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Jefferson, Richard Grainger (1980) *The phytophagous insect fauna of mercurialis perennis L.*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7487/

THE PHYTOPHAGOUS INSECT FAUNA

OF

MERCURIALIS PERENNIS L.

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(B.Sc. HONS. C.N.A.A.)

This dissertation is submitted in part fulfilment of the requirements for the award of a Master of Science degree at the University of Durham

DEPARTMENTS OF
BOTANY AND ZOOLOGY

DURHAM UNIVERSITY 1980

"In Nature's infinite book of secrecy ...
A little I can read."

William Shakespeare. 1564 - 1616.

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ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Lewis Davies for his help and advice, particularly with regard to species identification, at all times during the preparation of this dissertation.

I would also like to thank the following people for species identification and helpful comments:-

Mr. P. N. Lawrence, Dr. V. F. Eastop, Mrs. J. Palmer, Mr. C. Johnson, Dr. I. Hodgkinson, Mr. T. C. Dunn, Mr. J. Flint.

In addition, I am very grateful to Mr. M. L. Smith, Dr. M. G. Morris, Dr. R. C. Welch, Dr. L. K. Ward, Rev. G. G. Graham, Dr. J. H. Lawton and Mr. G. Banbury for advice, information and general assistance.

Research was carried out during the tenure of an N.E.R.C. advanced course studentship for which I am grateful.

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1. INTRODUCTION

The phytophagous insect fauna of both lower and higher plants (with the exception of trees) in the British flora is imperfectly known and few detailed studies have been undertaken with the exception of work on Pteridium aquilinum (Lawton 1976); Urtica dioica (Davis 1973); Sarothamnus scoparius (Waloff 1968); Juniperus communis (Ward 1977) and Viburnum lanata (Side 1955).

It is possible to compile lists of insect species associated with British plant species from data obtained from texts on the various orders of phytophagous insects, from lists published in papers in the Biological flora of the British Isles and from a literature search of biological papers. However, such lists are frequently incomplete and in some cases may be inaccurate.

It must be stressed that European and American data on phytophagous insects associated with plant species, genera or families are much more complete due to extensive detailed research for biological weed control purposes. (Goeden 1968, 1971a, 1971b, 1974, 1976, Goeden and Ricker 1974, Malicky et al. 1970 and Zwolfer 1965).

The paucity of data stimulated a detailed study of the phytophagous insect fauna of Dog's Mercury (Mercurialis perennis) (a woodland perennial herb) at three sites in County Durham with an accompanying literature search for records of associated insect species. In addition, data on seasonal changes in the number of associated species and seasonal changes in plant "architecture" (stem height, leaf number and leaf area) were collected. It is thought that changes in plant architecture may partly influence changes in the number of associated species. (Lawton 1978).

M. perennis is suitable for detailed study in the time period available (April to July) due to the fact that (a) it is fairly common, (b) it often forms extensive pure stands, (c) it produces a fresh set of aerial shoots in February or March and (d) it reaches maximum above ground biomass in late June and then remains summergreen until October (Hutchings and Barkham 1976, Mukerji 1936, Wilson 1968). In addition its size renders it suitable for the removal of individual plants for insect extraction in the laboratory.

The literature concerned with insect/plant relationships in general, is enormous and obviously only a brief resumé of the more relevant work can be presented.

The factors determining the total number of phytophagous insect species to which a particular plant species is host has received much attention and has been reviewed by May (1979). A primary factor seems to be the geographical range of the host plant; that is the greater the geographical range of a plant species the more insect species will be associated with it (Janzen 1968). This has been documented for insects on Hawaiian and British trees (Southwood 1960, Strong 1974b); Leaf mining Lepidoptera on Californian oaks (Opler 1974); larval agromyzids mining British Umbelliferae (Lawton and Price 1979); the arthropod pests of cacao and sugarcane (Strong 1974a, 1977) and insects on British herbs and woody bushes (Lawton and Schroder 1977, 1978, Lawton 1978).

Accordingly when one plant species is studied in isolation, a similar species/area pattern emerges. Ward and Lakhani (1977) studied the fauna of *J. communis* in Britain and found that the number of specific phytophagous insect species of juniper (of a total of twenty nine) found at any one site was largely explained by the site size; that is the number of juniper bushes. The species seemed to be related to site size in a sequential manner and therefore Ward and Lakhani (loc. cit.) could actually predict which species would be present according to the site size. Similarly, Davis (1975) and Lawton (1978) demonstrated the species/area effect for U. dioica and P. aquilinum respectively. The causes of the species/area relationships for insects on host plants are not at all clear (Strong 1979) and there are notable exceptions to the rule.

Claridge and Wilson (1978) for example, believe that species/area effects are not always the norm and that in many cases the data used for such analyses is not always complete or accurate. They studied a mesophyll feeding guild of leafhoppers associated with trees in Britain (see Claridge and Wilson 1976). Species/area correlations were calculated for this data and no significant correlations emerged. They put forward the hypothesis that co-evolutionary interactions are more important in determining patterns of insect/plant relationships in diverse plant communities.

Superimposed on the species/area pattern, is the influence of plant architecture. Architecturally or structurally complex plants have more insects associated with them than less complex ones as they permit greater niche diversification (Denno 1977, Lawton and Schroder 1977, 1978, Lawton 1978, Lawton and Price 1979). For example, woody shrubs support more phytophagous insect species than perennial herbs when geographical range is equal. One other possible influence is the life history strategy of the plant. However, Lawton and Schroder (1978) found no significant difference between the number of insects exploiting

Perennial European Cynareae compared to annual or biennial Cynareae and similarly Lawton and Price (loc. cit.) were unable to determine any significant difference in the number of agromyzid species associated with annual, biennial or perennial Umbelliferae.

Although geographical range and architectural complexity seem to be major determinants of the number of insects associated with a plant species, they do not necessarily explain all or most of the variation. For example, Lawton and Price (loc. cit.) found that these two factors accounted for 50% of the variation in the number of larval agromyzids mining various British Umbelliferae and Southwood (1961b, 1977) noted that Ilex aquilifolium and Taxus baccata have fewer associated insects than would be predicted from their geographical range. Therefore what other factors might be important?

It has been suggested that some plants may be less palatable to insects than others due to being nutritionally inadequate or possessing a greater variety of toxic secondary plant compounds (Southwood 1961b, Swain 1977). This is disputed by Lawton (1978) who states that plant chemistry has a profound effect on which species of insects attack each plant and a profound effect on the season at which a species is able to exploit its host plant, but only a small or perhaps no effect on the total number of insect species which eventually evolve to exploit a plant. P. aquilinum, contains a diverse number of secondary plant compounds (Lawton 1976, Cooper/Driver 1978) including tannins, lignins, phenols, ecdysones and also possesses the ability to produce free cyanide when fronds are damaged, yet it still has forty species of arthropod associated with it (Lawton 1976). In addition, Lawton and Price (1979) cite the case of Conium maculatum which is very toxic to vertebrates but is host to five species of leaf mining insects, not including other insect guilds. It seems that given time and exposure to a new potential host or a particular array of secondary toxins, insects (and other organisms) will eventually evolve detoxification mechanisms (Southwood 1961b, Feeny 1976, Van Emden 1978).

Plants do possess other defence mechanisms including physical defences such as spines (Atsatt and O'Dowd 1976) and association with ants; the latter being most highly evolved in the swollen thorn acacias in the Ethiopian and Neotropical regions (Hocking 1970). Many plants possess extra floral nectaries which are attractive to ants, but whether they help in defence against herbivorous insects in every case is unknown (Lawton 1976).

Other factors which might influence total numbers include taxonomic isolation, habitat and "time". The theory behind the first idea is that the more taxonomically isolated a plant is, the fewer the species of insects it will have associated with it on the grounds that the exchange of herbivores between closely related plant species is easier due to biochemical and structural similarities than exchange between unrelated species (Lawton and Schroder 1978). This theory was tested by Lawton and Schroder (loc. cit.) for each of the plant genera in the Biological Flora accounts and the European Cynareae data and none of the relationships were statistically significant. However, it must be stated that when a non-native plant is introduced into a new country or area, either accidentally or for agricultural purposes, the subsequent recruitment of insect species from the native fauna follows a pattern in that many of the species switch to the introduced species from closely related (biochemically or taxonomically) native plant genera (Southwood 1961b, Goeden 1971, Goeden and Ricker 1974, Strong 1974a & b, Strong et al. 1977, Owen and Whiteway 1980).

Secondly, the habitat of a particular plant species may determine associated insect numbers. Aquatic higher plants support very low numbers of phytophagous insects and this may be due to a lack of suitable pupation sites (Lawton and Price (loc. cit.). Habitat, then, may well be important in some cases.

Finally, the "time" factor may be of initial importance in determining numbers of associated species depending on the stage of colonisation being observed. The introduction of a new species to a new area will result in the recruitment of a fauna and it will take time for the asymptote of species richness to be reached.

According to Strong (1974a, 1974b, 1979) and Strong et. al. (1977), this asymptote is attained within a few hundred years, but there is some disagreement, as research into the biological control of certain introduced weeds in California and Australia by phytophagous insects indicated that there is short term accumulation of non-specialist species but not of specialist endophagous species (Goeden 1971b, Goeden and Ricker 1974, Wapshere 1974). Lawton and Price (loc. cit.) are of the view that given time, some of the currently unutilised British Umbelliferae may well be utilised by newly evolving specialist leaf miners. This might result in much variability if the various agromyzid/umbellifer associations were at many different stages along the path to eventual equilibrium (May 1979). Most evidence though, suggests an asymptote is reached after relatively short periods of evolutionary time. However, longer term accumulation of specialist species must not be completely ruled out.

The determinants of the equilibrium number of insect species a particular plant can support are very complex and there is dispute as to whether the mechanism of competition is important in this context.

Lawton (1978) and Rathcke (1976a) state that competition is not particularly important whereas Janzen (1973) states the opposite and makes the point that even though many insects on a living plant are never in direct competition, they will be indirectly competing as all parts of an individual plant are connected through the medium of its resource budget.

Further research is clearly required in this whole area of study in order to gain a better understanding of the observed patterns.

At the individual species level, there are more subtle seasonal changes in insect species richness and diversity on a particular host plant. A number of hypotheses have been advanced to explain such changes, but none are totally satisfactory. Seasonal variation in the levels of secondary plant compounds and nutrients in plants has been correlated with changes in the insect community (Feeny 1970, Lawton 1976). Feeny (1970) hypothesises that the spring feeding by caterpillars of Operophtera brumata L. and other species of Lepidoptera on oak trees in England is related to seasonal changes in the texture and chemical composition of the leaves. Early feeding coincides with maximum leaf protein content and minimum leaf sugar content. In addition, oak leaf tannins are at relatively low levels in the spring but increase during the summer, possibly reducing leaf palatability. Dement and Mooney (1974) also detected seasonal changes in tannin and cyanide levels in the Chaparral shrub (Heteromeles arbutifolia) and stated that high levels of toxins provided protection when herbivore pressure was greatest.

Lawton (1976) tentatively correlated seasonal changes in species diversity on P. aquilinium with changing food quality and changes in levels of various secondary chemical defence compounds. However, in a later paper (Lawton 1978), he favoured a seasonal change in plant architecture as an explanation.

It is supposed that obtaining an adequate and balanced intake of amino acids and proteins from host plants may be a finely balanced problem for phytophagous insects (Van Emden 1966, Southwood 1973, McNeill and Southwood 1978). There is evidence that the phenology of some phytophagous insects may be linked to seasonal fluctuations in the levels of nitrogen in the leaves, stems and fruits in plants. Seasonal movement in host alternating aphids (for example the bird cherry-oat aphid - Rhopalosiphum padi L.) enables them to exploit a continuous supply of nutritionally favourable foliage (Dixon 1973).

The structure of the insect community associated with host plant species or groups of related species is a subject that has received little attention and many questions remain to be answered. Structure in this context refers to (a) the taxonomic structure, that is the proportional contribution of the various insect orders; (b) the proportional contribution of the various feeding guilds such as chewers, suckers, gall formers, stem and leaf miners and so on, and (c) the proportion of specialists and generalists. Lawton and Schroder (1978) used Biological Flora data, European Cynareae data and the Commonwealth Institute of biological control's (C.I.B.C.) data on woody shrubs to attempt to detect patterns in the structure of faunal assemblages associated with plants of a particular type. Analysis of gross differences in taxonomic composition were relatively inconclusive except that woody shrubs tend to have a greater proportion of Lepidoptera and fewer Diptera than non-woody herbs. Similarly, there were few discernible patterns in the feeding categories, with the exception that more widespread plants that are not taxonomically isolated have the greatest number of gall formers and miners associated with them. Lawton and Schroder (1978) attribute this to the fact that such specialists have had a greater opportunity for colonisation in evolutionary time.

A detailed study of P. aquilinum by Lawton (1976) revealed that the Hymenoptera (especially the Symphyta or Sawflies) make a disproportionately large contribution to the total fauna, as do the Hemiptera. This pattern is confirmed when the present literature on all insect/fern associations is analysed (Balick et al. 1978, Cooper/Driver 1978).

Balick et al. (loc. cit.) hypothesize that the predominance of the primitive Symphyta within fern feeding Hymenoptera is a result of co-evolution with ferns before the rise of Angiosperm dominance in the late Cretaceous.

Lawton and Schroder (1978) using the European Cynareae data, examined patterns of polyphagy, (species feeding on plants in more than one family) oligophagy (species which feed on a number of plant species from within the same family) and monophagy (specialists restricted to one species of host plant). They found that the proportion of polyphagous species increased significantly as the total number of species of insect on the plant increases and hence this in turn is related to the geographical range of a plant species. This contradicts Rhoades and Cates (1976) who stated that the proportion of generalist herbivores should be greater on rare than common species. However, analysis of the C.I.B.C. data revealed no discernible relationships. Analysis of the structure of phytophagous insect communities on various host plants is at a very early stage and no doubt much is still to be discovered. At present the available data is not comprehensive enough to draw any meaningful conclusions.

Secondary plant compounds have been previously mentioned in discussion and a brief résumé of their origin and function is deemed necessary. Secondary plant compounds are low molecular weight secondary metabolites found in higher plants and fungi, of which over 10,000 are known (Swain 1977). They are usually classed according to their chemical structure and include broad groups of compounds such as phenols, terpenoids, alkaloids and nitriles as well as a biochemical miscellany of other groups of substances of less widespread occurrence (Whittaker 1970).

A common view is that secondary plant substances arose as a defence against viruses, bacteria, fungi and animals (Whittaker 1970, Levin 1971, Feeny 1976, Swain 1977) and they are not, so far as is known, essential to the basic metabolism of the plant (Whittaker 1970). Obviously, the presence of such a selection pressure stimulated adaptation through the evolution of detoxification mechanisms by phytophagous insects (and other organisms). Secondary plant substances in a given plant species represent no barrier to adapted or co-evolved insect species, and such species use certain secondary compounds in host selection as attractants, phagostimulants or inhibitors (Fraenkel 1959, 1969, Thorsteinson 1960, Van Emden 1966, 1978, Jermy 1966, Bullock 1967, Feeny 1976).

Feeny (1976) has developed the hypothesis that there are two kinds of chemical defence in plants: (a) qualitative compounds (such as phenols and alkaloids) which are effective against non-adapted insects but are susceptible to rapid detoxification by adapted insects and (b) quantitative compounds such as tannins which are dosage dependent barriers even to insects which feed on leaves containing them. Furthermore, Feeny (1976) introduces the concept of "apparency" or the susceptibility of a plant to discovery by natural enemies in ecological time. Non-apparent plants are those that are small, rare or ephemeral and apparent plants are large, abundant and persistent. The nature of the defensive compounds present changes along a gradient of species apparency such that non-apparent plants which cannot afford the metabolic cost of quantitative defensive compounds contain qualitative defensive compounds and apparent plants contain quantitative compounds. Feeny's hypotheses are understandably interesting, but require rigorous testing.

Finally, at the community level a number of studies have been made on the effect of the "vegetational background" on the associated insect community of a specific plant species. Root (1973) and Cromatie (1975) looked at the fauna of Brassica oleracea in simple (a monoculture) and diverse (associated with other species) habitats and concluded that species diversity of insects associated with B. oleracea was greatest in the diverse habitats. Smith (1977) reached the same conclusion growing Rumex obtusifolius in experimental plots with different types of vegetational background. These findings seem to accord with current ideas in community ecology.

Research into the determinants of insect species diversity (usually with reference to one guild) in various habitats reveals a number of interesting points which may be of some relevance to single insect/plant interactions.

