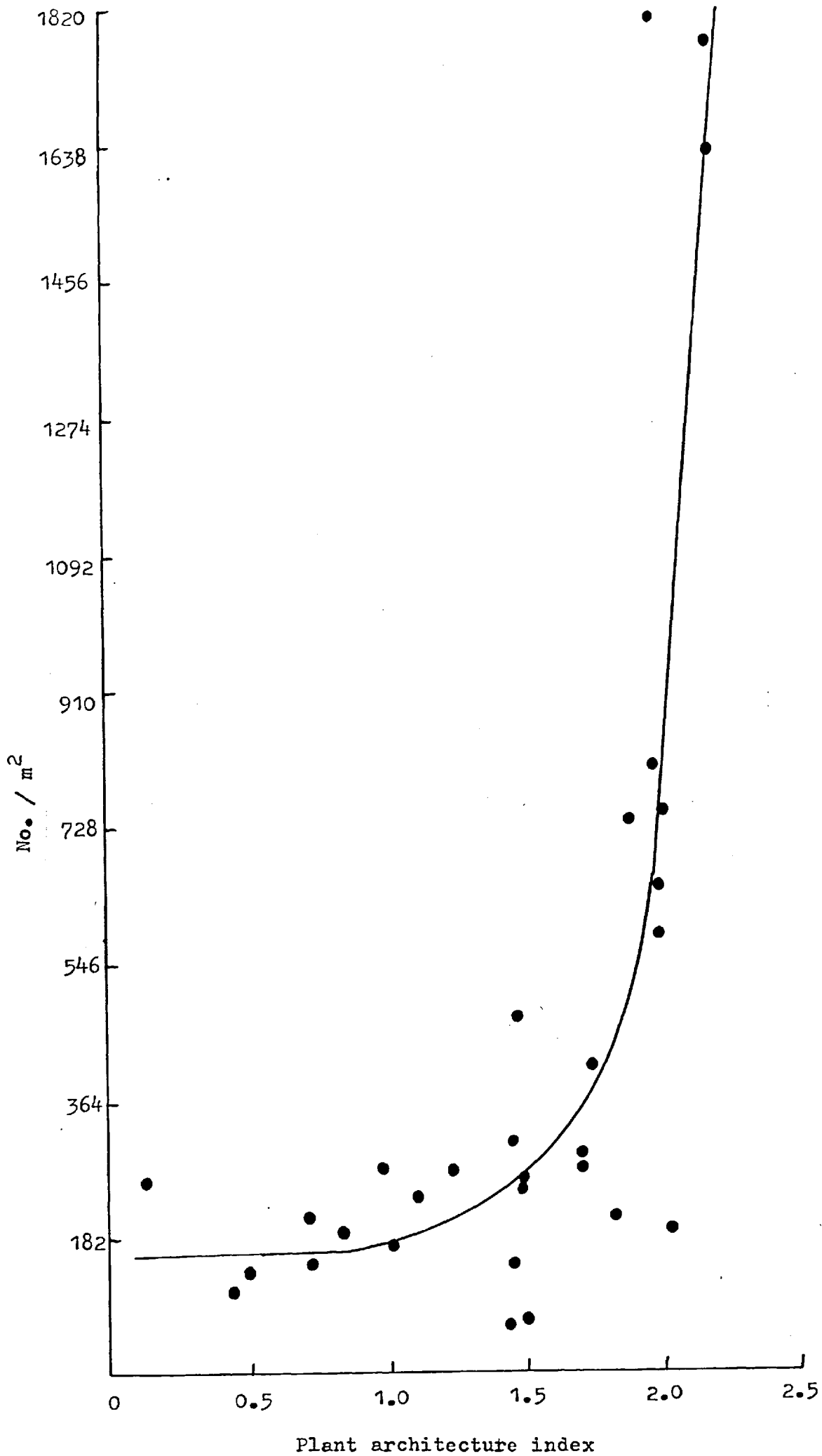
Fig.3.45. The density of Delphacidae associated with plant
architecture.

No. / m^2

Plant architecture index
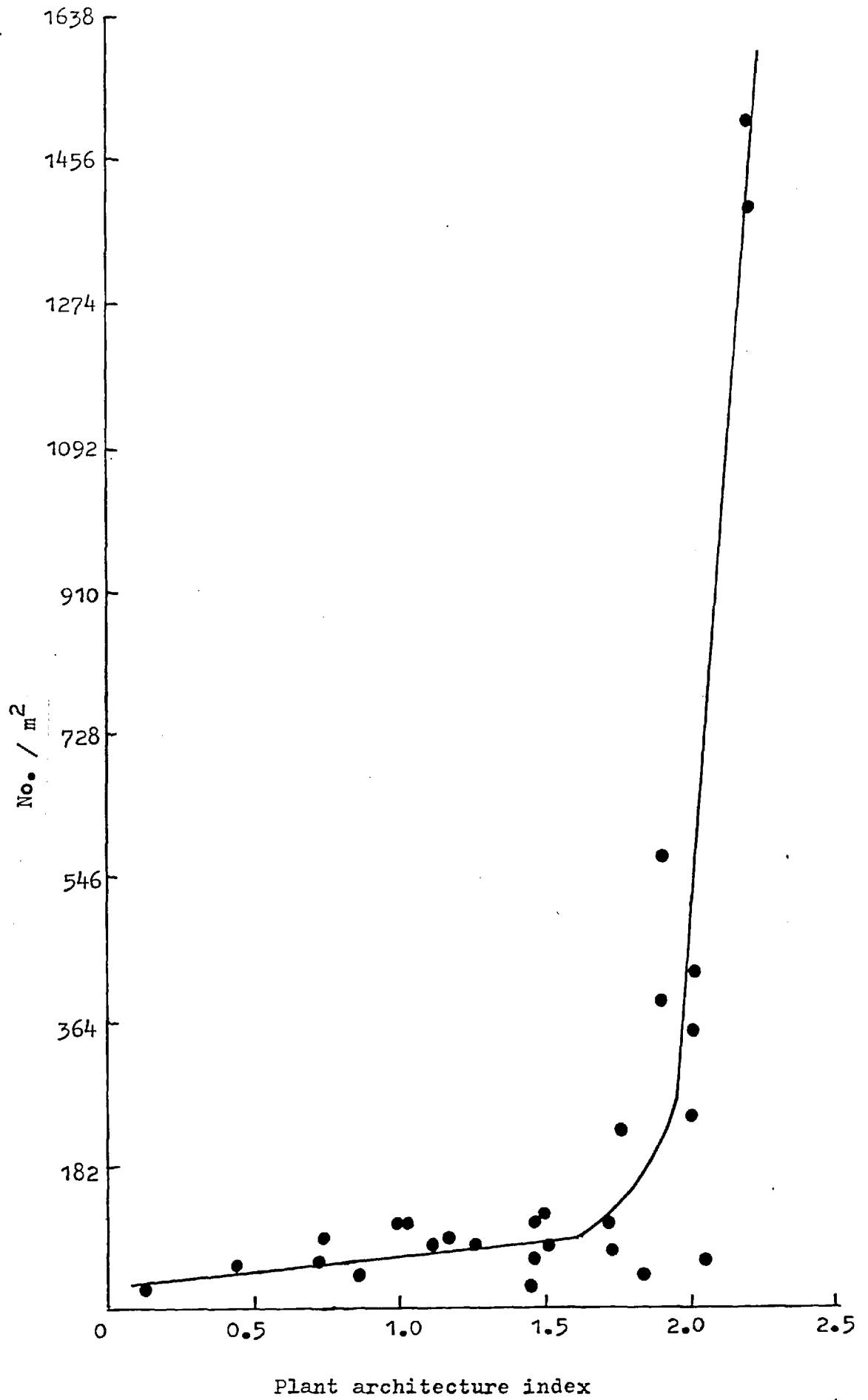
Fig. 3.46. The density of Cicadellidae associated with plant architecture.

Plant architecture index
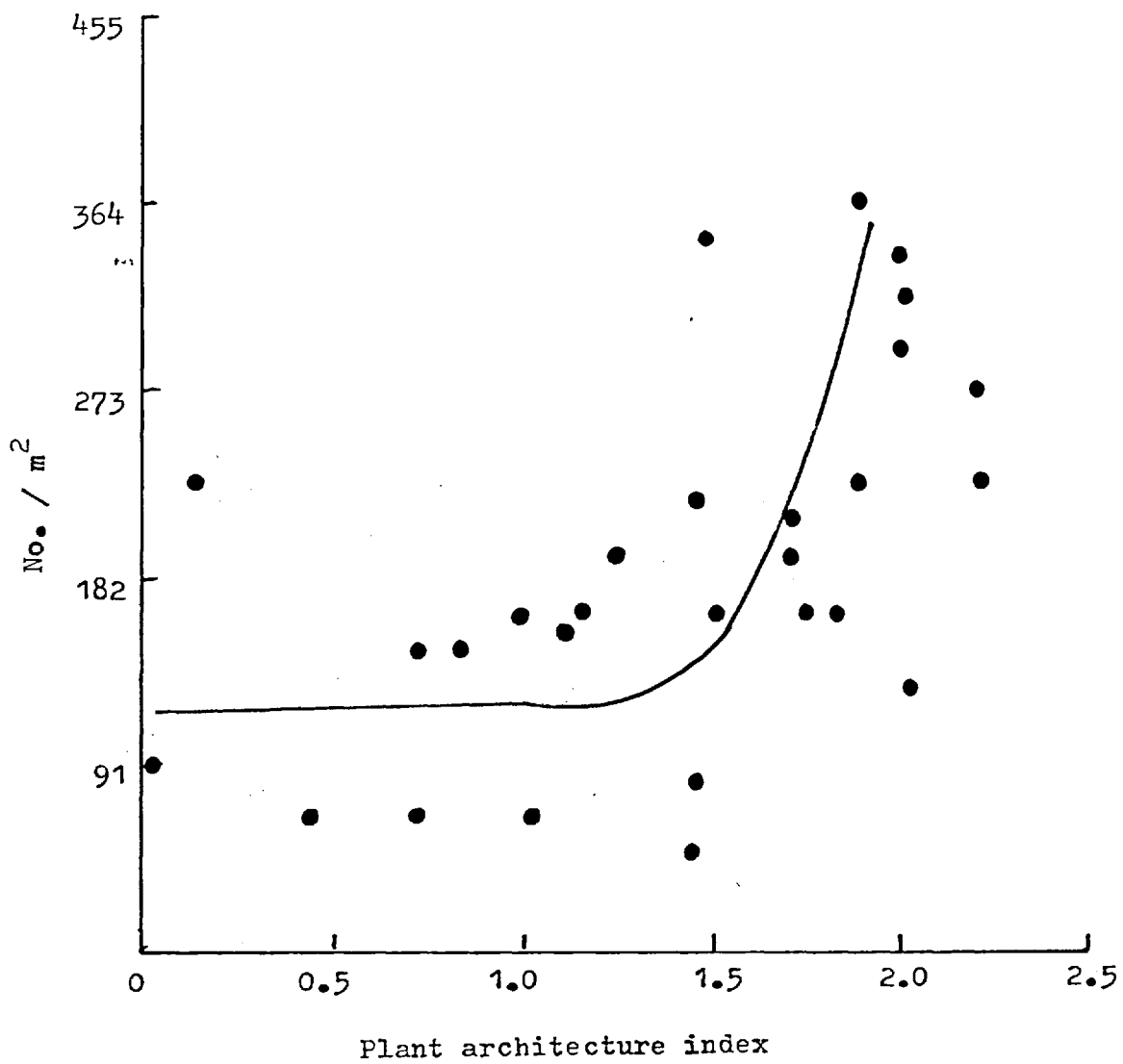
leafhoppers present (Fig.3.44). The population threshold for the leafhopper complex in question is about $360/m^2$, any populations exceeding this density become more and more dependant on the plant architecture. The Delphacidae (Fig.3.45) were responsible for the shape of Fig.3.44 as high populations occurred on those plots with the greatest amount of architecture. The population threshold level for the delphacids was considerably less than that for total leafhoppers, less than $180/m^2$. The Cicadellidae show a similar relationship with plant architecture (Fig.3.46) but never reach population levels above $360/m^2$. The population threshold level for cicadellids is about $250/m^2$, populations above this level becoming more dependent on levels of plant architecture.

Fig.3.47-3.49 show the influence of plant architecture upon the different Auchenorrhyncha feeding types. Leaf phloem feeders compete for the same resource irrespective of their taxonomic grouping. Phloem feeders (Fig.3.47) are the only feeding type to reach a population density to be markedly affected by plant architecture. As the population increases above a threshold value of $270/m^2$, plant architecture becomes increasingly important in determining phloem feeder abundance. Mesophyll feeders (Fig.3.48) never reach a high population density to be greatly affected by plant architecture. The shape of Fig.3.48, however, suggests that a similar relationship may exist as was demonstrated for phloem feeders. Xylem feeding leafhoppers (Fig.3.49) remained at such low population densities throughout the season that no correlation between populations and plant architecture was evident. It is conceivable, however, that at high population densities, plant architecture becomes important in determining the structure of xylem feeders in the same way as was shown for phloem feeders.

Fig. 3.47. The density of phloem feeders associated with plant architecture.

No. / m² (y-axis)

Plant architecture index (x-axis)
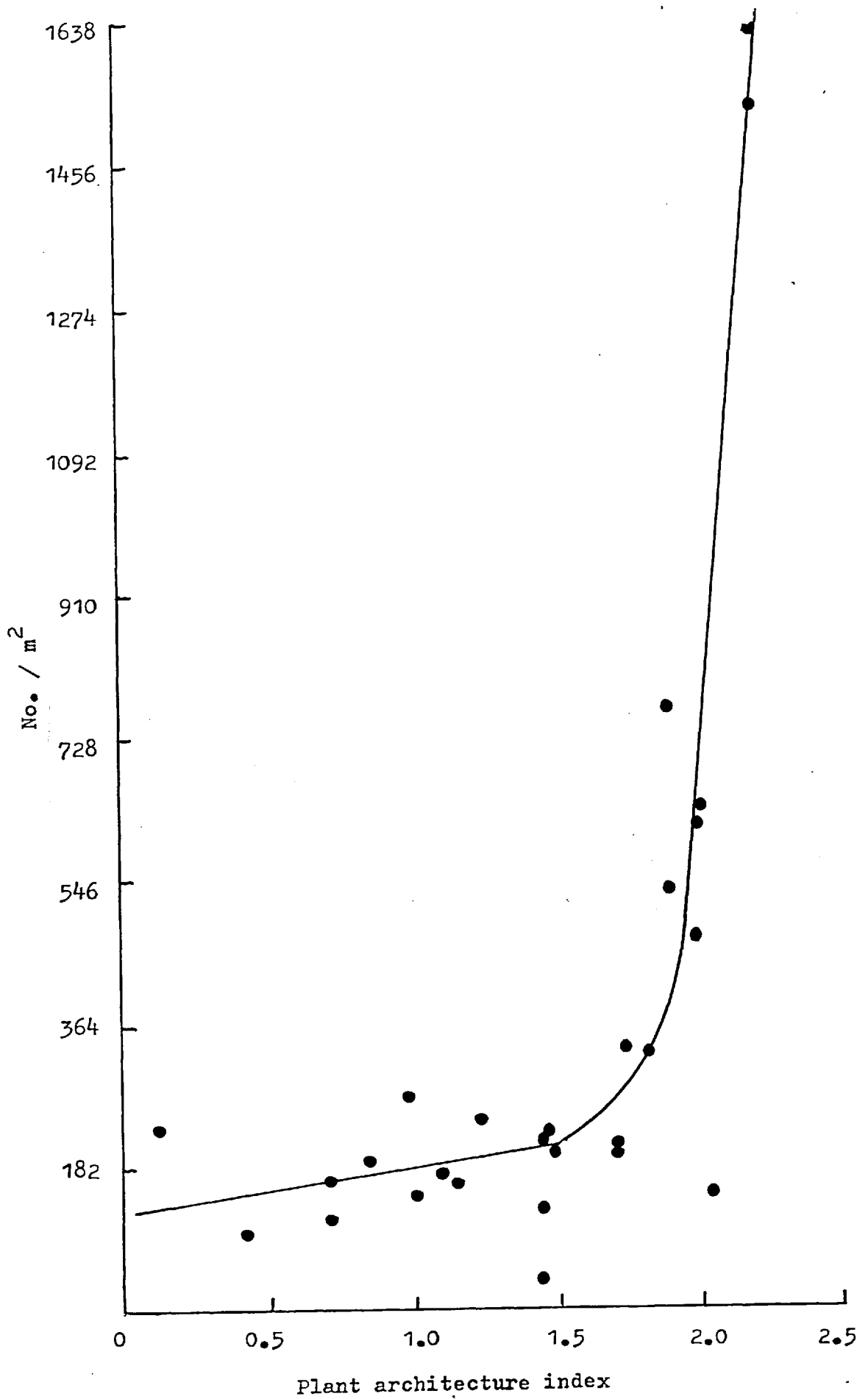
Fig.3.48   The abundance of mesophyll feeders assoc-
            iated with plant architecture.

Fig.3.49   The abundance of xylem feeders associated
            with plant architecture.

Plant architecture index

Plant architecture index
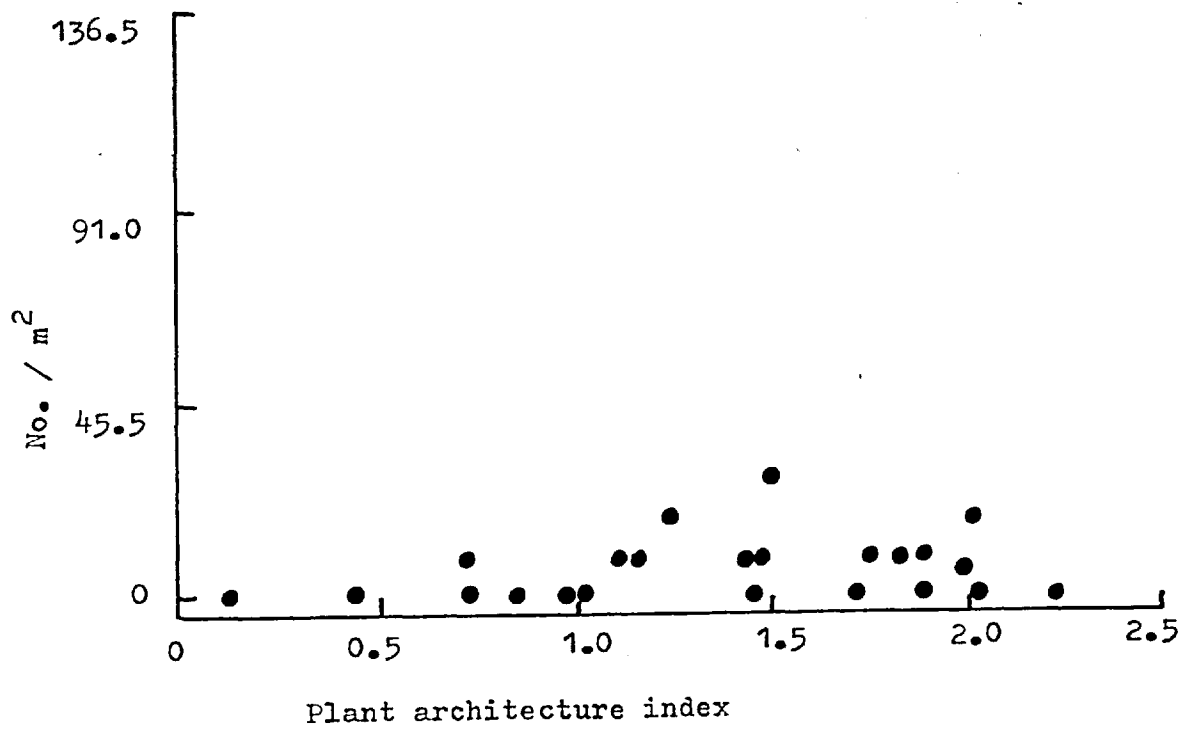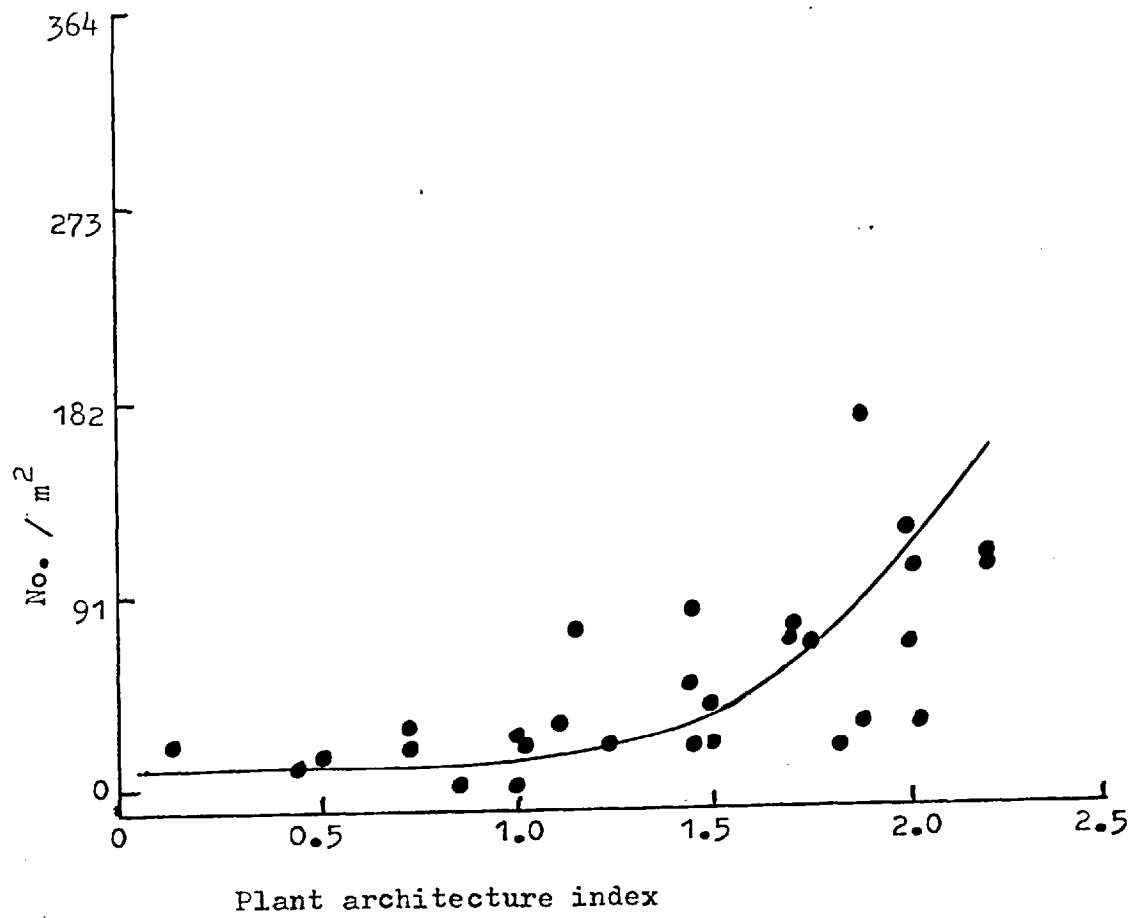
3.4 Discussion

The large differences in the total number of leafhoppers captured
in 1978 and 1979 reflect the general lability of the grassland
Auchenorrhyncha.   Waloff (1980) in her excellent review on grassland
Auchenorrhyncha comments that survival of leafhopper populations is to
some extent geared to the phenology and the nutritional stage of the host
plant during the nymphal stage, while the sizes of the adult popul-
ations are partly determined by their dispersal from one breeding site
to another.   However, survival is a life or death situation.   Many
of the influences of poor nutrition result in slow development and
reduced fecundity such that populations are reduced to a low level
until conditions again become favourable for rapid population growth.
By this method the dominant species and the population levels alter
but the absolute number of species remains stable over a short period
of time.

In 1979, parasitism rates were low (less than 20% of any species
being parasitised) reflecting the low level of control of leafhopper
populations by insect parasitoids.   Hill (1976) also found that
low parasitism rates existed in a leafhopper community dominated by
H.mollis and he dismissed parasitoids as one of the major regulators
of leafhopper populations.

Waloff (1975) noted that many of the parasitoids are polyphagous
and often restrict their attacks to family or subfamily levels of
their hosts.   The common dryinid and pipunculid species tend to attack
grassland leafhopper species in proportion to their abundance, in this
way their effects tend to be similar to those of predators.

Although no measure of predation was obtained, population levels
of two of the major predator groups were measured.   Nabids were more
abundant in the early part of the year and spider populations increased

and then stabilized after mid August. Rothschild (1966) and Solomon (1973) have shown that the importance of spiders as predators increases in the second half of the summer and in early autumn. Waloff (1980) considers that the spiders are showing a numerical and aggregative response to prey density, a response which could lead to density dependent predation and leafhopper population stability. It is also possible that the number of spiders may reflect increased spider reproduction at times of high prey density.

Petal et al. (1971) in Poland considered that ants play an important role as predators in grassland habitats. She showed that the number of Auchenorrhyncha caught by ants was greatest during the periods of intensive growth of larvae in the ants' nest. Most of the Auchenorrhyncha consumed by ants were nymphs or newly moulted adults. In her study, however, the estimated density of ants was ten orders of magnitude greater than the estimated maximum density in this study.

The conclusions to be drawn about the effects of parasitoids and invertebrate predators in controlling leafhopper populations must at best be very tentative. Invertebrate predators and parasitoids may be exerting a population stabilizing effect but in general the numbers of predators and parasitism rates are at such low levels (in 1979 at least) not to have any major population regulating influence. The results from the present study would tend to support the more detailed results of Waloff (1980).

The major plant parameter that has been altered with fertilizers is the quality of the food available to leafhoppers. The numbers of leafhoppers occuring on plots that received individual treatments were variable. If, however, the plots are divided according to a particular nutrient level, rather than according to the level of fertilizer applied, several patterns become obvious. Leafhoppers are responding to a particular nutrient level within the grasses. They attain maximum abundance

on grasses that have a particular nutrient level. The number of adults
is maximal at a particular leaf nutrient level. The highest number
of first instar nymphs/female occurred at a particular grass nutrient
level. Grasses with nutrient levels either side of this level had
less first instar nymphs/female present.

There is very little evidence to indicate that leaf nitrogen levels
are a more accurate index of food quality than leaf potassium or leaf
phosphorus levels. The graphs showing peak adult density are much
steeper when examining leaf nitrogen levels than when examining leaf
potassium and leaf phosphorus levels. All the species examined reach
maximum occurrence at about the same level potassium (22 mg K/gm dry
wgt) and leaf phosphorus (>3 mg P/gm dry wgt). High leaf phosphorus
levels were commonly outside the range normally recorded in plants.
In general, however, the leafhoppers associated with any one of the
index levels all show the same pattern. The number of leafhoppers
all increase to a maximum and then decrease at higher nutrient levels.
The reasons for choosing nitrogen levels as an index of food quality
must remain until a method is found that enables one element to be
manipulated without altering the other elements. The bulk of the
available evidence supports the view that nitrogen levels are generally
limiting to phytophagous insects.

The amino acid quality index provides an interesting and new
approach to the influences of food quality on phytophagous insect
populations. It utilizes the individual amino acid levels and groups
them according to their effects on insect performance. The groups are
loosely termed as being favourable and unfavourable to insect performance
and the ratio of favourable to unfavourable amino acids gave an index
of amino acid quality. At low values of the index (i.e. when favour-
able amino acid levels are low relative to unfavourable amino acid levels),

leafhoppers are restricted by the poor quality of the food. As the

amino acid quality increases, the size of the leafhopper population

increases. At high values of the index when amino acid quality is

high, the abundance of leafhoppers is restricted by other factors.

Amino acid quality index values of about 0.35 appear to be the

threshold value for D.hamata. Below the threshold value a low number

of adults/m^2 was present whilst above this value, a higher number was

present. It is most certain that different species of leafhopper

have different threshold values. A species that is present when amino

acid quality is low will probably have a lower threshold than a species

that is always present when amino acid quality is high. Indeed, natural

selection will favour those individuals who have a nutritional physiology

best suited to the grass nutrient quality. A.ocellaris adults showed

no difference in abundance on those plots with a threshold value as

small as 0.25. Further work is obviously required on the behaviour

and ecology of A.ocellaris in the light of this low threshold value.

It was the fourth most abundant species during the present study and

formed about 10% of the total Auchenorrhyncha fauna.

Another way to examine the plant's response to fertilizers is to

examine the effects of increased living space (Southwood 1972) to the

insect. Lawton (1978) found a very good correlation between living

area (or plant architecture) and the number and abundance of insects

inhabiting Pteridium aquilinum (L.). As the living area available to

insects increased during the season, the number and abundance of colon-

izers increased. He concluded that available living area rather than

plant chemistry was probably more important in determining the number

of insects utilizing bracken. Chemistry was more important in deter-

mining how the insect community was structured. Any insect that managed

to withstand the chemical defences of bracken was then restricted by the

living space available to it.

