INSECT HERBIVORE COMMUNITIES COLONISING THE FLOWER-HEADS OF BERKHEYA IN SOUTH AFRICA AND CARDUOIDEAE IN EUROPE AND CALIFORNIA

by

MAXWELL MAITLAND CLARK

Thesis submitted to the University of Cape Town
in fulfilment of the requirements of the degree of
Doctor of Philosophy

Department of Zoology
University of Cape Town
Rondebosch 7700
South Africa

November, 1988

CONTENTS

ACKNOWLEDGEMENTS

I am grateful to Prof V.C. Moran for his supervision of this thesis and his guidance over the years. I am also indebted to Dr J.H. Hoffmann for his constant help and advice.

I have also benefitted from discussions and correspondence at various times with Prof D. Goeden, Prof M.P. Hassell, Prof J.H. Lawton, Prof H. Zwölfer, Dr P.E.H Hulley, Dr J. Scott and Dr H. Zimmermann. Prof J.H. Lawton, Dr J.H. Hoffmann and Mr J.S. Donaldson kindly commented on the penultimate draft of this thesis.

I would like to thank the following people for their assistance: Dr M.W. Mansell, Dr G.H. Prinsloo, Mr J.S. Donaldson, Mr I.M. Miller, and Mr R. Oberprieller (insect identifications); the staff of the Bolus Hebarium at the University of Cape Town and Dr A. Jacot Guillardmod (plant identifications); Mr J. Perrera and Mr D. Wallace (technical assistance); Mr C. Castello-Villan and Miss C. Malony (statistics and computing).

This work was funded by grants from the FRD (C.S.I.R) and the Department of Agriculture and Water Supply to Prof V.C. Moran, and I was the recipient of a C.S.I.R. PhD studentship.

I am grateful to my parents for their continued interest and support. I would also like to thank my wife, Desiré: she drew the figures, typed the manuscript, and provided support and encouragement throughout.

RESUMÉ

The diversity and composition of insect herbivore communities are affected by characteristics of their host plant species. The genus Berkheya in South Africa and genera in the Cynaroideae (commonly called thistles) are morphologically similar but only distantly related plants in the Asteraceae. Berkheya and Cynaroideae therefore provide an opportunity to test some current ecological theory about how plants affect their insect herbivore communities.

Insect herbivore communities associated with the flower-heads of Berkheya, Californian thistles and European thistles were compared. The effects of the range, architectural complexity and taxonomic isolation, of the host plant, on the herbivore communities was investigated to explain why their communities appeared similar in some cases and why they differed in others.

Results show that herbivore flower-head communities associated with Berkheya and Californian thistles were similar. Herbivore communities associated with the flower-heads of European thistles were variable, but generally comprised fewer species and different taxa and guilds when compared to communities in the other two plant groups. Range, flower-head size and taxonomic isolation all had an effect on the herbivore communities but their effect differed between geographic regions and between plant species. The pool of insect herbivore species available to colonise flower-heads also had a marked effect on the herbivore communities.

CHAPTER 1

INTRODUCTION

Plants are known to have great influence on the diversity and composition of the insect herbivore communities that feed on them (Strong et al. 1984). Berkheya (Asteraceae: Arctoteae) and thistles (Asteraceae: Carduoideae) are herbaceous plants which, despite their taxonomic differences, show remarkable morphological similarities (Fig. 1.1). So, Berkheya and the thistles provide a novel template for comparison of herbivore communities and on which to test current ecological theories about how plants influence their associated insect herbivore communities.

Much of the ecological theory about insect herbivore/plant interactions has been derived from the recent, and fruitful, analytical approach to the study of insect communities (Root 1973, Lawton 1976, Seifert & Seifert 1976, 1979, Strong 1977, Simberloff 1978, Thompson 1978, Rey 1981). One of the main purposes of this study was to determine whether general conclusions can be made about the association of insect herbivores with Berkheya and thistles and whether there are any 'rules' that have influenced the evolution of these associations. It is shown repeatedly that there are significant and interesting correlations between characteristics of the plants and their herbivore communities, but these are not universal.

The study involved a comparison of the insect herbivore communities associated with three plant groups: Berkheya species sampled in South Africa, European thistles surveyed by Zwölfer (1965), and the Californian thistles

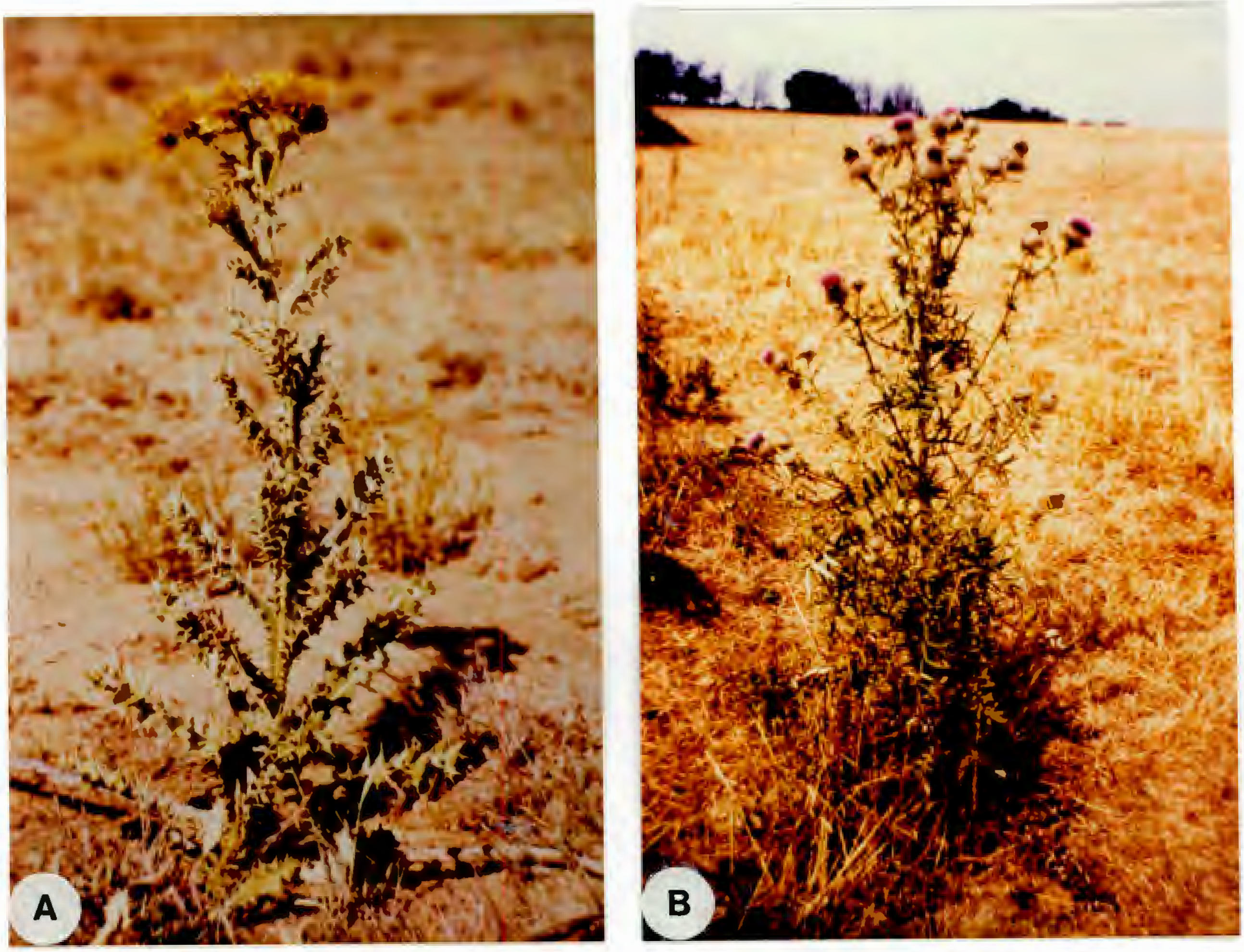


Fig. 1.1 Flowering Berkheya (A) and Cirsium (B) plants. Photographs taken by Dr H. Zimmermann.

recently sampled by Goeden & Ricker (1986a, 1987a, 1987b). The effects that these host plants have on their insect herbivore communities were also analysed to determine whether or not they can account for some of the similarities and differences observed between the herbivore communities from the three plant groups.