Diversity of Auchenorhyncha (Hemiptera) in limestone grassland (Morris 1974b); froghoppers and leafhoppers of woodland herbaceous vegetation (Whittaker 1969); arthropods in different types of arable field (Allan et al. 1975) and Homoptera of old fields (Murdoch 1972) seem to be related primarily to structural and botanical diversity of such habitats. The most important determinant of insect species diversity of the two factors mentioned, varies according to the habitat type and the guild studied. Claridge and Wilson (1976) looked at leafhoppers of mixed, broadleaved temperate woodland and concluded that tree species diversity was the most important factor in determining leafhopper species diversity. Presumably this is due to the fact that most leafhopper species in this case show close host plant specificity.

Rathcke (1976b) provides a note of caution in that determinants of insect diversity are often more complex than is often presumed. Studies of a guild of stem boring insects in tall grass prairie in Illinois revealed that plant resource diversity alone cannot adequately account for the patterns of abundance and exploitation shown by this stem boring guild.

Southwood et al. (1979) however, looked at changes in plant and insect diversity (Heteroptera and Coleoptera only) through succession from fallow field to birch woodland. They found that in the early seral stages, insect diversity parallelled plant taxonomic diversity but at later stages when plant taxonomic diversity is falling, the increase in plant architecture maintained the increase in insect species diversity.

2. THE SAMPLE SITES

M. perennis was sampled at three sites in County Durham. In this county there are very few sites where M. perennis attains similar abundance and extent to sites in Central, Eastern and Southern England, presumably due to lack of suitable habitat (see Chapter 3). The sites selected were those which had relatively large, extensive stands of the plant. However, these sites were relatively small in extent compared to many sites in Southern Britain and elsewhere.

Site 1 (Little high wood: Grid reference NZ 268403) is open, broad leaved woodland situated on sandstone of the Coal measures (Upper Carboniferous) which is in turn covered by undifferentiated alluvium which forms the parent material of the soil. M. perennis grows both in pure and mixed stands at this site on a gently sloping bank.

Site 2 (Elemore Hall: Grid reference NZ 352445) is again open, broad leaved deciduous woodland on the Magnesium Limestone (Permo - Triassic) which is covered at this site by undifferentiated Boulder Clay and glacial drift of Pleistocene age. The species grows in both pure and mixed stands, although pure stands are more extensive at this site than the former.

Site 3 (Shadforth dene: Grid reference NZ 351398) is relatively open scrub interspersed with small areas of grassland situated on the Magnesium Limestone. M. perennis grows in pure stands in concentric rings at the base of the various shrub species.

Site size is not given as in all cases other areas of M. perennis were present in the immediate vicinity and thus the effect of site size and isolation on the number of species present will be minimal.

Tables 1 - 3 give details of the associated species at each site. These lists include species actually growing interspersed with the plant and those growing in immediately adjacent areas. In addition, species found throughout the sampling period (May to July) are included in each case. Nomenclature follows Clapham, Tutin and Warburg (1962) for convenience.

TABLE 1

PLANT SPECIES ASSOCIATED WITH M. PERENNIS AT SITE 1

TREES AND SHRUBS

* Acer pseudoplatanus
Crataegus monogyna
Fagus sylvatica
Fraxinus excelsior
* Ulmus procera

OTHER ANGIOSPERMS

Agropyron repens
Anemone nemorosa
Anthriscus sylvestris
* Arrhenatherum elatius
Cirsium arvense
Conopodium majus
Endymion non scriptus
* Galium aparine
* Geum urbanum
* Hedera helix
Heracleum sphondylium
Milium effusum
* Ranunculus ficaria
Rubus idaeus
Silene dioica
* Stachys sylvatica
* Urtica dioica

BRYOPHYTES

* Thuidium tamariscinum (forms a discontinuous carpet).

* denotes abundant species

TABLE 2

PLANT SPECIES ASSOCIATED WITH M. PERENNIS AT SITE 2

TREES AND SHRUBS

* Acer pseudoplatanus
Crataegus monogyna
Fagus sylvatica
* Sambucus nigra
* Tilia platyphyllos
Ulmus glabra

OTHER ANGIOSPERMS

Aquilegia vulgaris
Arctium pubens
Arrhenatherum elatius
Bromus ramosus
Cirsium arvense
Cirsium vulgare
Dactylis glomerata
Endymion non scriptus
* Epilobium angustifolium
Fragaria vesca
* Galium aparine
* Geranium robertianum
* Geum urbanum
Glechoma hederacea
Heracleum sphondylium
Holcus lanatus
Lapsana communis
* Ranunculus ficaria
Ribes uva-crispa
* Rubus fruticosus agg.
* Rubus idaeus
Rumex obtusifolius
Rumex conglomeratus
* Silene dioica
* Stachys sylvatica
Taraxacum officinale agg.
* Urtica dioica
Veronica montana
Vicia sepium

TABLE 3

PLANT SPECIES ASSOCIATED WITH M. PERENNIS AT SITE 3

TREES AND SHRUBS

Corylus avellana
* Crataegus monogyna
Prunus spinosa
Rosa canina agg.
* Ulex europaeus
Viburnum opulus

OTHER ANGIOSPERMS

Achillea millefolium
* Agrostis tenuis
Alchemilla sp.
Anemone nemorosa
Bellis perennis
Betonica officinalis
Brachypodium pinnatum
Campanula rotundifolia
Carex flacca
* Centaurea nigra
Cirsium arvense
* Cynosaurus cristatus
* Dactylis glomerata
Fragaria vesca
* Galium aparine
Galium cruciata
Geum urbanum
Helianthemum nummularium
Heracleum sphondylium
* Holcus lanatus
Linum catharticum
Lolium perenne
* Lotus corniculatus
Orchis mascula
Plantago lanceolata
Pontetilla sterilis
Poterium sanguisorba
* Primula veris
Prunella vulgaris
Ranunculus bulbosus
Ranunculus ficaria
Sanicula europaea
Solanum dulcamara
* Stachys sylvatica
Taraxacum officinale agg.
Teucrium scorodonia
* Trifolium pratense
Viola riviniana

3. THE BIOLOGY OF MERCURIALIS PERENNIS

M. perennis is a perennial dioecious, rhizomatous herb of woodlands and other shady habitats which often forms extensive pure stands, particularly in old undisturbed woodland.(Mukerji 1936, Wilson 1968, Knight 1974). It occurs over the whole of Central Europe eastwards to the Caucasus mountains, northwards to Southern Norway and mid-Sweden, southwards to North Africa and westwards to Ireland. Altitudinally, it reaches as high as 2,000 metres in Switzerland but the ultimate height attained varies with latitude and other geographical factors.

In the British Islands (except Ireland), M. perennis is found in 72% of the ten kilometre grid squares (Perring and Walters 1976). Areas where the plant is absent include the extreme north of Scotland, the Outer Hebrides, the Shetlands, Orkneys, the Isle of Man, the Fens and Anglesey. In Ireland it is thought that with the exception of a site in County Clare, it has everywhere been introduced (Boatman 1956). In County Durham it occurs in woodland, scrub and hedgerows in 44.5% of the two kilometre grid squares covering the county (Data from G. G. Graham pers. comm.). Grid square occurrence, however, is only a crude measure of abundance as it only works on a presence/absence basis.

There are a number of records of M. perennis fruits from the Hoxnian and Ipswichian interglacials and also from the Devensian glacial and postglacial Flandrian periods (Reid 1899, Godwin 1975). Pollen records, which Godwin (loc. cit.) has interpreted as being M. perennis rather than the less common Mercurialis annua include ones from the Ipswichian, late Devensian and early Flandrian. It is therefore probable that it has been present in Britain at least since the Hoxnian and it survived periods of ice advance in refugia, at open sites.

The following account of the morphology, growth and reproduction of M. perennis has been compiled mainly from Mukerji 1936, Wilson 1968, Hutchings 1976, Hutchings 1978, Hutchings and Barkham 1976 and from personal observations.

The plant produces aerial shoots from mid-February to mid-March from a dense mat of rhizomes buried to a depth of one to five centimetres (cms.) below the ground surface. Shoots are erect, unbranched, up to 55 cms. tall and bear up to twelve opposite pairs of leaves arranged in a spiral manner up the stem horizontally to the ground surface. There are three types of aerial shoots, male, female and sterile. The ratio of male to female shoots from the sampled material in County Durham (see methods section) was 3 : 1. The petiole is short (0.3 - 1 cms.) and the leaves are simple, bistipulate, elliptic - ovate to elliptic - lanceolate in shape, finely serrated and hirsute. The first leaf pair tends to be small (1 - 2 x 0.3 - 1 cms.) compared to subsequent pairs which may be up to 11.3 x 5.8 cms. Most leaf pairs are borne between 10 and 30 cms. above ground level with 71% of the total leaf area occurring between 15 and 30 cms. above the ground. Average leaf area per leaf pair increases from the lowest layers in the profile upwards, except for the highest strata where many leaves are not fully expanded.

Sterile shoots, which often do not survive after May, rarely exceed 8 - 10 cms. in height and have a much reduced leaf area.

Flowers are normally borne in the axils of all leaf pairs present at the time of flowering with the exception of the first. The flowering period is usually between February and May but in Northern England flowering occurs towards the end of this time span. Male flowers are borne in clusters of up to ten on long pedicels which droop downwards. Female flowers occur in groups of two to six on initially short pedicels which elongate after fertilisation. The flowers are chiefly wind pollinated but this method may be augmented by insects. After flowering extension growth and leaf expansion recommence until mid June - early July, after which no new leaf pairs are produced. The male flowers and the pedicels die and are shed after flowering whereas on female shoots the pedicels elongate and the bilocular fruits enlarge. The seeds are shed during July. M. perennis has a very low seed output compared to most plants and percentage seed germination in its natural habitat is very low and reproduction is principally by vegetative means. The rare occurrence of seedlings is brought about by a variety of factors which include (a) the high percentage of defective seeds; (b) many seeds are destroyed by birds, mammals and invertebrates; (c) many are destroyed by fungal attack; (d) premature shedding of immature seeds and (e) conditions required for germination are very rigorous.

Shoots are connected by a branching rhizome system. The times of active rhizome growth are spring and early autumn and most additions to shoot populations being the result of rhizome spread and the production of new shoots upon the rhizomes. Rhizomes fragment after four or five years and ramets (vegetatively produced progeny) become separated from their parents.

As a consequence of the rarity of seedlings, spread into new areas away from the original population is extremely slow. M. perennis has thus been used as an indicator of woodland relic hedges and old undisturbed woodland (Pollard 1973).

The plant grows under a wide range of woodland light intensities, and particularly in the North of England, frequently occurs as a plant of hedgerows, partially shaded banks and as a component of the grike vegetation in limestone pavements. However, it cannot flourish in situations with too intense an illumination and it is rare to find it growing completely in the open. Normal light intensity range for the plant is between 5% and 50% of full visible daylight. Outside these limits light intensity exerts a reducing effect on both shoot number and shoot size. However, in any given situation other environmental variables will also be important and synergistic effects may be operating.

M. perennis will grow in soils with a pH range from 4.5 to 8.5, but usually attains its greatest abundance between 5.8 and 7.2. However, contrary to that stated by Hope/Simpson (1937), pH is not often a direct cause of distributional patterns shown by the species (Martin 1969). Similarly, levels of major nutrients seem to have little influence on the plant. However, the species is very sensitive to waterlogging (Mukerji 1936, Wardle 1959, Martin 1969). Intolerance of the latter is linked with oxygen diffusion rates which need to be high for M. perennis. Oxygen supply is not, though, the only factor involved and the presence of toxic quantities of ferrous ions in poorly drained soils is also important as the species is very intolerant of ferrous ions (Martin 1969).

The plant is susceptible to trampling and other forms of disturbance which tend to reduce shoot density and may permit invasion by other species given suitable ecological conditions (Wardle 1959, Wilson 1968, Knight 1974).

As has already been mentioned, M. perennis often forms pure stands which may have a shoot density of up to 500 m^{-2} (Hutchings and Barkham 1976).

In this situation the herb canopy is virtually closed with few gaps where light can penetrate directly to the ground. At some sites, though, where the woodland is relatively young or conditions do not permit dominance, M. perennis grows with other species (See Tables 1 - 3 for examples). How does M. perennis manage to achieve and maintain pure dominance? Contributory factors include its growth form, method of reproduction and phenology, its extreme shade tolerance and its ability to maintain vigorous growth over tens or hundreds of years without exhibiting ageing phenomena (Wilson 1968). In addition, it may well be less nutrient demanding than other woodland species. For example, Pigott and Taylor (1964) found that it could survive in shade in areas of low available phosphate, whereas common associates such as U. dioica could not. Indeed, coining the terminology of Grime (1979) M. perennis is a stress tolerant competitor.

M. perennis contains a number of secondary plant compounds and as a result is poisonous to livestock and other vertebrates (Eaton 1941, Forsyth 1968). It contains an alkaloid Mercurialine (Eaton loc. cit., Forsyth loc. cit.), and a number of phenolic compounds including three flavonoid compounds, Kaempferol, Quercetin and Kaempferol di-glucoside and two phenolic acids, p-coumaric and ferulic (Bate Smith 1962, Dumkow 1969). It is thought that these compounds evolved as defence mechanisms, especially against bacterial and fungal infection, although Whittaker (1970) documents a number of situations where phenolic acids are used as allelopathic substances by higher plants.

The living plant is host to a number of fungi throughout its range in Britain, including Zythia mercurialis Kickx., Ascochyta mercurialis (Imperfect fungi), Capnodium footii (mildew), Synchytrium mercurialis

(Phycomycetes : Chytridiales) and Melampsora rosrupii Wag (rust). The uredospore and teleutospore stages of the latter are found on Populus tremula and Populus alba and the Aecidiospore stage is found on M. perennis. M. rosrupii (rust) and a virus disease causing yellowish mottling of the leaves were observed affecting the plant at all three sites (see Appendix table 1).

Various species of mollusc are known to feed on the living and senescing leaves of the plant (Grime et. al. 1968, Mason 1970, Jenning and Barkham 1975) and R. C. Welch (pers. comm.) observed considerable foliar damage caused by snails at sites in Southern England. Similar foliar damage was observed at the sampling sites in County Durham and Cepaea hortensis (a possible feeder) was found on the plant at Sites 1 and 2.

Wilson (1968) states that M. perennis is surprisingly free of invertebrate pests and R. C. Welch (pers. comm.) states that the fauna is very limited. It is hoped that this dissertation will show that these views, based possibly on limited evidence, are in fact incorrect.

4. METHODS

At each site, cut samples of complete M. perennis stems were taken during daylight hours at the beginning of each month from May to July. In each case 100 one stem samples were removed by carefully cutting off individual shoots at ground level without jarring the plant, and then rapidly placing each cut sample in a separate large polythene bag. No attempt was made to sample the roots, rhizomes or leaf litter underneath the herb canopy. At sites 1 and 2 shoots were selected at random along a zig-zag transect line to avoid retracing areas already traversed and hence avoiding too much disturbance. At site 3, ten scrub "islands" (see Chapter 2) with surrounding rings of M. perennis were selected and in each case, ten samples were taken in the manner described above. After each sampling, a general collection of insect species was carried out for comparison purposes. In addition, due to the presence of large pure stands of the plant at Site 2, sweep netting was also employed at this site. However, general collecting and sweep netting did not reveal any new species not found by the cut shoot sampling method, suggesting the number of samples taken and the sampling method was adequate. This fact was also substantiated when no new species were added after doubling the sample size on one occasion in June at Site 2.

Sweep netting is a good method for collecting fast moving insects but it is not very useful for sampling one plant species (unless the species is growing in pure stands) as it is obviously not discriminatory. Cut samples have the advantage that smaller insects are collected (for example Thysanoptera and Collembola) whereas these would normally be overlooked. Sampling during daylight hours is obviously the most feasible system. However, some phytophagous insects are nocturnal feeders and the possibility of missing such species cannot be ruled out. The large weevil, <u>Barynotus moerens F.</u>, which feeds chiefly on <u>M. perennis</u> tends to feed at night and during the day it is often found on the ground under the host plant making it inconspicuous (Morris 1976, Read 1978, M.G. Morris pers. comm.).

Samples waiting to be analysed were kept in a $1^{o}C$ constant temperature room.

Each sample was emptied and shaken over a white enamel tray and any phytophagous insects were collected and recorded. In addition, each leaf was carefully searched and the stem of every fifth sample was dissected to check for stem miners. Small insects such as Thysanoptera, Collembola and immature Heteroptera were removed with a small pooter. Predatory and scavenging species were ignored, as were other arthropod orders such as the Acari (mites) and the Araneae (spiders). For each cut sample the sex of the plant and any details of invertebrate damage, evidence of fungal and viral attack and leaf senescence were recorded. For every fifth cut sample, stem height, leaf number and the length and breadth of three randomly selected leaves (one of opposite equal pairs) excluding the top pair were recorded. These provide a crude but reliable measure of plant architecture to supplement the information already available.