In this study, the effects of the fertilizer was to increase the living space (biomass and height) available to the insect populations. The seasonal pattern of increase in living space has not altered, just the absolute amount available to the insects. McNeill & Southwood (1978) have shown that the number of different herbivorous insect species and their abundance rapidly increased to a maximum in late May through June. Although they linked this increase to the fluctuations in nitrogen in H.mollis, the dominant grass species, there is nothing to suggest that the increase was not due solely or partly to the increase in living space. After the nitrogen decreased in H.mollis the number and abundance of herbivore species remained relatively high.

In this study the effects of increasing the living space available to leafhoppers are not utilized at low population densities. Once populations exceed a threshold value however, living space becomes progressively more important. At high population densities, lack of available living space may restrict further population increase. Overcrowding and the effects of increased interference generally reduce feeding, growth and ovipositional rates, promote macroptery and emigration in a range of other Homopteran species (e.g. Van Emden et al. 1969; Hill 1976; Dixon 1979; Reader 1980).

Other authors have shown similar effects of habitat complexity on leafhopper populations (Andrzejewska 1965; Whittaker 1969; Murdoch et al. 1972; Waloff & Solomon 1973; McClure & Price 1975, 1976; Denno 1977; Tallamy & Denno 1979). Morris (1971, 1973) showed that species diversity decreased in grassland Auchenorrhyncha when the grass was mown. He also noted that a different leafhopper assemblage was present on short grassland. Tall grassland may allow resource partitioning

along a vertical height gradient. Andrzejewska (1965) found discrete

vertical stratification of sap-feeding Homoptera in grassland vegetation.

Denno (1980) found that the most niche separation among sap feeders on

Spartina patens was attributable to vertical partitioning of the grass

system.   In general, grasses that are tall or that have a complex

structure, support a larger and more diverse sap feeding fauna than short

grasses or grasses that have a simple structure.

In this study the individual effects attributed to plant height

and biomass have not been separated.   An increase in plant biomass

is likely to provide a greater diversity of microhabitats that could

be of potential use to herbivores for feeding, oviposition and refuge

sites.

It is possible to combine the effects of food quality and plant

architecture and then to examine the abundance of leafhoppers. Fig.

3.50 shows the relationship between the number of phloem feeders

$(no./m^2)$ per unit plant architecture (Biomass Kg x Height cm.) and

amino acid quality.   Above an amino acid quality threshold, the

abundance of phloem feeders/unit plant architecture is relatively

constant.   The threshold value is approximately 1 on the amino acid

quality index.   Below the threshold value, phloem feeder abundance per

unit plant architecture decreases dramatically as the quality of the

amino acids decreases.

Lawton (1978) showed that insect species diversity followed closely

the increase in plant architecture (plant area) and that the number of

species divided by the living space remained constant throughout the

season (Fig.3.51).   A plot of the number of leafhopper species/unit

amount of plant architecture for the experimental area is shown in

Fig.3.51.   It can be seen that the number of species divided by the

living space is not constant throughout the season.   Lawton's (1978)

Fig.3.50   The number of phloem feeders/unit arch-
            itecture associated with amino acid
            quality.
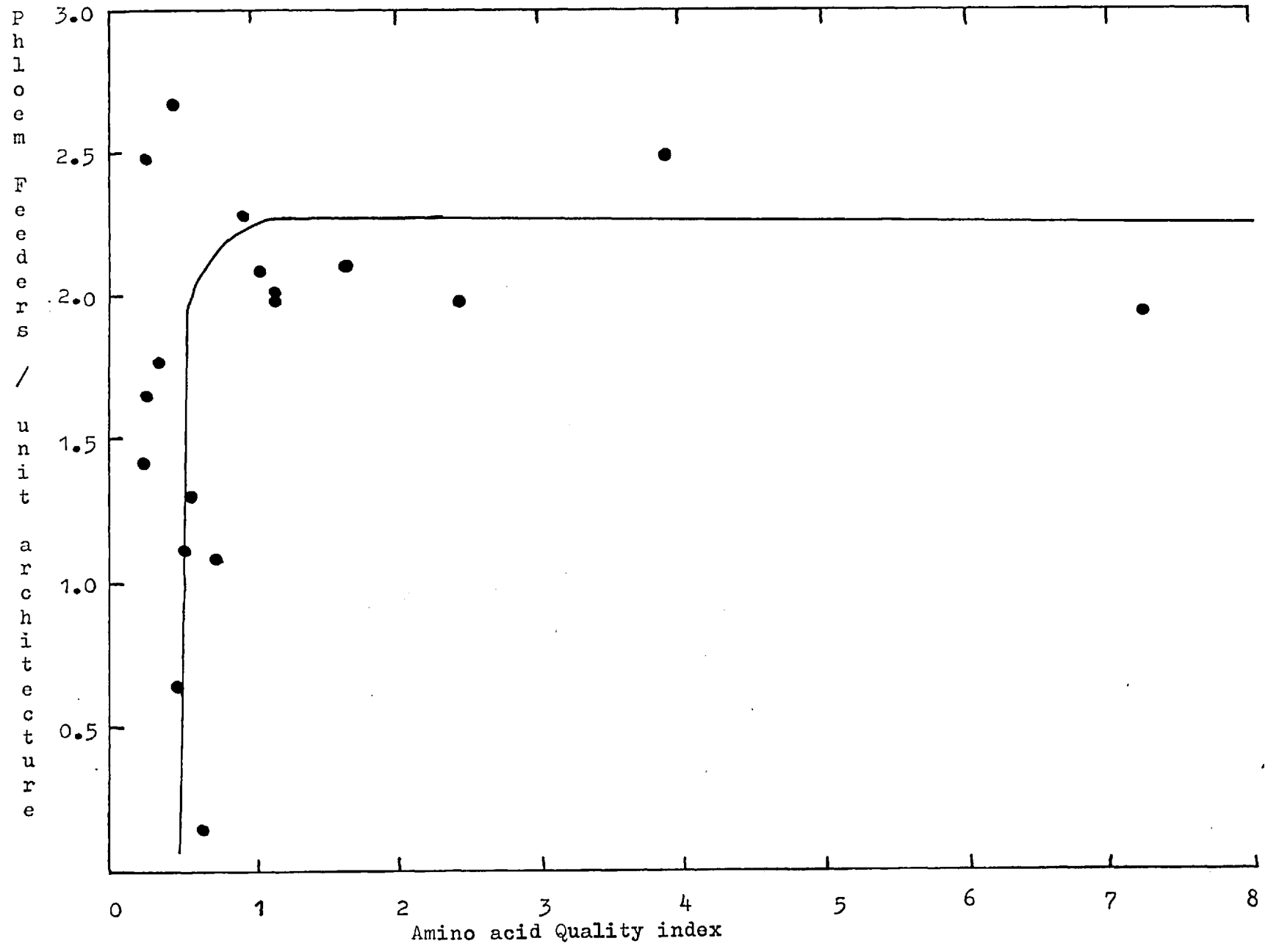
presentation of his data can be criticised on a number of points, the most important one being that only a fraction of his data has been plotted. Early in the season before most insect species have emerged the species/plant architecture index must be very low which would then make the shape of his graph similar to the shape of the graph from this study area. Addition of other herbivore species does not alter the basic shape of the graph but increases the species/architecture index so that comparison with other data sets would need to be exercised with caution.

Fig.3.51 shows that the number of leafhopper species rapidly increased early in the season before plant architecture has increased. One possible explanation for the large spring peak is that leafhopper species were responding to some parameter other than plant architecture. McNeill & Southwood (1978) maintain that the herbivore community on grassland is closely tied to the grass nutrient quality and that the number of species and their abundance is linked to the seasonal flushes in food quality. Support for this viewpoint is shown in Fig.3.52 which shows the number of species/unit food quality (in this case amino acid quality - see earlier). The area on the graph between mid-May and early September more closely resembles a straight line than a similar plot of the abundance of leafhoppers/unit plant architecture (Fig.3.51).

Further support has come from other sources (see Section 5) which show that the number of leafhopper species that colonized a pure grass sward increased after NPK fertilizer had been applied but before any increase in plant architecture was manifested (Fig.3.53). Plant architecture was still important, however, because the number of leafhopper species continued to increase after pasture height had increased and after the nitrogen levels had decreased.

Fig. 3.51. The number of leafhopper species / unit plant architecture in 1979.

(Lawton 1978)
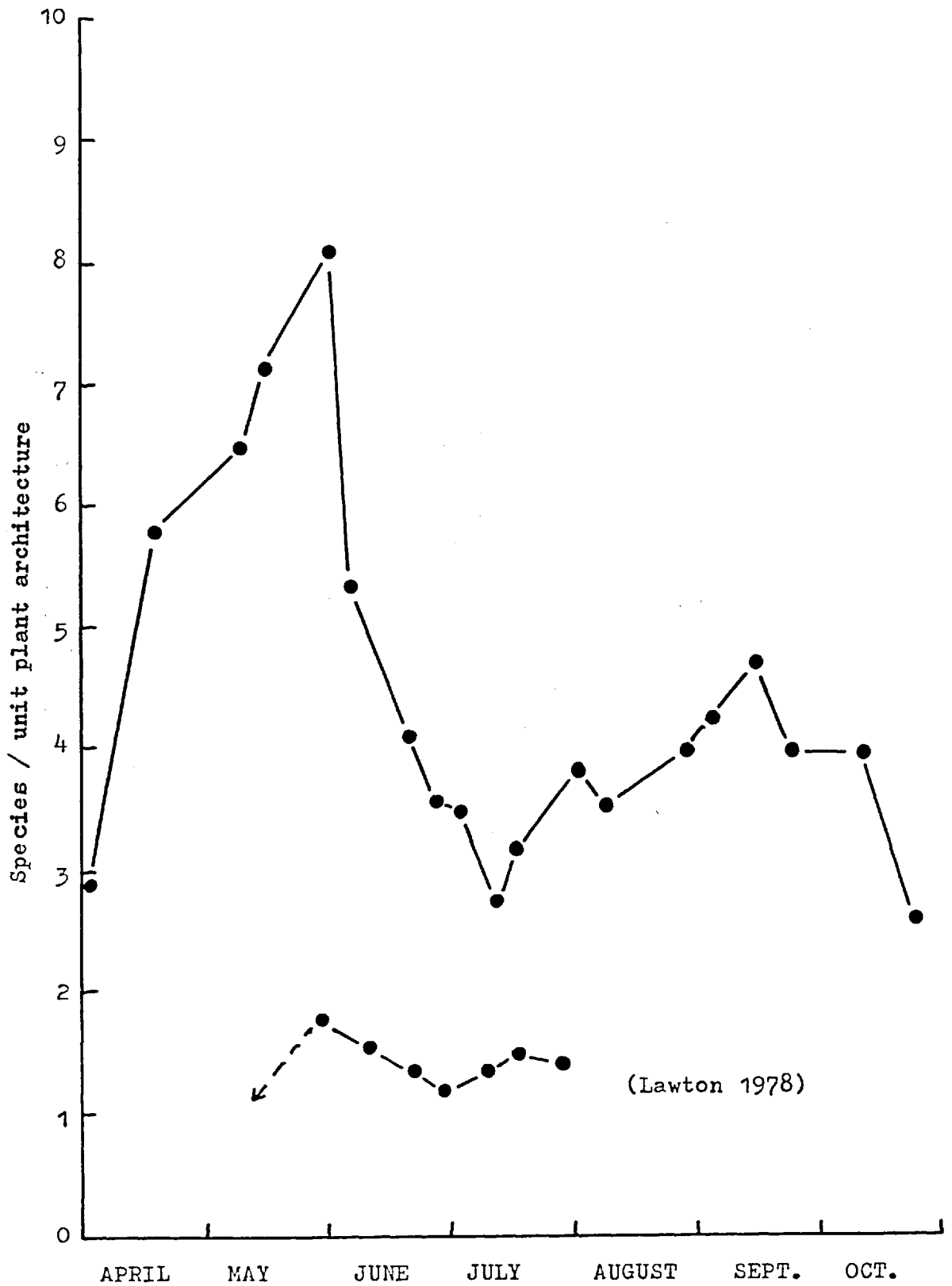
Fig. 3.52. The number of leafhopper species per unit amino

acid quality index.
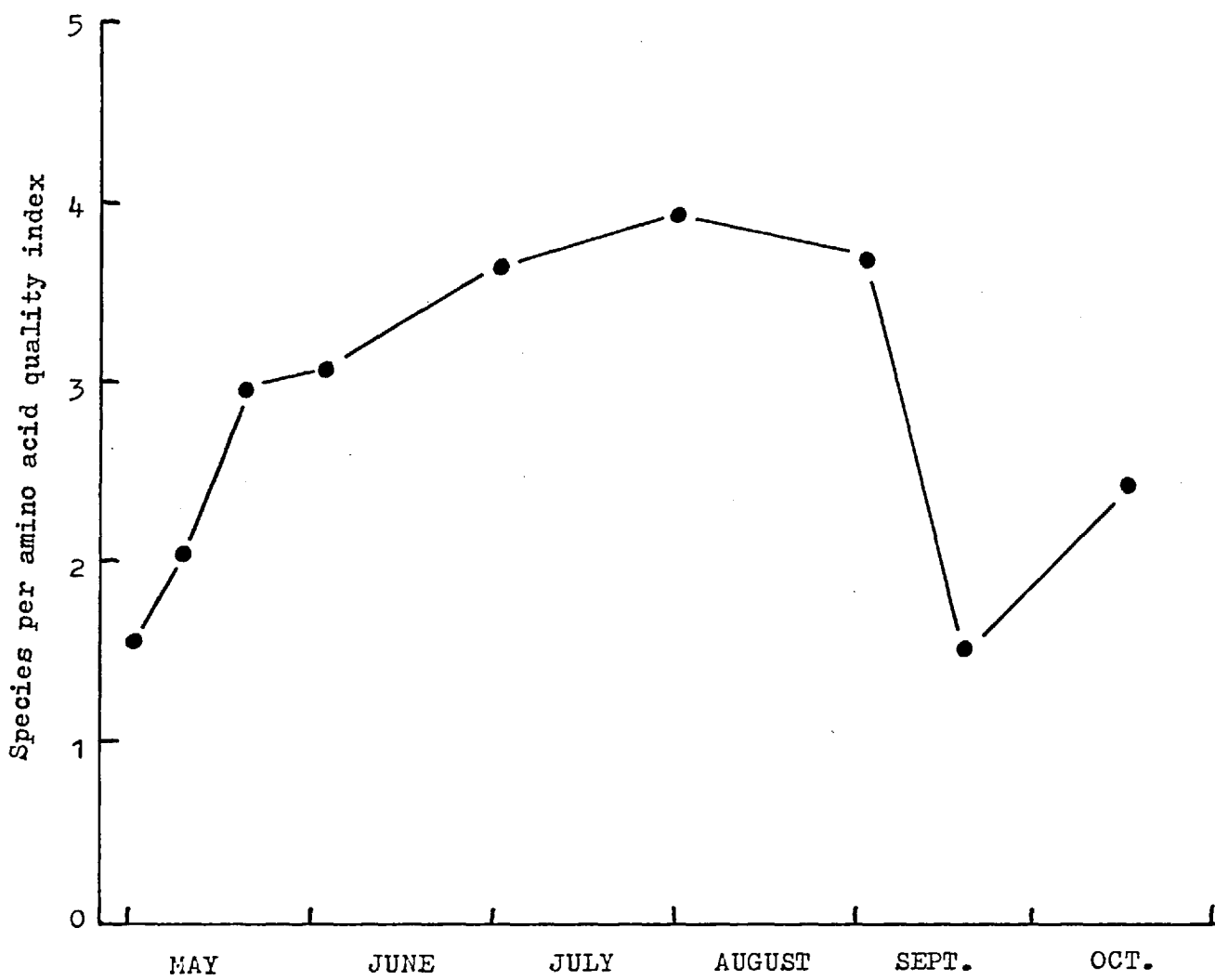
Fig. 3.53. The number of leafhopper species on pure swards
in response to fertilizer application. The arrow
represents the time when stem soluble nitrogen
rapidly increased. (●——●) leafhopper species,
(O—·-O) pasture height.
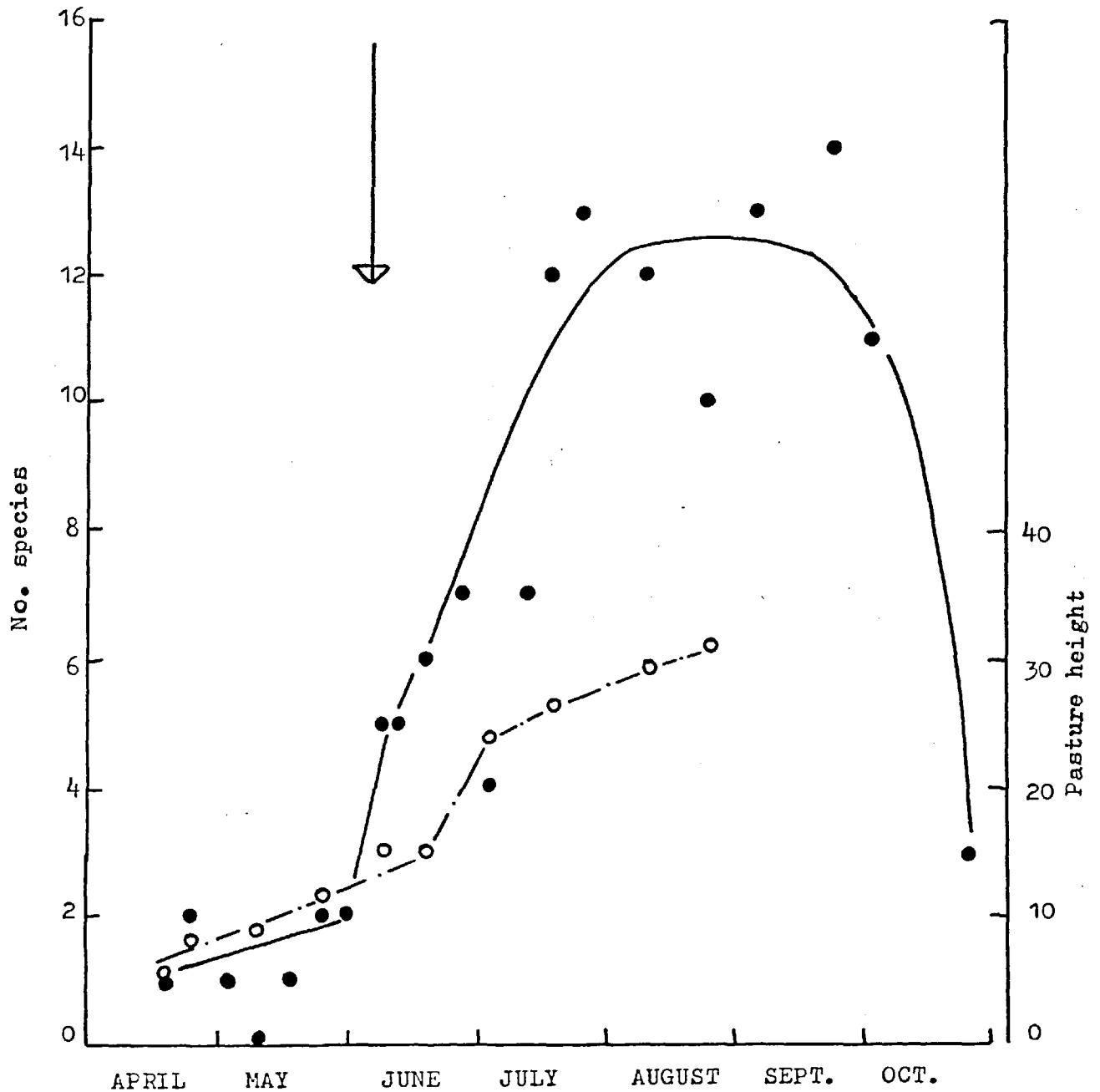
Interpretation of Figs.3.47-3.49 suggests that the abundance of the three feeding types are acting independently of each other. All feeding types occur together at the same time in the field but utilize a different food resource. This suggests that members belonging to similar feeding types are in direct competition for plant space and food resources but that members from different feeding types are able to coexist. A high level of abundance of one insect feeding type may have very little effect on the levels of abundance of another insect feeding type.

The mechanisms used by leafhoppers to space themselves on plants can only be speculation at this stage but two obvious types of mechanisms do exist, chemical and biotic. It is possible that chemicals salivated into the plant in the formation of sheaths may be transported by the plant and act as 'messengers' to other probing leafhoppers. Alternatively, the plant could release a chemical in response to insect probing which could also act as a chemical messenger to other leafhoppers.

The other major form responsible for maintaining a personal space must include leafhopper songs and the recent discovery of substrate vibrations. Leafhopper songs appear to be sex specific (Ossiannilsson 1949) and species specific (Strübing 1962, 1970, 1975, 1978; Moore 1961; Claridge & Howse 1968; Claridge & Reynolds 1973). Ossiannilsson (1949) and Claridge & Howse (1968) found that there may be more than one type of song, some possibly having strong ecological significance. Communication by substrate vibration on the plant (Strübing 1977) provides an interesting mechanism whereby phloem feeders can maintain spacing (or alternatively be kept together). Detection of the signal would probably be quite host specific providing an ideal means of communication between individuals of the same species.

In conclusion, the effect of fertilizers on grassland leafhopper communities is to alter the quality of the available food and to increase the available living space. Both have a beneficial influence and serve to increase the leafhopper populations that manage to find and take advantage of them. Food quality is considered more important in the first instance and only after populations have increased does the influence of plant architecture become more important in determining the structure of the leafhopper community.

In the next section, the effects of increased food quality on a number of leafhopper species are examined. To demonstrate the beneficial effects of increased food quality without altering plant architecture it has been necessary to experiment in constant environmental conditions.

3.5 Summary

(1) Low parasitism rates and low levels of predators suggest that other population controlling factors are operating.

(2) Leafhopper populations are characterised by great lability with resident populations possessing the potential to rapidly increase in abundance.

(3) Both nutrients and living space are increased as a result of fertilizer addition to the plant.

(4) When the levels of N, P, and K in the food are used as indices of food quality, maximum adult leafhoppers were present on those areas with a particular N, P and K level. Levels of N, P and K either larger or smaller than the optimum level had smaller numbers of adults present. Insects responded more strongly to leaf nitrogen levels than to leaf potassium or leaf phosphorus levels.

(5) Plant amino acids can be grouped as to whether they would be beneficial or detrimental to leafhopper performance. The ratio of the levels of beneficial to detrimental amino acids gave an index of amino acid quality.

(6) At low values of amino acid quality, leafhoppers (particularly phloem feeders) were present in low numbers. As amino acid quality increased, the numbers of phloem feeders also increased in a curvilinear fashion. Mesophyll feeders showed a similar but more variable pattern and xylem feeders did not show any pattern with leaf amino acid quality. Individual leafhoppers had an amino acid quality threshold, adults accumulating on those areas with high amino acid quality.

(7) Plant architecture (biomass and height) became progressively more important in restricting leafhopper populations once the population exceeded a threshold level ($250/m^2$ for phloem feeders and $136/m^2$ for mesophyll feeders).

(8) The number of species of leafhoppers was influenced more by food quality than by plant architecture, although both were important in determining the number of species and their abundance. At low population densities, food quality was more important than plant architecture. However, as the population increased due to the beneficial effects of food quality, plant architecture played an increasingly important role. The interaction between food quality and plant architecture can be used to explain the leafhopper community.

SECTION IV

Laboratory studies to examine the effects of food quality on repro-
ducing females

4.1 Introduction and review of literature

In Section III, it was shown that when the food quality was art-
ificially increased, the number of adults increased, levelled off, and

than decreased again. Further, the number of first instar nymphs/

female showed a similar pattern as food quality increased. For this

and subsequent sections, nitrogen has been chosen as the indicator of

food quality because of the sensitivity of the response to it by the

insects, relative to the other indicators measured (P,K) (Section 3.3.4),

its fundamental importance in protein metabolism and its wide intra-

season variability in the plants. Ideally, amino acid quality should

have been used as this was found to be the best indicator of food

quality (Section 3.3.4) but the time and expense involved in the large

numbers of determinations that would have been required made this approach

impractical.

Although many studies have been concerned with the effects of food

quality (particularly N) on aphid development and reproduction (e.g. see

reviews of Van Emden 1972; Hill 1976; Dixon 1977) there are surprisingly

few studies concerned with the influence of food quality on leafhopper

development and reproduction. Hill (1976) in a laboratory observation

has shown that adults of D.hamata, A.ocellaris, D.abdominalis, R.coronifera

and Z.scutellaris preferentially fed upon the developing flowers, seeds

and flower stem. Further, he linked high fecundity levels to high

leaf nitrogen levels during leaf senescence. Metcalf (1970) studying

the sugar cane leafhopper, Saccharosydne saccharivora Westw. correlated

fecundity levels to an increase in plant nitrogen levels following

nitrogen fertilization. Both Hinckly (1963) and Fennah (1969) found a positive correlation between leafhopper fecundity and host plant soluble nitrogen levels. Kalode (1974) showed that female brown plant-hopper, Nilaparvata lugens had high fecundity when reared on plants that received large amounts of nitrogen fertilizer. Pathak (1975) demonstrated in the greenhouse that increased applications of nitrogen fertilizer increased the number of progeny of N.lugens. Dyck et al. (1979) summarise much of the work of agricultural fertilizers on N.lugens. The reports of Kalode (1974), Pathak (1975) and Dyck et al. (1979) illustrate the fundamental problem with most of these results in that the researchers have little idea of the plant nitrogen levels and that their broad correlations are at best only associations between insects and the quantity of fertilizer applied.

Hill (1976) examined the relationship between an index of adult synchrony and an index of fecundity for D.hamata and A.ocellaris. Although no relationship between the indices was apparent for A.ocellaris, when D.hamata populations developed to adulthood before or during the period of nutrient mobilisation, population fecundity was high. If the adults missed the periods of nutrient mobilisation, fecundity was low.

Hill (1976) constructed a nitrogen budget in nymph and adult leaf-hoppers in an attempt to predict the points in the life cycle when high food quality was of greatest importance to the insect. Table 4.1 summarises nitrogen utilization efficiency data for his species. Reproductive nitrogen utilization efficiencies were higher than nymphal nitrogen utilization efficiencies in A.ocellaris and D.hamata. R.coronifera and Z.scutellaris had similar nymphal and reproductive adult nitrogen utilization efficiencies. From this and other data Hill (1976) concluded that food quality was important in influencing oviposition, but not nymphal or adult survival. He continued 'populations which can synchronise their

Table 4.1   Nitrogen Utilisation Efficiencies (NUE) of nymphs

and adults (modified from Hill 1976)

Species			NUE%
A.ocellaris	generation 1	nymphs	30.5
		reproducing adults	54.9
	generation 2	nymphs	32.4
		reproducing adults	50.7
D.abdominalis		nymphs	40.8
		reproducing adults	–
D.hamata		nymphs	24.1
		reproducing adults	43.1
R.coronifera		nymphs	21.8
		reproducing adults	19.4
Z.scutellaris		nymphs	32.1
		reproducing adults	30.7

times of adult emergence consistently with periods of high quality

food availability are abundant. Less well adapted species are rare,

but can show periodic outbreaks of abundance if they become synch-

ronised to periods of high food quality.

This section examines the effects of food quality on feeding,

growth and oviposition rates. Four leafhopper species were chosen for

study, D.hamata, Elymana sulphurella (phloem feeders), Eucelis incisus

(xylem feeder), and Z.scutellaris (mesophyll feeder). Information on

life history, voltinism and hibernation stages of these 4 species can

be obtained from Table 1.1 (Section I). Population sampling data are

given independently in Appendix XII.

4.2 Materials and Methods

All experiments were conducted at $20 \pm 1^{o}C$ and 16 hr photoperiod.

Leafhoppers were sorted live from sweepnet samples and caged individually

in glass sided cages of the type shown in Fig.4.1. They were left to

acclimatise to their new conditions for 10 days prior to any data being

recorded (preliminary experiments showed that female pre-ovipositional

periods were approximately 10 days in most species at $20^{o}C$). The

Holcus lanatus shoots were collected from the fertilized plots

(described in Section II) and renewed every 2 days.

4.2.1 Estimation of faeces/honeydew production

The method for determination of faecal/honeydew production has been

taken directly from Hill (1980). The walls of the glass cage (Fig.4.1)

and aluminium foil covering the cork were coated with 'repelcote'

(BDH Chemicals), a silicone based water repellent. The foil had a small

hole placed in it large enough to allow the passage of a grass stem to

be placed through into a water reservoir, but not to permit escape by

leafhoppers.