This study concentrated on the herbivore communities associated with the flower-heads of Berkheya and

Californian and European thistles. Flower-heads form discrete micro-habitats in which insect herbivores interact with each other and with their host plant. Because of the discrete nature of the flower-heads, these insect herbivore communities are more suitable to study than communities on the entire plant, especially since the flower-heads can easily be discretely sampled. In addition, much information is already available about the insect herbivore communities on thistle flower-heads in Europe due to the classical studies of Prof H Zwölfer (Zwölfer et al. 1971, Zwölfer 1965, 1979a, 1982a, 1985, 1987).

The insect herbivore communities on plants are influenced in several ways, three of which include; (1) the geographical distribution of the plant, (2) the morphological structure of the plant and (3) the taxonomic isolation of the plant. These aspects have been reviewed recently by Strong et al. (1984) but a brief account is given here to provide background information and to place this thesis in perspective.

1.1 A brief perspective

Initially, the insect herbivore community needs to be defined. A definitive description of a herbivore community is difficult because communities can be defined at different levels. For example, the community can range from the population of a single insect species found inside a particular flower-head, to all the insect species that feed on a particular vegetation type. Therefore, how the herbivore community is viewed is usually arbitrary and depends to a large extent on the type of ecological system that is studied. In this thesis, the insect herbivore community was considered to be the complex of insect herbivore species associated with a particular plant species over its entire natural range.

One of the best studied plant-effects on herbivore communities is host plant range. Southwood (1960, 1961a) was first to observe that more insects species feed upon widespread plants than on similar plants with a smaller range. Much has since been written about this species-area relationship with regard to insect herbivores (eg. Lawton & Schröder 1977, Strong 1979, Connor & McCoy 1979, Auerbach & Hendrix 1980, Neuvonen & Niemela 1981, Claridge & Wilson 1981, 1982). Several hypotheses have been proposed to explain this relationship and these are discussed by Price (1983) and Strong _et al_. (1984). In essence, widespread plants cover more kinds of habitats, to which certain insect species may be restricted, than rare plants and they therefore have a higher probability of being encountered by new insect herbivore species (Southwood 1961b, Williams 1964).

The architectural complexity of plants also affects the herbivore community and this subject has been reviewed by Lawton (1983a). Lawton & Schröder (1977, 1978) and Strong & Levin (1979) showed independently that an increase in plant size and morphological complexity results in a general increase in the number of herbivore species that inhabit the plant. Large plants have more exposure to herbivores and architecturally complex plants provide more micro-habitats for insects to colonise. A clear example, provided by Moran (1980) who looked at insects on _Opuntia_ species, clearly shows the effect of plant size and architectural complexity on species diversity.

The diversity of the host plants' closest relatives can also influence the herbivore community (Strong _et al_. 1984). Plants with many close relatives are expected to be colonised by more herbivore species than taxonomically isolated plants. This hypothesis is based on the assumption that related plants are biochemically more similar to each other than are unrelated plants. It is considerably easier for a herbivore to move onto another plant species that is biochemically similar to its conventional host plant. There are fewer hurdles to overcome and the herbivore may be considerably preadapted to the task. Taxonomic isolation is therefore expected to have a negative effect on species richness (Janzen 1968, 1973, Lawton & Schröder 1977, Lawton & Price 1979). The use of plant biochemistry to elucidate the taxonomy of plant groups provides some support for assumptions made by the hypothesis (eg. Valadon 1977). Several studies have shown that taxonomically isolated plants do have impoverished faunas (Cornell & Washburn 1979, Connor et al. 1980, Moran & Southwood 1982, Southwood et al. 1982), but the converse may also be true (Davis 1967) because plants that are taxonomically related are not always biochemically similar. Also, taxonomically unrelated plants can have certain similar secondary compounds that result in them sharing some herbivore species (Berenbaum 1981).

The size of plant taxa could also affect the kinds of herbivores in the community. If host shifts between biochemically similar and related plants are more simple, similar kinds of herbivores should be found on closely related plants. Thus a group of related plants that occur sympatrically could provide a pool of insect herbivore species capable of colonising each of the plant species. The size of this species pool would depend, to a large extent, on the number of related plant species.

Host plant range, architectural complexity and taxonomic isolation probably act together on the herbivore community. Therefore, if all these factors were similar in two or more groups of plants, it would be expected that their herbivore communities should be similar.

1.2 Thistles and Berkheya

Thistles and Berkheya are morphologically similar. Because of this similarity, members of Berkheya are known locally in South Africa as thistles. To prevent confusion, in this thesis only the members of the Cynaroideae will be called thistles.

Prior to the present study, nothing was known about the insect herbivores that fed on Berkheya, but the herbivore communities of thistles have been the subject of extensive study for the past 25 years (Zwölfer 1988). Interest in the herbivorous insects on thistles arose primarily because some thistles are important weeds in many parts of the world (Julien 1982) which has encouraged several biological control projects (Kok & Surles 1975, Goeden & Ricker 1977, 1978, Schröder 1980, Harris 1980, Boldt & Kok 1982, Boldt & DeLoach 1985, Kok & Pienkowski 1985, Harris 1986, Goeden et al. 1987). In addition, several studies have covered the biology and ecology of some of the insect species (eg. Cameron & Redfern 1974, Lalonde & Shorthouse 1984, Steck 1984, Redfern & Cameron 1985, Zwölfer 1979a, 1979b, 1980, 1982a, 1982b, 1984, 1985, 1986, 1987). Surveys have also been carried out on thistles, in the genus Cirsium, indigenous to California in North America but little is known about the insects' biology (Goeden & Ricker 1986a, 1987a, 1987b).

1.3 Scope of this thesis

The aims of this study were to compare the insect herbivore communities from the flower-heads of Berkheya, Californian thistles and European thistles, and to determine whether the effect of the host plants on their herbivore communities were responsible for any similarities or differences between the communities. Similarities were identified by; similar herbivore species numbers, similar numbers and proportions of specialist and endophagous herbivore species, similar kinds and relative proportions of insect orders or species and guilds.

Details about the distribution, morphology and taxonomic diversity of the host plants were required first, and these are reported in chapter 2. An initial survey was also carried out on one Berkheya species to help design a program to sample Berkheya in South Africa. The techniques used to sample the flower-heads are then described (chapter 3).

Because nothing was known about herbivorous insects on Berkheya, six Berkheya species were surveyed in South Africa to identify the insect species that feed on their flower-heads. In addition, the biology of the most commonly encountered herbivore species was studied to determine what parts of the flower-heads they ate (ie. to identify their guilds and also to determine how much they ate to establish what impact they had on the flower-heads and on any co-occurring herbivore species) (chapter 4).