Lepidoptera larvae and pupae were reared through to adults (unless parasitised) to facilitate identification. A feeding experiment was conducted with the weevil <u>Barypeithes pellucidus Bohn.</u>, as its association with the plant was uncertain. Four individuals were kept in a petri dish with fresh undamaged leaves of <u>M. perennis</u>. After three days no feeding holes were observed. Two individuals were transferred to a petri dish containing senescing and senescent leaves of the plant and immediately feeding holes were made in these leaves. Examination of faecal material under the microscope revealed the remains of glandular leaf hairs of *M. perennis*, providing further evidence for feeding. The two individuals kept with fresh leaves eventually died. A number of cut stems known to contain a stem mining larva which was suspected as being *Apion pallipes Kirb*. were kept upright in a container with a base of damp filter paper. After three weeks adult specimens of *A. pallipes* emerged, solving the problem.

As previously mentioned, a literature search for records of species feeding on *M. perennis* in the British Isles was undertaken. Literature consulted included standard text on the various insect orders, Royal Entomological Society identification handbooks, the Institute of Terrestrial Ecology's phytophagous insect data bank (L. K. Ward pers. comm.) and a number of specific papers.

5. RESULTS

Mean, standard deviation (S) and standard error (SE) values were calculated for stem height, leaf number and leaf area index (length x breadth) data for each monthly sampling at all three sites (Table 4). In addition, mean leaf area index per plant was also calculated (mean leaf number x mean leaf area index). A linear relationship exists between actual leaf area and the product of the maximum leaf length x the maximum leaf width (Wilson 1968) and therefore the leaf area index used would seem to be adequate. The data from Table 4 is presented graphically in Figures 1 - 4 and these form the basis for interpretation of seasonal changes in plant architecture.

Figure 5 shows the seasonal changes in the amounts of living shoot material of M. perennis and has been taken from Al. Mufti et. al. (1977). Miscellaneous data on percentage invertebrate damage, senescence, fungal and viral infection is presented in Appendix table 1.

Table 5 lists all the phytophagous insect species recorded as being associated with M. perennis in Britain derived from an extensive literature search. Flower feeding insects have been included even though these are not included in any later analyses (see below). The Hemiptera - Heteroptera records from Butler (1923) are not feeding records and represent records where entomologists have collected the species from M. perennis. Details of other host plants, geographical distribution, abundance and so on for all species listed can be found in Appendix 2.

The phytophagous insect species derived from the monthly sampling procedure for the three sites in County Durham are listed in Table 6.*

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* A key to the authority abbreviations used in Tables 5 and 6 can be found in Appendix 3.

Each species has been alloted a category according to its association with the host plant. The categories are not necessarily final and in many cases considerable doubt exists as to the association. Decisions as to which category a species should be placed in were based on (a) personal observation, (b) feeding and rearing experiments, (c) abundance and frequency of encounter of species, (d) information derived from the literature (e) personal communication with specialists and (f) intuitive reasoning. Further discussion of this follows below.

The categories require some explanation (see Table 7). Leaf feeders may be sap-sucking Hemiptera or chewing Lepidoptera and Coleoptera for example, while species associated with partially rotting or senescent leaves are probably only very loosely associated with the plant and feed on fungal hyphae, spores and so on. Species in the "uncertain" category include those which are known to be polyphagous and might plausibly be feeding on M. perennis. However, proof of feeding is not available. Casual species are those which are presumably resting on the plant and are not associated with it in a feeding sense and are presumably "strays" from adjacent plant species.

Casual flower feeders on the other hand may actually exploit part of the host plant, that is by feeding on nectar or pollen, but are not usually closely linked with M. perennis in this case (for example some adult species of Thysanoptera). Finally, the three species of Collembola: Entomobryidae listed in Table 6 are usually found in herbaceous vegetation, moss and decaying leaves (Lubbock 1873, Gisin 1960) and probably feed on leaf surface microflora, fungal hyphae, pollen and spores. They are probably not attached very closely to any particular plant species.

In some cases, generic or specific determination was not possible for various reasons, and numbers of individuals were not counted where a species was very numerous, for example Bourletiella sp. (Collembola : Sminthuridae). Many of the Lepidoptera larvae and pupae which were kept for rearing purposes were parasitised by species of Ichneumonidae (Hymenoptera : Apocrita) which prevented species determination.

Bourletiella sulphuren Koch., was discovered at a later stage, in samples thought only to contain one species, by P. N. Lawrence (pers. comm.) and has been omitted from Table 6 as the site is unknown.

Figures 6 - 9 are graphs, derived from the data in Tables 6 and 7, of seasonal changes in associated phytophagous insect species at each sampling site and also the gross changes with all three sites pooled. Figure 6 shows the leaf feeding category only; Figure 7 includes leaf feeders and species associated with senescent leaves; Figure 8 includes leaf feeders and species of uncertain status and Figure 9 includes all three aforementioned categories. These various combinations were tested to see if they would significantly change the observed pattern and in the case of species associated with senescing leaves, it is considered that they are part of the phytophagous fauna and are influenced by seasonal changes in plant architecture.

The taxonomic composition of the phytophagous insect fauna of M. perennis is shown in Figure 10. The data was derived from Tables 5 and 6 and includes only those species which actually feed on the living plant biomass, excluding the flowers, seeds, roots and rhizomes. The Lepidoptera column includes species A, B and H (See Table 6) which were pupae attached to the leaves of the plant and the individuals are presumed here to be phytophagous on M. perennis. Further detailed sampling and experimentation in other geographical areas may well reveal further phytophagous insect species records for M. perennis.

At all sampling sites, associated predatory arthropod species were present. The commonest species (adults and larvae) was Anthocoris nemorum L. (Heteroptera : Anthocoridae), a general predator of aphids, mites and other arthropods. Other predators included syrphid larvae (Diptera:Syrphidae), Chrysopa sp. (Neuroptera : Chrysopidae), a few species of ladybird (Coleoptera : Coccinellidae), various Staphylinid beetles (Coleoptera : Staphylinidae), a sawfly of the family Tenthredinidae (Hymenoptera : Symphyta) and numerous Harvestmen (Arachnida : Opiliones). In addition, scavengers such as Panorpa communis L. (Mecoptera : Panorpidae) and Forficula auricularia L. (Dermaptera : Forficulidae) were present.

TABLE 4

THE COMPUTED MEANS, STANDARD DEVIATIONS, AND STANDARD ERRORS FOR MEASURED PLANT ARCHITECTURE PARAMETERS FOR ALL SITES (FOR FURTHER EXPLANATION SEE TEXT)

SITE	MAY	JUNE	JULY
(a) SITE 1			
MEAN STEM HEIGHT IN CMS.	33.84	39.87	42.74
STANDARD DEVIATION (S)	4.50	5.02	4.43
SAMPLE SIZE (n)	25.00	20.00	23.00
STANDARD ERROR (SE)	0.90	1.12	0.92
MEAN LEAF NUMBER	13.92	14.00	13.65
S	2.20	1.72	2.16
n	25.00	20.00	23.00
SE	0.44	0.38	0.45
MEAN LEAF AREA INDEX (L x B) IN CMS.	19.56	22.66	23.45
S	10.12	8.48	8.23
n	74.00	58.00	77.00
SE	1.18	1.11	0.94
MEAN LEAF AREA INDEX PER PLANT IN CMS.	272.30	317.20	318.70
(b) SITE 2			
MEAN STEM HEIGHT IN CMS.	27.40	36.98	39.10
S	4.40	6.89	7.28
n	24.00	40.00	20.00
SE	0.90	1.09	1.63
MEAN LEAF NUMBER	13.91	13.95	13.50
S	1.95	2.21	2.58
n	24.00	40.00	20.00
SE	0.40	0.35	0.58
MEAN LEAF AREA INDEX	12.35	20.06	26.10
S	6.52	8.95	10.59
n	72.00	117.00	60.00
SE	0.77	0.83	1.37
MEAN LEAF AREA INDEX PER PLANT	171.80	279.80	352.30

TABLE 4 CONTINUED

SITE	MAY	JUNE	JULY
(c) SITE 3			
MEAN STEM HEIGHT IN CMS.	23.40	30.42	36.95
S	4.71	4.76	9.02
n	25.00	20.00	19.00
SE	0.94	1.06	2.07
MEAN LEAF NUMBER	12.80	13.50	14.00
S	1.99	2.23	2.30
n	25.00	20.00	19.00
SE	0.40	0.50	0.53
MEAN LEAF AREA INDEX	9.93	22.36	25.10
S	4.35	8.17	9.01
n	75.00	60.00	55.00
SE	0.50	1.05	1.21
MEAN LEAF AREA INDEX PER PLANT	127.10	301.90	351.40
(d) TOTAL FOR ALL SITES			
MEAN STEM HEIGHT IN CMS.	28.23	36.06	39.80
S	6.19	6.85	7.27
n	74.00	80.00	62.00
SE	0.72	0.76	0.92
MEAN LEAF NUMBER	13.54	13.85	13.71
S	2.07	2.09	2.29
n	74.00	80.00	62.00
SE	0.24	0.23	0.29
MEAN LEAF AREA INDEX	13.93	21.29	24.70
S	8.43	8.73	9.32
n	220.00	235.00	191.00
SE	0.56	0.57	0.67
MEAN LEAF AREA INDEX PER PLANT	188.60	294.90	338.60