Fig. 4.1. Cage used for rearing leafhoppers individually.

muslin covering open topped tube

3" X 1" glass tube

Leaf material

muslin covering cork

cork

water reservoir (2" X 3/8" tube)
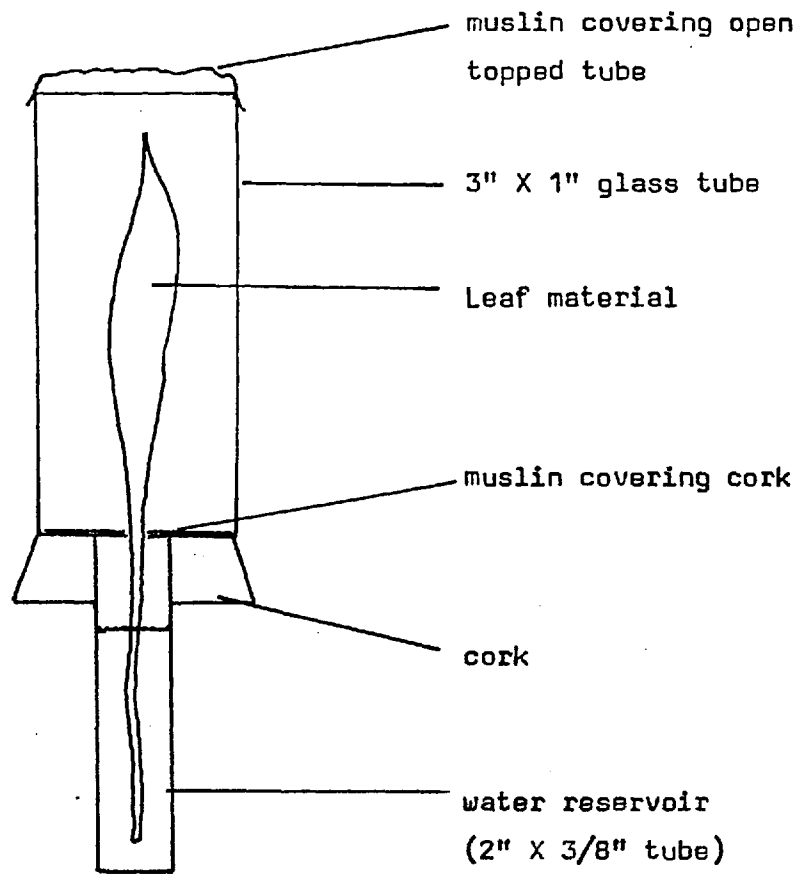
Every 2 days, leafhoppers were transferred to another acid washed replecote coated cage with a new grass shoot and the number of faeces droplets on the walls, foil and leaf blade were recorded. Droplets on the walls were counted after exhaling into the tube which allowed the droplets to absorb water vapour from the breath. Droplets then appeared as clear windows through the fogged glass. Droplets on the foil and on the leaf blade were counted under a binocular microscope.

Following counting of the droplets, samples were collected for the determination of the average dry weight and nitrogen content. Known numbers of droplets were collected onto small freeze dried, pre-weighed pieces of filter paper. The inside of the tube was again fogged and the droplets collected by capillary action into the paper. No visible residue was left after collection of the droplets. The paper and faecal material were then freeze dried and reweighed and the weight of faeces droplets found by difference. All weighings were made using a Cahn electro-microbalance to the nearest microgram. The paper containing the faeces was retained for nitrogen analysis. The amount of faecal material collected into individual pieces of filter paper were sometimes small (30 ug) but usually greater than 100 ug.

4.2.2 <u>Oviposition rate</u>

After the number of faecal droplets on the leaf blade had been counted it was examined to determine the number of eggs present. In all species it was possible to see and count the eggs through a binocular microscope. In the case of <u>D.hamata</u> which oviposits in grass stems, a short piece of stem was also included with a leaf blade. After 2 days the stem was dissected and the eggs present were counted.

4.2.3 Instar durations

First instar D.hamata nymphs were caged individually in glass cages at 15C and 20C by the method described earlier and with a food source (an excised leaf removed from the field fertilized plots), changed every two days. The cages were examined at the same time every day and a note of the day that insects moulted was recorded. The number of days between successive moults was then calculated as the average instar duration.

4.2.4 Adult longevity

When a virgin female emerged it was placed into a glass cage with an older male. Although not observed, fertilization was presumed to have taken place and after 4 days the male was removed. The total number of eggs laid by the female was summed to give a measure of total fecundity. Female longevity was calculated as the period from the day of emergence to the day of death.

Nitrogen determinations

The samples to be analysed for nitrogen were very small. A Kjeldahl method based on modifications of those used by Wright (1973) and Hill (1976) was used.

Digestion was carried out in 10 ml freeze-drier centrifuge tubes (Johnson and Jorgensen Ltd.), heated on standard micro-kjeldahl burners. The tube plus sample was weighed on a top loading balance to an accuracy of 0.01g. 500 μl of nitrogen free sulphuric acid and 50 μg of catalyst (containing Na_2SO_4, $CuSO_4 . 5H_2O$, $HgSO_4$ and Se in the ratio 50:4:4:1) were added. The sample was then digested and allowed to cool after which 3.0 gms of deionised water were added. The tube was thoroughly shaken to ensure uniform mixing and the contents were transferred to clean stoppered tubes to await analysis on the auto-analyser.

Digestion with a range of known weights of D-L Alanine gave 98.7% recovery. The results have been corrected for this loss.

This method was used to analyse the total nitrogen content of eggs and faeces of the 4 species of Auchenorrhyncha feeding on H.lanatus given different fertilizer treatments. Enough faecal material was collected onto the filterpaper to allow individual nitrogen determination but in a few cases, where very small amounts of faeces were collected, samples have been bulked. Controls showed that a very small amount of nitrogen was present when filter paper was wiped around a glass cage previously coated with replecote and allowance has been made for this.

Errors and assumptions

No attempt has been made to estimate waste metabolic nitrogen. Hill (1980) determined waste metabolic nitrogen in the form of uric acid, xanthine and hypoxanthine. He concluded that phloem feeders may be producing significant amounts of ammonia in the honeydew but that this was rapidly lost by evaporation and not detected in the analysis. Hill (1976) estimated that this would result in an increase of about 2% in the nitrogen utilization efficiencies.

In some cases, the assumption has been made that female body weight remained constant throughout the duration of the reproductive life. Many people (e.g. May 1971; Becker 1975; Hill 1976) have shown that this assumption is incorrect. However, this error is likely to be small relative to the body weight and weight of faecal and egg material. Since all 4 species have been treated in the same way the results will be comparable with themselves.

4.3 Results

The two phloem feeding species produced honeydew. E.incisus produced copious quantities of a watery excreta as is common for most xylem feeders. Z.scutellaris, which feeds on the mesophyll cells, produced small globules of dark brown liquid excreta. All types of excretment are referred to below as faeces.

The dry weight of faeces (mg) produced per female per day calculated as the product of the mean droplet size multiplied by the mean number of droplets per day is shown in Table 4.2.

The dry weight of faeces egested per milligramme female per day is shown in Table 4.3.

Egg production per female per day is shown in Table 4.4. D.hamata produced a large number of small eggs when compared to the number of eggs produced by E.sulphurella and E.incisus, species of approximately similar size. Oviposition rate increased as the level of nitrogen added to the grass increased. When high rates of nitrogen fertilizer were applied, egg production decreased in all the species except Z.scutellaris, which was still increasing egg production at the highest level of nitrogen applied. A comparison of Tables 4.3 and 4.4 shows that a greater number of eggs were produced on those plots with high ingestion rates.

No statistically significant differences existed between the individual dry weights of the eggs oviposited when fed on H.lanatus with different nitrogen treatments. The dry weight of egg material produced per female per day is given in Table 4.5 and the dry weight of material consumed per milligram female per day is given in Table 4.6. Z.scutellaris consumed an amount equivalent to 72% of its body weight each day at the maximum rate (i.e. nitrogen applied at 1200 Kg/ha). The phloem feeders consumed an amount equivalent to 25% of their body weight each day at their highest rate, whilst the xylem feeder consumed an amount equivalent to 12% of its body weight each day.

4.3.1 Assimilation efficiency

Waldbauer (1968) defined Approximate Digestibility (AD) as the weight of the food ingested minus the weight egested as faeces, divided by the weight of the food ingested, i.e.

Table 4.2   Dry weight of egesta mg/ ♀/day when fed H.lanatus
fertilized with different rates of nitrogen fertilizer.

Nitrogen kg/ha

Species		1200	900	600	300	100	0
D.hamata		0.0715	0.0822	0.0783	0.0967	0.0821	0.0650
	SE	0.009	0.014	0.010	0.011	0.008	0.005
E.sulphurella		0.1456	0.1494	0.2163	0.2322	0.1515	0.0905
	SE	0.015	0.011	0.027	0.024	0.015	0.008
E.incisus		-	-	0.0582	0.0937	0.0207	0.0313
	SE			0.016	0.016	0.004	0.008
Z.scutellaris		0.0832	0.0656	0.0450	0.0348	0.0312	0.0313
	SE	0.004	0.004	0.006	0.003	0.003	0.002

Table 4.3   Dry weight of egesta per milligramme female per day
when fed H.lanatus with different rates of nitrogen
fertilizer.

Nitrogen kg/ha

Species	1200	900	600	300	100	0
D.hamata	0.0917	0.1054	0.1004	0.1240	0.1053	0.0833
E.sulphurella	0.0941	0.0966	0.1398	0.1501	0.0979	0.0585
E.incisus	-	-	0.0347	0.0559	0.0124	0.0187
Z.scutellaris	0.4894	0.3859	0.2647	0.2047	0.1835	0.1841

Table 4.4   Eggs/♀/day when fed H.lanatus fertilized with different rates of nitrogen fertilizer.

Nitrogen Kg/ha

Species	1200	900	600	300	100	0
D.hamata	2.46	4.29	7.96	6.22	6.41	5.05
SE	0.42	1.40	1.27	1.02	0.91	1.27
E.sulphurella	1.09	1.96	3.57	4.23	2.97	1.45
SE	0.28	0.24	0.67	0.33	0.49	0.30
E.incisus	–	–	3.20	3.56	1.14	1.13
SE			0.59	0.82	0.28	0.28
Z.scutellaris	4.05	2.17	1.93	1.67	1.27	1.42
SE	0.28	0.24	0.53	0.58	0.26	0.35

Table 4.5   Egg biomass mg/♀/day when fed H.lanatus fertilized with different rates of nitrogen (dry weights)

Nitrogen Kg/ha

Species	1200	900	600	300	100	0
D.hamata	0.0347	0.0605	0.1122	0.0877	0.0904	0.0712
E.sulphurella	0.0403	0.0725	0.1321	0.1565	0.1099	0.0537
E.incisus	–	–	0.0979	0.1089	0.0349	0.0346
Z.scutellaris	0.0393	0.0210	0.0187	0.0162	0.0123	0.0138

Table 4.6   Biomass consumed per milligram female per day when fed
             H.lanatus fertilized with different rates of nitrogen.

Nitrogen Kg/ha

Species	1200	900	600	300	100	0
D.hamata	0.1362	0.1829	0.2442	0.2364	0.2212	0.1738
E.sulphurella	0.1202	0.1434	0.2252	0.2513	0.1690	0.0932
E.incisus	-	-	0.0932	0.1210	0.0332	0.0393
Z.scutellaris	0.7206	0.5094	0.3747	0.3000	0.2559	0.2653

Table 4.7   Approximate Digestibility (AD) for reproducing females
             when fed H.lanatus fertilized with different rates of
             nitrogen.

Nitrogen Kg/ha

Species	1200	900	600	300	100	0
D.hamata	32.7	42.4	58.9	47.6	52.4	52.3
E.sulphurella	21.7	32.7	37.9	40.3	42.4	37.2
E.incisus	-	-	62.7	53.8	62.8	52.5
Z.scutellaris	32.1	24.3	29.4	31.8	28.3	30.6

$$AD = \frac{\text{Weight of food ingested} - \text{Weight of faeces}}{\text{Weight of food ingested}} \times 100 \qquad (1)$$

where AD is approximate digestibility.

In this study, the weight of the food ingested has been found indirectly by assuming that female weight remains constant. AD can then be defined as

$$AD = \frac{\text{Weight of eggs produced}}{\text{Weight of food consumed}} \times 100 \qquad (2)$$

The difference between values obtained using equation 1 and 2 will be small, values using equation 2 will be slight underestimates of the true AD.

AD for the 4 leafhopper species has been calculated using equation 2 and the results are shown in Table 4.7. Z.scutellaris had the lowest maximum AD (30%), E.sulphurella and D.hamata had 40% and 60% respectively and E.incisus had the highest AD (63%). As the level of nitrogen fertilizer applied to the grass increased, the AD of D.hamata, E.sulphurella and E.incisus increased and then decreased but that of Z.scutellaris remained relatively constant.

4.3.2 Calculation of daily nitrogen utilization efficiency

A deal of controversy surrounds the use of the term utilization efficiency. Waldbauer's (1968) definition has been used here. He suggested that utilization 'should be reserved as a general term which included digestion, metabolism, and conversion (of food) to body substance'. The efficiency of utilization then is a measure with which a substance (in this case nitrogen) is utilised, i.e.

$$NUE\% = \frac{\text{Nitrogen used by insect}}{\text{Nitrogen consumed by insect}} \times 100$$

In this study the assumption has been made that reproducing females remain at constant weight throughout their reproductive life. In effect

this means that the amount of nitrogen in the body can be assumed to be constant, and the amount of nitrogen used for maintenance is equal to the nitrogen excreted with the faeces. Nitrogen consumption can then be estimated as the amount of nitrogen in the faeces plus the amount of nitrogen used in egg production, i.e.

$$NUE\% \quad = \quad \frac{N(egg)}{N(faeces)+N(egg)} \quad x \; 100$$

Table 4.8 shows the average amount of nitrogen egested (ug/♀/day) when fed on H.lanatus treated with different rates of nitrogen fertilizer.

The amount of nitrogen used for egg production (Table 4.9) has been calculated from the product of the mean number of eggs produced and the mean nitrogen content of the eggs.

Table 4.10 shows the daily nitrogen utilization efficiencies for reproducing females. NUE has been calculated from experimental means and not for individual leafhoppers; therefore the values have not been given standard errors.

The seasonal fluctuations in plant nutrients would suggest that the level of nitrogen in the food is dependent on the time when these experiments were undertaken. Further, as was shown in Sections II and III, although there is a general relationship between the amount of fertilizer applied to the plant and the level of nitrogen in the plant, the relationship does not hold in every case. Thus the results shown in Table 4.10 have been plotted against the leaf nitrogen content when these experiments were undertaken (Fig.4.2). All 4 species show the same pattern, NUE is maximised over a very narrow band of nitrogen concentration in the food. It is particularly interesting that in no case is NUE maximised at the highest nitrogen level.

Table 4.8   Nitrogen egested as faeces (ugN/♀/day) when fed
             H.lanatus fertilized with different rates of nitrogen.

Nitrogen Kg/ha

Species	1200	900	600	300	100	0
D.hamata	14.200	11.286	20.344	20.230	20.164	10.030
E.sulphurella	9.668	7.533	8.933	15.186	16.044	7.240
E.incisus	–	–	8.0202	6.203	3.571	5.330
Z.scutellaris	8.312	7.767	6.912	3.880	5.747	6.144

Table 4.9   Egg nitrogen production (ug N/♀/day) when fed
             H.lanatus fertilized with different rates of nitrogen.

Nitrogen Kg/ha

Species	1200	900	600	300	100	0
D.hamata	3.66	6.39	11.85	9.26	9.54	7.52
E.sulphurella	2.15	3.87	7.04	8.34	5.86	2.86
E.incisus	–	–	9.33	10.38	3.32	3.30
Z.scutellaris	2.61	1.40	1.25	1.08	0.82	0.92

Table 4.10   - Nitrogen Utilization Efficiency (NUE) for reproducing

females when fed H.lanatus fertilized with different

rates of nitrogen.

Nitrogen Kg/ha

Species	1200	900	600	300	100	0
D.hamata	20.5	36.1	36.8	31.4	32.1	42.9
						32.4*
E.sulphurella	18.2	33.9	44.1	35.5	26.7	28.3
E.incisus	-	-	53.8	62.6	48.2	38.2
Z.scutellaris	41.8	15.3	15.3	21.7	12.5	13.0

* Estimated when feeding on grass material removed from a sown monoculture

of H.lanatus described in Section V.

Fig.4.2   Nitrogen utilization efficiencies for
           reproducing females when feeding on a
           range of nitrogen concentrations in
           H.lanatus.

           (a)   Dicranotropis hamata
           (b)   Elymana sulphurella
           (c)   Eucelis incisus
           (d)   Zyginidia scutellaris

(a)

NUE%

Nitrogen content of food (mg N/gm dry weight)

(b)

(c)

NUE%

(d)

Nitrogen content of food (mg N/gm dry weight)
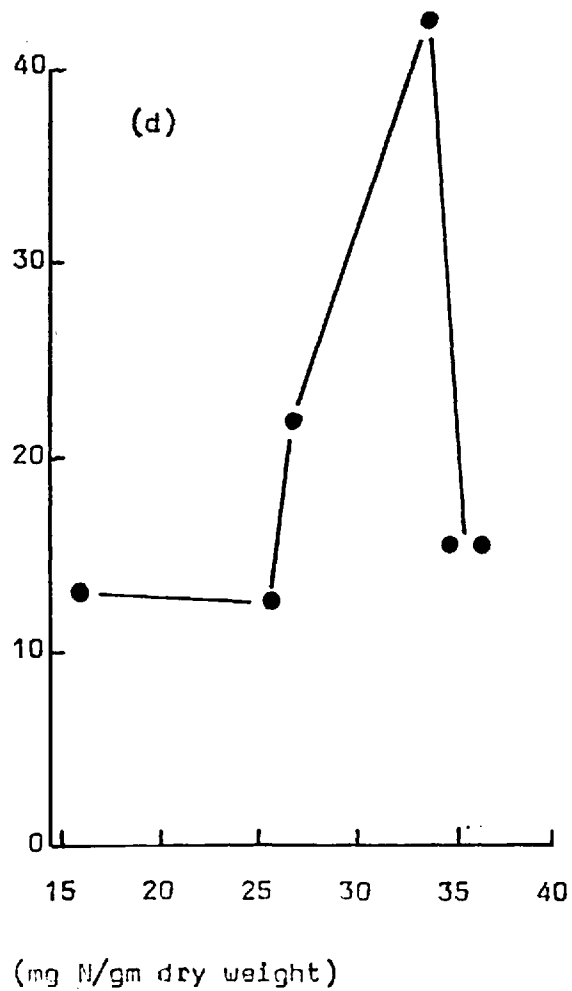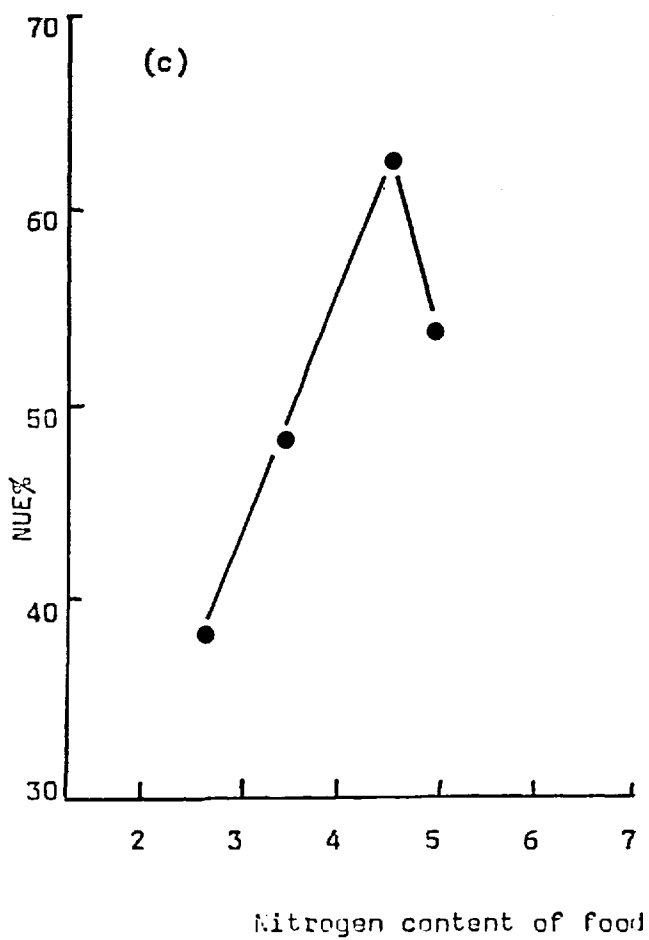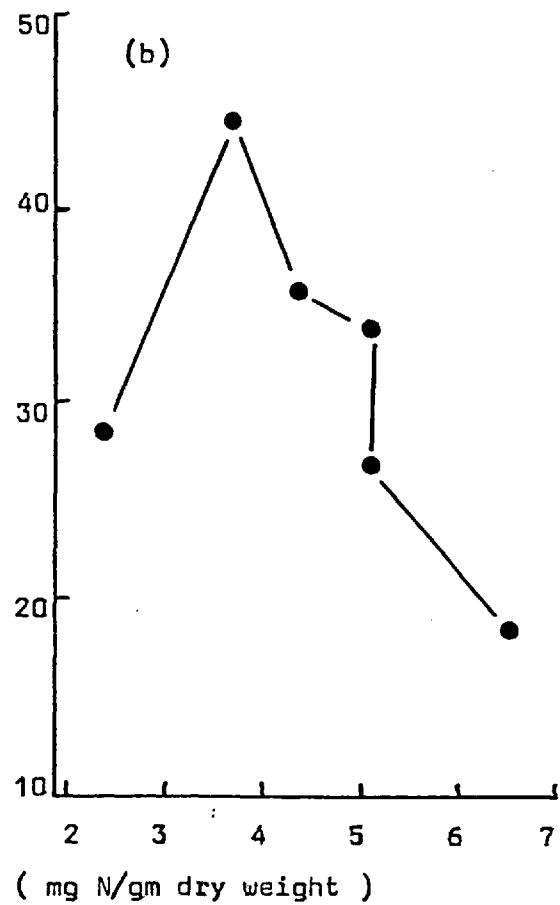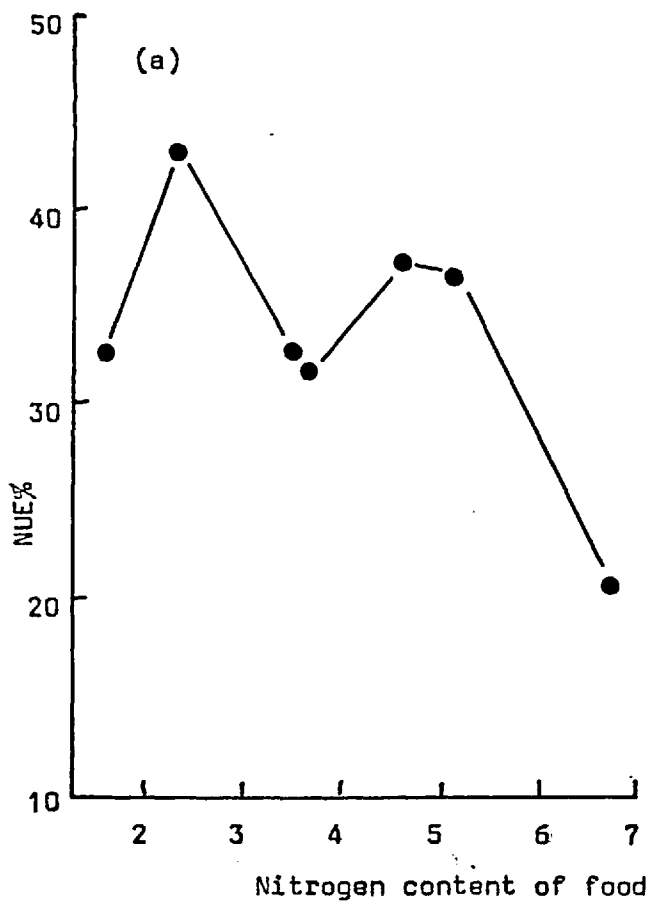
4.3.3 Instar durations

The data for the individual instars are listed in Table 4.11 and the total instar duration plotted against the level of leaf soluble nitrogen during the duration of the experiment is graphed in Fig.4.3. Differences do exist between the duration of the instars when feeding on different quality food. These differences are more pronounced at low temperatures. High levels of nitrogen in the food also depress instar duration.

Shortened nymphal periods necessarily imply less exposure to predators and parasitoids so that a greater number of nymphs reach reproductive stages provided no increase in background mortality.

4.3.4 Adult longevity

Only longevity of female D.hamata was examined and then only a small number of adults survived to die of full physiological age. This experiment was conducted in conjunction with the feeding experiments. No statistical differences were found between adult longevity when adults were feeding on H.lanatus taken from plots with different nitrogen treatments. Mean adult longevity was 41.2 days (N=11) at 20 C. When females died, the ovaries were dissected and on no occasion were the females reproductively spent, i.e. they had developed ova up to the time of their deaths.

Discussion

Because of the large number of parameters involved in the results of this section it has been decided to discuss the results from the individual feeding types separately.

Z.scutellaris consumed material at a maximum rate equivalent to 72% of its body weight. This is an extremely high ingestion rate and is most probably related to its food source, mesophyll contents. However,

176.

Table 4.11   D.hamata instar duration at 15 and 20° C when feeding

on H.lanatus fertilized with nitrogen.

20° C

Leaf soluble nitrogen

Instar	2.35	2.67	4.42	5.16	8.65
II	8.0	8.0*	7.0	9.0	8.0
SE	1.0	–	–	–	–
III	9.0	5.5	6.0	6.0*	9.7
SE	0.6	0.5	–	–	1.8
IV	7.5	7.8	6.0	7.3	6.0
SE	1.0	0.9	0.5	0.3	0.6
V	8.8	8.7	7.7	9.3	9.0
SE	0.2	0.7	0.3	0.3	1.0
Σ	33.3	30.0	26.7	31.6	32.7

15° C

II	28.5	28.5	20.0	21.0	21.0
SE	–	7.5	–	–	–
III	24.0*	24.0	21.0	16.0	34.0
SE	–	–	3.0	–	4.0
IV	25.5	22.0	19.3	22.0	21.5
SE	1.5	7.0	1.8	6.0	0.5
V	21.7	20.0	19.2	20.0	19.3
SE	2.9	2.0	0.5	–	0.9
Σ	99.7	94.5	79.5	79.0	95.8

* estimated

Fig. 4.3. D.hamata cumulative instar duration (II-V) when
feeding on H. lanatus fertilized with different
rates of nitrogen.

Leaf soluble nitrogen level (mg N/gm dry weight)
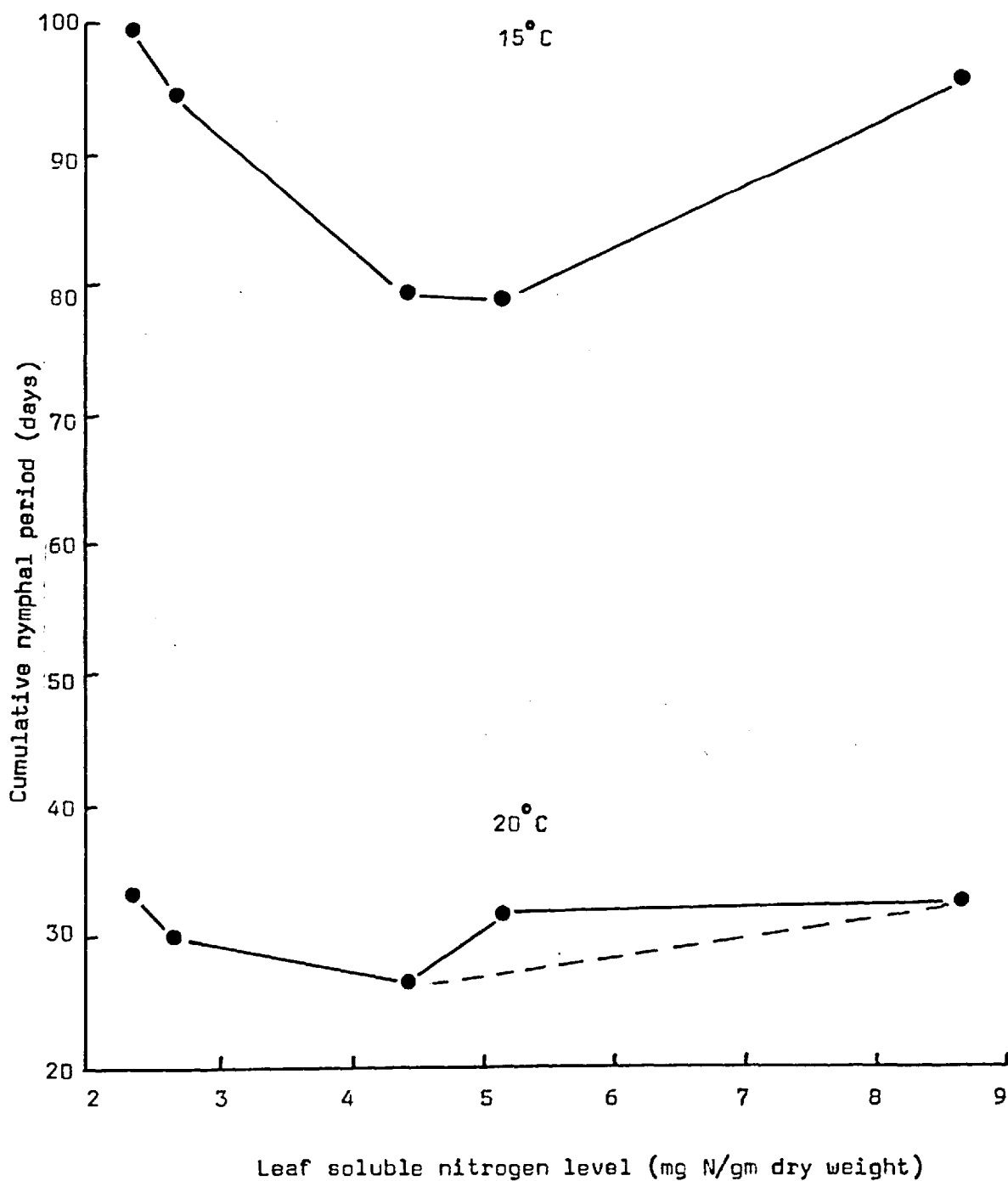
of its intake, it assimilated only a small proportion (32% maximum).
This presumably reflects the difficulty in obtaining adequate amino
acids and proteins when feeding on the mesophyll contents.   Many of
these compounds are likely to be bound into plant proteins and thus are
difficult and metabolically costly to extract.   Thus, Z.scutellaris
has a strategy of rapid throughput of material and removal of the more
easily digestible components.