Once these initial details were known, the herbivore communities could be analysed and compared. The approach adopted was to first compare the insect herbivore communities to identify any similarities (chapter 5). Next, the effect of plant range, architectural complexity and taxonomic isolation on the herbivore communities was analysed to determine whether these factors were, in fact, responsible for any similarities or differences observed between communities (chapter 6). This approach separates the analyses of the herbivore communities and plant effects. The influence of any previous assumptions about the relationships between herbivore communities and plants is avoided, and the chance of a circular argument when relationships are sought is thereby minimized (Field *et al*. 1982).

Finally, the conclusions made from the analyses are synthesised and the effect of plants on the evolution of herbivore communities in *Berkheya* and thistle flower-heads is discussed. The importance of preadapted species pools on the evolution of herbivore communities is also considered.

CHAPTER 2

HOST-PLANT PHENOLOGY, DISTRIBUTION, DIVERSITY AND FLOWER-HEAD STRUCTURE

Abstract

1. Information about Berkheya was required to design a sampling program to sample Berkheya flower-heads in South Africa. Therefore, a field study was initially carried out on B. heterophylla, which was chosen as a representative of the genus, and the plant phenology and timing of herbivore attack was examined. Four stages of flower-head development were recognised; young buds, mature buds, flowering heads and mature heads. Although at the end of the three month flowering period the mature heads formed only 53% of the number of flower-heads per plant, they formed 87% of the total flower-head resource per plant, measured by flower-head volume. Flower-heads were best sampled when mature because all the insect herbivore species that comprised the herbivore community were then collected.

2. A study of flower-head morphology showed that Berkheya and thistle flower-heads are structurally similar, and that they share many features of composite flower-heads. Therefore, similar kinds and numbers of niches are available to herbivores on Berkheya and thistle flower-heads.

3. The three plant groups, Berkheya in South Africa, thistles in California and thistles in Europe, are geographically separate so there has been little or no opportunity for mixing between the insect herbivore communities.

4. The taxonomic diversity of the host plants was compared to determine which plant species are related and which are taxonomically isolated. European thistles are the most diverse group with about 79 genera. Three thistle genera are native to North America and these species are closely related to the European thistles. Berkheya is the largest of 15 genera in the tribe Arctoteae, 14 of which occur only in southern Africa. Morphological and biochemical evidence suggested that Berkheya may have evolved from the thistles in Europe so the two groups could be more closely related to each other than their confamilial status implies.

In this chapter, basic information about Berkheya phenology and flower-head structure, and details about the distribution and diversity of Berkheya and thistles are provided.

2.1 Phenology of Berkheya

Berkheya are mostly biennial herbs. They produce a rosette in the first year and flower in the second year. Flowers are produced on a stem that grows vertically from the centre of the rosette and more than one flowering stem may be produced per rosette. For this study of Berkheya phenology, one species, B. heterophylla (Thunb.) was selected as a representative of Berkheya since it is typical of the genus.

The phenology of B. heterophylla was studied in a dense stand of B. heterophylla in a disturbed field on the outskirts of Grahamstown (33°23'S; 26°29'E). Twenty, one-year old plants, that had just started to produce a flowering stem from the rosette, were chosen at random. Each plant was marked with a metal tag for identification. To determine the amount of flower-head resource available, the number of flower-heads on each plant was counted and the flower-head diameter was measured. Flower-head diameter was taken as the maximum distance across the capitulum and was measured with vernier calipers. A separate record was kept of the growth of each flower-head from the time it first developed, until the end of the flowering period.

The timing of herbivore attack on the flower-head was determined from actual observations of the insects in the field and from oviposition and feeding scars on the flower-heads. If all the herbivore species that attacked the flower-heads were present at any one time during the growth of the flower-head, this would be the most appropriate stage to sample. Moreover, this growth stage should be easily recognised in the field. Therefore morphological features characteristic of the age of the flower-head were also noted.

These observations, counts and measurements were taken one week after marking the plants in November and at three-weekly intervals thereafter, until the end of the flowering period.

2.1.1 Flower-head development

Four stages in the growth and development of B. heterophylla flower-heads were recognised; young buds, mature buds, flowering-heads and mature heads.

Young buds were usually less than 7mm in diameter and were characterised by having immature florets completely covered by young bracts. When the florets pushed the bracts apart at the top of the flower-head, the mature bud stage was reached. In the mature bud stage only the tops of the florets, which were green at first, but soon turned yellow, were visible. The flowering-head stage was easily recognised. The florets opened dorsally when they flowered and they were less tightly packed together. In the final stage (mature heads) the florets died and turned brown while the achenes continued to grow and mature. Finally the flower-head stopped growing and all parts, except for the achenes, senesced. When the flower-head dried, the achenes sat loosely in the capitulum from which they were easily dislodged, and were free to disperse.

The flower-heads always developed on the flowering stem in a particular sequence, and they usually flowered in the order in which they appeared (Fig. 2.1). Individual flower-heads could therefore be identified by their