FIGURE 1 : GRAPH TO SHOW SEASONAL CHANGES IN THE MEAN STEM HEIGHT OF M. PERENNIS

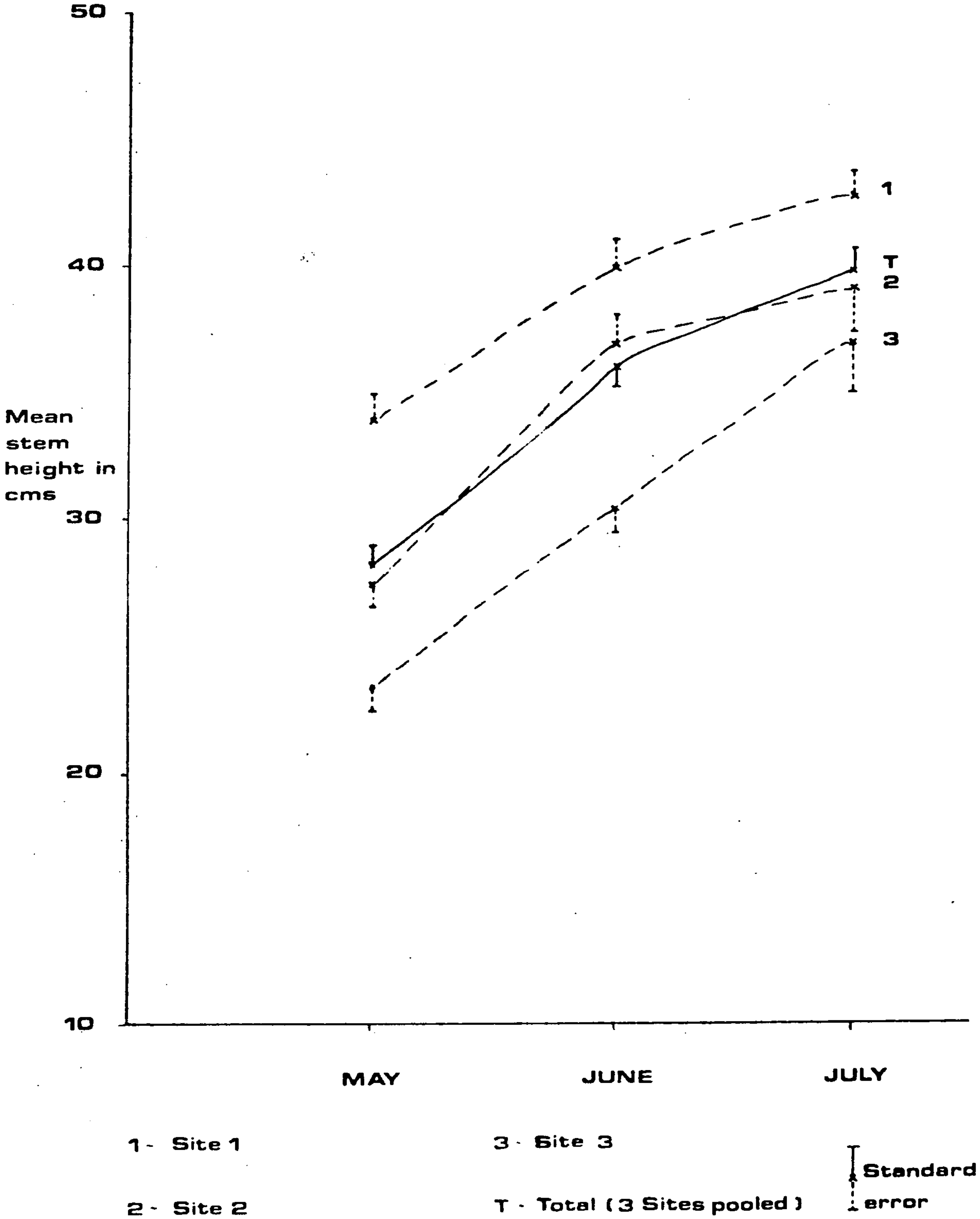


FIGURE 2: GRAPH TO SHOW SEASONAL CHANGES IN THE MEAN LEAF NUMBER OF M. PERENNIS

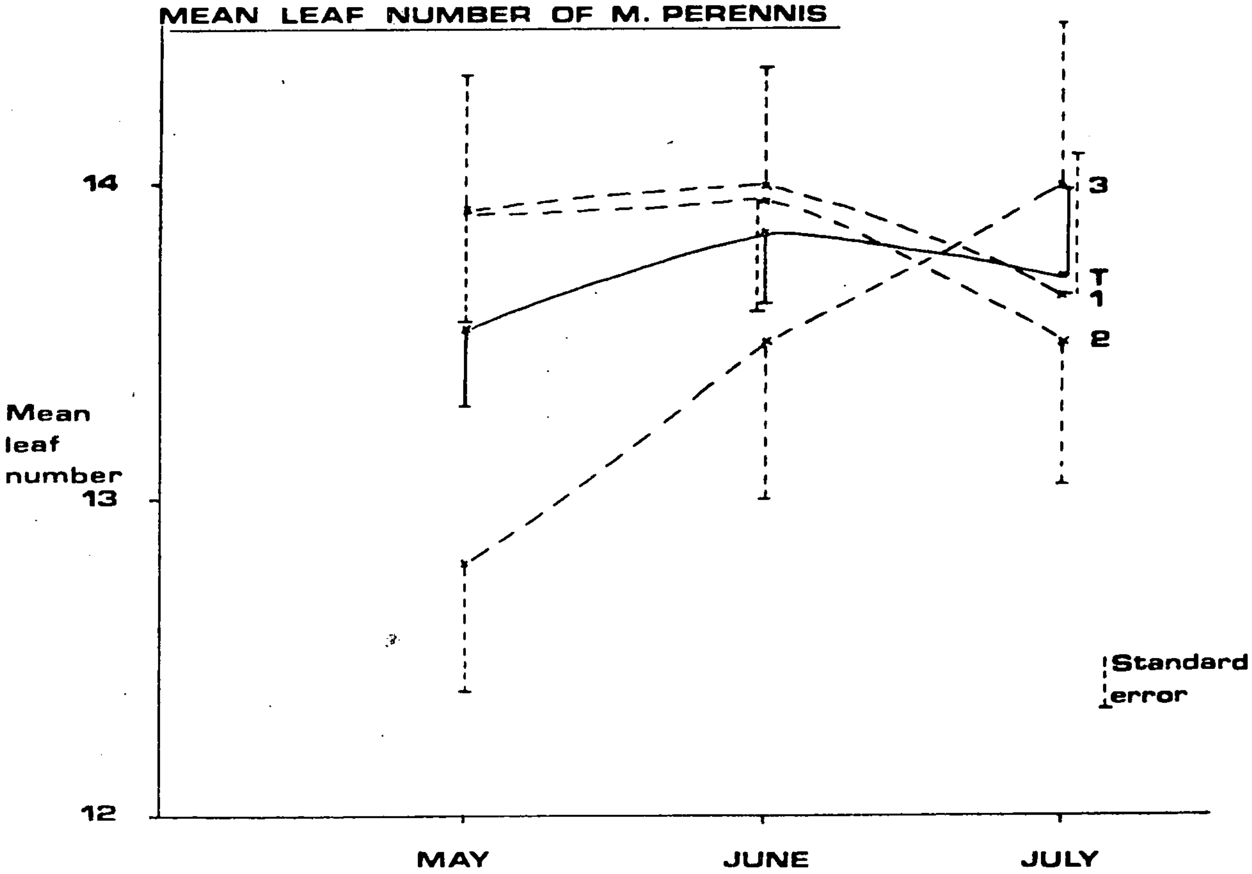
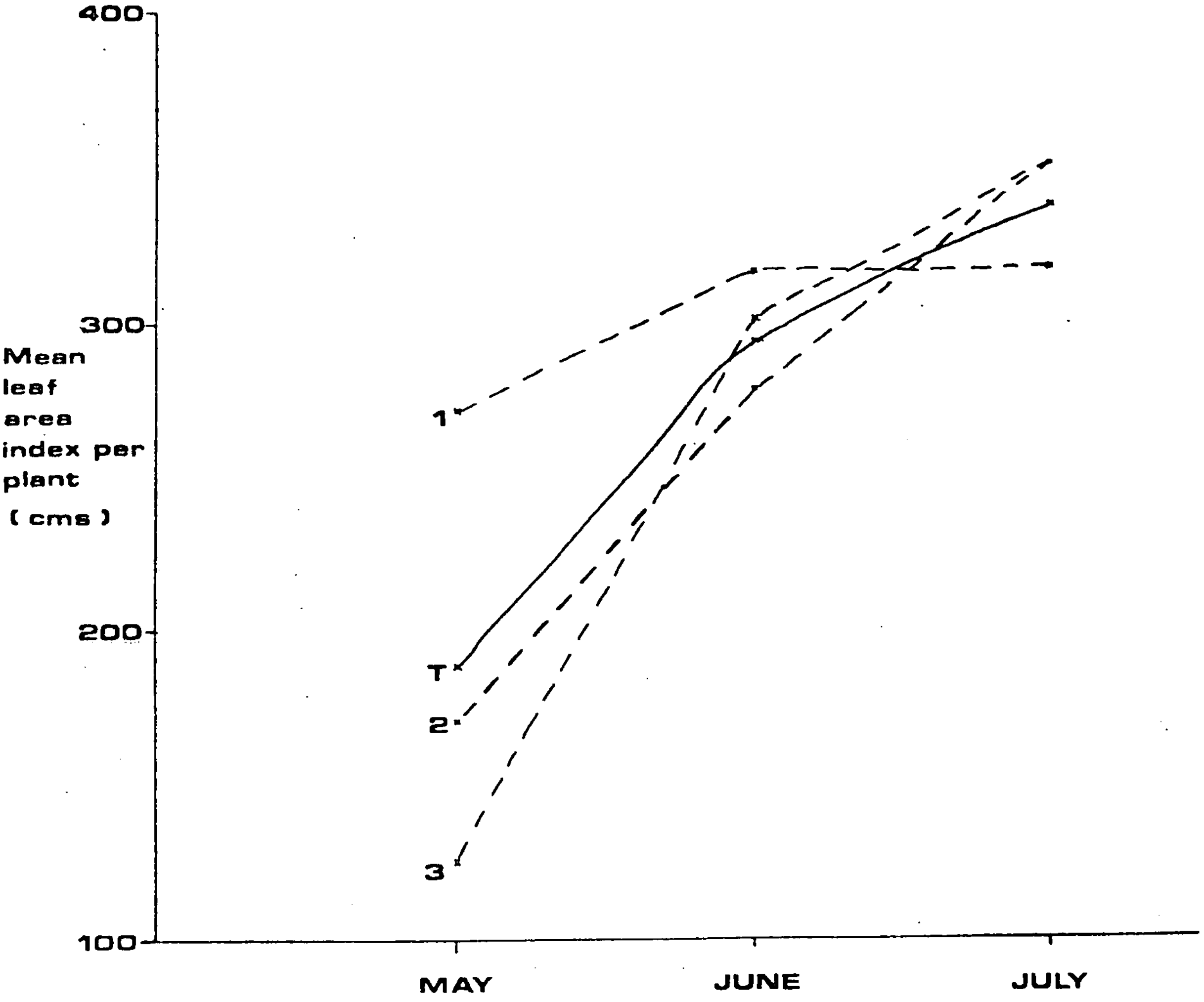
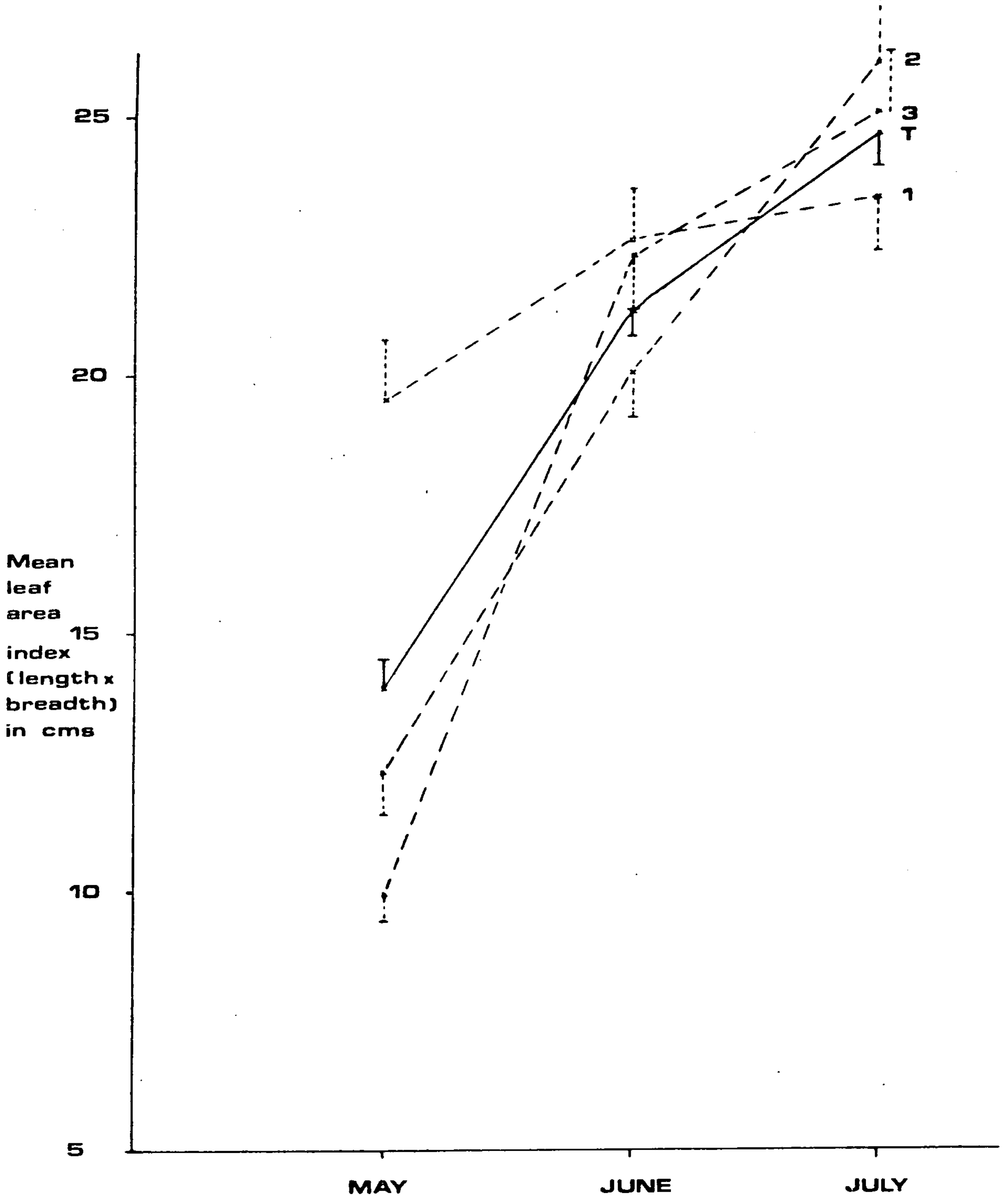


FIGURE 3: GRAPH TO SHOW SEASONAL CHANGES IN THE MEAN LEAF AREA INDEX PER PLANT (M. PERENNIS)



FOR KEY SEE FIGURE 1

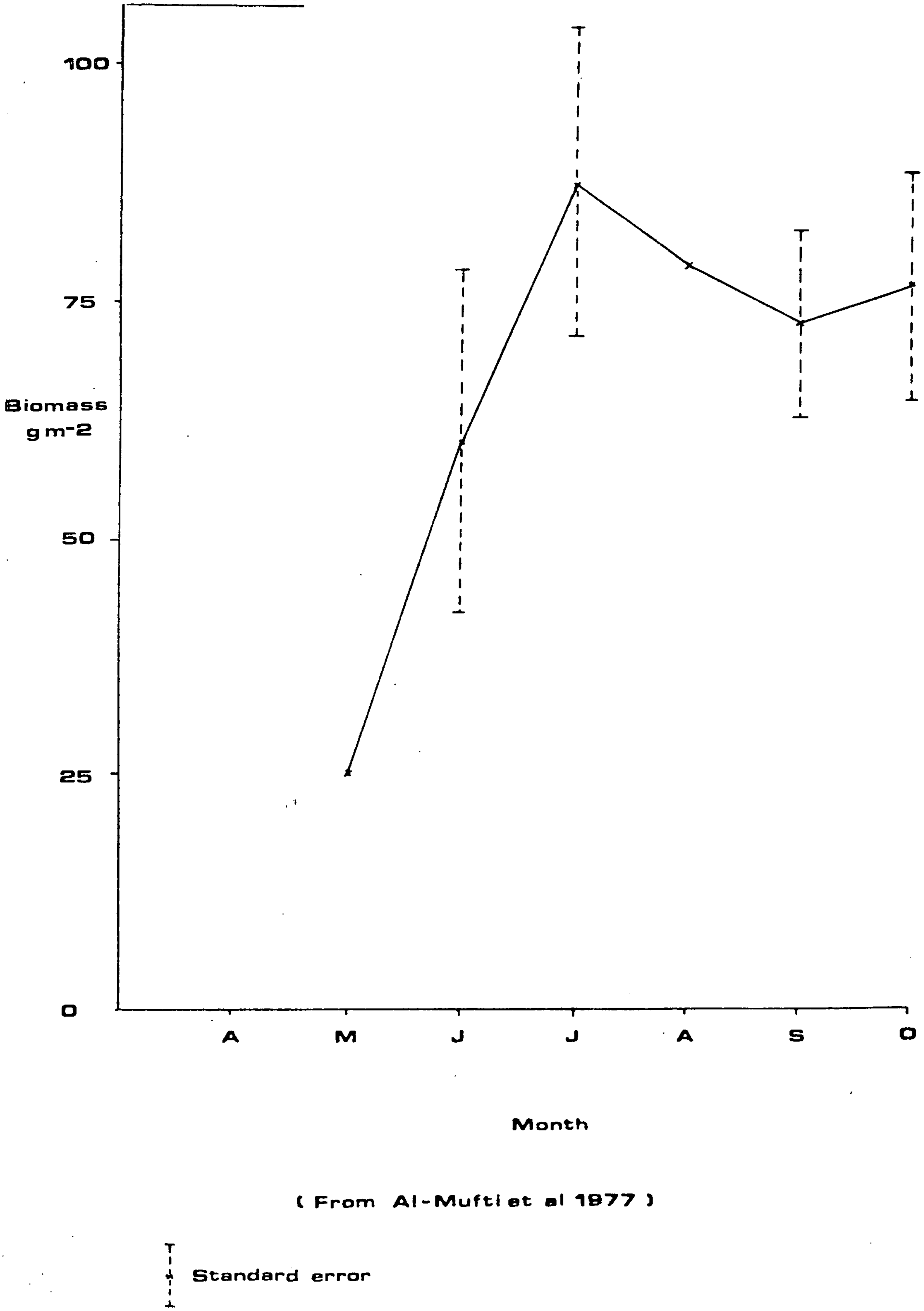
FIGURE 4: GRAPH TO SHOW SEASONAL CHANGES IN THE MEAN LEAF AREA OF M. PERENNIS



FOR KEY SEE FIGURE 1

FIGURE 5:

GRAPH TO SHOW THE SEASONAL CHANGE IN THE AMOUNT OF LIVING SHOOT MATERIAL OF M. PERENNIS (LATHKILLDALE DERBYSHIRE)



(From Al-Mufti et al 1977)

TABLE 5

A LIST OF PHYTOPHAGOUS INSECTS ASSOCIATED WITH M. PERENNIS IN THE BRITISH ISLES COMPILED FROM THE LITERATURE

SPECIES	MAIN SOURCES	ASSOCIATION WITH HOST PLANT
COLEOPTERA:-		
Chrysomelidae		
Hermaeophaga mercurialis F.	Fowler (1891), Joy (1932), Walsh (1954), Linssen (1959), Welch (1972), Walsh & Dibb (1975), L. K. Ward (pers. comm.)	Adult - Leaf feeder Larva - root feeder (Welch 1972)
Curculionidae		
Apion pallipes Kirb.	Fowler (1891), Joy (1932), Walsh (1954), Linssen (1959), Walsh & Dibb (1975) L. K. Ward (pers. comm.)	Leaf feeder
Barynotus moerens F.	Joy (1932), Walsh (1954), Linssen (1959) Walsh & Dibb (1975)	Leaf feeder
Tropiphorus elevatus Hbst.	L. K. Ward (pers. comm.) Joy (1932), Linssen (1959)	Leaf feeder
Tropiphorus obtusus Bons.	Joy (1932), Linssen (1959)	Leaf feeder
Tropiphorus terricola Newn.	Fowler (1891), Joy (1932), Walsh (1954), Linssen (1959), Walsh & Dibb (1975)	Leaf feeder
Nitidulidae		
Meligethes kunzei Er.	Fowler (1891), Walsh (1954), Walsh & Dibb (1975)	Flower feeder Polyphagous

TABLE 5 (CONTINUED)

SPECIES	MAIN SOURCES	ASSOCIATION WITH HOST PLANT
HEMIPTERA : HETEROPTERA		
Miridae		
Calocoris major Schol.	Butler (1923)	Collected from M. perennis (see text)
Calocoris sexguttatus F.	Butler (1923)	Collected from M. perennis (see text)
Dicyphus stachydis Reut.	Butler (1923)	Collected from M. perennis (see text)
Psallus variabilis Fall	Butler (1923)	Collected from M. perennis (see text)
Psallus varians Herr Schaeffer	Butler (1923)	Collected from M. perennis (see text)
HEMIPTERA : HOMOPTERA		
Aphididae		
Aulacorthrum solani Kltb.	L. K. Ward (pers. comm.)	Leaf/stem feeder Polyphagous
Cixiidae		
Cixius distinguendus	Whittaker (1969)	Leaf feeder
LEPIDOPTERA		
Micropterigidae		
Micropterix calthella L.	J. Flint (pers. comm.)	Pollen feeder Polyphagous
Noctuidae		
Phlogophora meticulosa L.	L. K. Ward (pers. comm.)	Leaf feeder

TABLE 5 (CONTINUED)

SPECIES	MAIN SOURCES	ASSOCIATION WITH HOST PLANT
Pyralidae		
Pyrausta nivealis F.	Ford (1949)	Leaf feeder
Pyrausta olivalis Schiff.	Ford (1949), Beirne (1952)	Leaf feeder
Tortricidae		
Olindia schumacherana F.	Ford (1949), Bradley et. al. (1973)	Leaf feeder
THYSANOPTERA		
Thripidae		
Thrips fulvipes Bagn.	Morison (1949), Mound (1967), Mound et. al. (1976), Pitkin (1976), Ward (pers. comm.)	Larvae monophagous Adult - will often visit other plant species. (foliage and flower feeder)
MISCELLANEOUS		
Ceutorhynchus moguntiacus Schultze (Coleoptera : Curculionidae)	Walsh (1954)	This record is erroneous. C. moguntiacus has been applied to both C. thomsoni Kolbe and C. timidus Weise, and does not exist anymore. (M. G. Morris pers. comm.)