Nitrogen utilization efficiency was low over most of the measured
range of total nitrogen except when NUE increased dramatically for a
narrow band around 30 mg N/gm dry weight.   The maximum value of NUE
(42%) was similar to the maximum value recorded for the phloem feeders.

D.hamata has a higher assimilation rate than E.sulphurella, the
other phloem feeder, although consumption rates and ovipositional rates
are similar per milligramme of female body weight.   This may be related
to a large number of individual differences between the two species, e.g.
the amount of time and energy spent moving, or differences in gut length,
etc.   The food quality of the grass taken from the experimental plots
did not differ between the two species as the experiments were undertaken
at the same time.

When fertilizer was added at high rates, both consumption and assim-
ilation decreased in the phloem feeders.   This is interesting as con-
sumption and assimilation rates are linked (Waldbauer 1968) such that
assimilation is partially determined by the gut retention time.   The
faster the consumption (and hence gut throughput time) then the lower is
the assimilation rate.   The reasons for the decrease in consumption and
assimilation rates are only conjecture at this stage but two explanations
are apparent.   The plant may have been made unsuitable for these two
species such that they are consuming and digesting only the small amount
of material necessary for adult maintenance.   Results with other

Homoptera show that restlessness increases as the plant becomes unsuit-
able (e.g. Dixon 1977). Preliminary results with _J.pellucida_ show that
the amount of time spent feeding decreases when the plants become un-
favourable. The second explanation is that nitrogen is no longer the
limiting element and that perhaps the insects have switched to an energy
limited metabolism as is often found in animals (e.g. Morowitz 1968).

Comparisons between consumption and AD of the two phloem feeders
when feeding on _H.lanatus_ taken from unfertilized plots (control plots)
show that _E.sulphurella_ has a consumption rate of approximately half and
an AD of approximately one third that of _D.hamata_. The answer to these
differences probably lies in the different life history strategies
involved. _E.sulphurella_ exhibits many of the characteristics of a
'K' strategist (MacArthur & Wilson, 1967). They live in a stable environ-
ment with a predictable (albeit low quality) food source, they lay single
large eggs and relative to _D.hamata_ are long lived and do not show much
potential to rapidly increase their abundance. In contrast, _D.hamata_
exhibit more 'r' characteristics than _E.sulphurella_. They persist in
an unstable environment (i.e. overwinter as nymphs) and utilize an un-
predictable food source (the timing, duration and quality of the nutrient
flushes are unpredictable with respect to the insect, e.g. McNeill &
Southwood 1978). The female lays batches of small eggs and the most common
morph is brachyopterous (c.f. _E.sulphurella_). This species has a great
potential to rapidly increase its population (e.g. it developed into 43%
of the total leafhoppers caught in 1979, Section 2). The advantages
to laying batches of eggs in an unstable environment which has an un-
reliable food source have been reviewed by Stearns (1976) amongst others.

The pattern showing NUE plotted against increasing leaf nitrogen
is similar in both species. NUE increased to a maximum and then decreased
as the levels of leaf nitrogen increased. The maximum NUE of _D.hamata_

and E.sulphurella are similar, but are reached at different levels of leaf soluble nitrogen.

E.incisus consumed only a small proportion equivalent to its body weight each day (3.9%) but digested a greater proportion than the other species. The low consumption rate is probably a reflection of the low carbohydrate content in the xylem. Phloem honeydew is comprised of 90% carbohydrate and hence the dry weight component is large. Xylem feeder excreta is predominantly water with a very low dry weight component. Because the food source to E.incisus is relatively more dilute than the food source to a phloem feeder, it processes a greater volume of material and has a more efficient method for extracting nutrients than the phloem feeder.

E.incisus had a higher NUE than the other 3 species. This is almost certainly associated with the low levels of nitrogen in the xylem (Beevers 1976). E.incisus was consuming a smaller quantity of nitrogen per body weight than the other species but was utilizing nitrogen much more efficiently. It is quite probable that the measured leaf soluble nitrogen level for E.incisus does not represent the actual level of nitrogen in the food source, however it is not unreasonable to assume that as leaf soluble nitrogen increased, the levels of nitrogen in the xylem also increased. E.incisus occasionally excreted faecal droplets which were similar in appearance to honeydew droplets excreted by phloem feeders. Port (1978) recorded E.incisus feeding on the xylem about 70% of the time and approximately 30% of the time it fed on the phloem contents. It is possible that this species can supplement its low nitrogen diet at times by feeding occasionally on the phloem material (c.f. partial predation strategy of mirid bugs, e.g. Southwood & Leston 1959). The physiology of this insect would warrant further investigation.

All 4 species maximised NUE at different levels of nitrogen in the plant. This suggests that natural selection should favour those individuals that are correctly synchronised with the plant nitrogen levels that allowed maximum NUE. There are two ways to approach this problem. Firstly, natural selection should favour monophagous individuals that are correctly synchronised to the nutrient levels in the dominant grass species. In years when insect life history and plant nitrogen levels are correctly synchronised, high ovipositional rates result which ensure rapid population increases. Hill (1976) and McNeill & Southwood (1978) provide partial evidence for this mechanism. They use peak adult D.hamata emergence and times of peak nitrogen flushes in H.mollis. A greater number of nymphs/adult was present in the following generation when fecund females and nutrient flushes were correctly synchronised. To ensure that the dominant grass species is not destroyed by insect damage, the plants response is to maintain differential nutrient flushing, both in quantitative amounts and in time.

The second way that natural selection can act is to promote polyphagy (or at least oligophagy) and favour highly mobile individuals capable of searching out and tracking a particular nutrient level in the grass species in its immediate habitat. Gibson (1976a, 1976b) studied grassland Heteroptera and showed that competition between co-existing species was rare and that different species were strongly correlated with a particular nitrogen level in a range of grasses. Insects switched host plant species as the different grass phenologies moved the different grass species in and out of the band of nitrogen concentrations that the insects were associated with; in this way, interspecific competition was avoided.

There is little justification for relating consumption and
oviposition rates in the laboratory to those occurring in the field.
However, the effects of increasing food quality on oviposition can-
not be ignored. Females captured in the field in 1979 were dissected
throughout the season and scored as to ovian development using the
method of Waloff (1973). No females were captured with spent ovaries
so it is reasonable to assume that oviposition continues for most, if
not all, of the adult life. Increased reproduction in the field is
due to increased ovipositional rates because adult longevity is rela-
tively unaffected by plant nitrogen levels.

In the next section analyses of host plant field data and leaf-
hopper performance when feeding on the different grass species are
presented in an attempt to further examine the hypothesis that leaf-
hoppers are associated with a particular nitrogen level in the
plant.

Summary

(1) Instar durations and oviposition rate are dependent on food
quality whereas adult longevity is unaffected by the level of food
quality.

(2) Irrespective of its dry weight consumption, Z.scutellaris digests
only about 30% of its intake. Maximum consumption was equivalent to
72% of its body weight each day. E.incisus had a low dry weight con-
sumption rate (the maximum was equivalent to 12% of its body weight
each day) but a more variable higher digestion rate such that it can
partially compensate for low consumption. The phloem feeders had
intermediate consumption rates (equivalent to 25% of body weight each
day) but variable digestion rates.

(3) When nitrogen utilization efficiencies were plotted for different

species against the level of nitrogen in the food, they reached maximum

values on different plant nitrogen levels. This suggests that leaf-

hopper species may be associated with a particular nitrogen concentration

in the grasses.

SECTION V

Insect-host plant associations

Introduction

Host plant associations of grassland Auchenorrhyncha have received little attention. This is not surprising when one considers the species composition and habitat complexity even in a relatively small area of a natural grassland. Indeed, natural grasslands are character- ised as having a mosaic of grass species and much of the localised patterns in grassland leafhopper distribution may be attributed to the mosaic of grass (e.g. Murdoch et al. 1973).

Two studies in particular have contributed greatly to our know- ledge of grassland leafhopper-host plant associations. Whitcomb et al. (1973) studied host relationships of grassland Cicadellidae in North America and concluded that examples of monophagy and polyphagy are relatively uncommon. Nutritional adaptation and patterns of seasonal rhythmicity were the major factors responsible for the main- tenance of host specificity. Waloff & Solomon (1973) examined grass- land Auchenorrhyncha-host plant relationships at Silwood Park, Berkshire, England. They concluded that only a few species showed consistant host plant specificity.

Most grassland leafhoppers are restricted to members of the gramineae by the presence of allelochemicals (Whittaker 1972) in other plant taxa. Host associations between leafhoppers and different grass species are maintained by the rhythmical seasonality and nutrient com- position of the grasses and nutrient requirements of the leafhoppers. Evidence to support this claim comes from a number of sources. (1) Amino acid balances are known to be critical for rearing other Homoptera. (2) Many species can be reared successfully on a number of graminoceous species. Port (1978) found no differences in the

feeding behaviour in the majority of his 53 test species when feeding on _Avena sativa_ (L.), and when feeding on their known host. Waloff & Solomon (1973) report that strong host associations are uncommon. They analysed results from breeding experiments which included identification of species that emerged from grass dug up in the field and potted in an outdoor insectary. (3) Biochemically most grass species are very similar. Gibbs (1963) and Butler & Bailey (1973) review the biochemical similarities of grasses and note the general lack of secondary chemicals. (4) There are many recorded instances of limited maintenance of insect species on plants in the field that are not their primary host nor, in many instances, evolutionary closely related.

Thus there is a need to examine and clarify some of the host associations of grassland Auchenorrhyncha and attempt to unravel some aspects of the nutritional adaptation of leafhoppers to their 'primary' host.

The best method for comparison of host specificity is collection from a number of similarly aged monocultures within a very narrow time period. At Silwood Park, areas of relatively pure swards of grasses are absent (except for areas of _H.mollis_) so it was necessary to sow monocultures of the six most dominant species. Collections were also taken occasionally from an area of almost pure _H.mollis_ but as this had been in monoculture since before 1966 (McNeill 1969) comparison of the results with those from recent sown plots may not be valid as time to colonization is considerably different. Hill (1976) worked on this area of _H.mollis_ so that species differences between his data and this study may be attributed to a combination of host plant and other effects. In 1979, only two species recorded regularly on _H.mollis_ were not captured on this experimental site, _Macustus griesescens_ (Zetterstedt) and

Diplocolenus abdominalis (Fab.).   In 1979, D.abdominalis was relatively

common on Hill's (1976) H.mollis site (i.e. 50.1/m^2 @ 5/6/79 and 31.9/

m^2 @ 4/7/79) but no M.griesescens were captured. Therefore it is probable

that D.abdominalis may be closely associated with H.mollis.

In this section, examination of Auchenorrhyncha-host plant assoc-

iations are presented with respect to the physical, phenological, and

chemical characteristics of the host species.   The evidence suffers

from only 2 years data and then the results are taken from within a

small area at Silwood Park.   An extensive national survey is obviously

required in the light of some of these results.

Materials and Methods

The experimental site was situated on a cultivated field on Silwood

Bottom (SU 687946)   at Silwood Park, Ascot, Berkshire, England. To

the west of the area was rough grassland dominated by a H.mollis and

H.lanatus complex.   50m North of the site was cultivated in 1977 and

then left fallow for the duration of this study, to the south was winter

and spring wheat and the area to the East was planted with potatoes in

1978 and Black Field Beans in 1979.

In autumn 1977, 5 grass species were sown in small plots (15m^2) in

a latin square design.   A 1m wide border (a mixture of the 5 grass species)

surrounded each plot.   The grasses sown included most of the dominant

grass species at Silwood Park plus perennial ryegrass and included:

Dactylis glomerata (L.) (Variety 'Bopa Pajbjerg')

Festuca pratensis (Huds.) (Variety 'S215)

Holcus lanatus (L.) (Variety Unknown origin)

Lolium perenne (L.) (Variety 'Cropper')

Poa pratensis (L.) (Variety 'Prato')

A sixth grass species, Agrostis tenuis (Sibth.) (Variety 'Browntop')

was sown below the original area in Autumn 1978, the size of this plot

was $150m^2$.

Grass seed was broadcast at 34 gm/m^2 with a basal fertilizer (NPK

Growmore 7:7:7) dressing at 40 gm/m^2. Growmore fertilizer at 40 gm/m^2

was applied to the area each spring.

The experimental plots were handweeded in the spring and invading

grasses and other species were removed. In this way, the plots

remained as monocultures for the duration of the study.

Plant material was removed at random from the indvidual plots and

samples of similar grass species were bulked. Material was transferred

to a freeze drier within 10 minutes of collection and after drying was

stored in airtight containers for future analysis.

Plant height was measured with a one metre rule at 3 random stations

within each plot.

Biomass estimates were calculated from the dry weight of live plant

material clipped at ground level within two $0.01/m^2$ quadrats. One

quadrat/plot was removed and estimates from similar grass plots were

bulked. For A.tenuis in 1979, three $0.01/m^2$ quadrats were removed and

bulked at each sampling occasion.

Nitrogen levels of freeze dried plant material were determined by

the standard micro-Kjeldahl method described in Section II and Appendix

III.

Peak flowering times of the different grass species were estimated

by counting the number of flower stems present in an 0.25 m^2 quadrat

that had been randomly placed at 3 intervals within each plot. The

results from individual plots of similar grass species have been bulked.

Insects were sampled at weekly intervals with a motorised D.vac.

suction sampler as described in Section III. One, 60 second suck per

plot was taken at random from within two plots (chosen from a table of

random numbers) of the same grass species and the contents bulked to form one sample. Plots were sampled only when the grass was dry and at the same time of day (1500 hr). The contents of the sample were killed immediately and the leafhoppers present were removed, identified and counted in 70% alcohol under a binocular microscope.

Discussion of Results

Physical characteristics

A penetrometer was made based on the design of Williams (1954) and Tanton (1952) which measured the weight of sand necessary to push a pin through the epidermis of a leaf. The results (Fig.5.1) give only a relative measure of leaf toughness allowing the grass species to be ranked according to decreasing toughness:-

F.pratensis = P.pratensis ⟩ D.glomerata = L.perenne>>H.lanatus

H.lanatus was half as hard as the other 4 species (which were of similar hardness) but was the only species to have numerous hairs on the leaves; the other species being relatively hairless.

Water content of plant material has been associated with Lepidopteran larval growth (Scriber 1977; Scriber & Feeny 1979) but it is doubtful whether water requirements vary a great deal between leaf-hopper species. In times of acute water stress, nitrogen and amino acid levels are known to increase in the aerial parts of plants (Bates 1971; White 1976). This increase in food quality may be more advantageous to resident leafhoppers than the direct effects of water shortage. It is probable that in years of extreme water shortage, individuals either emigrate or die. The results showing the water content for the individual grass species are given in Appendix XIII. Water content was determined by the equation (Chapman 1976)

$$Wd = \frac{100(f-d)}{d}$$

where Wd = water content, f = fresh weight and d = dry weight of plant material.

Fig.5.1   Leaf toughness of 5 grass species as
          measured with a penetrometer. Like
          symbols denote not significantly differ-
          ent at p<0.001.

Fig.5.2   The abundance of leafhoppers associated
          with an index of plant architecture.
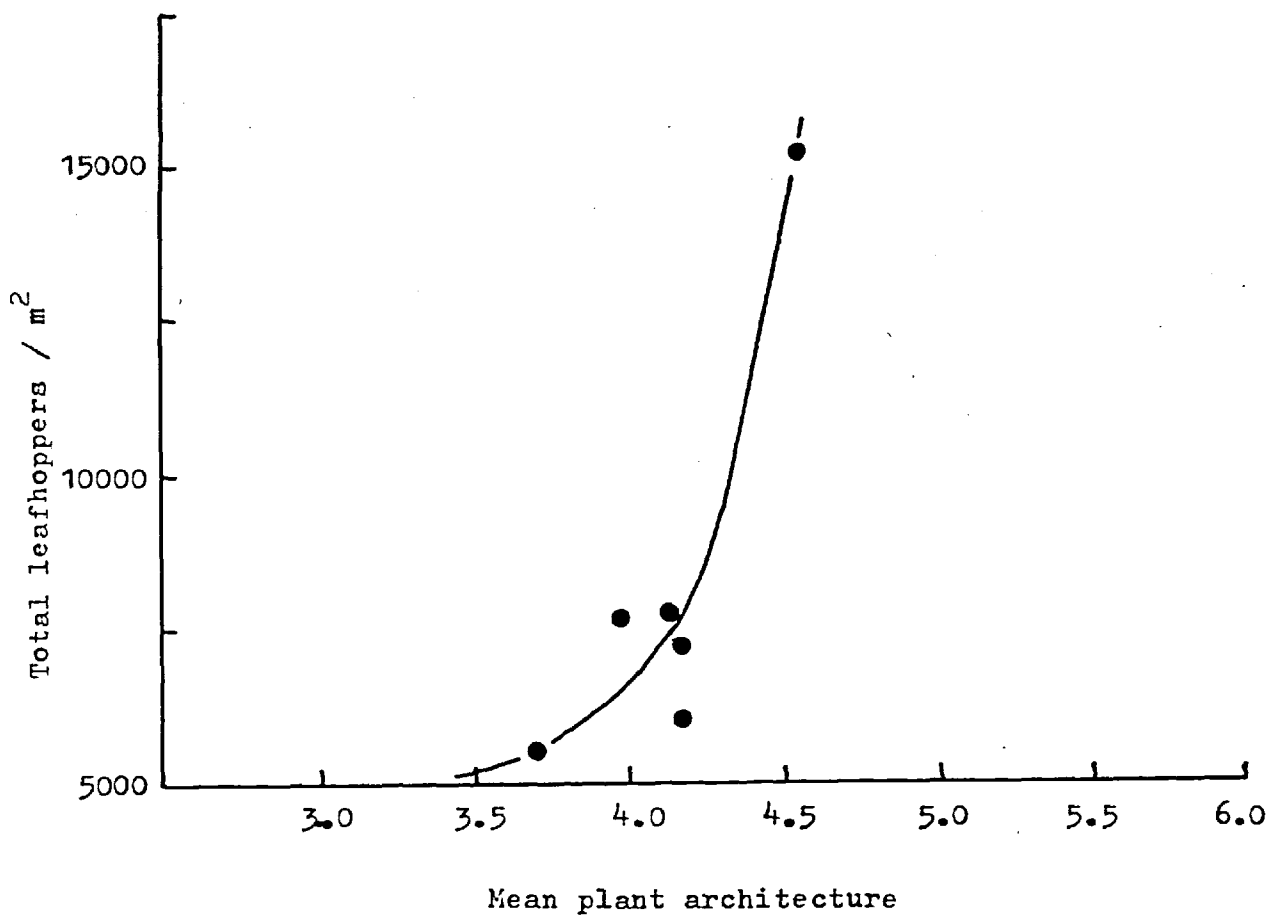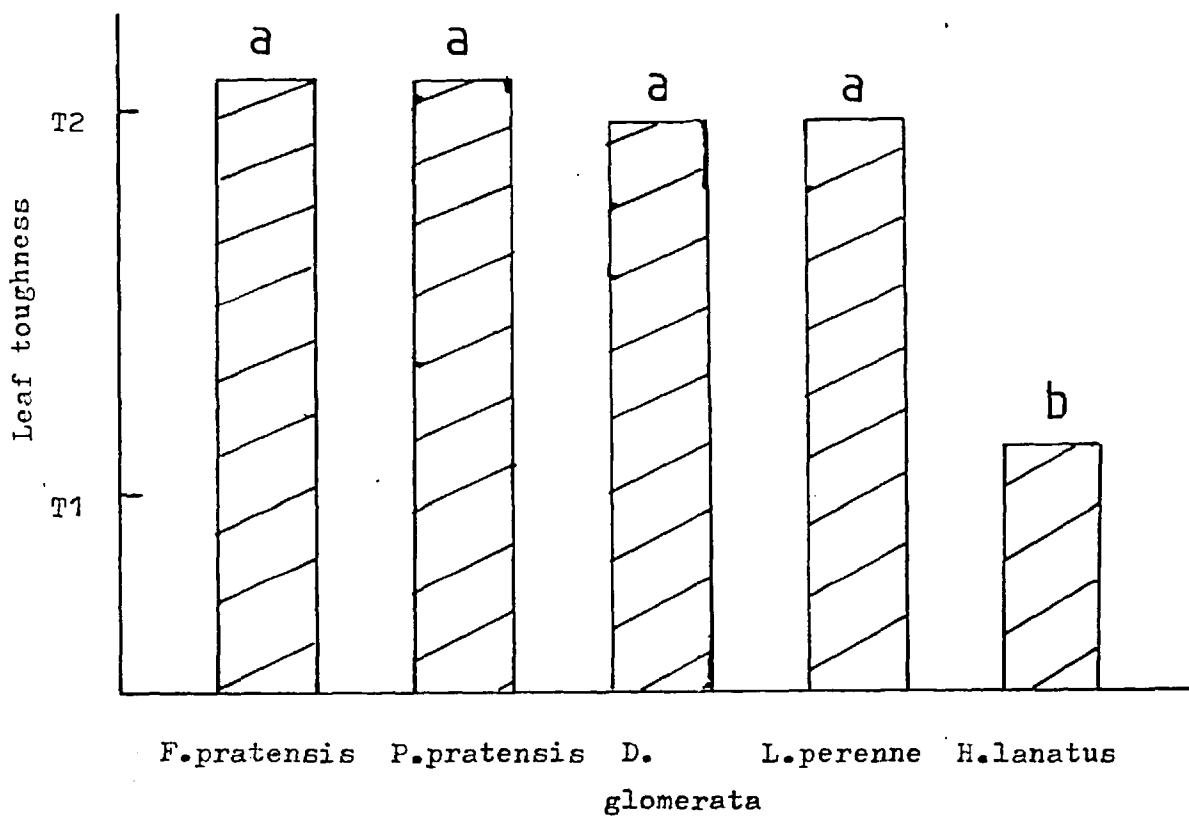
Plant height (Appendix X) and plant biomass (Appendix V) have been combined to give an index of plant architecture, such that

$$\text{plant architecture} = \log_{10} (\text{height} \times \text{biomass})$$

The results of plant architecture in 1979 (Table 5.1) show that grasses can be ranked according to the mean of plant architecture, D.glomerata > H.lanatus = L.perenne > F.pratensis > P.pratensis > A.tenuis.

Nutrient characteristics

No attempt was made to determine the quantitative or qualitative presence or absence of plant secondary chemicals. An exhaustive literature search, however, revealed that secondary chemicals (alkaloids, terpenoids, phenols, etc.) were absent in the majority of grasses (e.g. Gibbs 1963; Raffauf 1970; Butler & Bailey 1973). Raffuaf (1970) lists eleven alkaloids of varying molecular weights that have been found in Lolium but at present their function remains unknown. Harborne & Williams (1976) examined the flavonoid content of representatives from 121 genera of the gramineae and concluded that flavonoids are widespread but at very low concentrations. The ecological effects of these chemicals to sucking insects must remain unknown at this stage.

Total and soluble leaf nitrogen and soluble stem nitrogen levels were determined for the individual grass species in 1978 (Appendix XVI) and 1979 (Appendix XVII). Each grass species had a different mean nitrogen level and in general they all followed the characteristic seasonal pattern described earlier (Section II). In 1978 the late addition of 'Growmore' fertilizer to the experimental area increased the nitrogen levels at a time when they are usually low (i.e. late June/early July) (Appendix XVIII). The soluble stem nitrogen and total leaf nitrogen levels in 1978 returned to a level similar to that which existed prior to the addition of fertilizer. Leaf soluble nitrogen levels, however,

Table 5.1   Index of plant architecture (biomass x height) during 1979

Date	H.lanatus	L.perenne	D.glomerata	F.pratensis	P.pratensis	A.tenuis
9/5	2.14	2.44	3.95	2.39	2.73	1.83
21/5	3.39	3.00	4.18	3.95	3.51	2.96
31/5	3.58	3.62	4.16	3.85	3.48	3.02
8/6	3.89	3.86	4.36	3.97	3.73	3.30
14/6	4.40	4.28	4.60	4.45	4.25	3.98
21/6	4.29	4.29	4.56	4.44	4.25	4.07
28/6	4.58	4.22	4.86	4.29	4.15	3.93
6/7	4.64	4.74	4.70	4.41	4.28	4.27
13/7	4.78	4.91	5.00	4.46	4.23	4.27
20/7	4.89	5.02	4.82	4.42	4.44	4.35
2/8	4.94	4.91	4.76	4.56	4.27	4.24
15/8	4.50	4.78	4.63	4.32	4.25	4.14
$\bar{x}$	4.17	4.17	4.55	4.13	3.96	3.70

remained at a higher level than that prior to fertilizer addition.

In 1978 flowering was very sporadic probably because of nutrient deficiencies during and after floral initiation. Dates of peak flowering in 1979 (Table 5.2) correspond closely to those set out in NIAB Handbook 'Recommended Varieties of Grasses" (Anon 1977) and although there is some degree of overlap, peak flowering times of the 6 grass species are separated temporally.

Insect analysis

Species captured within the experimental area and information on the most common host plants are listed in Table 5.3. The numbers of the 10 most abundant species captured on the different grass species in 1978 and 1979 are given in Table 5.4 and 5.5. All species of leafhopper occurred on all the grass species except Stenocranus minutus which was restricted to D.glomerata. Although most host associations are weak each grass species had a dominant leafhopper species. In some cases when more than one dominant species were present they were often temporally separated. Evolutionary related grasses, e.g. F.pratensis and D.glomerata (Festuceae) share similar faunal character- istics shown well by Z.scutellaris occurring in large numbers on both these grasses.