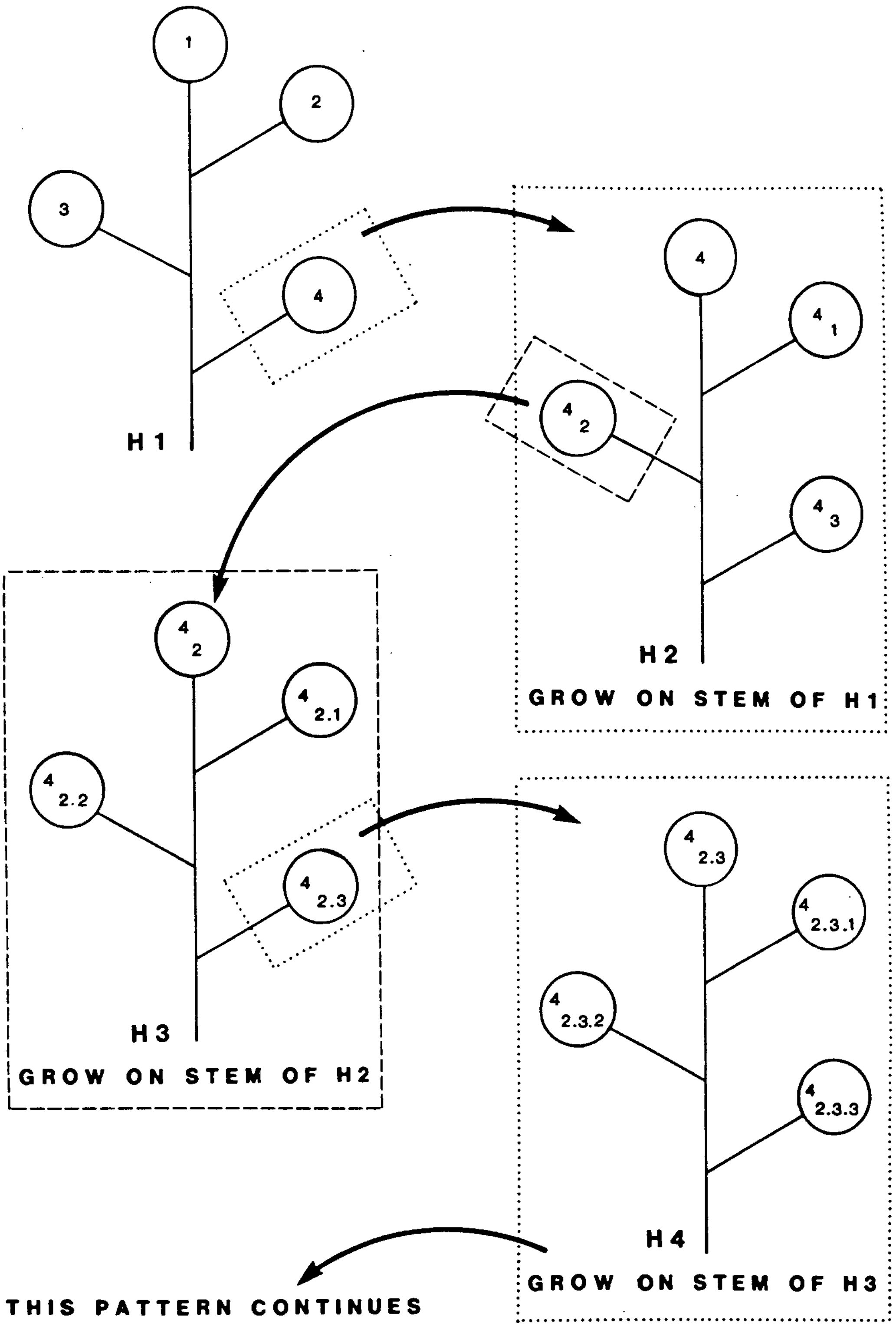


Fig. 2.1 Diagrammatic representation of the pattern in which flower-heads developed on the flowering stem of B. heterophylla. The notation was used to identify each flower-head every time they were measured, so that each flower-head did not have to be labeled. Primary heads (H1) developed first on the main flowering stem, then secondary heads (H2) developed on the stem of each H1 head, and H3 heads in turn developed on the stem of each H2 head. This pattern continued until the flowering stem died. Four flower-heads of each type are illustrated but up to 16 occurred on a plant.

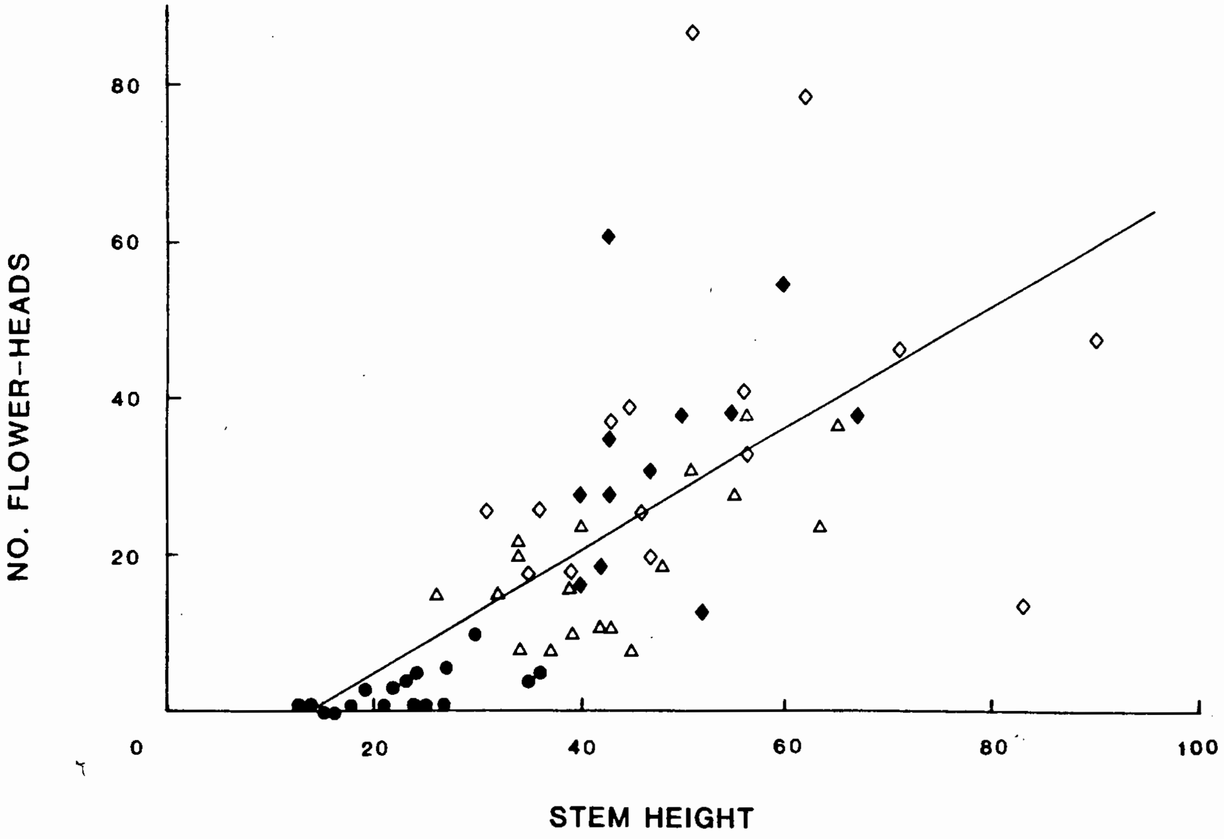


Fig. 2.2 The relationship between the height of the B. heterophylla flowering stem and the number of flower-heads on the stem. Counts and measurements were taken after 3 weeks (closed circles), 6 weeks (open triangles), 9 weeks (closed diamonds), and 12 weeks (open diamonds). $y = 0.79 x - 10.28$, $r^2 = 0.48$, $P<0.001$.

position on the flowering-stem and there was no need to label them. Tall flowering stems produced more flower-heads than short stems (Fig. 2.2) and flower-head production continued until the flowering stem died.

The production and development of flower-heads during the flowering season is illustrated in Fig. 2.3. Forty-seven