TABLE 6

PHYTOPHAGOUS INSECTS COLLECTED FROM SAMPLES OF M. PERENNIS FROM 3 SITES IN COUNTY DURHAM (MAY TO JULY)

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
SITE 1: MAY		
COLEOPTERA		
Curculionidae		
Apion pallipes Kirb.	1	Adult - leaf feeder Larva - stem miner
Barynotus moerens F.	3	Adult - leaf feeder Larva - root feeder
Rhychaenus fagi L.	2	Casual
Phyllobius calcaratus F.	2	Widely polyphagous - uncertain relationship with host plant
COLLEMBOLA		
Sminthuridae		
Bourletiella repanda Agr.	Very numerous	Leaf feeder
HEMIPTERA : HETEROPTERA		
Acanthosomatidae		
Elasmostethus interstinctus L.	1	Casual
Miridae		
Calocoris major Schol. (4th instar)	23	Leaf feeder
Dicyphus stachydis Reut.	1	Casual
Plesiocoris rugicollis Fall. (early instar)	2	Polyphagous - uncertain relationship with host plant

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
HEMIPTERA : HOMOPTERA		
Aphididae		
Drepanosiphum sp.	numerous	Casual
LEPIDOPTERA		
Geometridae		
Perizoma didymata L.	3	Leaf feeder
THYSANOPTERA		
Thripidae		
Taenothrips inconsequens Uzel	1	Casual: flower feeder
Thrips atratus Hall.	3	Polyphagous - uncertain relationship with host plant
Thrips fulvipes Bagn.	7	Adult: leaf and flower feeder
SITE 1: JUNE		
COLEOPTERA		
Chrysomelidae		
Chaetocnema concinna Marsh.	1	Associated with senescing leaves
Cryptophagidae		
Atomaria berolinensis Kr.	4	Associated with senescent leaves
A. fuscicollis Man.	1	Associated with senescent leaves

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
A. pusilla pk.	1	Associated with senescent leaves
A ruficornis Marsh	1	Associated with senescent leaves
Curculionidae		
Apion pallipes Kirb.		
Adults	5	Leaf feeder
Larvae	numerous	Stem miner
Barynotus moerens F.	2	Leaf feeder
Barypeithes pellucidus Bohn.	28	Feeds on leaves which are beginning to senesce
Liosoma deflexum Panz.	2	Casual
Sciaphilus asperatus Bons.	1	Polyphagous - uncertain relationship with host plant
Lathridiidae		
Corticaria crenulata Gyll.	1	Associated with senescent leaves
Enicmus histrio Joy	2	Associated with senescent leaves
Lathridius nodifer Westw.	1	Associated with senescent leaves
COLLEMBOLA		
Entomobryidae		
Entomobrya nivalis Linné	numerous	See text
Lepidocyrtus lignorum F.	numerous	

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
Sminthuridae		
Bourletiella bicincta Koch.	numerous	Leaf feeder
B. flava Gisin	numerous	Leaf feeder
B. repanda Agr.	numerous	Leaf feeder
HEMIPTERA : HETEROPTERA		
Miridae		
Calocoris major Schol	15	Leaf feeder
Calocoris quadripunctatus Vill.	1	Casual
Calocoris sexguttatus F. (4th instar)	27	Leaf feeder, also partly predatory
HEMIPTERA : HOMOPTERA		
Aphididae		
Drepanosiphum sp.	numerous	Casual
LEPIDOPTERA		
Noctuidae		
Phlogophora meticulosa L.	1	Leaf feeder
Tortricidae		
Olindia schumacherana F.	1	Leaf feeder
Miscellaneous		
Unidentified species pupa parasitised (A)	1	Probably a leaf feeder
Unidentified species pupa parasitised (B)	3	Probably a leaf feeder

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
PSOCOPTERA		
Unidentified immature species	2	Associated with micro-flora of senescent leaves or organic debris
THYSANOPTERA		
Thrips fulvipes Bagn.		Leaf and flower feeder
Adults	5	
Immature individuals	4	
SITE 1: JULY		
COLEOPTERA		
Cryptophagidae		
Atomaria atricapilla Steph.	1	Associated with senescent leaves
A. fuscata Schor.		Associated with senescent leaves
Curculionidae		
Apion pallipes Kirb.		Leaf feeder
Adults	3	
Larvae	Numerous:- 84% of samples mined (n = 40)	Stem miner
Barynotus moerens F.	3	Leaf feeder
Barypeithes pellucidus Bohn.	5	Feeds on leaves which are beginning to senesce
Lathridiidae		
Corticaria elongata Gyll.	1	Associated with senescent leaves

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
COLLEMBOLA		
Entomobryidae		
Entomobrya nivalis Linné	10	See text
Lepidocyrtus lignorum F.	5	See text
Sminthuridae		
Bourletiella bicincta Koch.	numerous	Leaf feeder
B. flava Gisin	numerous	Leaf feeder
B. repanda Agr.	numerous	Leaf feeder
HEMIPTERA : HETEROPTERA		
Calocoris major Schol.	2	Leaf feeder
Calocoris sexguttatus F.	12	Leaf feeder, also partly predatory
Plesiocoris rugicollis Fall.	4	Polyphagous - uncertain relationship with host plant
3 unidentified immature species :- C	2	Casual
D	1	Casual
E	2	Casual
LEPIDOPTERA		
Unidentified 'macro' species - larva parasitised (F)	1	Leaf feeder
THYSANOPTERA		
Unidentified species - immature, probably Thrips fulvipes. Bagn.	1	Leaf feeder

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
SITE 2: MAY		
COLEOPTERA		
Curculionidae		
Apion pallipes Kirb.	2	Adult - leaf feeder Larva - stem miner
Barynotus moerens F.	2	Adult - leaf feeder Larva - stem miner
Phyllobius calcaratus F.	2	Polyphagous - uncertain relationship with host plant
Rhynchaenus fagi L.	1	Casual
HEMIPTERA : HETEROPTERA		
Acanthosomatidae		
Elasmostethus interstinctus L.	1	Casual
Miridae		
Calocoris major Schol. (4th instar)	10	Leaf feeder
Calocoris sexguttatus F. (2nd instar)	6	Leaf feeder, also partly predatory
HEMIPTERA : HOMOPTERA		
Aphididae		
Drepanosiphum sp.	1	Casual

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
THYSANOPTERA		
Thripidae		
Thrips atratus Hall.	2	Polyphagous - uncertain relationship with host plant
Thrips fulvipes Bagn.	4	Leaf and flower feeder
SITE 2: JUNE		
COLEOPTERA		
Chrysomelidae		
Chrysolina polita L.	4	Oligophagous - uncertain relationship with host plant
Cryptophagidae		
Atomaria berolinensis Kr.	1	Associated with senescent leaves
Curculionidae		
Phyllobius viridiaeris Laich.	1	Polyphagous - uncertain relationship with host plant
Rhychaenus fagi L.	1	Casual
Sciaphilus asperatus Bons.	1	Polyphagous - uncertain relationship with host plant
Nitidulidae		
Micrurula melanocephala Marsh.	1	Flower feeder - casual

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
Salpingidae		
Rhinosimus viridipennis Lat.	1	Refuse feeder
COLLEMBOLA		
Sminthuridae		
Bourletiella pallipes Bour.	numerous	Leaf feeder
Bourletiella repanda Agr.	numerous	Leaf feeder
HEMIPTERA : HETEROPTERA		
Miridae		
Calocoris major Schol.	8	Leaf feeder
Calocoris sexguttatus F. (4th instar)	20	Leaf feeder also partly predatory
Dicyphus stachydis Reut.	2	Casual
Harpocera thoracica Fall.	1	Casual
HEMIPTERA : HOMOPTERA		
Aphididae		
Drepanosiphum sp.	numerous	Casual
Cercopidae		
Philaenus spumarius L. (immature)	1	Widely polyphagous - leaf feeder
Cicadellidae		
Unidentified immature species	1	Casual

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
LEPIDOPTERA		
Geometridae		
Perizoma didymata L.	3	Leaf feeder
Pyralidae		
Pyrausta olivalis Shiff.	6	Leaf feeder
Miscellaneous		
Unidentified species - parasitised (G)	3	Leaf feeder
Unidentified species - pupae parasitised (H)	3	Probably a leaf feeder
THYSANOPTERA		
Unidentified species - immature, probably Thrips fulvipes Bagn.	2	Leaf feeder
SITE 2: JULY		
COLEOPTERA		
Cryptophagidae		
Atomaria berolinensis Kr.	4	Associated with senescent leaves
A. nigriventris Steph.	1	Associated with senescent leaves
COLLEMBOLA		
Entomobryidae		
Entomobrya nivalis Linne	5	See text

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
Lepidocyrtus lignorum F.	9	See text
Orchesella cincta L.	3	
Sminthuridae		
Bourletiella flava Gisin	numerous	Leaf feeder
Bourletiella pallipes Bour.	numerous	Leaf feeder
B. repanda Agr.	numerous	Leaf feeder
HEMIPTERA : HETEROPTERA		
Miridae		
Calocoris major Schol.	5	Leaf feeder
Calocoris sexguttatus F.	18	Leaf feeder, also partly predatory.
Plesiocoris rugicollis Fall.	3	Polyphagous - uncertain relationship with host plant
Unidentified Miridae (1st instar)	2	Casual
HEMIPTERA : HOMOPTERA		
Cercopidae		
Aphrophora alni Fall.	1	Casual
LEPIDOPTERA		
Unidentified 'macro' species-larva parasitised (F)	1	Leaf feeder
THYSANOPTERA		
Unidentified individuals probably Thrips fulvipes Bagn.	3	Leaf feeder

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
SITE 3: MAY		
COLEOPTERA		
Chrysomelidae		
Batophila rubi Pk.	2	Casual
Curculionidae		
Barynotus moerens F.	1	Adult: leaf feeder Larva: root feeder
Phyllobius calcaratus F.	2	Polyphagous - uncertain relationship with host plant
Nitidulidae		
Meligethes sp.	2	Flower feeder(s) - polyphagous. Probably casual
HEMIPTERA : HETEROPTERA		
Calocoris sexguttatus F. (2nd instar)	2	Leaf feeder - also partly predatory
HEMIPTERA : HOMOPTERA		
Cercopidae		
Philaenus spumarius L. (immature)	3	Widely polyphagous - leaf feeder
THYSANOPTERA		
Thripidae		
Limothrips cerealium Hall.	1	Casual: flower feeder

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
Limothrips denticornis Hall.	1	Casual: flower feeder
Thrips atratus Hall.	2	Polyphagous - uncertain relationship with host plant
Thrips fulvipes Bagn.	10	Adult: leaf and flower feeder
SITE 3: JUNE		
COLEOPTERA		
Chrysomelidae		
Batophila rubi Pk.	2	Casual
Crepidodera transversa Marsh.	3	Polyphagous - uncertain relationship with host plant
Longitarsus sp.	1	Casual
Curculionidae		
Phyllobius calcaratus F.	2	Polyphagous - uncertain relationship with host plant
Phyllobius pyri L.	2	Polyphagous - uncertain relationship with host plant
Nitidulidae		
Meligethes sp.	1	Flower feeder - polyphagous probably casual

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
COLLEMBOLA		
Entomobryidae		
Entomobrya nivalis Linné	2	See text
Lepidocyrtus lignorum F.	5	
Sminthuridae		
Bourletiella repanda Agr.	numerous	Leaf feeder
HEMIPTERA : HETEROPTERA		
Miridae		
Calocoris sexguttatus (3rd instar)	1	Leaf feeder, also partly predatory
Dryophilocoris flavo-quadrimaculatus DGr.	1	Casual
Leptopterna dolabrata L.	1	Casual
HEMIPTERA : HOMOPTERA		
Cercopidae		
Philaenus spumarius L. (immature)	4	Widely polyphagous - leaf feeder
Cicadellidae		
Unidentified immature species	3	Casual
Psyllidae		
Psylla peregrina Fors. (immature)	2	Casual

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
LEPIDOPTERA		
Geometridae		
Perizoma didymata L.	2	Leaf feeder
THYSANOPTERA		
Unidentified species, immature. Probably Thrips fulvipes Bagn.	13	Leaf feeder
SITE 3: JULY		
COLEOPTERA		
Chrysomelidae		
Crepidodera transversa Marsh.	4	Polyphagous - uncertain relationship with host plant
COLLEMBOLA		
Entomobryidae		
Entomobrya nivalis Linné	14	See text
Lepidocyrtus lignorum F.	18	
Sminthuridae		
Bourletiella repanda Agr.	numerous	Leaf feeder
HEMIPTERA : HETEROPTERA		
Miridae		
Calocoris sexguttatus F.	1	Leaf feeder, also partly predatory

TABLE 6 CONTINUED

SPECIES	NUMBER OF INDIVIDUALS	ASSOCIATION WITH HOST PLANT
Leptopterna do~~t~~labrata L.	1	Casual
HEMIPTERA : HOMOPTERA		
Aphididae		
Uroleucon sp.	5	Casual
Cercopidae		
Aphrophora alni Fall.	1	Casual
Philaenus spumarius L.	2	Widely polyphagous - leaf feeders
Psyllidae		
Psylla peregrina Fors.		
Adult	4	Casual
Immature	3	Casual
LEPIDOPTERA		
Unidentified 'macro' species - larva parasitised (F)	1	Leaf feeder
THYSANOPTERA		
Unidentified species probably Thrips fulvipes Bagn.		
Adult	11	Leaf feeder
Immature	5	

TABLE 7

NUMBERS OF PHYTOPHAGOUS INSECT SPECIES ALLOTED TO EACH FEEDING CATEGORY FOR ALL SITES DURING THE SAMPLING PERIOD (FOR FURTHER EXPLANATION SEE TEXT)

ASSOCIATION WITH HOST PLANT	NUMBERS OF SPECIES		
	MAY	JUNE	JULY
SITE 1			
1. Leaf feeder	6	13	10
2. Associated with senescing leaves	-	9	3
3. Casual	4	3	3
4. Uncertain relationship with host plant	3	1	1
5. Casual - flower feeder	1	-	-
6. Other	-	2	2
TOTAL	14	28	19
SITE 2			
1. Leaf feeder	5	10	7
2. Associated with senescing leaves	-	2	2
3. Casual	3	5	2
4. Uncertain relationship with host plant	2	3	1
5. Casual - flower feeder	-	1	-
6. Other	-	-	3
TOTAL	10	21	15
SITE 3			
1. Leaf feeder	4	5	5
2. Associated with senescing leaves	-	-	-
3. Casual	1	6	4
4. Uncertain relationship with host plant	2	3	1
5. Casual - flower feeder	3	1	1
6. Other	-	2	2
TOTAL	10	17	13

FIGURE 6: GRAPH TO SHOW SEASONAL CHANGES IN THE NUMBER OF INSECT SPECIES IN CATEGORY 1 (SEE TABLE 7) ASSOCIATED WITH M. PERENNIS

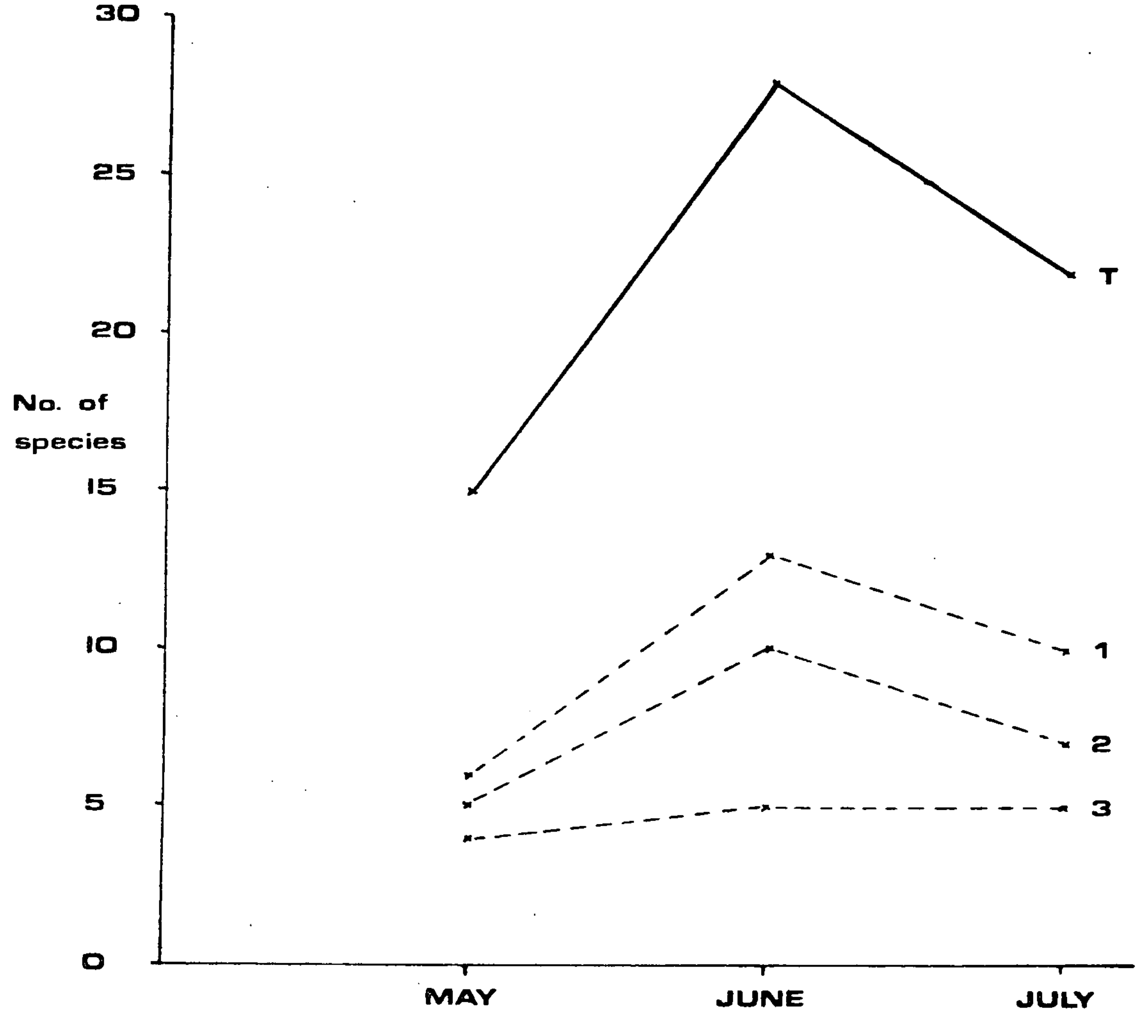


FIGURE 7: GRAPH TO SHOW SEASONAL CHANGES IN THE NUMBER OF INSECT SPECIES IN CATEGORIES 1 & 2 COMBINED (SEE TABLE 7) ASSOCIATED WITH M. PERENNIS