Although plant physical defences may be important to chewing insects (perhaps this is part of the reason why larval lepidoptera are relatively rare on grassland), the feeding behaviour of leafhoppers is such that physical defences can be circumvented. Plant water content was sufficient to sustain lepidoptera growth (e.g. Scriber 1977). Examination of the number of leafhoppers present on the grasses in 1979 revealed that D.glomerata had about twice as many leafhoppers than the other plant species. A.tenuis had the smallest number of leaf- hoppers present whilst L.perenne, H.lanatus, F.pratensis and P.pratensis

Table 5.2   Peak flowering times in 1979

Grass species	Peak flower heads/m^2	Dates
Poa pratensis	4	2.VII
Holcus lanatus	240	13.VII - 2.VIII
Lolium perenne	176	13.VII - 2.VIII
Dactylis glomerata	12	14.VI - 2.VIII
Festuca pratensis	77	13.VII - 2.VIII
Agrostis tenuis	36	6.VII - 13.VII

Table 5.3   Species captured and the most common host plant

Species	Host plant
(1) Cercopidae	
Neophilaenus lineolatus (L.)	D.glomerata;H.lanatus; Holcus spp.
(2) Cicadellidae	
Aphrodes albifrons (L.)	—
A.bicinctus (Schrank)	—
A.fuscofasciatus (Goeze)	—
Artheldeus pascuellus (Fall.)	L.perenne; F.pratensis; A.tenuis[1]
Balclutha punctata (Thunberg.)	Deschampsia flexuosa[1]
Doratura stylata (Boheman)	A.tenuis[1]; Festuca rubra[1]
Elymana sulphurella (Zetterstedt)	H.lanatus; Holcus spp.[1]
A.ocellaris. (Fall.)	H.lanatus; H.mollis[2]
Eucelis incisus (Krischbaum)	L.perenne; F.pratensis
E.lineolatus (Brulle)	L.perenne
Graphocraerus ventralis (Fall.)	—
Macrosteles laevis (Ribaut)	P.pratensis; H.lanatus; A.tenuis[1]
M.sexnotatus (Fall.)	—
M.variatus (Fall.)	D.glomerata
Mocydiopsis parvacauda (Ribaut)	A.tenuis; H.lanatus
Psammotettix confinis (Dahlbom)	A.tenuis; F.pratensis
Recilia coronifera (Marshall)	Holcus spp[1]. ; H.mollis[2]
Streptanus aemulens (Kirschbaum)	—
S.sordidus (Zetterstedt)	A.tenuis
Zyginidia scutellaris (Herrich-Schaeffer)	D.glomerata; F.pratensis Holcus spp.[1]
Deltocephalus pulicaris (Fall.)	A.tenuis
Rhytistylus proceps (Kirschbaum)	F.rubra[1]
(3) Delphacidae	
Ribautodelphax angulosa (Ribaut)	L.perenne; D.glomerata
Struebingianella dalei (Scott)	A.tenuis[1]
Dicranotropis hamata (Boheman)	H.lanatus; Holcus spp.[1,2]
Javesella pellucida (Fab.)	F.pratensis; D.glomerata
Stenocranus minutus (Fab.)	D.glomerata

[1]   Waloff & Solomon 1973

[2]   Hill 1976

Table 5.4   The total leafhoppers/m^2 associated with different grass species in 1978

Species	L.perenne	H.lanatus	F.pratensis	P.pratensis	D.glomerata
A.ocellaris	9.1	195.8	13.7	0	22.8
Z.scutellaris	31.1	90.9	908.3	212.9	991.8
A.pascuellus	236.7	0	18.2	218.5	31.9
P.confinis	82.0	45.7	285.9	50.2	54.7
J.pellucida	1195.4	1191.7	1995.8	1030.2	1076.3
R.angulosa	1121.7	1153.3	716.7	600.6	516.5
E.incisus	1325.1	658.9	1059.6	1053.2	494.2
E.lineolatus	541.7	82.1	318.6	168.6	204.8
M.laevis	177.6	841.9	204.9	732.9	164.1
S.minutus	0	0	0	0	109.3
Σ	4720.4	4260.5	5521.7	4067.1	3666.4

Table 5.5   The total leafhoppers/m^2 associated with different grass species in 1979

Species	L.perenne	H.lanatus	F.pratensis	P.pratensis	D.glomerata	A.tenuis
A.ocellaris	95.4	3497.6	81.7	132.0	13.6	36.4
Z.scutellaris	2378.6	1643.1	3296.6	4180.3	4891.8	2545.3
A.pascuellus	2102.6	40.8	2453.8	1454.5	214.8	177.5
P.confinis	347.8	72.8	221.1	313.0	68.3	541.5
J.pellucida	677.7	373.1	995.7	853.5	1424.1	1018.8
R.angulosa	352.4	181.7	659.0	497.2	1000.8	705.6
E.incisus	286.7	177.3	409.9	293.1	215.7	168.2
E.lineolatus	409.6	300.2	195.6	95.4	259.5	91.0
M.laevis	45.5	1078.4	22.6	236.6	18.1	310.4
S.minutus	4.6	18.2	18.2	22.8	7294.1	9.1
Σ	6700.9	7383.2	8354.2	8078.4	15400.8	5603.8

197.

had about the same number. This pattern correlates well with the data describing plant architecture (Fig.5.2). An architecturally more diverse plant will have a greater surface area and a greater number of niches and should theoretically support a greater density of leafhoppers than a plant that is less diverse.

Tables 5.6 and 5.7 list the total number of adult leafhoppers captured on the different grass species in 1978 and 1979 respectively. Only A.ocellaris and S.minutus showed consistent host associations with H.lanatus and D.glomerata respectively. The other species had host shifts between generations (e.g. J.pellucida 1978, 1979, M.laevis 1978, P.confinis 1979 and (perhaps) E.incisus 1979 and E.lineolatus 1979), and between years (e.g. Z.scutellaris-partial host shift although there is a strong association with D.glomerata in both years, A.pascuellus, P.confinis, J.pellucida, R.angulosa, M.laevis, and (perhaps) Eucelis spp.). In some cases the numbers captured were too small to be conclusive (e.g. Eucelis spp.).

The nitrogen content in the food, 10 days prior to and during the time when adults were present in the field, is shown in Tables 5.8 and 5.9. A considerable amount of variation existed between the nitrogen levels in 1978 and 1979 due predominantly to the difference in timing of fertilizer application. Because of the varying degrees of leafhopper-plant association, the underlying principles are difficult to grasp. Therefore a consideration of the individual species with the grasses is presented. Associations were tested for significance using polynomial regression techniques available on minitab (Ryan et al. 1978).

Adarrus ocellaris

This species was strongly associated with H.lanatus. Leaf nitrogen levels in 1979 were 1.84 ± 0.19 (S.E.) mg N/gm dry weight and 1.66 ±

Table 5.6   The total number of adult leafhoppers/m^2 associated with different grass species in

1978

Species	gen.	L.perenne	H.lanatus	F.pratensis	P.pratensis	D.glomerata
A.ocellaris	1	0	0	0	0	0
	2	0	86.5	13.7	0	0
Z.scutellaris		368.8	136.7	1633.7	382.6	1724.7
A.pascuellus	1	0	0	4.6	0	9.2
	2	4.6	0	9.1	50.1	0
P.confinis	1	0	0	4.6	0	4.6
	2	63.8	13.7	22.8	32.0	13.7
J.pellucida	1	14.3	0	0	0	0
	2	50.1	9.1	59.2	45.6	81.9
R.angulosa	1	0	0	0	0	0
	2	154.8	86.7	31.9	18.2	45.6
E.incisus	1	5.4	3.6	7.3	1.8	5.4
	2	141.2	9.2	63.7	54.8	45.6
E.lineolatus	1	0	4.6	4.6	4.6	4.6
	2	95.6	68.4	141.1	45.6	59.2
M.laevis	1	13.7	32.0	18.3	73.0	9.2
	2	77.4	486.8	104.7	241.2	63.9
S.minutus		0	22.8	0	0	22.8

Table 5.7   The total number of adult leafhoppers/m^2 associated with different grass species in 1979

Species	gen.	L.perenne	H.lanatus	F.pratensis	P.pratensis	D.glomerata	A.tenuis
A.ocellaris	1	9.1	286.7	9.1	9.1	0	0
	2	18.2	969.2	22.8	63.7	9.1	4.5
Z.scutellaris		1428.1	937.7	2434.9	2678.5	3350.3	2060.5
A.pascuellus	1	305.1	9.2	332.4	173.1	51.1	31.0
	2	254.9	0	441.6	154.9	0	4.6
P.confinis	1	54.6	0	9.1	0	0	31.9
	2	18.4	9.2	22.9	50.2	4.6	136.6
J.pellucida	1	93.8	153.0	293.1	205.9	199.4	47.4
	2	182.2	141.3	204.8	177.6	145.8	248.0
R.angulosa	1	4.6	0	4.6	0	22.8	54.6
	2	36.4	9.2	22.9	50.1	63.8	134.3
E.incisus	1	13.7	9.1	12.7	15.5	1.8	0
	2	27.4	4.6	18.3	18.2	4.6	18.4
E.lineolatus	1	22.9	13.7	31.9	18.3	36.4	22.9
	2	9.1	13.7	18.3	18.4	0	9.2
M.laevis	1	4.6	22.9	0	9.2	13.7	18.3
	2	4.6	76.0	4.6	0	0	18.3
S.minutus		4.5	18.2	0	13.7	2138.5	0

Table 5.8   The mean nitrogen content of the food during the time when females are present in the field in 1978 (mg N/gm dry weight).

Species gen.	L.perenne	H.lanatus	F.pratensis	P.pratensis	D.glomerata
A.ocellaris 2	3.03	3.03	2.37	3.90	2.10
Z.scutellaris	30.7	38.7	24.5	43.7	28.9
A.pascuellus 2	3.03	3.03	2.37	3.90	2.10
P.confinis 2	3.25	3.05	2.33	4.08	2.45
J.pellucida 2	3.75	3.40	2.75	5.13	2.80
R.angulosa 2	3.70	3.37	2.97	5.13	3.13
E.incisus 2	3.25	3.05	2.33	4.08	2.45
E.lineolatus 2	3.03	3.03	2.37	3.90	2.10
M.laevis 2	3.25	3.05	2.33	4.08	2.45
S.minutus	2.63	2.40	2.40	3.30	2.63

Table 5.9   The mean nitrogen content of food during the time when females are present in the field in 1979 (mg N/gm dry weight).

Species	gen.	L.perenne	H.lanatus	F.pratensis	P.pratensis	D.glomerata	A.tenuis
A.ocellaris	1	2.07	1.84	2.28	2.50	2.21	2.54
	2	1.42	1.66	2.16	1.39	2.06	1.42
Z.scutellaris		25.2	24.8	24.3	20.5	22.9	20.5
A.pascuellus	1	1.83	1.74	1.91	2.39	2.01	2.28
	2	1.89	1.75	2.13	2.15	2.19	1.33
P.confinis	1	1.83	1.74	1.91	2.39	2.01	2.28
	2	1.89	1.75	2.13	2.15	2.19	1.33
J.pellucida	1	3.70	2.53	5.64	3.92	3.87	4.04
	2	1.33	1.75	2.23	1.36	2.18	1.49
R.angulosa	1	4.57	2.70	6.74	4.35	4.35	4.81
	2	1.53	1.65	2.38	1.45	1.67	1.53
E.incisus	1	1.33	1.80	1.61	1.74	2.47	1.95
	2	1.71	1.92	2.10	2.83	2.69	1.39
E.lineolatus	1	2.07	1.84	2.28	2.50	2.21	2.54
	2	1.57	1.56	2.30	1.39	1.72	1.46
M.laevis	1	1.83	1.74	1.91	2.39	2.01	2.28
	2	1.64	1.49	2.41	1.30	1.81	1.41
S.minutus		3.16	2.52	4.50	3.64	3.90	2.78

0.30 during the two flight periods. In 1978, the leaf nitrogen level during the second generation flight period was 3.03 $\pm$ 0.39, a level unusually high due to fertilizer addition. L.perenne had a similar nitrogen level (3.03 $\pm$ 0.42) and no A.ocellaris were captured on this grass species. Thus, the host association is sufficiently strong to suggest that mechanisms other than nitrogen levels are responsible for the association between A.ocellaris and H.lanatus.

Zyginidia scutellaris

Z.scutellaris had the strongest association with D.glomerata but it also had the ability to occur in equal abundance on other grass species, for example, F.pratensis in 1978 and perhaps F.pratensis, P.pratensis and A.tenuis in 1979. In 1978, the nitrogen content in the food during the adult flight period was (mg N/gm dry weight) D.glomerata 28.9 $\pm$ 3.52 (S.E.) and F.pratensis 24.5 $\pm$ 3.29. The nitrogen levels in 1979 were D.glomerata 22.9 $\pm$ 0.92, F.pratensis 24.3 $\pm$ 1.70, P.pratensis 20.5 $\pm$ 1.51 and A.tenuis 20.5 $\pm$ 1.51. In 1978, grasses with nitrogen levels higher than those in D.glomerata supported a lower population of Z.scutellaris. Therefore, there is good evidence to link the size of Z.scutellaris populations to the nitrogen content in the food. The strongest association is with D.glomerata for which some form of chemical may be responsible (e.g. Hultin & Torrssell 1965).

Artheldeus pascuellus

Although this species occurred in low numbers in 1978, the greatest number was caught on P.pratensis. In 1979, highest numbers were captured on F.pratensis and L.perenne. High nitrogen levels in 1978 produced by fertilizer addition were probably outside the range usually encountered by the species. In 1979, leaf nitrogen levels

in F.pratensis were 1.91 ± 0.28 (S.E.) mg N/gm dry weight and 2.13 ± 0.09 during the two adult flight periods respectively. Leaf nitrogen levels in L.perenne in 1979 were 1.83 ± 0.27 and 1.89 ± 0.18 during the two adult flight periods respectively. A.pascuellus occurred in the third highest numbers on P.pratensis, leaf nitrogen levels of which were similar to F.pratensis and L.perenne i.e. 2.39 ± 0.62 and 2.15 ± 0.72 during the two adult flight periods respectively. Considering the large standard errors associated with the nitrogen level of P.pratensis, it is possible that A.pascuellus may be associated with leaf nitrogen levels of 1.90-2.00 mg N/gm dry weight.

Psammotettix confinis

Low numbers of this species were present in 1978 and maximum numbers were captured on L.perenne. In 1979, the first generation was associated strongly with L.perenne but the second generation was most strongly associated with A.tenuis. Waloff & Solomon (1973) suggest that A.tenuis is the most common plant associated with P.confinis. It may be that P.confinis could breed and survive successfully on L.perenne but when A.tenuis is present (as in 1979) it moves to its preferred host. Nitrogen levels in the leaves during adult emergence in 1979 would reinforce this view. The leaf nitrogen levels in L.perenne are similar during both adult flight periods. However, the leaf nitrogen level in A.tenuis during the first generation flight period was considerably higher perhaps delaying the switching from L.perenne to this species. Nitrogen levels during the second generation flight period in A.tenuis more closely resembled the levels in L.perenne i.e. L.perenne generation one, 1.83 ± 0.27 (S.E.) mg N/gm and A.tenuis generation two, 1.33 ± 0.06. However, the leaf nitrogen level in L.perenne during the second generation flight period was 1.89 ± 0.33

suggesting that mechanisms other than leaf nitrogen levels may also be partly responsible for the host associations.

Javesella pellucida

This species occurred on most of the grass species (except H.lanatus) in 1978 in equal numbers but probably showed greater affinity to D.glomerata. In 1979, adult population levels in generation one were highest on F.pratensis and in generation two on A.tenuis. This species probably showed the least degree of host association. The leaf nitrogen level in D.glomerata in 1978 was 2.80 ± 0.43 (S.E.) mg N/gm dry weight. In 1979, the nitrogen level in F.pratensis was 5.64 ± 3.37 and in A.tenuis was 1.49 ± 0.09 during the first and second adult flight periods respectively.

Ribautodelphax angulosa

In 1978 and 1979 the greatest number of adult R.angulosa were present on L.perenne and A.tenuis respectively. The size of the adult populations in both years was similar which suggests that either R.angulosa's optimum host has not been represented or else the nitrogen levels are outside the range which allows a high level of fecundity. In 1979, grasses with similar nitrogen levels to A.tenuis during the second generation flight period supported smaller numbers of R.angulosa so that perhaps the evidence is weighted in favour of having an incorrect host.

Eucelis incisus

This species was associated with L.perenne in 1978 and 1979. In 1979, P.pratensis may have supported an equal number to L.perenne during the first generation flight period but because of low populations, it cannot be stated conclusively. Leaf nitrogen levels in L.perenne in 1978 were 3.25 ± 0.44 (S.E.) mg N/gm dry weight. In 1979, leaf nitrogen levels in L.perenne and P.pratensis during the first generation flight

period were 1.33 ± 0.27 and 1.74 ± 0.42 respectively. During the

second generation, the nitrogen level in L.perenne was 1.71 ± 0.34.

This species is strongly associated with plant nitrogen levels.

Eucelis lineolatus

This species is also clearly associated with plant nitrogen

levels. The greatest number were captured in 1978 on F.pratensis

with a leaf nitrogen level of 2.37 ± 0.18 (S.E.) mg N/gm dry weight.

In 1978, the greatest number was captured on D.glomerata (generation

one) with a leaf nitrogen level of 2.21 ± 0.24 and in generation two,

the greatest number was captured on F.pratensis with a leaf nitrogen

level of 2.30 ± 0.33.

Macrosteles laevis

This species has been characterised as being an early colonizer

of disturbed habitats (Andrzejewska 1962) which perhaps explains why

it was more abundant in 1978 than 1979. In this study, M.laevis

was primarily associated with H.lanatus (to be fair, in 1978 first

generation adults were more abundant on P.pratensis than the other

grass species). Leaf nitrogen levels in 1978 during the adult flight

periods were P.pratensis (generation one) 8.73 ± 1.95 (S.E.) mg N/gm

dry weight; H.lanatus (generation two) 3.05 ± 0.34. In 1979, the

levels of leaf nitrogen were lower, for example, H.lanatus 1.74 ±

0.24 and 1.49 ± 0.14 for generations one and two respectively.

Generation one adults were present on the lowest nitrogen levels at

this time so it may be possible that the nitrogen levels were outside

their optimum range.

Stenocranus minutus

This species was so strongly associated with D.glomerata in 1978

and 1979 to suggest the presence of allelochemicals in D.glomerata.

May (1977) studied S.minutus in detail and suggested that it oviposits

and feeds solely on <u>D.glomerata</u>. Such strong associations are generally rare in grassland Auchenorrhyncha.

Thus, the major leafhopper species except <u>S.minutus</u> show varying degrees of association with plant nitrogen levels, these have been summarised in Table 5.10.

The association of <u>J.pellucida</u> and <u>R.angulosa</u> with plant nitrogen levels is difficult to unravel. Both species overwinter as nymphs and the fecund females of the first generation have a high nitrogen food source during the spring nutrient flush. Members of the second generation become adult at a time when plant nitrogen levels are considerably lower. It is possible then that members of the two generations are following two different strategies. The spring adults tending towards monophagy of the dominant host plant and develop their timing with the nutrient flush in the plant. The summer generation adults with a predictable but low quality food source could be moving towards a strategy of oligophagy and feeding from a number of different grass species.

The results so far show that different grass species have a dominant leafhopper fauna and that in the majority of cases, individual leafhopper species are associated with plant nitrogen levels. Different grass species have different levels of leaf nitrogen which may vary each year depending on the environmental, biotic, and other factors that are responsible for nutrient cycling.

Some leafhopper species track the grass nitrogen levels, that they 'perform' best at, in a range of grass species and thus are oligophagous feeders. Other species tend to favour monophagy but then have a phenology closely geared towards a plant species. For these species, timing of the periods when nitrogen is most important (i.e. reproductive stage) to high levels of leaf nitrogen, is critical.

Table 5.10   A summary of the strength of the association

between leafhopper species and plant nitrogen

levels.

Strong associations   Weak associations

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E.incisus   S.minutus

E.lineolatus   A.ocellaris

Z.scutellaris   P.confinis

A.pascuellus   J.pellucida

M.laevis (?)   R.angulosa

S.minutus overwinter as adults but the females do not develop eggs
until the spring when they can take advantage of the spring nutrient
flush.   D.hamata, recorded at low population levels on this trial,
may also use this strategy (Hill 1976). He suggested that this
species was cued into the nutrient flushes of the dominant grass
species, H.mollis. His data for the first generation adult population
supports this view but it is difficult to justify for the second gener-
ation.

It is possible that the different numbers of leafhoppers captured
on the different grass species may represent a host plant trapping
effect.   Feeding and ovipositional trials, however, would not support
this view.   Data on pre-reproductive periods, daily egestion, con-
sumption and ovipositional rates,and approximate digestibilities for
female E.incisus when feeding on different grass hosts in the labor-
atory are given in Table 5.11.   When feeding on F.pratensis, consum-
ption rates and egg production were greatest, pre-oviposition periods
were shortest and AD was lowest.   Daily nitrogen budgets for reproducing
E.incisus on different grass species are summarised in Table 5.12.
Nitrogen utilization efficiencies were low but similar to those from
unfertilized grass in earlier experiments (Section IV) and differed
depending on the grass species.   Consumption was highest on
F.pratensis and NUE was lowest.

Unfortunately, no estimate of the nitrogen content in the food is
available for this experiment.   However, it is not unreasonable to
assume in the light of earlier results that the different grasses had
different leaf nitrogen levels and that the leafhopper NUE is a re-
flection of the nitrogen levels in the food.   Examination of the
number of E.incisus on the grass species during 1979 showed that the
greatest number was present on F.pratensis with approximately similar

Table 5.11   Female pre-reproductive period, daily ingestion,
oviposition, and consumption rates, and Approximate
Digestibility (AD) for reproducing Eucelis incisus
on different grasses at $20^{\circ}C$.

Parameter	Gramineae			
	F.pratensis	H.lanatus	A.tenuis	D.glomerata
Pre-reproductive period (days)	6.5	10.0	14.0	14.0
Dry weight egested mg/♀/day	0.0505	0.0380	0.0269	0.0240
Eggs/♀/day	1.20	1.13	0.91	0.67
Consumption mg/♀/day (Egg wgt.= 0.0306 mg.)	0.0972	0.0726	0.0547	0.0445
% AD	42.1	47.6	50.9	46.1

Table 5.12   Daily nitrogen budgets for reproducing female Eucelis
              incisus when feeding on different grasses at 20°C

Parameter	Gramineae			
	F.pratensis	H.lanatus	A.tenuis	D.glomerata
Nitrogen egested/♀/ day (µg N/ mg. dry wgt.)	6.999	5.267	3.728	3.326
Egg nitrogen/ ♀/day (µg N/ mg dry wgt.)	3.499	3.295	2.654	1.954
Nitrogen con- sumed/♀/day (µg N/mg dry weight)	10.498	8.562	6.382	5.280
NUE %	33.3	38.5	41.6	37.0

numbers on H.lanatus, D.glomerata and A.tenuis.

Conclusions

Plant physical defences were similar between grass species and would appear to have little effect in determining leafhopper-host plant associations. Grass phenology and plant nutrient levels differed considerably between the grasses.

Most species of leafhopper were present on all the grasses sampled but each grass species had a different dominant leafhopper fauna.

The strength of the leafhopper-plant association varied depending on the leafhopper species in question. Species that were strongly associated with one host were relatively rare and these species utilized phenological adaptations to synchronise ovipositional periods with periods of high food quality in the grass. Other more oligophagous species were associated with a particular nitrogen level in the grass. These species were found on grasses that had a nitrogen content within a narrow nitrogen concentration band. As the plant nitrogen levels altered (associated with flowering, seed setting, and senescence) leafhoppers switched onto other food plants that had a suitable nitrogen level.

SECTION VI - DISCUSSION

Fertilizers have provided a method of manipulating plant nutrient levels and the levels of food quality with respect to phytophagous insects. The advantage of increased food quality to the Auchenorrhyncha fauna fit the general theories on the effects of plant chemistry on the growth rates, fecundity and survival of plant feeding insects (e.g. see reviews of Van Emden & Way 1973; Beck & Reese 1976; Feeny 1976; Rhoades & Cates 1976; Chapman & Bernays 1978). The literature concedes that the low nitrogen (protein or amino acid content) and high levels of quantitative (Feeny 1976) defences, singly or in combination, result in reduced feeding rates, slow growth rates, long developmental times, poor survival and reduced fecundity. Poor nutrition may also result in smaller or weaker individuals which may be more easily killed by disease (Anderson 1979) and weather (McNeill 1973).

In the present study, high levels of food quality resulted in enhanced consumption, growth and ovipositional rates. Increased consumption in turn places more pressure on the plant. The effects of sucking insects are more subtle than the effects of grazing insects where removal of leaf material may represent a photosynthetic loss (and hence subsequent net production loss) to the plant. However, there are many examples in the literature to show that moderate levels of insect consumption are likely to be stimulatory to vegetative growth and yield production when carbohydrate reserves in the plant are high (e.g. see review of Harris 1973).

Although the amount of plant material removed by sucking insects is often substantial, documented quantified results have been difficult to find. Dixon (1971) correlated the size of the annual ring in sycamore (Acer pseudoplatanus L.) with the number of sycamore aphids (Drepanosiphum platanoides Sehr.) present on the tree through the year.

He calculated that in the absence of aphids, sycamore could conceivably produce 280% more stem wood. In laboratory studies Dixon (1971) showed that aphid infestation can regulate leaf size and leaf growth and that leaves that had been infested with aphids had a net dry matter production rate 1.7 times greater than uninfested leaves. From the results of laboratory studies, Mittler (1958) has suggested that in 1 day an individual willow aphid, _Tuberolachnus salignus_ (Gmelin) can ingest the photosynthetic products of between 5 and 20 cm^2 of leaf.

However, such visual methods (e.g. Dixon 1971) do not lend themselves easily to studying production losses on grasses. Researchers have resorted to exclusion techniques, generally insecticidal treatments, to restrict sucking insects from selected areas (e.g. Andrzejewska & Wojcik 1971; Clements & Henderson 1977; Hawkins et al. 1979). Production losses estimated by insecticidal exclusion of leafhoppers vary, for example, Smith & Medler (1959) estimated 48% loss of alfalfa yield by _Empoasca fabae_ (Harris); Hawkins et al. 1979 estimated an average loss of 17.9% by a leafhopper complex feeding on coastal bermuda grass; Clements & Henderson (1977) estimated 33% increase in yield from areas treated with insecticide to exclude a leafhopper complex. Andrzejewska (1971) estimated production losses of about 40% by the total phytophagous community of which leafhoppers formed by far the most dominant biomass.

The results of such experiments often prove that the situation is complex and that plant production losses are not due solely to the losses acrued from consumption alone. This problem has recently been highlighted by Whittaker (1979) who considered the effects of invertebrate grazing on food plants that were competing with members of the same and other plant species. His results show that invertebrate grazing not only markedly affected plant production but also affected

plant species diversity; insects were selectively grazing on some plants and not others, which in turn altered the competitive balance. In the light of these results the effects of invertebrate grazing pressure in relation to the population dynamics of the plant are obviously needed.

Auchenorrhyncha can affect plant production in other ways not related to the quantity of material actually removed. They transmit several plant pathogens in the gramineae but are not generally recognised as serious pests in the United Kingdom (Medaiyedu 1975). However, in other countries the insects often reach pest status e.g. Rose (1974); Pathak (1968), Anon 3 (1977).

Direct probing damage by phloem feeders is a serious problem often resulting in serious cases of hopperburn. For example, _Nilaparvata_ _lugens_ and _Nephotettix_ _cincticeps_ feeding on rice (Sogawa 1970a, 1971a; Bae & Pathak 1970); _Empoasca_ _flavescens_ feeding on castor bean leaves (Jayaraj 1967); _D.pellucida_ feeding on oats (Raatikainen & Tinnila 1959).

Parenchyma feeders produce little damage when compared to the damage caused by phloem feeders. In most cases the contents of the palisade and spongy parenchyma cells are removed giving rise to the appearance of chlorotic spots on the leaves (see Smith & Poos 1931; Pollard 1968).

In the present study it is possible to calculate the amount of material that was consumed by the phloem feeders in 1979. The calculations have been based on consumption data (Section 5) and insect biomass data (Section 3).

Monthly temperature data in 1979 are given in Appendix XVI. The mean temperature for the 4 summer months was 14.7°C. Consumption rate at 15°C were 51% of the consumption rate at 20°C (unpublished data). The dry weight of the sap consumed has been calculated from the mean

Table 6.1   The average monthly phloem feeder biomass/m^2 on control and NPK+Lime fertilized plots in 1979 (mg/m^2 dry weight).

	Unfertilized	Fertilized
June	37.85	39.21
July	55.55	51.85
August	77.39	307.85
September	57.00	108.16

Table 6.2   Phloem feeder consumption (mg/m^2) during the summer months in 1979.   (Consumption on unfertilized plots = 0.0673 mg/mg ♀ /day; consumption on NPK+Lime fertilized plots = 0.1183 mg/mg ♀ /day)(dry weights)

	Unfertilized	Fertilized
June	76.6	139.2
July	115.9	190.2
August	161.5	1129.1
September	115.1	383.9
Total	544.6	2662.8
Mean of total	1603.7	

phloem feeder dry weight consumption rates at 15°C. The average

monthly phloem feeder biomass (mg/m^2/month) on control and NPK+Lime

fertilized plots is shown in Table 6.1. The dry weight of the sap

consumed per month from June to September is shown in Table 6.2.

Estimates varied from 0.545 .g/m^2 on the unfertilized plots to 2.663

g/m^2 on the NPK+Lime plots, the average being 1.604 g/m^2.

Andrzejewska (1971) estimated total leafhopper consumption on an un-

fertilized meadow at 1.700 .g/m^2. Her consumption rates were determined

in laboratory studies but temperature data were not presented.

If we assume that the actual calorific value of the plant sap to

be about 4.2 cal/mg dry weight (Rathcke 1968), the approximate calorific

equivalent of the dry weight of plant biomass consumed per summer is

about 2.289 Kcal/m^2 on unfertilized plots and 11.185 Kcal/m^2 on

NPK+Lime fertilized plots ($\bar{x}$ = 6.737 Kcal/m^2). It is reassuring

to note that these production losses are of the same order as

recorded by Andrzejewska (1967) (i.e. 92.7 Kcal/m^2) when working

in a nutrient rich experimental area.

Migration of leafhoppers was not monitored. Adults readily colon-

ized the sown monocultures during late summer 1977 and early summer 1978

and these migrants formed the basis of the following populations. Most

of the species in the present study have been recorded in aerial suction

traps by Waloff (1973), who has analyzed migration of grassland

Auchenorrhyncha in detail. Some of the fluctuations in numbers of leaf-

hoppers captured on successive sampling dates in the present study are

primarily due to the effects of small scale migrations. Indeed, one of

the conclusions in the present study is that adults are extremely mobile

and readily disperse from one feeding site to another in search of a

particular plant nutrient level. Waloff (1973) concluded that although

the number of leafhoppers captured in the suction traps was small, all

the species dispersed when they were immature and mature adults tended to 'flit', the scale of the dispersion being closely associated with the degree of wing polymorphism. Taylor & Taylor (1977, 1979) have shown that insect populations fluctuate in space and suggested that on a small scale, interchanges in local populations are relatively common.