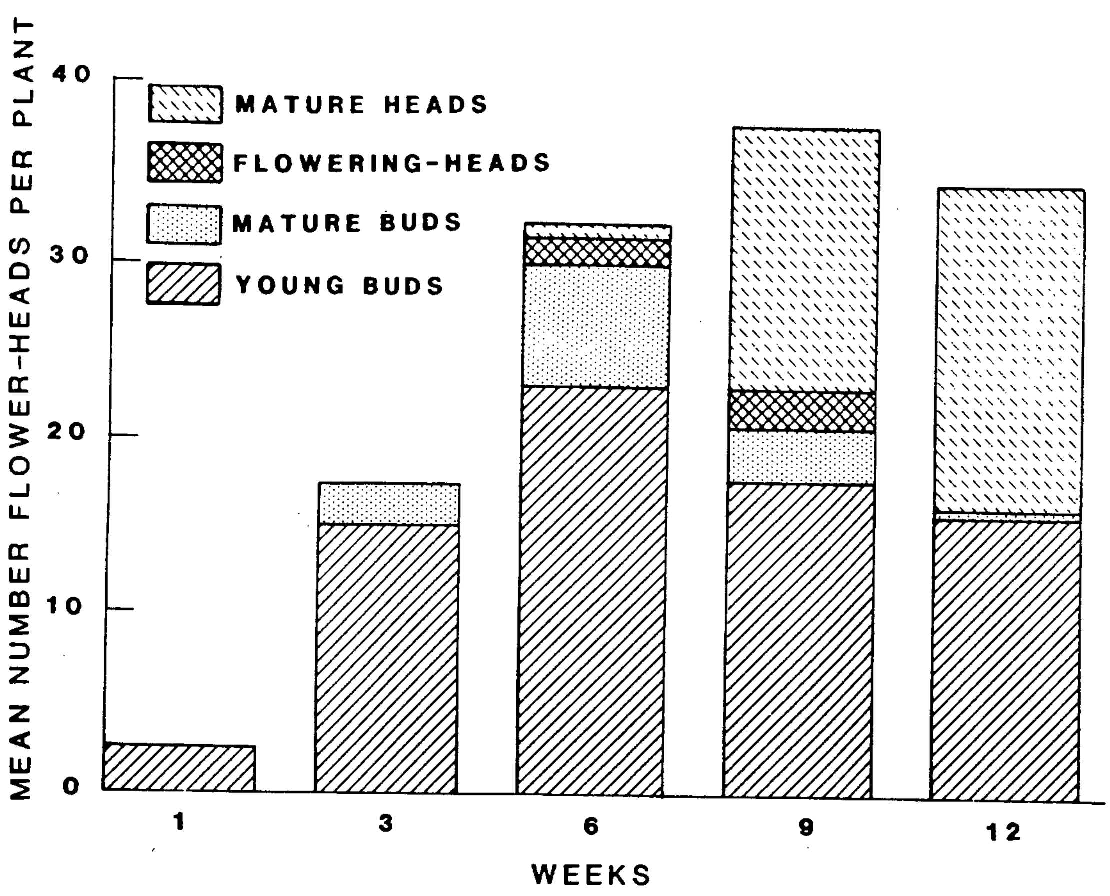


Fig. 2.3 The mean production of flower-heads per plant, on 20 B. heterophylla, during the flowering period. The development of the flower-heads from young buds to mature heads is also illustrated.

percent of the flower-heads never reached maturity because young buds that were produced late in the flowering period died with the flowering stem before they had time to develop. The proportion of heads in the mature bud and flowering-head stage at any one time was less than 25% of the total number of flower-heads present but the number of mature-heads increased towards the end of the flowering period and reached 53% of the total number of heads per plant. Most of the flower-heads were produced within the first 6 weeks of the flowering season (84%), after which very few flower-heads were produced. Some flower-heads were entirely removed by insect herbivores. This accounted for the reduction in total flower-head numbers from the ninth to the twelfth week (Fig. 2.3).

While flower-head numbers illustrate flower-head production, these numbers do not reflect the amount of resource available to insect herbivores. This is better illustrated using flower-head volume (Fig. 2.4). Although the mature-heads formed just over 50% of the total number of flower-heads (Fig. 2.3) at the end of the flowering

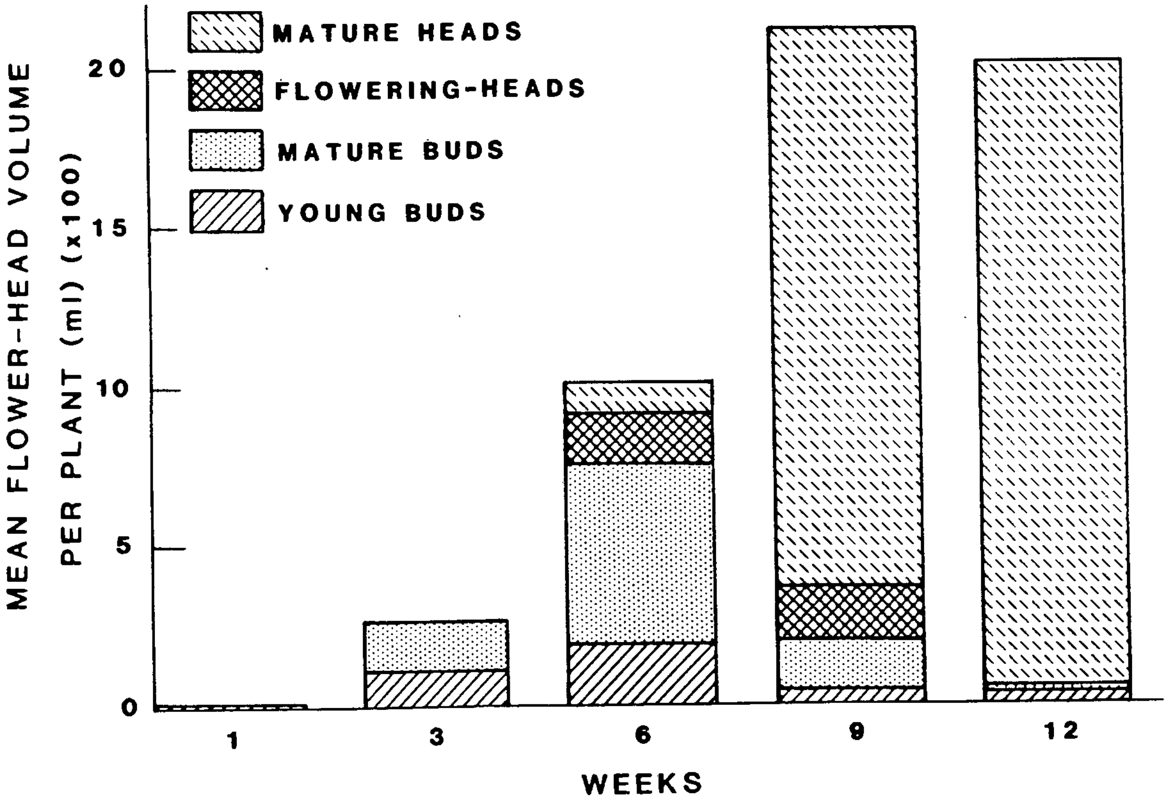


Fig. 2.4 The mean change in volume per plant, of each flower-head stage present on 20 B. heterophylla during the flowering period.