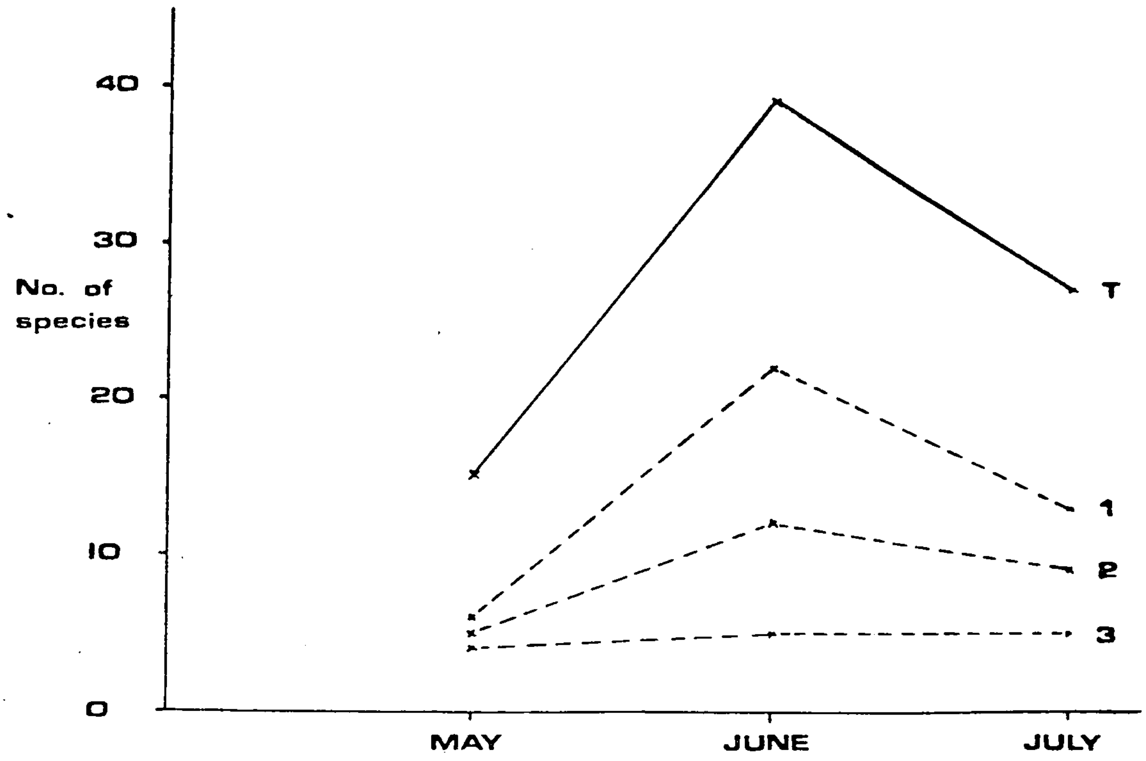


FIGURE 8: GRAPH TO SHOW SEASONAL CHANGES IN THE NUMBER OF INSECT SPECIES IN CATEGORIES 1 & 4 COMBINED (SEE TABLE 7) ASSOCIATED WITH M. PERENNIS

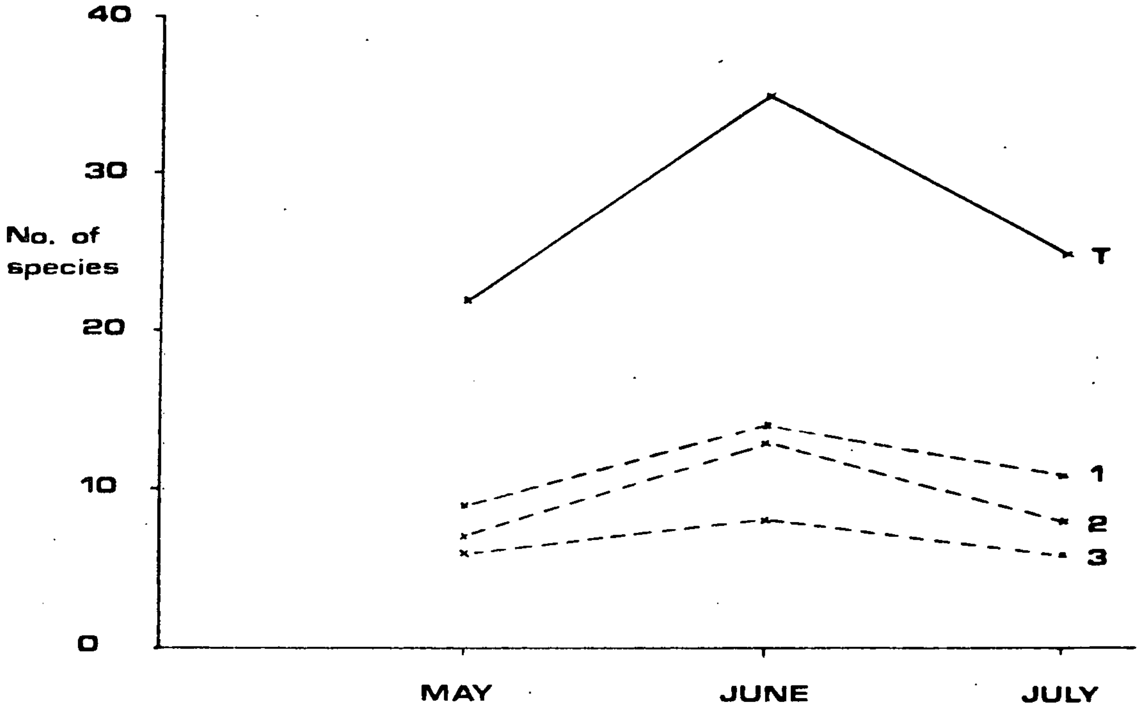


FIGURE 9: GRAPH TO SHOW SEASONAL CHANGES IN THE NUMBER OF INSECT SPECIES IN CATEGORIES 1, 2 & 4 COMBINED (SEE TABLE 7) ASSOCIATED WITH M. PERENNIS

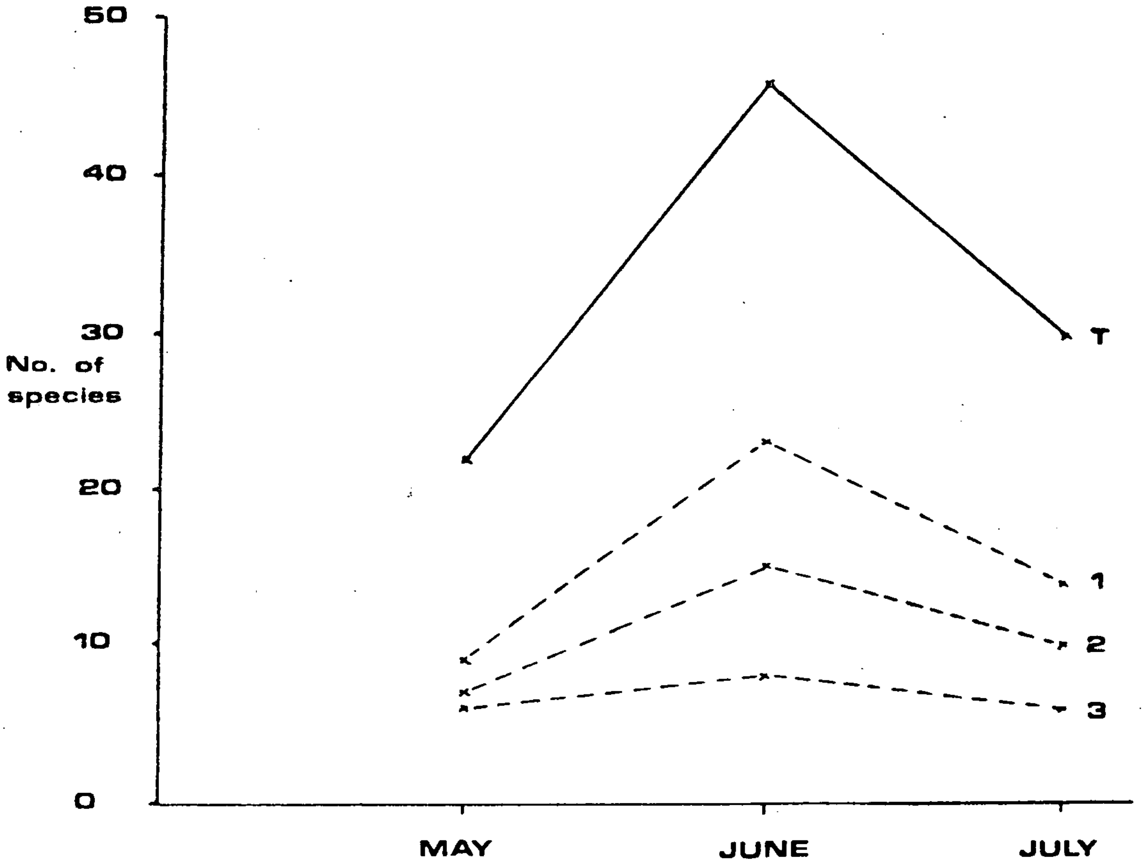
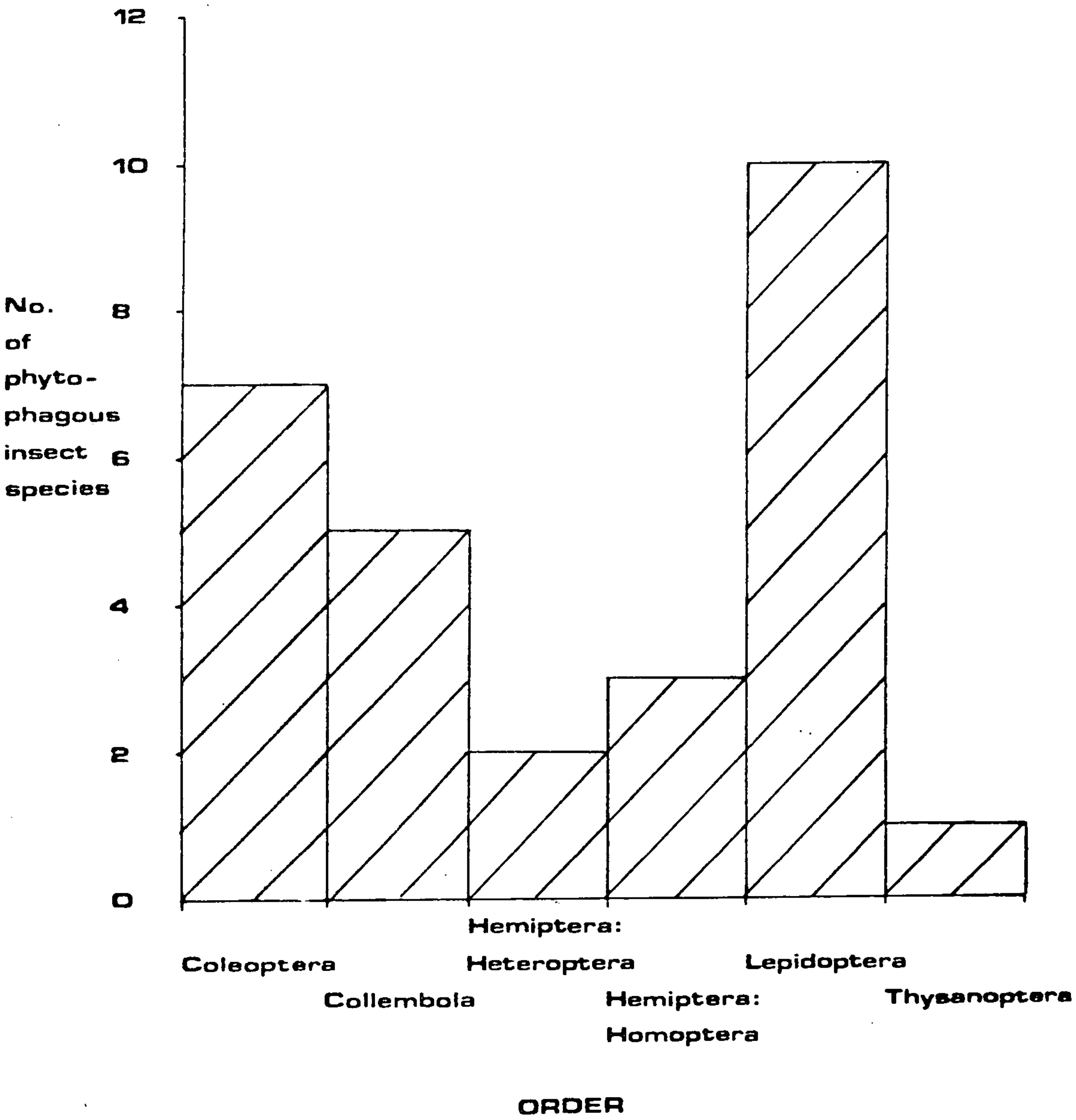


FIGURE 10:

GRAPH TO SHOW THE TAXONOMIC COMPOSITION OF THE PHYTOPHAGOUS INSECT FAUNA OF M. PERENNIS



6. DISCUSSION

Contrary to the opinions of Wilson (1968) and R. C. Welch (pers. comm.), M. perennis does not appear to have a particularly limited phytophagous insect fauna. Percentage invertebrate foliar damage of plant samples from the three study sites (see Appendix Table 1) is well above 50% at the earliest sampling date and by July damage can be as high as 100%. Some of this damage is caused by molluscs, but much is caused by phytophagous insects, particularly Coleoptera and Lepidoptera. Sampling in County Durham (Table 6) revealed twenty species feeding on the living plant biomass and a literature search (Table 5) revealed thirteen species, making a net total of twenty eight. M. perennis occurs in 72% of the 10 kilometre grid squares covering England, Wales and Scotland (Perring and Walters 1976). The relationship between the geographical range of a plant species and the number of associated phytophagous insect species has been expressed graphically for four groups of plant life forms including perennial herbs, by Lawton and Schroder (1977), using Biological flora data. If using this graph in Lawton and Schroder (1978), a straight line is drawn vertically from the value of 72% (the estimated geographical range of M. perennis in the British Isles) on the X axis to meet the regression line fitted for this data, and a horizontal line is then drawn from this point to intercept with the Y axis, a figure of 22 species is derived. This can thus be taken as the "expected" number of species exploiting M. perennis in the British Isles. This figure may be an underestimate, as the insect data used by Lawton and Schroder (1977) in their analyses are not entirely complete and rarely include small orders such as Collembola and Thysanoptera. Further detailed work in other areas of the British Isles could feasibly reveal further species feeding on the plant, as yet unrecorded, which would increase the total. However, the evidence that the two species of Calocoris (Heteroptera : Miridae), are phytophagous on the host plant is only circumstantial and although Calocoris major Schol. and Calocoris sexguttatus F. were found on M. perennis particularly at Sites 1 and 2 in large numbers throughout the sampling period (see Table 6 for details) the uncertainty must remain. These two species are recorded as feeding on U. dioica (Saunders 1892, Butler 1923, Southwood and Scudder 1956, Southwood and Leston 1959) but Butler (loc. cit.) reports that immature and adult individuals of both species have been collected from M. perennis. These two species have been listed in the leaf feeding category, but should future experimental work prove this to be an incorrect assumption then the species total would be reduced accordingly. In addition, the five closely related species of Bourletiella, although almost certainly foliage feeders (Southwood 1973), have not been studied in depth and their separate identities are open to question (P. N. Lawrence pers. comm.) which may again mean a reduction in the species number.