Many of the different (and often conflicting) results reported in the literature concerning insect performance and fertilizer addition (e.g. Jones 1977; Table 3.1) can now be explained with reference to some of the above results. Present day insects have coevolved with their common hosts to a degree where they are closely cued to the host plant. Species that are present in times of low available food quality have evolved strategies to increase the levels of available nutrients. McNeill & Southwood (1978) have discussed many of the ways used by herbivorous insects to increase a poor quality food supply. The Silwood Park grassland Auchenorrhyncha can be viewed as operating on a monophagous -polyphagous continuum. Species in a stable environment but with a poor quality food source have adapted their nutritional physiologies to a maximum performance at a particular plant nutrient concentration. They then search for and feed on a number of grass species that have that particular nutrient concentration. Populations of these oligophagous leafhoppers can be viewed as being extremely mobile (on a small scale) with numbers in local populations being extremely fluid. At the other end of the continuum are the monophagous species that have coevolved with the phenology of the most dominant host plant. These species live in an unstable environment and have cued the period when the nutrient demand is high into the nutrient flushing of the dominant host plant. The selective forces that maintain the feeding strategy are obviously complex and represent a number of trade-offs between the advantages (high quality food source, reduced levels of interspecific competition

and reduced predator/parasitoid activity) and the disadvantages
(unreliable timing of the food source and mortality due to weather) in
a hostile competitive habitat.

To monophagous species, the effect of a spring fertilizer application
is to standardize the plant differential nutrient flushing times and
therefore decrease the importance of synchrony of insect timing and plant
nutrient flushes.   To the polyphagous feeding species, the effects of
a spring fertilizer addition is to make the plant nutrient levels higher
and therefore outside the range usually encountered in the hosts by these
insects.   Although insect development and fecundity levels may be im-
paired for a short time, plant nutrient levels rapidly decrease from a
peak to a level that existed prior to fertilization.   The population
response to fertilizer application then will depend on the feeding and
life history strategy being followed by the insect and the physiological
plasticity of the individual species to varying levels of plant nutrients.

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APPENDIX I

Relative abundance of plant species in 1978 and 1979

KEY

1	Control		8	K
2	NPK+lime		9	P
3	PK		10	N_{300}
4	N_{100}		11	NK
5	Lime		12	NPK
6	N_{600}		13	N_{900}
7	NP		14	N_{1200}

APPENDIX I   Relative abundance of plant species in 1978

						Treatment						
	1	2	3	4	5	6	7	8	9	10	11	12
Agrostis tenuis	38.2	12.8	37.9	36.4	26.7	17.2	30.8	34.5	25.8	31.2	30.5	17.8
Anthoxanthum odoratum	18.7	–	–	1.8	5.0	51.7	35.4	–	8.0	16.4	18.7	4.4
Festuca rubra	16.2	–	1.7	0	18.3	5.2	–	–	11.3	–	–	4.4
Holcus lanatus	24.4	9.3	5.2	25.4	36.6	24.1	33.8	10.3	12.9	31.2	44.1	6.7
Holcus mollis	–	73.3	51.7	29.1	6.7	–	–	51.7	25.8	–	–	66.7
Poa annua												
Poa pratensis												
Dactylis glomerata								*				
Stellaria media	1.6	4.6	–	–	6.7	5.2	–	3.4	11.7	19.7	3.4	–
Rumex acetosa	0.8	–	3.4	7.3	1.7	–	–	–	4.9	1.6	3.4	–
Cirsium arvense												
Urtica diocea		*	*									

APPENDIX I   Relative abundance of plant species in 1979

Treatment

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Agrostis tenuis	62.3	11.2	51.1	51.2	27.8	47.9	31.7	38.5	33.7	39.3	42.2	7.9	41.7	15.9
Anthoxanthum odoratum	18.9	0.9	0.7	3.1	1.3	1.4	25.4	1.0	3.7	3.4	15.7	1.6	1.7	1.0
Festuca rubra	26.4	0.9	0.7	0.8	25.3	4.1	0.8	0.5	12.3	–	–	0.8	–	–
Holcus lanatus	1.9	0.9	0.7	15.7	29.1	2.7	27.8	0.5	0.6	41.6	39.8	0.8	1.7	0.5
Holcus mollis	1.9	84.1	43.8	19.7	5.1	2.7	11.9	59.0	49.1	6.7	1.2	87.3	51.7	81.7
Poa annua	–	–	–	–	–	2.0	–	–	–	–	–	–	–	–
Poa pratensis	–	–	–	–	–	–	–	–	–	–	–	–	–	1.0
Dactylis glomerata	–	–	–	–	–	–	–	*	–	–	–	–	–	–
Stellaria media	2.5	0.8	0.4	1.0	1.3	7.1	2.0	0.5	0.2	0.3	–	–	1.0	–
Rumex acetosa	3.2	–	0.6	0.6	–	30.2	3.4	–	0.4	0.8	1.2	1.6	2.3	–
Cirsium arvense	–	–	–	–	–	2.0	–	–	–	–	–	–	–	–
Urtica diocea	–	1.0	0.8	–	–	–	–	–		–	–	–	–	–

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APPENDIX II   Treatments on study area

				N_{1200}	N_{900}
NPK	NK	N_{300}	P	K	
NP	N_{600}	Lime	N_{100}	PK	NPK + Lime
	Control				
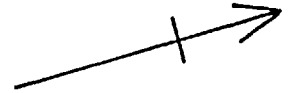
APPENDIX III - CHEMICAL METHODS

Nitrogen

Leaf nitrogen was estimated using the standard micro-kjeldahl technique (Bradstreet 1965).

Total nitrogen

(i) Weigh 60 mg finely ground, freeze dried, plant material directly into a long necked micro-kjeldahl flask.

(ii) Add 1 selenium catalyst tablet.

(iii) Add 2 mls of nitrogen free sulphuric acid (H_2SO_4).

(iv) Reflux (gently at first but slowly increasing the heat) for about 3-5 hours until the digestion is completed.

(v) Allow to stand and when cool dilute the sample to 100 ml.

(vi) Prepare blank solutions following the same procedure.

(vii) Remove 10 ml subsample for calorimetric analysis on auto-analyser* using standard alkaline phenate/sodium hypochlorite solutions.

(* The autoanalyser used in this study was a Technicon Mk 7.)

Soluble nitrogen

The soluble nitrogen content was extracted by the same method as Van Emden & Bashford (1969).

(i) Weigh 100 mg of finely ground, freeze dried, plant material into a 2 x 1 inch stoppered tube.

(ii) Add 2 mls of buffer (2.5% Trichloroacetic acid with 0.02% phenol) and shake for 8-10 hours.

(iii) Centrifuge at 5000 r.p.m. for 6 minutes and pipette 1 ml. of the supernatant into a kjeldahl flask.

(iv) Continue as with Total Nitrogen (ii).

Amino acids

The extraction procedure for leaf soluble amino acids was that used by Van Emden & Bashford (1971).

(i) Weigh 100 mg of finely ground, freeze dried plant material into a 2 x 1 inch stoppered tube.

(ii) Add 2 ml of buffer pH 2.2 and shake for 8-10 hours.

(iii) Centrifuge at 5000 r.p.m. for 6 minutes and pipette the supernatant into a clean polytopped tube. The sample can now be stored at $0^{\circ}C$ for a short period until ready for use.

In this study all samples were analysed on a Mk 4 Amino acid analyser obtained from The Locarte Company.

Potassium

The technique for analysis of leaf potassium was based on oxidation of the organic material by acid digestion and subsequent analysis by flume emission (Chapman 1976).

(i) Weigh 100 mg of finely ground, freeze dried plant material into a conical flask.

(ii) Add 20 ml concentrated Nitric acid (NHO_3) and allow to stand overnight (or until organic material thoroughly wetted).

(iii) Add 5 ml of concentrated Hydrochloric acid (HCl) and 5 ml of perchloric acid ($HClO_4$).

(iv) Digest at moderate heat until white fumes are evolved.

(v) Heat strongly for a few minutes to drive off most of the $HClO_4$ and allow to cool.

(vi) Dilute to 100 mls with deionized water.

(vii) Prepare blank solutions following the same procedure.

Sub-samples were analysed on flame photometer against standards of known concentration.

Phosphorus

Sub-samples of acid digested material (see analysis for leaf potassium) were analysed on a Technicon MK7 auto analyser using the standard ascorbic acid/ammonium molybdate colorimetric reaction (Chapman 1976).

APPENDIX IV

Key		
1	Control	8 K
2	NPK + Lime	9 P
3	PK	10 N_{300}
4	N_{100}	11 NK
5	Lime	12 NPK
6	N_{600}	13 N_{900}
7	NP	14 N_{1200}

APPENDIX IV   Biomass in 1979 (gm/m^2)

Treatment

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14
9/5	124	232	130	200	61	164	140	190	141	250	55	252	149	73
21/5	127	169	117	324	66	118	113	422	63	409	120	292	489	497
31/5	133	401	139	141	130	118	325	248	121	137	73	260	195	423
8/6	270	476	566	530	326	198	530	467	310	470	250	460	1010	761
14/6	300	829	557	467	200	372	322	730	344	350	263	601	593	1283
21/6	681	2204	1088	1959	863	624	1020	779	845	456	448	1296	2550	2473
28/6	630	2659	733	2334	898	803	1200	1484	824	900	800	3453	2219	3348
6/7	530	1459	1143	1470	572	570	1489	969	1724	810	1290	1881	2300	2530
13/7	1061	2965	1913	1623	1202	1512	1302	1130	942	1581	996	1649	1960	2791
20/7	830	4205	1367	1793	1395	806	2051	1655	1484	1308	970	2855	1080	2923
2/8	1271	2266	1185	1862	792	754	1573	1313	1565	1180	890	2395	2213	3289
15/8	1082	2537	2065	1375	895	989	1262	1650	1795	1322	810	2403	3091	3150
29/8	2035	3267	2121	2775	2124	1669	2289	3570	2549	2124	1578	3921	3056	4581
17/9	848	3819	2475	1738	1363	1737	1880	1630	2065	1403	970	2699	4500	3810

APPENDIX V

Key   1 Control   8 K

Key	1	Control		8	K
	2	NPK + Lime		9	P
	3	PK		10	N_{300}
	4	N_{100}		11	NK
	5	Lime		12	NPK
	6	N_{600}		13	N_{900}
	7	NP		14	N_{1200}

APPENDIX V   Pasture height in 1979 (cm)

Date	Treatment													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
21/5	12.6	19.6	17.9	14.7	15.1	10.2	14.0	18.1	17.0	13.3	12.7	21.5	18.9	20.8
31/5	14.9	23.3	23.3	21.2	15.9	12.7	17.6	21.7	19.9	13.7	12.6	29.1	21.7	29.6
8/6	17.8	30.3	34.2	32.7	18.8	14.4	21.0	40.5	14.8	19.5	28.6	32.3	31.3	41.1
14/6	19.8	39.6	41.8	35.1	21.7	16.8	26.2	37.4	30.5	24.9	15.8	45.9	33.9	43.3
21/6	23.7	47.1	46.0	43.1	31.0	19.7	29.4	43.9	36.9	27.3	21.2	47.6	42.4	47.2
28/6	28.1	45.4	46.8	41.8	30.7	22.3	34.1	50.3	43.0	36.2	23.3	52.2	44.3	51.8
6/7	24.7	52.7	52.1	41.1	30.8	20.0	31.8	46.1	39.7	32.2	22.2	51.1	43.9	53.4
13/7	28.1	59.7	58.1	54.7	38.6	24.5	36.1	58.1	53.1	43.8	24.4	56.8	49.6	56.2
20/7	27.6	59.1	56.3	47.9	31.8	24.6	33.8	54.8	38.8	35.9	25.8	55.7	45.8	55.2
2/8	35.7	59.6	62.9	56.8	41.8	30.3	40.4	64.5	53.3	40.9	29.5	73.7	57.4	75.1
15/8	33.6	70.1	64.2	50.3	36.3	27.9	39.9	62.2	56.7	36.0	30.1	63.9	57.9	70.6

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APPENDIX VI

Key

1	Control	8	K	
2	NPK + Lime	9	P	
3	PK	10	N_{300}	
4	N_{100}	11	NK	
5	Lime	12	NPK	
6	N_{600}	13	N_{900}	
7	NP	14	N_{1200}	

APPENDIX VI   Stem soluble nitrogen 1978 (mgN/gm dry weight)

Date	1	2	3	4	5	6	7	8	9	10	11	12	$\overline{X}$
17/4	4.32	4.32	4.06	4.14	4.00	4.80	4.72	4.28	4.36	4.35	4.18	4.28	4.32
24/4	2.32	6.22	6.16	4.22	4.26	3.88	2.90	2.68	2.80	2.08	5.50	5.82	4.07
3/5	3.30	3.96	4.82	6.42	4.30	6.12	4.66	4.68	5.08	3.72	4.24	4.52	4.65
8/5	2.80	5.18	4.90	1.26	3.86	3.58	3.44	1.92	3.46	5.44	3.40	3.64	3.57
15/5	3.20	5.74	3.22	5.26	4.48	3.84	3.88	4.28	6.60	4.16	5.02	3.46	4.43
23/5	3.60	5.68	3.82	4.72	12.48	5.10	3.24	3.82	4.16	3.64	3.78	4.74	4.90
12/6	2.02	1.70	4.10	2.62	2.34	6.60	2.76	2.68	2.68	3.94	3.10	3.50	3.17
27/6	1.08	3.50	2.18	2.94	1.18	7.44	3.00	2.56	2.84	3.10	3.22	3.00	3.00
3/7	1.24	3.58	2.94	2.42	2.24	2.26	1.20	1.78	3.60	2.78	3.52	5.18	2.73
24/7	1.60	5.48	2.66	1.96	2.00	2.94	2.92	2.50	2.54	2.38	2.32	3.80	2.76
17/8	1.40	3.86	2.54	2.12	1.94	3.02	4.14	2.36	2.32	4.00	2.96	3.40	2.84
31/8	1.28	3.34	2.68	3.06	2.16	4.46	6.52	1.64	2.04	3.22	2.98	3.60	3.08
12/9	1.40	3.36	2.36	3.88	2.10	7.92	3.44	2.88	2.00	3.22	2.08	3.00	3.14
3/10	2.14	4.22	1.86	3.44	1.76	4.04	3.06	1.94	2.78	3.08	3.00	3.12	2.87
26/10	2.08	3.28	2.08	3.08	2.76	5.84	2.40	2.82	3.36	2.92	4.08	3.40	3.18
3/11	1.12	6.88	2.48	2.34	2.40	8.94	3.76	3.04	3.34	3.84	3.52	4.28	3.83
$\overline{X}$	2.24	4.39	3.31	3.37	3.39	5.05	3.50	2.80	3.37	3.49	3.56	3.92	

APPENDIX VI   Stem soluble nitrogen 1979 (mg N/gm dry weight)

Treatment

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	$\overline{X}$
17/4	2.00	6.58	5.46	2.48	7.00	14.92	4.44	1.28	0.96	6.02	3.14	4.40	3.00	3.00	4.48
4/5	4.00	5.72	6.06	2.40	7.28	6.36	6.88	6.12	3.36	4.22	5.86	5.20	4.00	4.00	5.11
14/5	2.82	5.66	3.18	4.86	4.02	10.04	9.86	3.40	4.76	4.40	2.12	6.42	7.98	5.16	5.33
21/5	3.60	4.86	6.58	7.68	4.16	12.16	12.58	5.56	4.42	8.80	5.18	6.54	8.58	14.20	7.49
4/6	5.46	5.70	3.64	3.43	3.16	8.90	9.08	4.80	5.46	5.86	6.28	3.00	10.42	3.36	5.61
12/6	0.84	9.30	2.56	2.88	3.08	7.28	6.98	1.44	3.10	4.74	3.18	4.88	9.26	3.12	4.47
20/6	2.38	4.46	2.90	2.78	3.72	3.88	4.36	2.34	2.28	6.04	5.74	4.86	4.02	7.28	4.07
3/7	2.48	4.26	1.46	1.94	3.38	6.50	4.86	1.64	1.92	2.22	3.72	4.20	4.98	3.66	3.37
16/7	1.66	2.90	2.26	2.20	1.64	4.52	2.34	1.36	3.08	4.88	4.50	1.64	2.50	3.20	2.76
2/8	2.12	2.02	1.60	1.76	2.16	4.56	1.74	1.20	1.40	2.82	4.08	2.18	2.88	4.38	2.49
20/8	3.42	2.30	2.00	4.20	4.36	6.62	3.72	2.64	2.64	3.22	4.10	4.04	3.28	3.68	3.59
5/9	3.54	3.02	2.08	2.96	2.14	6.78	3.98	2.16	1.86	2.70	5.94	4.00	5.72	4.30	3.66
24/9	2.32	2.68	1.68	2.52	1.52	5.78	3.42	2.44	3.52	2.92	3.32	2.10	3.56	4.28	3.00
12/10	3.72	6.04	2.22	2.88	3.54	6.68	3.72	2.56	2.48	3.10	4.20	4.28	4.52	5.86	3.99
19/10	1.82	6.50	3.70	3.94	1.76	8.00	5.10	3.28	1.94	3.32	2.60	5.30	3.92	13.66	4.63
$\overline{X}$	2.81	4.80	3.16	3.26	3.53	7.53	5.52	2.81	2.88	4.35	4.26	4.20	5.24	5.54	

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APPENDIX VI　　　　Leaf soluble nitrogen 1978　(mg N/gm dry weight)

						Treatment							
Date	1	2	3	4	5	6	7	8	9	10	11	12	$\bar{X}$
24/4	3.28	4.64	3.98	3.80	4.18	4.04	3.84	3.80	3.98	4.82	3.86	4.62	4.07
3/5	3.50	3.86	4.04	4.50	4.66	3.96	3.68	5.28	4.50	4.02	4.26	3.40	4.14
8/5	4.14	5.50	4.48	3.76	3.38	3.64	3.16	3.58	3.84	3.26	4.06	3.52	3.86
15/5	3.20	4.10	3.46	3.70	3.90	3.58	3.62	3.06	4.12	4.52	3.52	3.26	3.67
23/5	3.08	4.50	3.52	4.60	10.56	7.46	2.74	3.44	4.16	3.40	3.10	4.94	4.63
12/6	2.42	4.94	4.16	3.84	2.88	8.38	3.04	2.94	3.06	4.56	3.08	3.76	3.92
27/6	2.34	3.90	3.04	3.58	2.50	7.16	4.42	2.92	3.20	3.78	4.34	4.04	3.77
3/7	2.32	4.04	3.06	3.18	3.30	4.32	4.00	3.16	3.78	3.74	4.02	4.34	3.61
24/7	2.32	6.32	3.24	3.82	3.04	4.86	4.42	1.42	4.06	3.62	1.88	5.38	3.70
17/8	2.56	4.76	4.48	4.48	3.28	2.44	5.56	3.98	2.84	4.04	2.92	3.60	3.75
31/8	2.30	6.28	2.46	7.02	2.68	3.58	5.20	2.52	2.78	5.38	2.78	3.90	3.91
12/9	2.94	3.56	2.96	4.82	2.90	6.30	3.02	2.86	2.62	3.72	2.54	3.48	3.48
3/10	3.34	3.42	2.62	4.56	2.28	5.74	2.94	2.40	3.18	2.94	2.62	3.36	3.29
26/10	2.62	3.66	3.34	3.08	2.92	4.42	3.50	4.04	2.66	2.48	3.48	2.02	3.19
3/11	2.26	4.66	2.68	3.18	2.90	9.22	3.38	2.48	4.40	3.70	3.12	3.58	3.80
$\bar{X}$	2.84	4.54	3.44	4.13	3.69	5.27	3.77	3.19	3.55	3.87	3.31	3.81	

APPENDIX VI   Leaf soluble nitrogen 1979 (mg N/gm dry weight)

Date	Treatment														$\overline{X}$
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
17/4	3.50	4.48	4.56	1.72	4.74	10.26	5.40	7.38	5.44	3.58	5.94	4.52	5.00	5.00	5.11
4/5	3.50	4.08	4.06	3.98	4.60	5.36	5.82	4.58	4.30	4.68	6.52	3.88	3.80	3.80	4.50
14/5	2.30	7.26	2.72	4.06	3.02	9.82	6.60	2.82	3.46	6.12	7.30	6.56	10.18	10.02	5.87
21/5	4.40	6.20	4.54	5.52	3.78	8.48	7.78	4.06	4.36	9.02	8.92	4.44	6.38	12.40	6.45
4/6	4.94	4.48	3.38	3.44	2.78	6.40	5.64	3.54	4.10	5.60	5.24	4.46	7.28	7.42	4.91
12/6	3.02	3.02	2.84	2.58	2.90	5.70	4.78	3.38	2.52	5.54	5.26	4.32	7.48	7.58	4.35
20/6	3.46	3.54	2.54	2.94	2.78	4.86	2.64	3.08	2.40	6.46	3.24	3.38	4.88	7.72	3.85
3/7	2.90	4.88	2.34	2.30	2.30	5.12	3.16	2.92	2.72	2.90	4.20	2.80	2.76	5.00	3.31
16/7	3.16	4.70	3.54	3.12	2.56	5.36	2.02	3.32	3.48	4.86	3.38	5.54	4.76	5.84	3.97
2/8	3.28	3.92	3.22	2.80	2.82	3.64	2.88	2.14	3.08	2.06	4.00	3.38	4.12	5.78	3.37
20/8	3.52	4.84	3.90	2.48	3.78	5.78	4.30	3.60	4.94	4.00	4.74	4.40	4.78	7.88	4.50
5/9	2.44	5.30	2.10	1.08	1.10	5.06	3.94	3.50	1.78	1.96	3.36	3.34	6.30	11.76	3.79
24/9	2.14	5.28	3.24	2.08	2.06	4.12	3.14	2.10	4.72	2.24	2.32	4.92	4.24	6.52	3.51
12/10	2.46	4.54	2.48	3.20	3.04	4.60	3.98	3.46	2.98	2.22	2.94	8.08	4.94	4.92	3.85
19/10	1.20	5.62	3.88	4.43	1.48	6.22	4.52	3.06	1.92	2.94	2.62	5.84	1.84	12.16	4.12
$\overline{X}$	3.08	4.81	3.29	3.18	2.92	6.05	4.44	3.53	3.48	4.15	4.67	4.66	5.46	7.80	

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APPENDIX VI   Leaf total nitrogen in 1978 (mg N/gm dry weight)

Date	Treatment 1	2	3	4	5	6	7	8	9	10	11	12	$\overline{X}$
24/4	24.7	36.3	37.1	34.9	35.6	27.5	24.8	35.1	34.0	39.4	29.6	22.0	32.4
8/5	28.4	37.0	36.7	30.2	33.5	33.3	29.5	38.6	28.2	25.9	32.6	33.4	32.6
15/5	26.9	30.3	30.1	32.9	32.9	34.7	32.1	30.9	29.9	26.9	33.0	26.4	30.9
23/5	22.8	30.8	27.2	32.7	39.9	34.5	26.5	28.4	29.5	10.2	9.6	34.6	27.6
12/6	16.5	42.1	12.3	23.8	24.5	45.6	43.0	22.1	22.1	35.2	25.7	23.3	29.1
27/6	13.8	35.1	28.3	29.1	20.5	44.4	29.2	21.7	27.9	28.3	26.9	31.7	29.4
3/7	15.4	34.8	21.3	24.7	31.5	33.5	10.8	22.9	26.6	33.0	38.9	32.5	28.2
24/7	17.9	39.2	15.6	19.8	27.1	32.5	27.2	22.4	23.3	23.6	39.5	26.0	26.9
17/8	15.4	37.7	28.5	24.1	20.3	28.8	44.2	22.9	24.4	32.3	23.7	32.6	29.1
31/8	14.5	31.4	29.3	29.1	16.6	30.6	42.3	18.9	21.6	28.9	21.3	30.1	27.3
12/9	20.1	43.5	25.7	25.9	19.9	44.2	27.8	23.6	21.5	25.2	19.6	28.3	27.8
3/10	22.8	26.6	18.6	26.3	17.3	42.5	24.5	20.1	23.6	28.9	21.1	26.5	25.1
26/10	15.4	35.3	23.9	19.4	16.5	30.6	21.8	24.4	21.5	24.6	24.7	27.3	24.5
3/11	10.9	32.2	17.7	20.1	20.6	35.0	27.3	18.6	20.3	20.8	23.1	25.3	23.7
$\overline{X}$	19.6	35.2	25.2	26.6	25.5	35.6	29.4	25.0	25.3	27.4	26.4	28.6	

APPENDIX VI   Leaf total nitrogen 1979 (mg N/gm dry weight)

Date	Treatment														$\bar{X}$
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
17/4	34.7	38.0	40.5	35.1	39.9	38.6	31.1	38.6	33.2	31.1	26.9	42.2	34.7	34.7	35.7
4/5	28.4	34.0	29.0	34.0	30.2	30.9	42.4	30.2	35.5	27.3	33.2	28.8	30.4	30.4	31.8
14/5	26.9	37.2	29.8	36.8	26.7	39.3	38.2	23.9	36.5	51.9	42.2	32.1	44.1	51.7	37.0
21/5	29.2	37.3	31.3	46.9	29.2	44.7	50.0	35.5	37.2	37.1	48.7	35.1	43.6	55.9	40.1
4/6	33.3	36.5	29.4	37.2	29.6	42.0	36.3	37.6	29.4	37.2	46.0	42.2	38.4	47.5	37.3
12/6	25.2	38.4	30.7	30.0	30.5	42.6	40.1	25.8	23.9	37.6	41.0	37.4	46.4	46.4	35.4
20/6	23.6	31.0	24.2	26.5	24.6	33.7	24.6	21.1	20.2	35.6	31.1	28.2	35.5	42.7	28.8
3/7	22.3	30.9	17.0	20.6	16.4	35.7	24.8	16.4	19.3	27.9	31.1	27.1	33.2	39.1	25.1
16/7	17.6	31.9	26.0	26.0	12.6	37.8	17.2	20.4	20.4	29.4	21.8	26.7	38.6	33.8	25.7
2/8	29.8	24.8	21.6	19.5	21.0	27.3	22.1	20.2	17.0	20.2	27.3	26.0	37.9	28.6	24.5
20/8	19.5	30.0	17.6	24.6	28.8	32.6	23.1	25.8	26.7	20.0	25.6	19.5	37.2	35.9	26.2
5/9	20.8	27.3	16.8	20.6	17.0	32.3	28.1	23.3	14.7	17.6	26.7	16.8	37.2	36.3	24.0
24/9	17.2	22.7	17.9	16.0	10.7	27.3	17.9	14.5	23.1	13.0	17.4	22.3	24.8	27.5	19.5
12/10	11.6	27.3	15.5	22.5	14.3	24.8	23.9	14.1	15.8	12.8	16.6	23.1	31.7	28.1	20.7
19/10	11.8	33.4	24.2	27.3	13.0	31.1	25.4	20.2	15.1	16.8	15.3	22.9	21.6	37.4	22.5
$\bar{X}$	23.46	32.05	24.77	28.24	22.97	34.71	29.68	24.51	24.53	27.70	30.06	28.69	35.69	38.40	

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Key   1   Control   8   K

2   NPK + Lime   9   P

3   PK   10 N_{300}

4   N_{100} 11   NK

5   Lime   12   NPK

6   N_{600} 13 N_{900}

7   NP   14 N_{1200}

APPENDIX VII   Leaf Total Phosphorus in 1979 (mg P/gm dry weight)

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	$\bar{x}$
17/4	3.65	5.97	5.19	4.37	3.78	3.13	3.29	4.43	4.56	3.35	2.88	5.51	3.65	3.65	4.10
4/5	3.27	4.43	4.28	3.47	3.35	2.87	4.14	3.81	3.68	2.78	3.31	3.84	3.27	3.27	3.56
14/5	3.09	4.34	5.01	3.21	2.96	2.72	5.33	3.53	3.99	2.77	3.22	4.95	3.13	3.14	3.67
21/5	2.80	4.68	5.16	3.57	2.91	3.26	3.68	3.14	4.01	2.81	3.00	5.98	3.44	3.37	3.70
4/6	2.29	5.30	5.22	3.41	2.65	2.93	4.84	4.00	6.51	2.78	2.86	5.85	3.14	4.12	3.99
12/6	2.55	4.34	5.53	3.04	2.82	2.75	4.28	3.50	3.37	2.43	2.83	4.26	3.48	3.06	3.45
20/6	2.35	4.20	3.84	3.12	2.41	2.53	3.62	3.12	4.17	2.34	2.42	4.12	3.19	2.73	3.15
3/7	1.90	3.88	4.13	2.51	2.61	2.30	3.35	2.82	4.29	2.38	2.01	6.46	3.22	2.90	3.20
16/7	1.90	3.56	3.57	2.50	1.74	2.25	2.44	2.59	3.73	1.74	1.70	3.12	2.60	2.03	2.53
2/8	2.20	2.86	3.47	2.04	2.09	1.65	1.88	2.19	2.15	1.70	1.79	2.36	2.25	2.20	2.20
20/8	1.96	2.41	3.35	2.44	2.99	2.37	2.77	2.85	4.30	1.74	2.26	2.92	2.94	2.89	2.73
5/9	1.67	3.87	3.51	2.33	2.39	2.54	3.12	2.98	2.70	1.89	1.77	3.81	3.30	2.81	2.76
24/9	1.88	3.39	3.54	2.52	1.78	1.99	2.03	2.69	4.05	1.76	1.77	3.29	1.91	2.37	2.50
12/10	1.56	3.65	2.56	1.89	1.71	2.41	3.42	2.17	4.78	1.53	1.39	4.38	2.92	2.73	2.65
19/10	1.87	5.38	4.55	3.22	2.47	3.52	3.05	3.37	3.08	1.97	1.92	5.16	2.14	3.93	3.26
$\bar{x}$	2.33	4.15	4.19	2.91	2.58	2.61	3.42	3.15	3.96	2.26	2.34	4.40	2.97		3.01