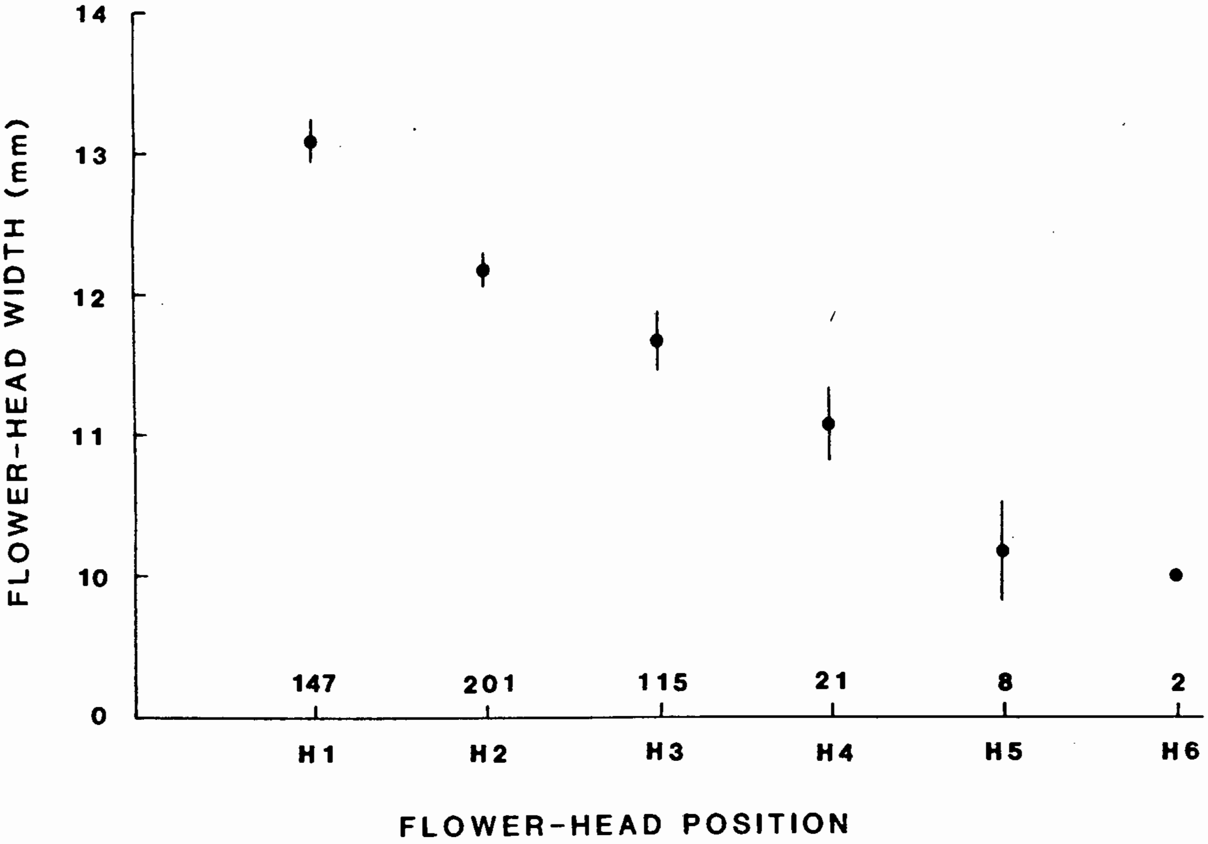


Fig. 2.5 The relationship between flower-head width and the position of the flower-head on the flowering stem (see Fig. 2.1 for an explanation of flower-head positions). Vertical lines represent standard error of the mean and the numbers above the horizontal axis represent the number of flower-heads.

period, mature-heads formed 87% of the flower-head resource available per plant.

During the flowering period, the later a flower-head matured the smaller it was likely to be (Fig. 2.5) and the less chance it had of reaching maturity (Table 2.1). Flower-heads that developed in position H3 and later, had 50% chance of maturing and most of these flower-heads died as young buds along with the flowering stalk (Fig. 2.3).

Table 2.1 Chance of a B. heterophylla flower-head reaching full maturity in relation to its position on the flowering stem (see Fig. 2.1 for an explanation of flower-head positions). The total number of flower-heads, on 15 plants, at each position is given by **N**.

	Flower-head position						
	H1	H2	H3	H4	H5	H6	H7
% Maturing	80	57	33	44	45	28	0
N	183	353	348	70	18	7	4

2.1.2 Timing of herbivore attack

General observation indicated that although the insect herbivore species may colonise flower-heads at different stages of their development, all species were present on the mature flower-heads.

The insects that fed on the outside of the flower-head, like the Hemiptera, were mobile and could move from head to head and were usually present on mature buds, flowering-heads, and mature heads. The immature stages of holometabolous species fed upon the inside of the flower-head. They were confined to a single flower-head for their entire development.

Observation of ovipositing curculionid females and the scars that they made on the flower-heads, showed that these insects first colonised mature buds and sometimes flowering-heads. Tephritids were also seen ovipositing in mature buds. None of the endophagous species completed their development before the flower-head reached the mature head stage (Table 2.2).

Table 2.2 Stages in the development of *B. heterophylla* flower-heads that were colonised by insect herbivores. More information about these herbivore species is provided in Table 4.3.

	Flower-head stage colonised			
Herbivore species	Young buds	Mature buds	Flowering heads	Mature heads
Coleoptera				
Dichelus sp 1			X	X
Larinus sp 1		X	X	X
Chrysolina sp		X	X	X
Diptera				
Urophora agromyzella Bezzi		X	X	X
Hemiptera				
Sciocoris sp		X	X	X
Brachycaudus helichrysi (Kaltenbach)	X	X	X	X
Sphaerocoris testudogrisea de Geer			X	X
Lepidoptera				
sp 1			X	X

These observations influenced the way in which *Berkheya* flower-heads were sampled.

2.1.3 Implications for sampling *Berkheya* flower-heads

In *B. heterophylla* flower-heads most of the food resource available to herbivorous insects was in the mature heads. If the endophagous insect species colonised the young buds, many would not mature because of the high mortality of flower-heads in this stage. The mature buds and flowering-heads were available for only a short time. Mature heads therefore represent the most stable and predictable habitat for the endophagous species.

The optimal stage of flower-head development for sampling, in order to obtain a representative sample of the herbivore population is the mature head, before the flower-head begins to senesce. Further advantages of collecting this stage are; (1) the endophagous insects have completed their development, and are not killed by removal of the flower-head from the plant, (2) these insects are therefore still able to emerge from the flower-head in an emergence box in the laboratory, (3) the adult insects thus obtained are easier to identify than the immature stages and (4) the achenes are fully developed in the mature heads so the damage caused by the herbivores can be assessed.

2.2 Flower-head morphology

One of the most characteristic features of the Asteraceae is the structure of the flower-head. The flower-head, also known as the capitulum, comprises many small individual flowers called florets. The capitulum is surrounded by protective bracts that form the involucre, so that the whole flower-head resembles a single flower. This basic flower structure is constant throughout the family, although it can be modified in different ways (Heywood 1978). Modifications have been used by plant taxonomists to differentiate between species. Berkheya and thistle flower-heads may therefore appear different when examined in detail, but, on a larger scale they appear similar since they have all the common structures characteristic of composite flower-heads (Fig. 2.6).

Echinops differs from the other thistles because each floret is surrounded by an involucre. The flower-head comprises a cluster of involucres (Moore & Frankton 1974).

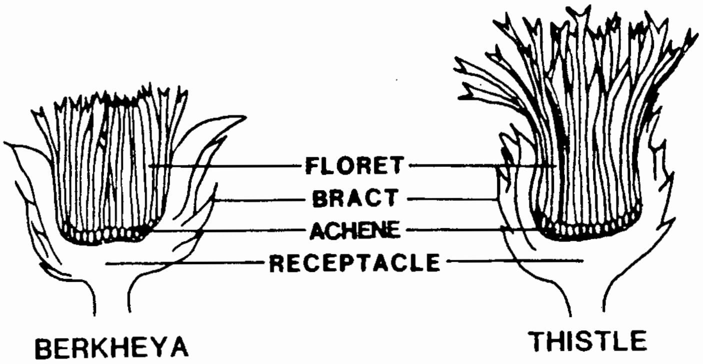


Fig. 2.6 The generalised internal structure of Berkheya and thistle flower-heads to show the similarity between the two.

The flower-head habitats of Berkheya and thistles are homologous and the same niches are present in the flower-heads of each plant group. According to the hypothesis that plant architectural diversity influenced the herbivore community (Lawton 1983a), Berkheya and thistle flower-heads should support similar numbers of herbivorous insects. However, host-plant range and the taxonomic diversity of the host plants' sympatric relatives will also affect herbivore numbers.

2.3 Geographical distribution and range of host plants

The Asteraceae, in which the thistles and Berkheya are found, evolved before the major continental drift that split up Gondwanaland (Turner 1977) and in consequence the family is now spread throughout most of the world. Berkheya is confined to sub-saharan Africa and has its centre in South Africa where 70 of the 73 described species occur (Gibbs Russell 1984). The Cynaroideae occur mostly in the palearctic region with their evolutionary centre in eastern Europe (Zwölfer 1988), but 3 genera are also indigenous to North America (Cirsium, about 120 species*; Saussurea, about 8 species; and a few Centaurea species) (Moore & Frankton 1974, Dittrich 1977), and a few Centaurea species are endemic to South America (Dittrich 1977). The Cynaroideae have not been successful in colonising sub-saharan Africa and only a few species of Carduus, Centaurea and Volutaria are present and their distributions are limited to tropical Africa (Dittrich 1977). The map in Fig. 2.7 shows that the distributions of Berkheya and Cynaroideae do overlap in central Africa, but because few Cynaroideae species are present in central Africa, Berkheya is almost completely separated from the European thistles and their associated herbivore species.