Species of uncertain association with M. perennis could increase the species total for the plant if proved unequivocally to be feeding on it. The following species come into this category:- Chrysolina polita L., Crepidodera transversa Marsh.(Coleoptera:Chrysomelidae), Phyllobius calcaratus F., Phyllobius pyri L., Phyllobius viridiaeris Laich., Sciaphilus asperatus Bons. (Coleoptera : Curculionidae) Plesiocoris rugicollis Fall. (Heteroptera : Miridae) and Thrips atratus Hall. (Thysanoptera : Thripidae). The three Phyllobius species are probably casuals or strays and according to Ward (1977), Phyllobius species often stray onto J. communis when present in high numbers in the local habitat. S. asperatus is also probably casual. C. polita, which was found at Site 2 only in June, is normally associated with food plants in the Labiatae family (Marshall 1979). At Site 2, a number of individuals of C. polita were found in one localised area of pure M. perennis resting in the top leaf axils, after a search following sampling. It is just possible that C. polita may feed on M. perennis in the North of England but it must be noted that one of its recorded food plants Glechoma hederacea, was present at Site 2 (See Table 2). Crepidodera transversa, found only at Site 3 (it is a species of rough grassland) is normally associated with Cirsium sp. and U. dioica (Fowler 1891, Joy 1932) but it is probably polyphagous and M. perennis could well be a food plant when growing in a suitable habitat for the beetle.

P. rugicollis normally feeds on Salix spp. and Myrica gale but since 1914 it has been found on apple (Malus domestica), Ribes spp. (Butler 1923, Southwood and Leston 1959, Wightman, 1967) and it seems to be extending its food plant range. Both adults and immature individuals were found on M. perennis at Sites 1 and 2 and with the exception of the presence of Ribes uva-crispa at Site 2 (Table 2) seemingly at relatively long distances from any of its listed food plants.

Finally, Thrips atratus is a polyphagous species and is found on many plant species, especially the Caryophyllaceae (Mound et. al. 1976, Pitkin 1976). It could well be breeding on M. perennis, but unfortunately immature individuals collected were not identifiable and the problem remains.

Host switching is known to occur, often suddenly (Dethier 1954, Strong 1979) with polyphagous phytophagous insect species and this makes it difficult to draw conclusions on the association of some of the "uncertain" species with the host plant, without rigorous observation and experimentation. In addition, some species vary their food plant geographically and retain limited ecological plasticity permitting local adaptations to new hosts (Zwolfer et. al. 1971).

Some of the insect species listed in Table 5 were not found at any of the sampling sites in County Durham. The three species of Tropiphorus (Coleoptera : Curculionidae) are all either local or rare (Joy 1932) and T. elevatus and T. obtusus have not been recorded from County Durham (M. G. Morris pers. comm.). Hermaeophaga mercurialis (Coleoptera : Chrysomelidae) is absent from Northern England presumably due to climatic and edaphic factors. The larvae seem to require a light, preferably calcareous, dry soil and the species is unable to overwinter in cold, wet, heavy soils and therefore the distribution is closely associated with the chalk, Tertiary, Greensand and Oolitic limestone deposits of S. E. England (Welch 1972). Pyrausta olivalis (Lepidoptera : Pyralidae) is a very common species and most certainly occurs in County Durham even though it was not found. Cixius distinguendus (Homoptera : Cixiidae) and Aulacorthrum solani (Homoptera : Aphididae) were also absent for reasons unknown. The possibility that some species were missed due to daytime sampling or the lack of sampling in early spring and late summer cannot be ruled out.

Careful observation of the available data (Table 6 and Figures 6 - 9) shows distinct inter-site differences in species composition and species number, with regard to phytophagous species and senescent leaf feeding species. In terms of total numbers, Sites 1 and 2 are similar when phytophagous species are considered (15 and 14 species respectively) but Site 3 is very species poor (7 species). A possible explanation for the paucity of species at Site 3 is that most M. perennis feeding species prefer the woodland microclimate and this is obviously lacking at the open scrub site. Species associated with senescent leaves are most abundant at Site 1 (12 species); Site 2 only has three species and Site 3 has no species in this category. The latter is explained by the fact that few actually senescent/dead leaves were present at this site even in July. The figures in Appendix Table 1 pool records for leaf browning and senescence, which can be a bit misleading as it includes leaves just beginning to senesce and those which are actually dead or senescent. Site 1 has most species in this category due to the abundance of dead, rotting leaves which is presumably related to the dampness of the habitat which is condusive to rapid rotting in situ of the leaves.

There are a number of differences in species composition between sites which may be real or apparent. Some examples are discussed below. Differences are probably in most part due to microclimatic or edaphic differences as the host plant is not the total environment of any species (Morris 1974a). In addition, in some cases the presence or absence of other associated plant species (See tables 1 - 3) may be of importance from a dietary point of view (polyphagous species) or if required for some other reason such as part of a species' total habitat. Site 1 is the only site with a moss carpet (Thuidium tamariscinum) which may be of importance to some species and possibly explains the presence of B. pellucidus at that site and not at the other two sites, as Fowler (1891) states it usually occurs or spends inactive periods in moss.

An earlier reference was made to the genus Bourletiella, stating that the seemingly separate identities of each species was open to question. Interestingly enough, two of the five species were found only at one site: B. pallipes was restricted to Site 2 and B. bicincta to Site 1. This might be good evidence for the validity of separating the individuals into species and it is interesting that B. bicincta, which Gisin (1960) states is found in damp habitats, is in fact found at the "dampest" site of the three.

C. major is completely absent from Site 3 and this is probably due to its preference for woodland areas or alternatively, absence could be due to the lack of its preferred host plant, U. dioica, at this site. The absence of other species, found at the two woodland sites, from Site 3 (for example A. pallipes) could also be attributable to the unsuitability of the habitat for the species concerned. Differences between Sites 1 and 2 and other inter-site variation in faunal composition are more difficult to explain without additional information on species autecology.

There are two possible reasons for the seemingly poor fauna of M. perennis indicated by R. C. Welch (pers. comm.) in Southern England.* Firstly, many sites for M. perennis in S. England contain large pure stands of the plant in dense, shady woodland without many other associated plant species. Thus, low habitat complexity may lead to lower insect species richness and diversity (Root 1973, Cromatie 1975, Smith 1977). Secondly, deep shade may be a contributory factor in that it is often not a favourable habitat for many phytophagous insects. (In contrast the two woodland sites sampled in County Durham permitted a fair degree of light penetration to the herb layer). Atsatt and O'Dowd (1976) cite the case of a crucifer (Dentaria diphylla) which is apparently protected from at least three flea beetles by growing in shady woodland habitats. There are also many other examples of shade being inhibitory to insect species.

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* Not substantiated

With regard to seasonal changes in the numbers of phytophagous insects exploiting the plant, the first idea to examine is whether variations in plant architecture influence these changes in numbers. Mean stem height (See Figure 1) increased through the sampling period as one would expect but it would seem with the exception of Site 3, that the gradient of the line is decreasing and that mean stem height probably reaches its maximum in July. Clearly, changes in leaf number and leaf area are of more significance to phytophagous insects and it would seem from Figure 2 that the maximum mean number of leaves is reached by May, possibly with the exception of Site 3. The standard errors are large and thus it would be incorrect to state that further new leaves were being produced by the plant even though this would seem to be the case, especially between May and June, when examining the curves. The graph seems to suggest that leaf number actually decreases between June and July. This is probably a function of the large standard errors but in the case of Sites 1 and 2 it may represent leaf rotting and senescence and subsequent drop. Leaf expansion continues after the actual number of leaves reaches a maximum (Figures 3 and 4). Mean leaf area index and Mean leaf area index per plant show very similar patterns in that leaf area increases throughout the sampling period with the exception of Site 1 where a plateau situation is reached at an earlier stage. Presumably a fourth sampling at the beginning of August would show that leaf expansion ceases about this time in County Durham. This cessation in leaf expansion occurs earlier in Southern Britain than in the North (Hutchings 1976, Hutchings and Barkham 1976). Data from Al Mufti et. al. (1977), on the seasonal changes in the amounts of living shoot material of M. perennis (See Figure 5) from a steeply sloping, North facing terrace on Carboniferous limestone in Upper

Lathkilldale (Derbyshire) shows that biomass (g/m^{-2}) increases to a maximum in July and then begins to fall or stabilise (standard errors are large) in August. This pattern is similar to that shown by other plant architecture parameters measured in the present work (See Figures 1 - 4). Other more subtle changes in architecture occurred throughout the study period. Firstly, there was the onset of flowering and then subsequently the loss of male flowers and their pedicels, and the development of seed capsules on the female plants. Obviously the presence or absence of flowers is significant to flower feeders but it is of little significance in the present study. Similarly, the same can be said for the presence or absence of seed, although a small number of seeds were damaged, probably by an invertebrate, at Site 3 (See Appendix Table 1) and the organism responsible for this was never discovered.

Examination of Figures 6 - 9 and Table 7 reveal that changes in insect numbers do not mirror changes in plant architecture parameters. The four graphs (see above for detailed explanation) essentially show the same pattern; that is an increase in numbers from May to a maximum in June and a subsequent drop in July, but not to below the number found in May. Site 3 is a partial exception in that Figures 6 and 7 (definite phytophagous species, and the latter plus senescent leaf feeders) show the same numbers of species exploiting the plant in June as in July. However, if species with an uncertain relationship with the plant are added (Figures 8 and 9) then the pattern is the same as shown by the other two sites and the totals for all sites pooled.

If plant architecture was the main influence on species number as tentatively hypothesised by Lawton (1978) then one would not expect a drop in numbers in July. It would be interesting to find out the subsequent numbers of insects exploiting the plant in August and September to see if the drop in numbers is maintained. Casual inspection of sites at the end of July suggested that species richness declined from early July to late July. In addition, similar data from Southern Sites would be useful as the pattern shown in the North of England is perhaps controlled by a different set of interacting environmental variables.

A further point of interest concerns the species associated with rotting/senescent leaves. The numbers of such species does not increase from June to July yet the available "habitat" space available to such species does increase. For example, Appendix Table 1 shows that leaf browning/senescence increased from 53.5% of plants showing leaf senescence, to 84% for Site 2 between June and July. This seems to confirm the earlier observation that plant architecture does not seem to be the main factor responsible for the observed seasonal pattern. Is it possible that this pattern is purely a reflection of the fact that many phytophagous species exploit the host plant at the most favourable part of the season in terms of macro and microclimate variables, and the decrease in species feeding on the plant continues through August and September? This may be inextricably bound up with the following hypothesis.

Seasonal changes in the nutrient concentrations (especially nitrogen and phosphorous) and the balance and quantity of amino acids in plant foliage have important consequences for herbivores, and particularly phytophagous insects. (Feeny 1970, Feeny 1976, McNeill and Southwood 1978, Hodgkinson et. al. 1979, Chapin et. al. 1980). Plants also show seasonal patterns in the levels of various nutrients in different tissues. It is hypothesised that at the onset of shoot growth in the spring, nutrient or assimilate translocation takes place from the roots and rhizomes into the leaves, and the foliage of M. perennis remains nutritionally favourable for phytophagous insect species until leaf expansion and shoot growth stops in mid June - early July. Assimilates are then channelled into rhizome formation/growth, the chief method of reproduction, and the foliage declines in quality and is less suitable as a diet for phytophagous insects. Thus the insect herbivores are synchronising their phenologies with changes in foliage quality. This does not explain why the number of associated species is not higher in May, and this may be due to unfavourable climatic conditions or possibly that the levels of Mercurialine and the various flavonoid compounds is greater at this time and has an inhibitory effect. These ideas require testing before any definite conclusions can be drawn.

The taxonomic composition of the phytophagous insect fauna associated with M. perennis is shown in Figure 10. Although the data are not complete, qualitative comparisons can be made between these data and data from all perennial herbs covered in the Biological flora of the British Isles, compiled by Lawton (1978). If the two small orders (Collembola and Thysanoptera) are excluded and the Homoptera and Heteroptera are combined for both data sets, then the following crude comparisons emerge:-

(a) The proportions of Lepidoptera and Hemiptera exploiting M. perennis are similar to the proportions for all plant species pooled from the Biological flora data.

(b) There are proportionately more species of Coleoptera utilising the host plant compared to the Biological flora data.

(c) Phytophagous Diptera and Hymenoptera are completely absent from M. perennis whereas they make up 0.16 and 0.06 respectively of the proportions for the Biological flora data.

These comparisons must be treated with caution for reasons cited elsewhere but in any case, it is difficult to find any explanation for the observed taxonomic structure, as pointed out by Lawton and Schroder (1978). In fact, such differences could arise from historical and evolutionary accidents (chance) and have no discernible deterministic cause. It is interesting to note that B. pellucidus, a species included in the 'phytophagous' category has an unusual association with the plant. Feeding experiments showed that it will only feed on senescing leaves of the plant and will not make feeding holes in fresh leaves. Microscopic examination of faecal material revealed small glandular hairs from the leaves of the plant, which supports the above experiment. It is not known whether this weevil is relatively catholic or whether it is specific or narrowly oligophagous. It does, however, seem to favour woodland herbaceous vegetation in Danish beechwoods which may or may not be of significance (Neilson 1975).

Details of other food plants of the species associated with M. perennis are given in Appendix 2. However, it is worth pointing out that M. perennis does not lack 'specialist' species. Monophagous species include H. mercurialis, T. fulvipes and probably the three Tropiphorus species and species such as B. moerens and A. pallipes feed on very few other plant species.

7. SUMMARY

A detailed study of the phytophagous insect fauna of M. perennis at three sites in County Durham was undertaken over a three month period. A literature search for records of phytophagous insect species associated with the plant in the British Isles was conducted to provide additional data.

One hundred one stem samples of the plant were removed from each of the sites in May, June and July. In the laboratory, phytophagous insects were collected from the samples, recorded and identified.

Measurements of stem height, leaf number and leaf area were taken from a sub sample of plant samples in each case, to provide data on plant architecture. Other information such as percentage invertebrate damage, percentage leaf senescence and so on, were also recorded.

The data collected was used to see if seasonal changes in plant architecture had any influence on the numbers of associated phytophagous insect species. Additional analyses undertaken included inter site comparisons with regard to faunal composition, and the taxonomic composition of M. perennis compared to other perennial herbs.

Twenty species were found to utilise the living plant biomass and a number of other species were loosely associated with the senescent leaves. If the species recorded from the literature are added to this total, the figure is increased to 28 for the British Isles. Species of uncertain association with the plant are not included in this total. These figures apparently contradict the opinion that the plant has an impoverished fauna. A hypothesis is advanced that the changes in insect species richness over time is influenced by seasonal changes in the

quality/palatability of the plant's foliage. Differences in insect species richness and faunal composition between sites are discussed and possible explanations are put forward.

Phytophagous Diptera (for example Agromyzidae, Anthomyiidae, Cecidomyiidae) and Hymenoptera (for example Tenthredinidae) are completely absent from the plant which thus differs from the "averages" derived from the Biological flora data on perennial herbs.

APPENDIX TABLE 1

MISCELLANEOUS DETAILS OF INVERTEBRATE DAMAGE, LEAF SENESCENCE, AND FUNGAL AND VIRAL INFECTION. FIGURES ARE EXPRESSED AS PERCENTAGES OF CUT PLANT SAMPLES (100 AT EACH SITE MONTHLY) AFFECTED

DETAIL	MAY (6/7.5.80)	JUNE (5/6.6.80)	JULY (4/5.7.80)
SITE 1.			
NO INVERTEBRATE DAMAGE	1	-	-
TOTAL INVERTEBRATE DAMAGE	99	100	100
FEEDING HOLES	96	100	99
OTHER DAMAGE	76	94	95
LEAF BROWNING/SENESCENCE	17	47	79
FUNGAL INFECTION	14	1	2
VIRAL INFECTION	-	1	1
DAMAGED SEED	-	-	-
SITE 2.			
NO INVERTEBRATE DAMAGE	45	*24	16
TOTAL INVERTEBRATE DAMAGE	55	76	84
FEEDING HOLES	31	48.5	61
OTHER DAMAGE	42	58.5	61
LEAF BROWNING/SENESCENCE	16	53.5	84
FUNGAL INFECTION	8	21.5	10
VIRAL INFECTION	4	4	3
DAMAGED SEED	-	-	-
SITE 3.			
NO INVERTEBRATE DAMAGE	42	18	19
TOTAL INVERTEBRATE DAMAGE	58	82	81
FEEDING HOLES	33	57	55
OTHER DAMAGE	34	62	68
LEAF BROWNING/SENESCENCE	42	47	63
FUNGAL INFECTION	2	2	1
VIRAL INFECTION	-	2	2
DAMAGED SEED	-	4	1

*SEE TEXT (METHODS)

APPENDIX 2

This appendix gives details of geographical distribution, abundance and host plants for all phytophagous (including senescent leaf feeders) insects listed in Tables 5 and 6. Additional information is included where relevant. The information in this list is derived from identification manuals (see references), personal correspondence, personal observation and experimentation and various scientific papers which are acknowledged when used. Distribution information should be treated only as a very general guide.