APPENDIX VIII

Key   1   Control   8   K

2   NPK + Lime   9   P

3   PK   10 N_{300}

4   N_{100} 11   NK

5   Lime   12   NPK

6   N_{600} 13 N_{900}

7   NP   14 N_{1200}

APPENDIX VIII   Leaf Total Potassium in 1979 (mg K/gm dry weight)

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	$\bar{x}$
17/4	24.1	30.4	28.8	24.5	23.1	27.4	22.3	31.9	24.8	22.3	29.8	28.1	24.1	24.1	26.1
4/5	18.4	22.6	22.8	17.8	18.3	15.7	21.9	16.0	20.0	16.7	20.3	20.4	18.4	18.4	19.1
14/5	21.8	22.8	29.6	24.9	22.1	17.6	21.0	26.6	23.5	21.7	23.0	27.1	23.0	20.3	23.2
21/5	21.0	28.1	30.8	22.3	21.3	20.8	21.3	28.7	24.4	23.9	20.3	25.5	23.5	22.8	23.9
4/6	20.2	24.9	34.1	23.7	18.4	21.7	22.8	32.4	30.0	22.2	21.7	27.0	23.2	23.4	24.7
12/6	30.4	25.1	31.1	21.3	21.4	27.2	21.4	26.2	18.7	21.7	29.8	30.7	25.3	20.8	25.1
20/6	18.5	24.8	26.8	18.9	21.1	18.5	18.8	26.0	22.8	21.0	23.8	19.7	15.5	18.2	21.0
3/7	19.0	24.6	27.9	19.1	20.9	21.6	8.8	28.8	21.9	15.5	23.6	29.9	21.6	15.9	21.4
16/7	16.6	26.4	25.6	15.4	15.7	23.0	14.2	23.5	20.2	15.4	21.7	25.0	19.5	18.7	20.1
2/8	17.7	17.7	22.8	13.6	18.7	13.8	16.7	38.7	11.8	12.2	23.0	19.5	11.8	12.9	17.9
20/8	20.1	14.1	19.4	22.1	20.8	22.5	19.4	16.4	16.1	16.1	29.6	21.2	19.4	15.9	19.5
5/9	16.7	24.9	27.1	17.2	23.0	24.5	22.0	26.3	20.9	14.1	26.6	22.5	23.4	23.4	22.3
24/9	16.5	21.3	17.1	21.0	15.6	13.5	16.7	23.4	20.3	12.7	17.7	21.6	15.3	16.4	17.8
12/10	15.1	25.6	21.4	21.4	18.0	19.7	21.3	20.3	18.3	11.5	19.2	25.0	20.7	26.8	20.3
19/10	15.2	26.9	22.7	20.3	15.2	29.3	20.4	26.1	21.0	12.3	18.7	26.4	15.6	26.2	21.2
$\bar{x}$	19.4	24.0	25.9	20.2	19.6	21.1	19.3	26.1	21.0	17.3	23.3	24.6	20.0		20.3

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APPENDIX IX

1	control	8	K
2	NPK+Lime	9	P
3	PK	10	N_{300}
4	N_{100}	11	NK
5	Lime	12	NPK
6	N_{600}	13	N_{900}
7	NP	14	N_{1200}

Asp.	Aspartic acid	Iso.	Isoluecine
Threo.	Threonine	Leu.	Leucine
Amide	Amide	L Dopa	L Dopa
Glut.	Glutamic acid	Tyro.	Tyrosine
Pro.	Proline	β Phen.	β Phenylalanine
Gly.	Glycine	γ Amino	γ Aminobutyric acid
Ala.	Alanine	Hist.	Histidine
Val.	Valine	Lys.	Lysine
Meth.	Methionine	Arg.	Arginine

Leaf soluble amino acids (nm/100 mg dry weight) at 4.5.79

Treatment

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	293	470	164	111	94	199	626	825	134	93	449	68	293	293
Threo.	425	273	332	145	698	879	809	756	299	319	1095	167	425	425
Amide	695	462	531	875	657	1469	513	1031	410	667	1685	363	695	695
Glut.	569	359	585	873	671	804	346	440	559	512	584	149	569	569
Prol.	683	221	317	380	1311	1775	258	1029	472	588	1011	166	683	683
Gly.	21	28	8	15	23	43	14	12	36	29	41	29	21	21
Ala.	1120	842	818	737	1171	1069	1711	1675	924	804	1911	1546	1120	1120
Val.	108	103	98	101	75	142	94	153	111	101	57	61	108	108
Meth.	T	T	T	T	T	T	T	T	T	T	T	T	T	T
Isol.	36	40	31	25	57	44	11	33	34	41	34	34	36	36
Leu.	165	159	139	117	219	269	141	171	180	195	147	179	165	165
L Dopa	256	373	315	253	189	296	240	249	347	183	289	433	256	256
Tyro.	22	16	26	15	30	59	13	25	12	16	12	9	24	24
β Phen.	24	17	26	15	79	56	4	2	12	17	13	9	24	24
γ Amino	1331	1457	1324	1006	1399	2588	1394	1631	1551	1015	1193	1350	1331	1331
Hist.	48	110	17	35	16	33	26	73	104	40	119	117	48	48
Lys.	47	48	43	56	45	133	47	37	52	55	40	39	47	47
Arg.	34	54	9	36	8	95	77	54	65	95	101	60	34	34
Total	5843	4978	4900	4793	6735	9858	6246	8143	5337	4673	8698	4718	5843	5843

APPENDIX IX   Leaf soluble amino acids (nm/100 mg dry weight) at 14.5.79

Treatment

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	21	125	21	26	33	60	217	22	54	106	98	139	268	102
Threo.	222	4791	170	351	544	7343	1732	213	400	2831	2450	3824	4506	7695
Amide	252	5791	225	485	437	2631	1057	313	258	1821	1535	1871	2774	2731
Glut.	117	551	78	116	241	661	574	75	210	472	859	607	786	1018
Prol.	204	258	125	121	532	2093	1217	299	247	364	1040	242	274	1115
Gly.	70	178	78	74	116	419	296	75	91	182	130	186	217	336
Ala.	1250	2344	1263	1779	1574	2586	2890	1318	1591	2272	2520	3279	2379	3022
Val.	50	114	50	51	80	223	158	51	40	85	91	100	100	137
Meth.	T	6	T	T	T	T	T	T	T	T	T	4	T	161
Isol.	26	38	38	35	19	173	89	32	30	47	129	28	27	134
Leu.	150	189	141	167	172	270	269	154	215	278	280	214	196	245
L Dopa	340	638	428	1307	253	351	287	343	1118	303	447	992	502	609
Tyro.	12	54	14	60	23	40	6	9	27	29	10	24	6	64
β Phen.	30	48	32	33	35	40	7	33	25	28	19	24	17	60
γ Amino	1061	1768	1053	1152	1000	2907	2262	914	1432	1521	1388	2106	2175	2293
Hist.	15	32	14	24	28	40	15	12	80	52	30	7	20	T
Lys.	26	72	53	32	45	100	67	24	27	70	50	50	49	81
Arg.														
Total	3846	17,000	3783	5811	5130	19,889	12,781	3887	5843	10,461	11,053	12,548	16,277	19,813

APPENDIX IX   Leaf soluble amino acids (nm/100 mg dry weight) at 21.5.79

Treatment

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	146	76	29	105	29	682	43	83	88	223	81	66	177	274
Threo.	480	627	228	404	242	2011	2234	286	225	2173	2446	380	3125	6319
Amide	763	760	408	529	211	1969	1681	352	270	2744	2353	470	1789	7889
Glut.	243	121	137	293	125	658	631	250	157·	817	825	369	1936	1801
Prol.	217	278	117	91	278	224	243	305	47	576	269	108	104	717
Gly.	113	98	44	47	55	103	138	63	117	266	103	62	98	339
Ala.	2632	2622	1970	2708	1833	2953	4469	1656	1792	4209	2799	2361	4118	7566
Val.	186	70	48	99	109	78	88	88	99	126	111	93	152	256
Meth.	T	T	T	T	38	T	T	T	T	T	T	T	T	T
Isol.	93	48	117	257	247	55	417	169	36	115	59	69	409	396
Leu.	233	182	90	56	29	234	53	97	272	571	217	143	68	98
L. Dopa	300	609	892	1310	295	343	578	471	561	558	338	653	471	301
Tyro.	45	22	15	9	23	22	18	15	32	20	21	20	10	77
β Phen.	75	26	40	29	43	44	58	32	44	50	34	27	44	188
γ Amino	1313	2354	1484	1620	1323	2049	3165	1654	1860	2780	2456	1740	3358	3967
Hist.	40	38	29	28	38	65	45	31	26	45	35	26	42	78
Lys.	92	47	43	198	38	58	61	41	14	58	71	37	80	192
Arg.	129	60	65	10	50	80	96	119	41	32	86	57	46	363
Total	6969	7975	5756	7782	4956	11,547	13,922	5593	5636	15,331	12,217	6623	16,025	30,458

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APPENDIX IX Leaf soluble amino acids (nm/100 mg dry weight) at 4.6.79

Treatment

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	56	139	75	87	99	133	35	76	33	214	72	171	208	228
Threo.	197	250	240	173	275	1074	586	193	201	1140	187	170	1195	1007
Amide.	293	826	583	176	242	2128	758	558	308	1389	366	252	2580	4112
Glut.	98	55	109	126	77	350	204	45	41	944	42	138	323	303
Prol.	164	264	111	228	347	320	69	140	85	418	692	66	237	515
Gly.	81	78	135	87	81	96	152	89	114	128	84	112	107	178
Ala.	988	1511	1631	1191	1013	2027	2667	1492	716	1027	2237	1579	2000	2836
Val.	74	158	150	111	133	89	101	89	70	81	241	120	194	252
Meth.	T	T	T	T	T	T	122	T	67	T	126	T	T	T
Isol.	92	94	56	50	119	139	143	124	93	64	36	100	134	218
Leu.	75	97	221	73	211	116	224	148	99	164	165	194	228	197
L. Dopa	104	150	675	1490	423	761	295	154	219	226	536	1145	270	302
Tyro.	21	22	55	75	T	93	81	51	40	67	72	86	72	143
β Phen.	42	15	70	71	T	25	37	15	67	39	40	81	50	78
γ Amino	860	1284	1541	1005	795	1198	1408	1394	1780	1672	1222	888	1339	1943
Hist.	32	43	48	74	20	26	75	32	29	63	76	85	43	89
Lys.	46	53	83	41	31	37	67	61	44	64	94	104	72	100
Arg.	40	33	29	37	33	50	116	26	38	34	50	50	72	135
Total	3223	5039	5782	5056	3865	8610	7024	4660	3006	7701	6287	5292	9049	12,499

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Leaf soluble amino acids (nm/100 mg dry weight) at 3.7.79

Treatments

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	27	89	15	18	34	152	58	16	28	19	60	36	59	107
Threo.	89	376	72	64	109	1227	141	57	61	119	716	398	588	871
Amide.	73	1059	79	64	147	883	197	49	57	120	489	595	620	966
Glut.	58	59	44	27	22	247	52	34	24	53	137	245	217	209
Prol.	222	399	127	140	136	929	98	47	120	189	934	339	376	354
Gly.	46	78	66	87	102	294	104	45	62	62	149	184	172	139
Ala.	587	1880	634	670	798	1807	1184	474	798	582	1713	1528	1512	1912
Val.	44	176	52	45	30	113	85	23	32	87	60	167	74	170
Meth.	T	T	T	T	T	T	T	T	T	T	T	T	T	T
Isol.	49	177	36	25	26	108	89	25	46	82	97	129	76	110
Leu.	65	269	49	67	76	185	112	54	76	125	141	203	156	167
L. Dopa	55	201	98	70	28	103	39	39	51	30	159	200	129	174
Tyro.	14	62	5	8	23	T	22	21	44	8	57	65	13	50
β Phen.	19	52	29	15	20	T	31	15	30	26	54	T	10	43
γ Amino	761	1953	588	714	794	1404	773	486	817	637	1323	1366	1257	1630
Hist.	11	641	53	29	31	28	39	234	38	44	39	47	31	40
Lys.	24	100	23	58	22	40	52	17	37	40	35	83	25	58
Arg	15	90	21	18	25	34	21	16	8	15	17	52	54	77
Total	2144	7572	1970	2099	2397	7519	3074	1635	2325	2223	6163	5584	4056	7001

APPENDIX IX   Leaf soluble amino acid (nm/100 mg dry weight) at 2.8.79

Treatments

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	26	56	19	12	24	38	39	15	17	21	29	49	35	82
Threo.	104	262	90	44	130	251	128	76	52	41	247	243	251	395
Amide	83	718	114	52	129	298	183	98	90	73	244	225	129	420
Glut.	65	102	36	25	43	43	13	31	35	18	84	194	199	198
Prol.	52	121	34	50	51	134	161	58	78	59	123	132	163	51
Gly.	28	72	61	57	114	118	45	98	52	53	55	86	87	60
Ala.	418	1187	399	423	711	574	696	556	347	453	416	1584	1000	858
Val.	111	55	15	19	18	12	22	24	21	22	27	27	23	104
Meth.	T	T	3	T	3	T	T	T	T	T	T	T	T	T
Isol.	59	72	7	19	18	10	54	10	16	16	29	198	87	104
Leu.	122	119	24	35	71	93	114	36	21	51	111	183	54	102
L. Dopa	113	6	9	12	20	5	20	15	4	19	16	29	16	12
Tyro.	48	14	19	4	17	3	21	13	5	8	13	13	20	23
β Phen.	56	18	9	8	22	13	12	10	7	10	18	9	17	12
γ Amino	516	1087	667	444	942	592	791	517	331	529	1494	2053	1543	1127
Hist.	25	38	9	32	19	13	40	26	19	8	19	26	22	48
Lys.	75	30	17	23	22	13	18	19	16	17	18	23	17	38
Arg.	69	27	14	7	12	5	103	18	11	5	17	8	14	38
Total	1900	3901	1530	1257	2354	2208	2358	1611	1110	1399	2943	5073	3660	3634

APPENDIX IX Leaf soluble amino acids (nm/100 mg dry weight) at 5.9.79

Treatments

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	40	152	69	90	64	167	141	68	46	46	178	90	184	65
Threo.	99	663	122	165	123	545	171	130	58	62	206	211	716	1142
Amide	43	1503	170	233	91	401	383	232	52	43	227	251	1499	1775
Glut.	16	20	6	59	41	60	5	13	20	15	163	136	120	474
Prol.	28	218	29	139	58	416	311	134	31	139	129	241	422	179
Gly.	25	21	47	19	6	21	27	16	13	48	25	99	127	13
Ala.	586	867	480	680	457	1626	1050	645	308	605	1113	713	1320	1478
Val.	40	150	49	55	33	132	98	42	19	42	76	75	127	111
Meth.	T	T	T	T	T	T	T	T	T	T	T	T	T	T
Isol.	18	78	13	14	5	49	127	19	15	14	35	45	61	41
Leu.	205	157	87	183	28	374	322	90	56	169	344	170	242	219
L Dopa	57	126	54	94	58	182	199	71	6	33	186	100	236	192
Tyro.	18	19	17	20	16	62	22	7	6	29	27	18	33	19
β Phen.	58	18	48	20	45	76	22	8	7	29	35	18	31	19
γ Amino	616	1356	544	853	627	2362	1104	838	321	363	1229	1063	2476	3229
Hist.	13	48	17	23	35	27	13	9	15	17	16	16	25	25
Lys.	19	139	52	38	32	127	66	18	13	30	48	62	88	40
Arg.	3	22	7	28	7	10	45	23	57	8	8	58	81	8
Total	1881	5534	1801	2685	1719	6627	4061	2339	983	1682	4036	3306	7709	9019

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APPENDIX IX   Leaf soluble amino acids (nm/100 mg dry weight) at 24.9.79

Treatments

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	81	219	89	166	101	1568	265	259	527	117	568	374	194	378
Threo.	213	1250	559	213	121	2210	548	262	2130	107	673	2210	1046	3119
Amide	209	2000	567	199	339	1615	547	263	3610	110	410	1616	704	4538
Glut.	226	311	168	311	16	1614	394	387	945	256	1204	896	736	899
Prol.	86	294	302	249	59	639	228	56	1122	61	241	326	688	1065
Gly.	25	42	22	10	15	101	45	15	75	9	50	23	37	49
Ala.	682	542	426	2013	200	1254	410	425	598	158	399	542	773	541
Val.	47	114	71	20	18	65	56	33	183	45	41	122	85	118
Meth.	6	T	4	T	8	T	4	T	9	T	T	10	19	16
Isol.	7	69	39	11	10	87	16	12	168	9	37	90	51	93
Leu.	152	133	86	93	51	379	165	106	174	102	142	212	258	239
L Dopa	17	T	4	T	8	13	5	10	12	T	T	20	T	T
Tyro	4	37	12	11	8	15	12	23	52	15	25	20	39	33
β Phen.	21	47	50	16	20	40	46	33	39	14	17	35	64	44
γ Amino	681	999	569	461	230	1533	676	702	521	340	370	767	797	739
Hist.	18	73	32	16	12	41	45	23	119	22	33	70	49	96
Lys.	15	51	52	28	17	47	45	16	80	14	35	57	41	57
Arg.	16	40	20	19	10	54	19	16	80	30	20	28	37	38
Total	2489	6282	3052	3816	1231	12,922	3506	2626	10,454	1389	4246	7390	5495	12,091

APPENDIX IX   Leaf soluble amino acids (nm/100 mg dry weight) at 19.10.79

Treatments

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asp.	61	133	59	128	34	151	121	36	27	47	30	143	163	305
Threo.	109	984	297	721	42	1398	732	227	241	327	101	699	531	3133
Amide	131	3363	544	1631	91	1189	1228	480	409	614	216	1323	882	9121
Glut.	89	650	187	96	4	1113	852	117	73	291	129	100	77	973
Prol.	29	123	145	114	33	86	581	175	256	103	112	110	323	142
Gly.	28	126	15	33	58	67	46	84	43	94	49	57	100	166
Ala.	446	2688	627	916	369	1544	973	1489	1071	1579	1160	1223	809	3964
Val.	24	186	64	71	17	110	129	86	98	138	72	138	49	333
Meth.	T	84	T	T	T	T	T	T	T	T	T	T	T	35
Isol.	19	372	26	25	7	53	51	22	28	57	27	59	46	259
Leu.	69	363	106	141	48	295	258	230	121	279	162	199	247	510
L Dopa	T	96	35	11	T	22	23	25	T	21	19	95	T	129
Tyro	T	98	46	25	5	27	29	21	37	42	28	25	12	73
β Phen.	14	98	18	44	7	45	73	18	48	51	34	26	14	161
γ Amino	436	3878	1107	1243	494	1564	1190	1392	1157	1678	1186	1493	1274	3116
Hist.	12	300	24	40	8	35	66	70	25	90	10	45	44	247
Lys.	14	116	65	45	17	57	55	69	61	47	33	107	46	171
Arg.	15	91	36	17	8	22	20	15	30	20	14	10	67	107
Total	1480	13,657	3364	5143	1233	7757	6421	4542	3695	5458	3366	5841	4615	23,036

APPENDIX X

Key

1	Control	8	K
2	NPK + Lime	9	P
3	PK	10	N_{300}
4	N_{100}	11	NK
5	Lime	12	NPK
6	N_{600}	13	N_{900}
7	NP	14	N_{1200}

Total Auchenorrhyncha /m^2 in 1978

Treatment

Date	1	2	3	4	5	6	7	8	9	10	11	12
17.4	36	0	0	9	18	0	64	36	27	27	109	9
24.5	9	27	9	36	9	27	9	27	9	36	36	9
10.5	18	9	9	18	209	146	118	109	36	27	55	64
16.5	9	27	18	9	55	9	64	218	91	0	27	46
22.5	18	9	46	9	73	91	200	55	9	27	18	27
30.5	18	36	109	9	18	85	82	73	64	73	18	36
6.6	18	0	0	46	55	27	46	9	127	46	36	73
12.6	36	27	27	0	46	9	18	0	9	36	0	0
20.6	18	0	46	27	55	36	0	0	55	36	18	36
27.6	82	0	18	18	18	18	9	27	36	36	18	18
4.7	18	9	36	0	36	9	9	27	46	0	18	27
11.7	55	0	27	55	55	9	9	18	55	18	55	9
17.7	27	27	46	18	9	27	9	82	36	18	9	36
25.7	137	264	200	137	191	55	300	255	200	164	100	146
10.8	364	164	282	228	109	391	455	273	73	91	182	755
15.8	100	410	410	73	282	291	246	291	173	309	191	446
22.8	73	319	309	18	109	82	555	−	146	0	46	46
11.9	36	100	55	9	73	883	737	9	46	18	9	637
18.9	64	182	164	18	91	109	155	164	100	173	473	1292
27.9	−	100	82	309	137	173	118	100	228	27	91	173
11.10	−	865	719	482	364	1101	1201	364	209	628	855	1329
23.10	−	355	519	692	36	73	1593	355	291	209	100	789

APPENDIX X Total Auchenorrhyncha/m^2 in 1979

Treatment

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14
18.4	137	118	155	64	109	291	291	9	73	209	118	218	137	137
9.5	382	173	218	218	91	237	237	146	91	55	100	309	27	510
15.5	191	118	73	228	55	673	319	200	273	64	46	173	100	437
1.6	127	109	127	373	55	300	400	200	191	137	473	164	127	127
6.6	182	182	264	264	127	64	155	391	255	182	373	228	255	309
20.6	200	209	537	282	291	255	319	337	100	218	127	273	218	100
27.6	328	118	146	291	391	146	455	428	601	264	191	191	309	137
3.7	272	173	364	328	173	218	419	846	255	64	291	400	364	373
12.7	246	1147	309	328	309	200	255	728	437	64	64	792	564	455
17.7	155	400	455	510	100	173	255	501	437	300	209	1274	291	883
23.7	100	1620	783	91	118	155	300	1638	683	246	200	2175	501	1128
2.8	237	828	1219	1356	237	273	173	1720	309	164	209	1547	1210	983
10.8	264	2557	728	428	200	528	537	1047	683	328	200	819	446	1128
16.8	428	1656	473	855	337	146	255	910	446	291	282	1656	701	555
28.8	510	1101	992	428	391	246	646	1602	519	410	809	3258	755	737
5.9	828	2430	874	655	182	546	974	555	391	364	337	1611	637	937
14.9	273	2557	1247	510	546	337	601	901	719	501	646	628	619	2584
25.9	364	1174	2175	510	928	391	501	1138	710	573	364	2821	1411	2302
12.10	218	3158	2894	1947	637	446	446	400	1274	410	64	2994	3294	1711
29.10	219	5806	2557	1101	573	446	300	2566	974	355	155	1347	237	1047

APPENDIX XI   Mean weight ± 95% Fiducial Limits of Nymphs and
Adults of the major species of Auchenorrhyncha
on experimental area.

Species	Stage	Mean Weight* (mg)	95% Fiducial Limits (mg)	Numbers Examined
D.abdominalis	♀	.913	.0533	91
	♂	.722	.0246	90
	V	.468	.0285	87
	IV	.212	.0356	25
	III	.057	.0050	21
	II	.032	.0024	29
	I	.013	.0013	33
	Egg	.026	.006	5
A.ocellaris	♀	.642	.0406	67
	♂	.462	.0273	70
	V	.248	.0153	97
	IV	.116	.0073	86
	III	.053	.0004	82
	II	.024	.0009	121
	I	.011	.0008	109
	Egg Gen.1	.018	.0031	65
	Gen.2	.021	.004	165
R.coronifera	♀	.698	.0958	41
	♂	.372	.0350	28
	V	.249	.0192	35
	IV	.116	.0234	51
	III	.049	.0045	99
	II	.027	.0020	33
	I	.014	.0018	39
	Egg	.020	.003	250
D.hamata	♀	.780	.469	122
	♂	.513	.0139	86
	V	.469	.0252	104
	IV	.143	.0052	77
	III	.066	.0041	110
	II	.031	.0022	80
	I	.014	.0011	39
	Egg	.013	.0002	250
Z.scutellaris	♀	.170	.0079	74
	♂	.091	.0017	56
	V	.057	.0060	49
	IV	.029	.0034	80
	III	.013	.0094	86
	II	.009	.0010	110
	I	.006	.0009	45
	Egg	.006	.0002	80

APPENDIX XI   cont.

Species	Stage	Mean Weight* (mg)	95% Fiducial Limits (mg)	Numbers Examined
E.sulphurella	♀	1.547	0.121	8
	♂	0.624	0.037	9
E.incisis	♀	1.675	0.092	8
	♂	0.911	0.095	8
	V	0.519	0.041	5
	IV	0.377	0.025	2
	III	0.270	0.025	5
	II	0.120	0.004	7
J.pellucida	♀	0.945	0.084	5
	♂	0.344	0.019	12
	V	0.320	0.039	13
	IV	0.155	0.008	5
	III	0.066	0.005	8
	II	0.031	0.002	7
	I	0.014	0.001	9
M.parvicauda	♀	0.944	0.041	5
	♂	0.639	0.042	5
	V	0.516	0.052	3
	IV	0.300	0.021	8
	III	0.150	0.009	9
	II	0.041	0.003	4
	I	0.012	0.004	5
M.laevis	♀	0.641	0.023	8
	♂	0.304	0.023	6
E.lineolatus	♀	2.060	0.007	3
	♂	1.196	0.156	2
S.minutus	♀	1.749	0.078	11
	♂	1.221	0.033	8
N.lineolatus	♀	3.905	0.021	2
	♂	1.870	0.012	2

* All weights were made on a Cahn electromicrobalance to an accuracy of ± 0.001 mg.