Only one genus of the Cynaroideae, Rhaponticum, occurs in Australia naturally (Dittrich 1977). The absence of Berkheya from Australia suggests that this plant genus evolved only after the land mass that is now known as Australia split off from southern Africa. Also, because the Cynaroideae have not successfully colonised southern Africa, there was little opportunity for the thistles to colonise Australia via this route.

This study deals with three geographically separate groups of plants; Berkheya in southern Africa, Cynaroideae that were sampled by Zwölfer (1965) in Europe and Cynaroideae that were sampled by Goeden & Ricker (1986a, 1987a, 1987b) in California. A comparison of the herbivore communities of each group will show to what extent geographical distribution can influence the kinds of insects in the herbivore communities.

*If subspecies and hybrids are excluded, the number of Cirsium species in North America is 90. I am grateful to Dr P. Harris for this information. (Added after examination).

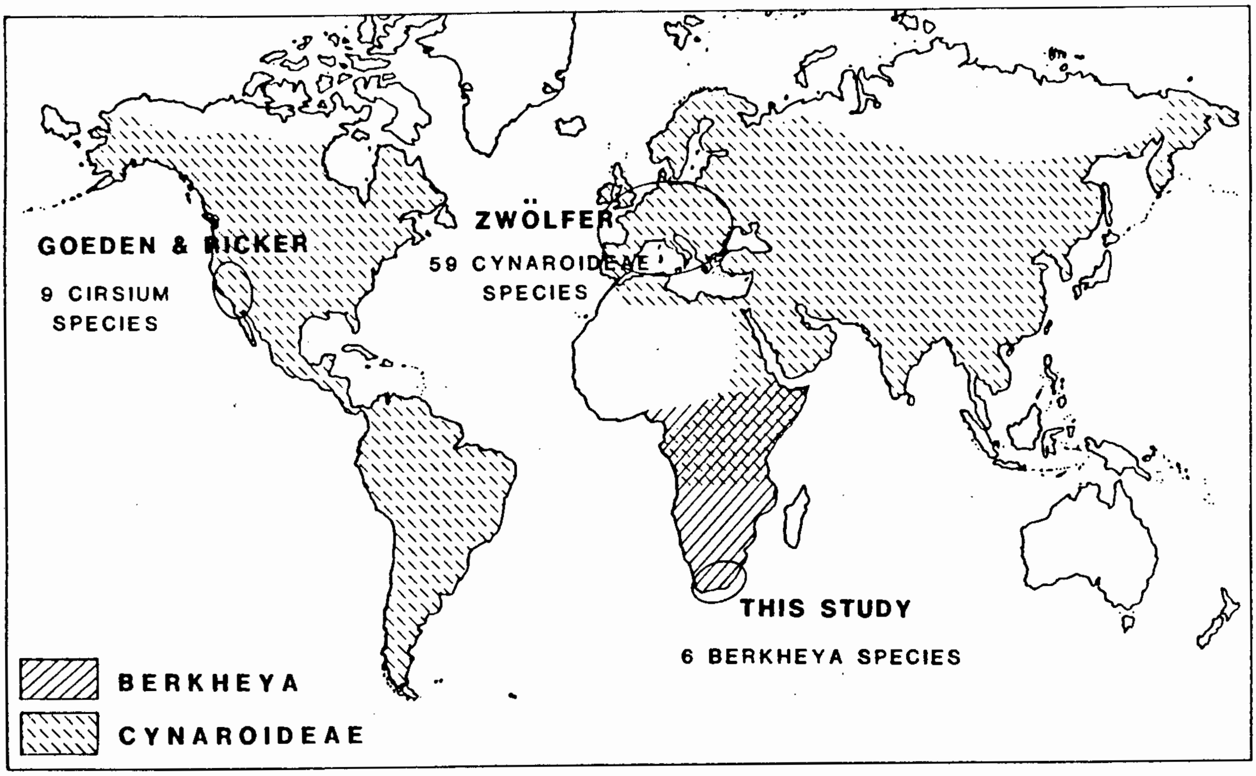


Fig. 2.7 World map illustrating the general distribution of the Cynaroideae and the Berkheya. The regions sampled by Goeden & Ricker (California), Zwölfer (Europe) and during this study (western and eastern Cape province, South Africa) are circled. Distributions were obtained from Dittrich (1977).

Several Cynaroideae species are agricultural weeds and have spread throughout the world (Julien 1982, Maw 1984). Thirteen Cynaroideae species have invaded South Africa (Carduus 2 spp, Cirsium 2 spp, Silybum 1 sp, Centaurea 4 spp, Microlonchus 1 sp, Cyanus 1 sp, Carthamus 1 sp and Cnicus 1 sp) (Gibbs Russell 1984), but all are without their native insect fauna.

If the thistles from Europe were introduced into South Africa together with their native insect fauna, these insects could colonise the local Berkheya species, which would change the herbivore communities on Berkheya. A tephritid, Urophora stylata F. has been released in South Africa for the biological control of Cirsium vulgare (Sâvi) Tenore (H.G. Zimmermann, personal communication), but this introduction was unsuccessful. Herbivore communities on Berkheya have therefore not been affected by exotic introductions on European thistles in South Africa.

Several insects from thistles in Europe have been successfully introduced into North America (Kok & Surles 1975, Harris 1980, Kok & Pieňkowski 1985). One of these introduced herbivores, Rhinocyllus conicus (Froelich) (Curculionidae: Coleoptera), has subsequently been found breeding in the flower-heads of Cirsium californicum Gray, C. proteanum Howell and C. occidentale (Goeden & Ricker 1986a, 1987a). These Cirsium species are indigenous to North America. Because R. conicus is not part of the indigenous insect fauna of North America, it is excluded from the herbivore communities of these plants in the analyses described in later chapters.

2.4 Taxonomy and diversity of thistles and Berkheya

The taxonomy and diversity of thistles and Berkheya is relevant to this study because similar kinds of insects are expected to colonise closely related plants. The taxonomic classification of the plants is used to indicate their 'relatedness'. Congeneric species are obviously more closely related than species in different subtribes.

A high diversity of related plants should result in a large pool of preadapted herbivore species. These plants are therefore expected to have a higher species richness.

than taxonomically isolated plants. The number of thistle species in North America and in Europe and the number of Berkheya species in South Africa may be important factors affecting the herbivore species in these regions.

Berkheya and the Cynareae are both part of the family Asteraceae, a very old group, whose origins date back to the Cretaceous (Turner 1977). The phyletic relationships of the tribes in the Asteraceae are controversial because the family is so old, and the groups have diversified so far apart that there are no connecting genera to indicate relationships between the tribes (Turner 1977). The result has been several taxonomic studies, each with a different number and grouping of tribes (Lessing 1832, Bentham 1873, Cronquist 1955, Carlquist 1976, Wagenitz 1976).

Europe has about 79 thistle genera (Tutin et al. 1976) and North America has about 3 thistle genera (Moore & Frankton 1974, Dittrich 1977). Southern Africa has about 15 genera in the Arctoteae, which is the tribe to which Berkheya belongs.