COLEOPTERA

Chrysomelidae

Batophila rubi.

Generally distributed but local in England, Scotland and Ireland in woods and hedgerows. Chiefly on *Rubus sp.*

Chaetocnema concinna

Common and generally distributed throughout the British Isles. Found by sweeping herbaceous vegetation.

Chrysolina polita

Common and generally distributed throughout England, Wales and probably the greater part of Scotland and Ireland. Prefers damp and marshy habitats by streams and feeds on various Labiatae, including *Mentha aquatica*, *M. rotundifolia*, *M. palustris*, *M. longifolia*, *Melissa officinalis*, *Lycopus europaeus*, *Origanum vulgare*, *Glechoma hederacea*, *Nepeta cataria* and *Salvia sp.* (Marshall 1979).

Crepidodera transversa

Common and generally distributed throughout the United Kingdom and Ireland. In rough grassland probably on Urtica dioica and various species of Cirsium.

Hemaeophaga mercurialis

Locally common in woodlands in S. E. England with a light, dry calcareous soil. It does not occur further north than Leicestershire. The beetle is solely restricted to M. perennis and the larvae feed on the roots of the plant (Welch 1972).

Longitarsus sp.

Forty one species of this genus occur in Britain and many of the species are extremely closely allied and are hence difficult to determine. Most species feed on herbaceous higher plant species.

Cryptophagidae

Atomaria

Most species of this genus are to be found in rotting vegetation and organic waste in general, where they feed on fungal hyphae.

A. atricapilla

Common and generally distributed throughout the British Isles. In haystack and vegetable refuse.

A. berolinensis

Local but generally distributed throughout the British Isles. In haystack and vegetable refuse.

A. fuscata

Common and generally distributed throughout the British Isles. In haystack refuse and manure heaps and so on.

A fuscicollis

Local but generally distributed throughout the British Isles. In moss, dead leaves and vegetable refuse.

A. nigriventris

Common and generally distributed throughout the British Isles. In vegetable refuse.

A. pusilla

Common and generally distributed in England but not common in Scotland. In moss, haystack refuse and so on.

A ruficornis

Fairly common and generally distributed throughout the British Isles. In manure heaps, haystack refuse, dead birds and so on. It is a very common synanthropic species (C. Johnson pers. comm.).

Curculionidae

Apion pallipes

Local, but generally distributed in the British Isles. Mainly on M. perennis but also recorded on Allium ursinum. The larvae mine the stem of the host plant.

Barynotus moerens

Local but generally distributed in the British Isles. Feeds on M. perennis chiefly at night but has also been recorded as feeding on Ranunculus repens (Read 1978). The larvae feed on the roots of the former plant species (Morris 1976).

Barypeithes pellucidus

Very local in England as far north as County Durham? Fowler (1891) states it is found in moss in sandy places. Feeding experiments revealed its preference for senescing leaves of M. perennis but it is not known whether it feeds on any other plant species in a similar manner.

Liosoma deflexum

Local but generally distributed throughout England and Wales becoming increasingly scarcer further north. It is found in damp places in moss and around the roots of various grasses and feeds on various Ranunculaceae including Anemone nemorosa. The larvae feed on the roots of Ranunculaceae species (Morris 1976).

Phyllobius calcaratus

Common and generally distributed throughout the British Isles. Polyphagous, it is found on various trees especially Alnus glutinosa, on various shrubs and bushes and in hedgerows. The larvae of all Phyllobius species are root feeders.

Phyllobius pyri

Common and generally distributed throughout the British Isles. Polyphagous, it is found on Crataegus monogyna, on young trees in woods and on Urtica dioica.

Phyllobius viridiaeris

Common and widely distributed throughout the country. It is found on many herbaceous plants including Urtica dioica and on Crataegus monogyna, Prunus spinosa and so on in woods and hedgerows.

Rhynchaenus fagi.

Common and widely distributed throughout the British Isles. It feeds on Fagus sylvatica and the larvae mine the leaves of the tree. Adults overwinter among the leaves of evergreens and in spring they can often be found at long distances from the host plant (Morris 1968). It seems that the adult also has a small range of plants which are utilised for early spring feeding and pre-overwintering feeding (Bale and Luff 1978).

Sciaphilus asperatus

A local species generally distributed from the Midlands districts southwards, but rarer further North and only occasional in Scotland. It is found in woods and in hedgerows and is presumably polyphagous.

Tropiphorus elevatus

A very local species found in England and Scotland. Fowler (1891) states it is found in moss and under stones, but it is recorded as being associated with M. perennis.

Tropiphorus obtusus

A very rare species found in England, Scotland and Ireland. It is recorded as being associated with M. perennis.

Tropiphorus terricola

A local but not uncommon species found throughout the British Isles. It feeds on M. perennis.

Lathridiidae

Corticaria crenulata

Local but generally distributed throughout England, rarer further north and in Scotland. In decaying sea weed, haystack refuse, moss and so on. Species in this genus probably feed on fungal hyphae.

Corticaria elongata

Common and generally distributed throughout England but local in Scotland. In haystack refuse, moss and so on.

Enicmus histrio

Local throughout the British Isles in vegetable refuse.

Lathridius nodifer

Common and generally distributed throughout the British Isles. In vegetable refuse, woodstacks and moss.

Nitidulidae

Meligethes sp.

Thirty four species occur in Britain and they are often difficult to separate. The species of this genus occur on flowers of many species and very few seem to be confined to a single plant species.

Meligethes kunzei

This is a rare species found in England as far north as Yorkshire. Host plants include Lamium album, M. perennis, Stachys sylvatica, and Melampyrum pratense.

Micrurula melanocephala

A local species occurring throughout England but rare in the Northern counties and very rare in Scotland. It is found in flowers of many plant species, including trees.

Salpingidae

Rhinosimus viridipennis

Locally common throughout the British Isles. It is usually found under bark and in decaying plant material.

COLLEMBOLA

Entomobryidae

Entomobrya nivalis

A very common species found in many situations, especially on bushes and on pine trees. This species is probably feeding on organic debris, pollen, spores and leaf surface microflora.

Lepidocyrtus lignorum

A very common species found in similar situations to, and having a similar "diet" to E. nivalis.

Orchesella cincta

A common species found in fields, under the fallen boughs of trees, in moss, amongst decaying leaves and in other similar habitats.

Sminthuridae

These are the globular springtails and they have a worldwide distribution. They have been little studied but are usually found in soil, in decaying vegetable matter, amongst living foliage and under the bark of trees. Pollen, fungal spores, fungal hyphae, micro-organisms and foliage are all eaten by this family (Richards 1968, Southwood 1973, P. N. Lawrence pers. comm.).

Bourletiella

Many species in this genus feed extensively on the foliage of spermatophytes, and also on pollen and fungal spores. The following five species were all very abundant amongst the foliage of *M. perennis*.

B. bicincta

On herbs in woodland especially in damp conditions.

B. flava.

On herbs in woodland.

B. pallipes

In dry grassy places.

B. repanda

In fields and amongst herbaceous vegetation.

B. sulphuren

In fields especially in Spring and Summer.

HEMIPTERA : HETEROPTERA

Acanthosomatidae

Elasmostethus interstinctus

Found throughout the British Isles in mixed woodland. Its principal food plant is *Betula sp*. but it will also feed on *Corylus avellana*, *Fagus sylvatica*, *Populus tremula* and *Quercus sp*. The imago is the overwintering stage.

Miridae

Calocoris major

This is primarily a Northern species in the British Isles and is usually found in or at the margins of damp woods, where it is often abundant. Food plants probably include Urtica dioica and M. perennis but it has also been collected from Stachys sylvatica, Allium ursinum and Rubus idaeus. The eggs overwinter and the larvae reach the 4th instar by mid May and the adult stage is reached in the first week of June. A few females may survive until the end of July.

Calocoris quadripunctatus

Found throughout the British Isles on Quercus sp. It is partly predacious and adults will feed on aphids and the larvae of other Miridae as well as piercing the vascular system of its food plant.

Calocoris sexguttatus

Widely distributed in the British Isles in woodlands and in thickets. Food plants probably include U. dioica and M. perennis but it is also partly predacious. It is often observed on the blossoms of various Umbelliferae species. The eggs overwinter and the adults usually appear in the second or third weeks of June. A few females survive until early August.

Dicyphus stachydis

Widely distributed throughout the British Isles. Its foodplant is Stachys sylvatica but it has been collected from other species such as M. perennis. The imago is presented from May to October but Spring and early Summer individuals are probably overwintered adults.

Dryophilocoris flavoquadrimaculatus

Common and widely distributed in all parts of the British Isles. The adults, which first appear in the last week of May, feed on Quercus sp. and on aphids, small Diptera and the larvae of other Miridae.

Harpocera thoracica

Common and widely distributed in all parts of the British Isles. The adult stage is reached in the third or fourth week of May and the bug feeds on Quercus sp.

Leptopterna dolabrata

This bug is found throughout the British Isles in meadows and other grassy places in fairly moist conditions. Its chief food plants are Phleum pratense, Agropyron repens, Alopecurus pratensis, Dactylis glomerata and Holcus lanatus. The eggs overwinter and the first adults appear at the end of June.

Plesiocoris rugicollis

This bug is sparsely distributed throughout the British Isles. The eggs overwinter and the first adults are found from early June until the end of July. (For food plant details see text).

Psallus variabilis

This is a rare species probably confined to S. E. England. It is confined to Populus tremula and Salix atrocinerea. The adults are found from mid-June until July.

Psallus varians

Common throughout the British Isles on Quercus sp. although adults often 'stray' to other tree species. The eggs overwinter and the first adults appear in early June with a few adults surviving until early September.

HEMIPTERA : HOMOPTERA

Aphididae

Aulacorthrum solani

This species infests a large number of plants belonging to many different families. The case of hibernation as eggs, followed by normal development of the fundatrix (winged adults of the first generation) on a number of quite different unrelated plants is exceptional.

Drepanosiphum sp.

All Drepanosiphum species live on *Acer pseudoplatanus* and *A. campestre* and *D. platanoides*, the commonest species is common wherever its host plant, *A. pseudoplatanus*, flourishes.

Uroleucon sp.

Most species of this large genus are mono or oligophagous and feed on various *Compositae*. A few species occur on *Campanulaceae*. *Crepis sp.*, *Hieracium sp.*, *Hypochaeris sp.*, *Centauiea sp.* and *Cirsium sp.* and many other if not most British Compositae are quite commonly infested. Most *Uroleucon* feed on the flower stem (V. F. Eastop pers. comm.).

Cercopidae

Aphrophora alni

Widely distributed in the British Isles. It feeds on a considerable variety of trees and bushes.

Philaenus spumarius

A very abundant, widely polyphagous species. The nymphs live in a mass of froth or spittle. It is found throughout the British Isles on a wide variety of trees and herbaceous plants.

Cicadellidae

These are the leaf hoppers, a large family with over 250 British species. They are extremely numerous insects and large numbers can be beaten from trees, shrubs, herbs and grasses in the summer.

Cixiidae

Cixius distinguendus

Local but widely distributed in the British Isles. It is mainly found in woodland and according to Whittaker (1969) M. perennis is one of its food plants.

Psyllidae

The Psyllidae or jumping plant lice are an important component of the Hemipterous fauna of many dicotyledonous plants. 77 species are known to occur in Britain. The nymphal stages are usually host specific whereas adults will often disperse and feed (but not oviposit) on plants other than the main host.

Psylla peregrina

A very common species found throughout the British Isles. Its host plants are Crataegus monogyna and C. oxycanthoides. The eggs overwinter on the dormant buds of the host plant(s) and there is one generation a year.

LEPIDOPTERA

Geometridae

Perizoma didymata

This species is common in almost every part of the British Isles. *M. perennis* is a new food plant record for this polyphagous species which also feeds on *Teucrium scorodonia*, *Anemone nemorosa*, *Primula vulgaris*, *Stellaria media*, *Silene dioica*, *Oxalis acetosella*, *Ranunculus ficaria*, *Vaccinium myrtillus* and a few other species. The larva may be found from April to June and the imago is on the wing in July and August.

Micropterigidae

Micropterix calthella

This is the commonest of the five species in the genus. The adult is usually day flying and feeds on the pollen of various *Ranunculaceae* and other flowering plants including *M. perennis* during May and June. The larvae feed on various mosses and liverworts.

Noctuidae

Phlogophora meticulosa

This species is common throughout the British Isles and the larvae are widely polyphagous, feeding on a great many herbaceous plant species including *M. perennis*. The larvae and adults are found throughout the year, the former being most abundant in July, August and September and the latter being most abundant in May and June.

Pyralidae

Pyrausta nivealis

Common throughout the British Isles in hedgerows, scrub and woodland. The larvae feed on a great variety of trees, shrubs and herbs, including M. perennis, Stachys sylvatica, Urtica dioica, Corylus avellana and Rubus sp. to mention just a few. Larvae can be found between October and May (they hibernate over winter) and the adults appear in June and July.

Pyrausta olivalis

Common throughout the British Isles with the exception of Northern Scotland in woods and hedgerows. The larvae feed on a variety of herbs and shrubs including M. perennis, Stachys sylvatica, Urtica dioica, Glechoma hederacea, Sambucus nigra and Humulus lupulus. Larvae can be found between September and April (they hibernate over winter) and the adults appear in June and July.

Tortricidae

Olindia schumacherana

This species is widely distributed in the British Isles but is rather local and never very common. The larvae feed between April and June on M. perennis, Ranunculus ficaria, Aquilegia vulgaris, Vaccinium myrtillus and other herbaceous plants. The adult appears in June and July.

PSOCOPTERA

There are 90 species of Psocoptera recorded from Britain. Those species found outdoors are mainly found on vegetation, in leaf litter, and on bark. Many food stuffs are utilised including unicellular algae, pollen, fungal spores, yeasts, honeydew moulds and other organic debris. It is unlikely that any species are specifically associated with any particular plant species. (Information source : New. 1971, 1974).

THYSANOPTERA

There are 146 species of Thysanoptera (Thrips) recorded from Britain. Most species are phytophagous on Spermatophytes, a few feed on fungal hyphae and spores and some are predacious. Thrips are active insects and are frequently collected from plants on which they do not breed (Morrison 1949, Mound et. al. 1976, Pitkin 1976).

Thripidae

Limothrips cerealium

Associated with various Graminae and sometimes is quite abundant on cereals. Widespread in Europe.

Limothrips denticornis

In the florets of Graminae, particularly Avena fatua. Widespread in Europe - apparently more common in Southern England than in Scotland.

Taeniothrips inconsequens

Host plants include Pyrus sp. Malus sp. Prunus sp. and Acer sp. Widespread in Europe, locally common in Britain.

Thrips atratus

In the flowers of many plant species, but particularly of the Caryophyllaceae family. Widespread in Britain and Europe.

Thrips fulvipes

Locally common in Britain on M. perennis.

APPENDIX 3

KEY TO THE AUTHORITY ABBREVIATIONS USED IN TABLES 5 AND 6

Agr.	Agren
Bohn.	Boheman
Bons.	Bonsdorff
Bour.	Bourlet
DGr.	De Geer
Er.	Erichson
F.	Fabricius
Fall.	Fallen
Fors.	Forster
Gyll.	Gyllenhal
Hall.	Haliday
Hbst.	Herbst
Herr.	Herrich
Kltb.	Kaltenbach
Kirb.	Kirby
Kirs.	Kirschbaum
Kr.	Kraatz
Laich.	Laicharting
Lat.	Latreille
L.	Linnaeus
Man.	Mannerheim
Marsh.	Marsham
New.	Newman
Panz.	Panzer
Pk.	Paykull
Reut.	Reuter
Schiff.	Schiffermuller
Schor.	Schoenherr
Schol.	Scholtz
Schul.	Schultze
Steph.	Stephens
Vill.	Villers
Westw.	Westwood

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