APPENDIX XII   Dicranotropis hamata population data $\bar{x}/m^2$ - 1978/1979

1978
Stage

Date	I	II	III	IV	V	♂	♀
17.4			0.8	0.8	1.5	0.8	
24.4			1.6	0.8			
10.5			0.8	1.6	0.8		
16.5			1.6	0.8			
22.5				0.8	0.8		
30.5							0.8
6.6							
12.6							
20.6							
27.6							
4.7							
11.7		0.8					
17.7	0.8						
25.7	23.2	6.6					
10.8	0.8	2.3	12.1	0.8		6.6	8.3
15.8	8.3	10.8	1.6	2.5	3.31	5.8	5.0
22.8	1.6	0.8	0.8	1.7	0.8	5.0	1.5
11.9	29.0	18.2	9.1	6.6		0.8	0.8
18.9	52.1	9.9					
27.9	24.0	3.3	0.8				
11.10	115.8	158.0	81.1	1.7			
23.10	20.7	167.9	29.0				

1979

Date	I	II	III	IV	V	♂	♀
18.4			8.3	25.7	84.4		
9.5			2.6	4.6	42.9	2.0	2.0
15.5					34.3	9.8	6.3
1.6					2.8	5.6	4.9
6.6						4.2	2.8
20.6						6.5	4.6
27.6						5.2	3.3
3.7	78.7	16.9				2.8	2.8
12.7	27.3	60.5				5.2	3.9
17.7	119.0	96.2	28.6			3.3	4.6
23.7	190.5	171.0	69.6			0.7	
2.8	176.2	185.3	86.5	18.2			
10.8	37.1	172.3	85.2	27.3	3.9	2.0	
16.8	102.7	163.8	63.7	14.3	29.9	13.7	13.0
28.8	72.2	279.5	138.5	2.0	9.1	37.7	26.7
5.9	215.2	98.8	98.8	4.6	0.7	22.8	12.4
14.9	410.2	120.3	27.3			12.4	7.2
25.9	325.7	141.7	295.8	5.9		0.7	2.0
12.10	567.5	405.0	267.2	0.7			
29.10	249.6	507.0	399.8	1.3			

APPENDIX XII   Elymana sulphurella population data $\bar{x}/m^2$ 1978/1979

1978

Date	I	II	Stage III	IV	V	♂	♀
17.4							
24.4							
10.5							
16.5							
22.5	0.8						
30.5	15.2						
6.6	9.1	5.3	0.8				
12.6	6.1						
20.6	0.8	1.5	5.3	0.8			
27.6	0.8	1.5	3.0				
4.7		0.8	1.5	0.8	0.8		
11.7					1.5		
17.7					3.0	0.8	0.8
25.7				0.8	1.5	3.8	1.5
10.8						3.0	3.0
15.8							3.3
22.8							2.3
11.9							
18.9							
27.9							1.7
11.10							
23.10							

1979

Date	I	II	III	IV	V	♂	♀
18.4							
9.5							
15.5							
1.6	13.7	11.7					
6.6	16.8	25.9	6.3				
20.6	3.3	8.5	21.5	7.8			
27.6	2.0	5.9	11.7	22.8			
3.7		2.0	2.0	11.1	4.6		
12.7				2.6	13.0	2.6	0.7
17.7				1.3	6.5	9.8	9.1
23.7					5.2	11.1	10.4
2.8						7.8	11.7
10.8						4.6	7.2
16.8						3.9	9.1
28.8						0.7	10.4
5.9							5.2
14.9							4.6
25.9							5.2
12.10							1.3

APPENDIX XII   Eucelis incisus population data $\bar{x}/m^2$ - 1978/1979

1978

Date	I	II	Stage III	IV	V	♂	♀
17.4			2.3		0.8		
24.4							
10.5							0.8
16.5							
22.5							
30.5							
6.6							
12.6							
20.6							
27.6							
4.7							
11.7							
17.7							
25.7							
10.8			0.8				
15.8							
22.8							0.8
11.9	1.5						
18.9							2.3
27.9	1.5	0.8					0.8
11.10	3.0		3.0	1.5			
23.10	3.0		1.5				

1979

Date	I	II	III	IV	V	♂	♀
18.4						0.83	
9.5							
15.5							
1.6	2.0	3.9	5.9				
6.6	1.3	3.3	7.7	2.0	0.7		
20.6					2.0		
27.6					1.3		
3.7		1.3	0.7		3.9		
12.7						1.3	
17.7							
23.7							
2.8							
10.8							
16.8							
28.8		3.3	0.7				0.7
5.9		2.0	0.7				
14.9		0.7					
25.9	0.7	0.7					
12.10			0.7		0.7		0.7
29.10			1.3	0.7		0.7	

APPENDIX XII   Zyginidia scutellaris population data $\bar{x}/m^2$

1978 and 1979

1978

Date	I	II	III	IV	V	♂	♀
17.4							1.5
24.4							4.1
10.5							3.0
16.5							
22.5	1.5					0.8	1.5
30.5							
6.6							
12.6		1.5		1.5	0.8		
20.6			1.5			1.5	0.8
27.6		0.8		0.8			4.6
4.7						3.8	3.0
11.7			0.8	1.5	1.5	11.4	9.1
17.7					0.8	9.9	5.3
25.7			0.8	2.3	5.3	33.4	24.3
10.8		0.8	3.0	6.8	9.1	36.4	37.1
15.8		6.6	16.6	0.8	2.5	57.9	43.0
22.8		4.1	7.5	7.5	6.6	26.5	39.7
11.9			4.6	4.6	24.3	13.7	10.6
18.9			5.3	3.8	6.8	43.2	23.5
27.9		0.8	3.3	4.1	3.3	37.2	23.2
11.10				4.1	5.0	97.6	63.7
23.10				2.5	4.1	27.3	16.6

1979

Date	I	II	III	IV	V	♂	♀
18.4							7.4
9.5		0.7					2.6
15.5							7.0
1.6		0.7					2.0
6.6			1.4	2.1	1.4		1.4
20.6	1.3	5.9	5.2	5.2	2.6		0.7
27.6	0.7	5.2	7.8	9.8	5.9		
3.7	1.4	2.1	5.6	16.8	14.0	0.7	1.4
12.7	1.3	2.6	12.4	8.5	21.5	8.5	11.7
17.7		1.3	2.6	9.1	11.1	23.4	18.9
23.7			1.3	2.0	5.9	23.4	17.6
2.8		0.7	2.6	0.7	2.6	16.9	25.4
10.8		1.3	4.6	0.7	2.6	26.0	31.9
16.8	2.0	2.6	7.2	3.9	3.2	40.3	39.0
28.8	2.0	3.3	13.0	12.4	11.1	30.6	27.3
5.9		11.7	35.1	31.9	24.7	9.1	17.6
14.9		9.8	26.7	39.0	35.1	16.9	24.7
25.9			3.3	40.3	66.3	47.5	70.9
12.10			0.7	1.3	29.3	46.8	35.1
29.10					7.8	51.4	57.9

APPENDIX XIII   Percentage water content of   grass species during the growing season in 1978 and 1979

1978

Date	H.lanatus	L.perenne	D.glomerata	F.pratensis	P.pratensis	$\bar{x}$
17/4	81.3	79.5	91.4	83.6	-	84.0
17/5	83.3	86.2	90.0	85.7	90.0	87.0
30/5	80.6	78.4	79.5	78.6	77.1	78.8
16/6	78.3	83.4	84.2	85.6	85.1	83.3
28/6	95.2	89.0	92.1	91.8	95.0	92.6
11/7	71.4	62.3	78.6	76.5	75.6	72.9
5/9	70.8	69.3	71.6	69.7	57.8	67.8
$\bar{x}$	78.4	69.2	83.9	76.2	71.0	

1979

Date	H.lanatus	L.perenne	D.glomerata	F.pratensis	P.pratensis	A.tenuis	$\bar{x}$
9/5	68.0	65.0	60.6	62.3	59.9	68.0	64.0
21/5	70.0	70.6	75.4	68.0	65.6	65.6	69.2
31/5	79.1	81.1	81.3	72.5	77.1	79.9	78.5
8/6	79.1	77.6	85.3	74.5	71.1	80.8	78.1
14/6	79.2	74.0	78.2	76.1	73.7	75.4	76.1
21/6	74.8	72.5	72.9	73.2	68.9	51.7	69.0
28/6	72.6	70.6	64.0	70.8	66.1	60.0	67.3
6/7	65.9	62.9	61.0	62.2	59.2	61.6	62.1
13/7	69.8	62.1	55.6	68.1	64.1	58.5	63.0
20/7	64.3	59.7	58.4	58.0	57.2	53.0	58.4
2/8	61.6	58.4	64.8	59.9	58.7	54.7	59.7
15/8	72.6	52.7	51.7	55.6	57.4	55.3	57.6
29/8	52.8	55.5	45.0	37.8	46.5	27.7	44.2
17/9	58.8	55.3	54.4	41.6	50.8	42.2	50.5
$\bar{x}$	69.2	65.6	64.9	62.9	62.6	59.5	

APPENDIX XIV   Pasture height of grass species (cm.) during the growing season in 1978 and 1979

1978

Date	H.lanatus	L.perenne	D.glomerata	F.pratensis	P.pratensis	x̄
10/4	4.5	8.4	6.3	7.2	1.0	5.5
27/4	4.2	12.4	7.9	8.1	1.0	8.1
9/5	5.4	11.8	9.2	9.6	2.0	9.1
22/5	9.2	14.8	13.7	13.4	1.5	12.6
6/6	10.7	16.2	16.0	14.4	3.3	15.4
20/6	11.5	16.2	17.6	15.4	3.4	15.0
7/7	25.5	22.5	31.6	24.2	8.8	24.1
19/7	31.8	23.9	29.9	27.0	13.2	25.2
10/8	31.3	24.6	31.6	26.0	15.2	25.7
22/8	31.0	23.7	30.3	26.5	15.1	25.3
x̄	16.5	17.5	19.4	17.2	6.5	

1979

Date	H.lanatus	L.perenne	D.glomerata	F.pratensis	P.pratensis	A.tenuis	x̄
9/5	13.9	11.9	28.3	21.7	12.1	2.5	15.1
21/5	16.4	16.2	33.6	24.2	15.1	5.9	18.6
31/5	19.3	22.2	45.0	28.4	18.2	6.3	23.2
8/6	25.9	26.1	45.7	32.6	22.5	9.4	27.0
14/6	31.8	26.0	51.3	36.8	23.9	12.6	30.4
21/6	31.4	32.8	53.1	38.0	28.1	17.1	33.4
28/6	39.4	36.5	54.6	39.2	29.8	16.4	36.0
6/7	51.6	44.1	48.9	38.8	28.8	20.3	38.8
13/7	69.7	57.9	49.2	35.9	27.1	21.0	43.5
20/7	76.9	65.3	44.8	37.2	23.7	20.9	44.8
2/8	78.7	62.5	49.7	37.9	26.4	20.5	46.0
15/8	74.0	63.3	47.0	34.6	26.7	22.0	44.6
x̄	44.1	38.7	45.9	33.8	23.5	14.6	

277.

APPENDIX XV   Plant biomass (gm/m^2) estimated from the 6 monocultures in 1979.

Date	H.lanatus	L.perenne	D.glomerata	F.pratensis	P.pratensis	A.tenuis	$\bar{x}$
9/5	10	23	317	112	44	27	89
21/5	151	62	451	368	213	154	233
31/5	196	189	318	250	166	165	214
8/6	300	275	500	285	241	213	302
14/6	792	740	782	761	737	754	761
21/6	626	589	679	723	628	687	655
28/6	967	459	1330	502	473	520	709
6/7	839	1249	1034	658	659	921	893
13/7	873	1409	2021	809	631	888	1105
20/7	998	1618	1470	712	1150	1078	1171
2/8	1119	1289	1151	960	707	840	1011
15/8	423	951	901	610	672	632	698
$\bar{x}$	608	738	913	563	527	573	

APPENDIX XVI   Leaf soluble nitrogen in 1978 (mg N/gm dry weight)

Date	L.perenne	F.pratensis	H.lanatus	D.glomerata	P.pratensis	$\bar{x}$
25/4	2.8	2.5	1.4	2.9		2.4
3/5	2.5	3.1	2.6	3.1		2.8
16/5	2.0	2.1	2.0	2.2	2.3	2.1
30/5	1.9	2.4	1.5	3.0	2.2	2.2
6/6	0.7	1.8	1.7	1.2	2.4	1.6
16/6	2.8	5.5	5.5	5.2	7.5	5.3
23/6	4.6	7.7	14.8	8.8	14.6	10.1
1/7	5.9	5.3	3.7	8.3	13.8	7.4
7/7	5.0	4.6	7.7	3.0	8.9	5.8
20/7	3.6	4.2	4.2	2.7	5.2	4.0
4/8	3.6	2.5	2.8	3.2	5.6	3.5
18/8	3.9	2.2	3.1	3.5	4.6	3.5
3/9	3.9	2.1	3.5	1.8	5.1	3.3
13/9	2.8	2.7	3.4	2.2	3.6	2.9
22/9	2.4	2.3	2.2	2.3	3.0	2.4
$\bar{x}$	3.23	3.40	4.01	3.56	6.06	

APPENDIX XVI   Leaf total nitrogen in 1978 (mg N/gm dry weight)

Date	L.perenne	F.pratensis	H.lanatus	D.glomerata	P.pratensis	$\bar{x}$
25/4	28.6	37.4	38.6	39.4	40.0	36.8
3/5	37.8	31.0	41.6	36.4	40.0	37.4
16/5	29.2	22.0	15.6	24.6	37.4	25.8
30/5	16.4	21.4	22.8	25.4	28.8	23.0
6/6	16.6	53.0	53.8	20.2	33.0	35.3
16/6	24.8	36.0	38.4	30.2	49.0	35.7
23/6	40.8	50.2	83.8	59.4	84.8	63.8
1/7	46.8	52.4	39.4	65.0	47.6	50.2
7/7	42.0	42.0	79.2	31.8	73.8	53.8
20/7	34.0	17.8	34.6	45.2	50.8	36.5
4/8	27.8	25.8	29.2	30.4	39.6	30.6
18/8	39.4	27.6	34.0	32.4	42.2	35.1
3/9	31.0	17.6	36.0	17.6	36.4	27.7
13/9	19.2	18.6	31.0	19.0	30.0	23.6
22/9	21.4	21.8	27.0	25.8	33.0	25.8
$\bar{x}$	30.4	31.6	40.3	33.5	44.4	

APPENDIX XVI   Stem soluble nitrogen in 1978 (mg N/gm dry weight)

Date	L.perenne	F.pratensis	H.lanatus	D.glomerata	P.pratensis	$\bar{x}$
25/4	2.4	4.0	1.0	2.9	-	2.6
3/5	3.3	3.1	2.8	3.1	-	3.1
16/5	-	1.8	2.3	1.7	5.1	2.7
30/5	1.7	3.0	2.5	1.5	1.7	2.1
6/6	0.6	1.6	1.8	2.0	-	1.5
16/6	2.4	3.6	3.0	3.1	5.1	3.4
23/6	5.9	8.9	11.7	9.2	14.4	10.0
1/7	5.6	8.6	2.7	7.3	16.8	8.2
7/7	4.2	3.8	7.4	3.4	9.9	5.7
20/7	2.2	3.3	3.3	2.5	5.1	3.3
4/8	2.2	2.4	2.3	3.7	3.6	2.8
18/8	3.0	2.2	3.4	3.4	4.0	3.2
3/9	2.2	2.1	2.6	1.7	2.0	2.1
13/9	-	2.0	3.3	2.5	1.5	2.3
22/9	4.3	2.0	2.5	1.6	3.7	2.8
$\bar{x}$	3.1	3.5	3.5	3.3	6.1	

APPENDIX XVII   Leaf soluble nitrogen in 1979 (mg N/gm dry weight)

Date	L.perenne	F.pratensis	H.lanatus	D.glomerata	P.pratensis	A.tenuis	$\bar{x}$
17/4	3.90	3.92	3.08	3.90	2.70	2.02	3.25
4/5	1.08	2.34	2.02	2.40	2.60	1.70	2.02
14/5	8.60	14.36	4.10	8.22	6.90	8.86	8.51
4/6	2.78	3.40	2.12	2.78	2.80	3.30	2.86
12/6	2.34	2.46	1.88	2.06	3.36	2.28	2.40
20/6	1.74	1.64	2.06	2.20	2.58	3.02	2.21
3/7	1.42	1.62	1.28	1.78	1.24	1.54	1.48
18/7	0.84	1.58	2.06	3.42	1.40	1.30	1.77
2/8	1.34	1.96	1.76	1.46	1.66	1.58	1.63
23/8	1.80	3.16	1.42	1.66	1.02	1.58	1.77
8/9	1.46	2.02	1.76	1.90	1.68	1.44	1.71
24/9	1.66	2.06	1.30	1.86	1.20	1.22	1.55
19/10	2.54	2.32	2.18	2.80	3.56	1.32	2.45
29/10	1.18	1.98	2.42	4.20	4.88	1.56	2.70
$\bar{x}$	2.33	3.20	2.10	2.90	2.68	2.34	

APPENDIX XVII   Leaf total nitrogen in 1979 (mg N/gm dry weight)

Date	L.perenne	F.pratensis	H.lanatus	D.glomerata	P.pratensis	A.tenuis	$\bar{x}$
17/4	46.0	51.4	44.4	45.8	45.4	26.8	43.3
4/5	41.8	57.0	47.0	30.4	48.0	21.2	40.9
14/5	60.2	65.2	40.0	44.8	52.4	50.2	52.1
4/6	41.8	35.2	48.8	26.4	26.4	74.4	42.2
12/6	31.2	29.0	33.4	28.6	56.4	40.0	36.4
20/6	33.0	18.0	60.1	24.6	26.0	33.8	32.6
3/7	22.8	22.0	22.0	27.2	19.0	25.0	23.0
18/7	31.6	22.8	42.2	23.4	22.0	18.4	26.7
2/8	20.2	18.4	20.2	20.2	15.8	20.6	19.2
23/8	27.8	32.2	30.0	22.0	21.6	21.2	25.8
8/9	21.6	22.4	14.3	23.8	19.0	20.2	20.2
24/9	27.2	24.6	20.6	20.2	18.0	19.4	21.7
19/10	25.0	27.8	24.1	23.8	28.2	30.8	26.6
29/10	32.0	27.2	44.4	37.8	18.4	16.8	29.4
$\bar{x}$	33.0	32.4	35.1	28.5	29.8	29.9	

APPENDIX XVII   Stem soluble nitrogen in 1979 (mg N/gm dry weight)

| Date	L.perenne	F.pratensis	H.lanatus	D.glomerata	P.pratensis	A.tenuis	$\bar{x}$
17/4	4.26	4.52	4.00	4.36	1.10	1.94	3.36
4/5	8.04	2.64	7.00	2.82	2.20	1.60	4.05
14/5	17.36	10.32	5.66	7.50	2.24	5.96	6.13
4/6	2.06	2.30	2.84	3.44	4.52	2.44	2.93
12/6	2.26	1.96	2.02	2.16	4.82	2.10	2.55
20/6	1.76	1.80	1.52	2.92	2.66	1.70	2.06
3/7	1.42	1.88	1.22	1.42	1.10	1.06	1.35
18/7	1.54	1.72	1.14	1.30	1.86	1.44	1.50
2/8	1.46	1.58	1.16	1.30	1.38	0.86	1.29
23/8	1.40	2.28	1.18	1.50	1.00	1.16	1.42
8/9	1.20	2.44	1.66	1.76	1.62	3.84	2.09
24/9	1.10	2.04	1.90	1.34	1.04	0.88	1.38
19/10	3.04	3.72	2.34	3.26	2.22	1.04	2.60
24/10	2.20	3.08	2.48	2.24	2.62	1.48	2.35
$\bar{x}$	3.51	3.02	2.51	2.67	2.17	1.96	

Mean nitrogen content of monocultures.

● ——— ● 1979; o ------ o 1978.

(a) Leaf total nitrogen

(b) Leaf soluble nitrogen

(c) Stem soluble nitrogen

(a)

(c)
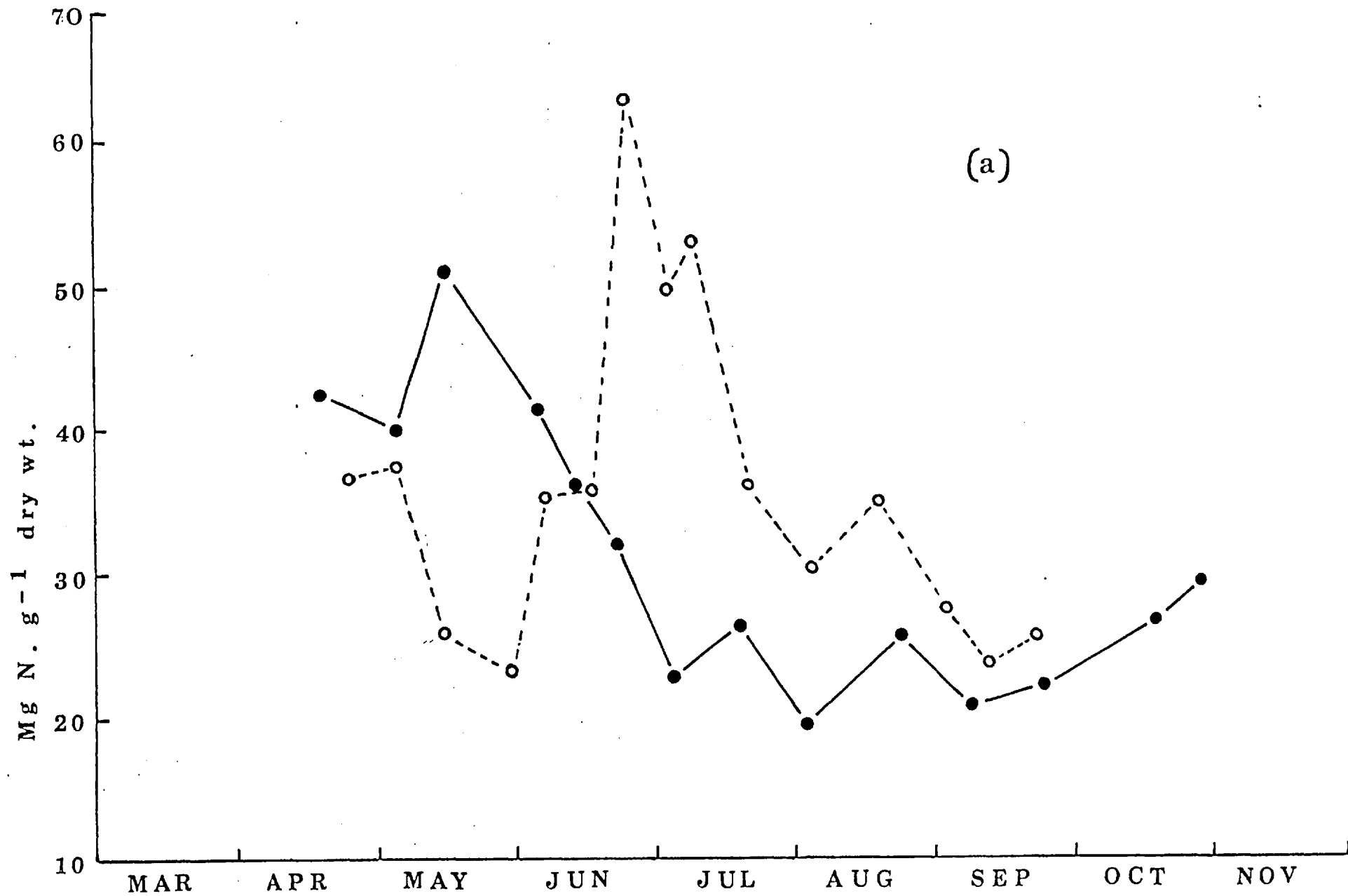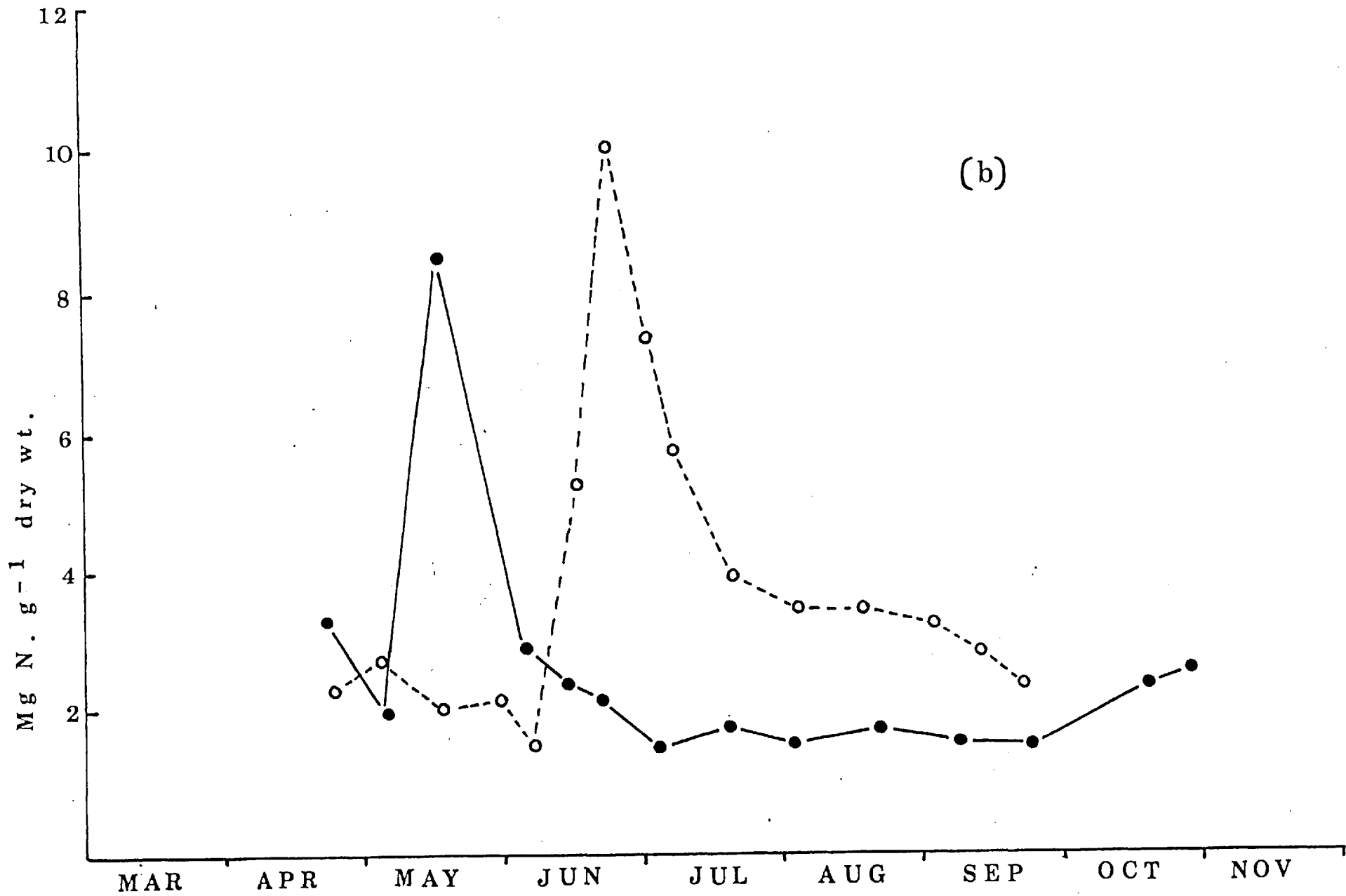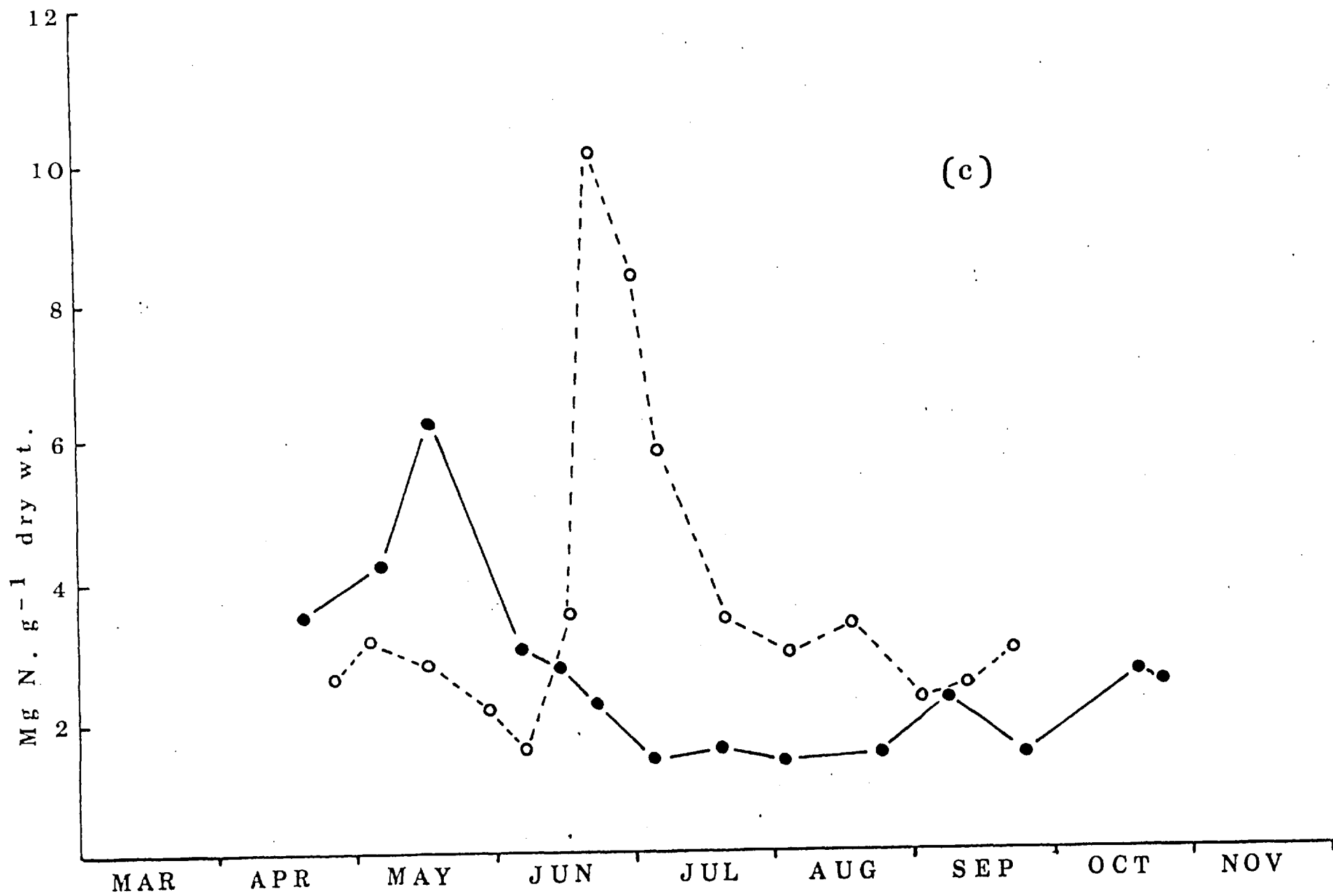
APPENDIX XIX

Mean monthly temperatures at Silwood Park, 1979

	Max.	Min.	Mean
May	15.2	5.7	10.2
June	18.4	9.6	14.1
July	21.5	11.3	16.8
August	19.7	9.9	14.8
September	18.4	7.6	13.1
October	15.3	6.3	10.8