2.4.1 Taxonomy of Berkheya

The genus Berkheya is part of the tribe Arctoteae in the Asteraceae. Most species of the Arctoteae, like the Berkheya, are restricted to sub-saharan Africa. The Arctoteae is a relatively small tribe with about 194 species in 15 genera of which Berkheya is the largest (about 73 species) (Fig. 2.8).

Members of the Arctoteae are so morphologically similar to the Cardueae (=Cynaroideae) that the Arctoteae was once

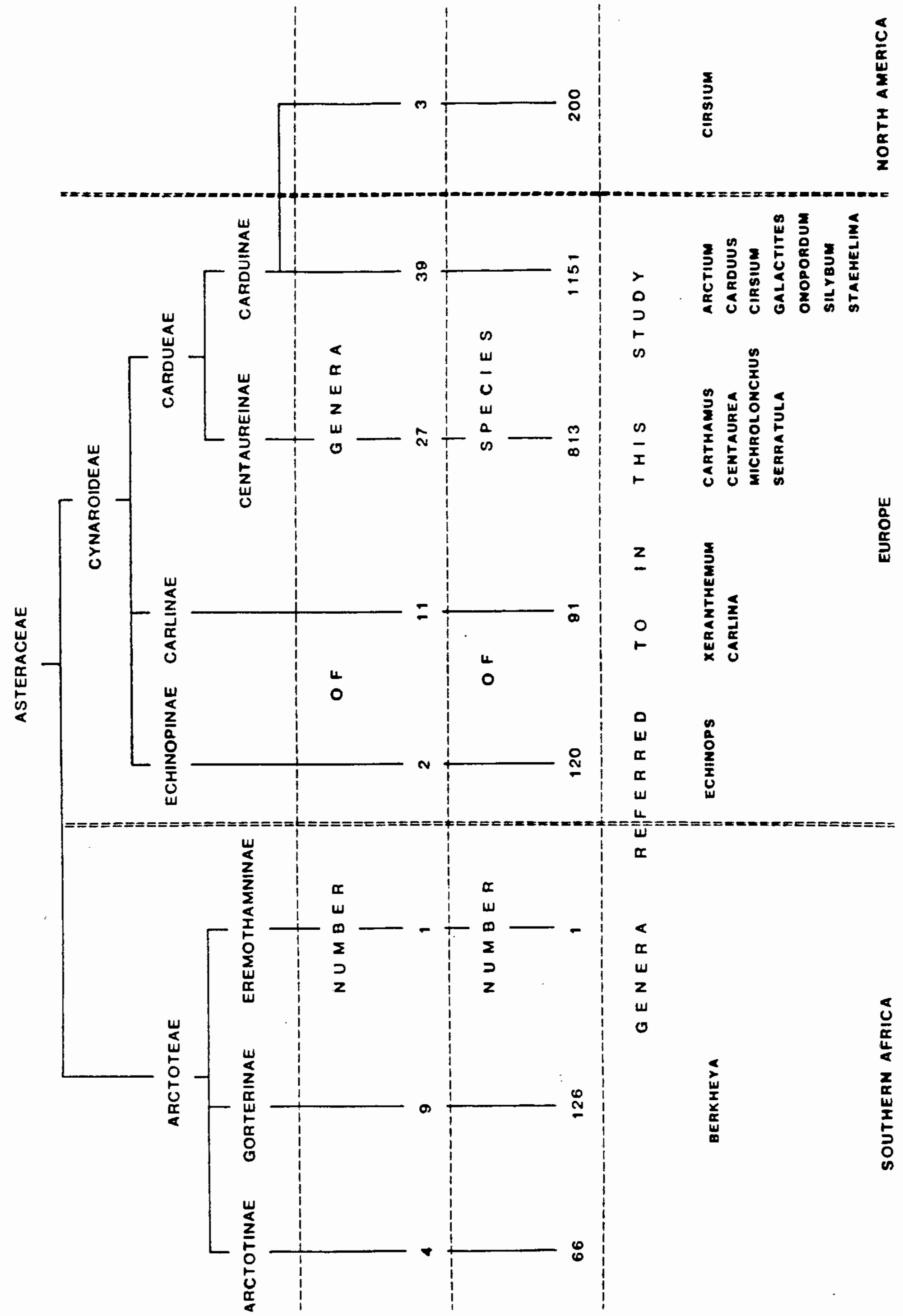


Fig. 2.8 The taxonomic relationship of *Berkheya* and thistle species dealt with in this study. Classification based on Dittrich (1977) and Norlindh (1977). The estimated number of species and genera in each of the regions sampled (see Fig. 2.8) is given to show the relative diversity of each group. Plant genera referred to in this thesis are also listed.

placed as a subtribe of the Cynareae (Cardueae) (Lessing 1832), and, although Bentham (1873) later raised the Arctoteae to tribal level, he still considered them to be southern representatives of the Cynareae. Morphological evidence therefore suggests that the Arctoteae and Cynaroideae are more closely related to each other than to the other taxonomic groups in the Asteraceae.

This relationship is further supported by biochemical evidence. Certain acetylenes, which are considered to be good taxonomic characters of the Arctoteae, are also present in genera of the Cynaroideae (Valadon 1977). Valadon (1977) considered Berkheya to be the primitive member of the Arctoteae and he found that Berkheya has certain chemical affinities with Echinops in the Cynaroideae.

2.4.2 Taxonomy of the Cynaroideae

The tribal name Cynareae, which is used by many authors, is illegitimate since it is predated by the name Cardueae described by Cassine in 1815 (Dittrich 1977). Cardueae was usually split into four subtribes; Echinopsidinae, Carlinae, Carduinae and Centaureinae. However, Dittrich (1977) re-examined the flower-head characters, and on the basis of new morphological characters, he created three tribes in the sub-family Cynaroideae: Echinopeae, Carlineae and Cardueae. Cardueae comprises two subtribes, Carduineae and Centaureinae. This division has also been supported by serological studies (Prof U. Jensen cited by Zwölfer 1988). Dittrich's (1977) classification of the Cynaroideae is followed in this study (Fig. 2.8).

Many hybrids of Cirsium occur in North America and this makes an estimate of the number of species difficult (Howell, 1960). A cytological investigation has shown that North American Cirsium species are closer to congenerics in Europe than to species in Asia Moore & Frankton (1963). Therefore it is difficult to accept Zwölfer's (1988) suggestion that the North American species originated from the Asian species and colonised North American via the Bering Strait.

This chapter provides information that was used to design a sampling program for Berkheya. In addition, details about the distribution, flower-head morphology and taxonomic diversity of Berkheya and the thistles were required so that the effect of these aspects on the insect herbivore communities could be determined and this is dealt with in later chapters.

CHAPTER 3

MATERIALS AND METHODS

Abstract

The Berkheya species sampled in South Africa are listed here with the methods used to sample their flower-heads. The thistle species sampled by Zwölfer in Europe and by Goeden & Ricker in California are also listed.

3.1 Berkheya species sampled in South Africa

In addition to B. heterophylla, five Berkheya species were selected for a detailed study of the herbivores that colonise their flower-heads (Table 3.1). This was to test the hypothesis that structurally similar flower-heads would be colonised by similar herbivore communities because similar niches are available. The initial selection was made after a careful examination of herbarium specimens. Only Berkheya species occurring in South Africa were considered.

Plant size, like structural complexity, also affects herbivore species richness (Strong et al. 1984). The thistle species surveyed in Europe and North America represented a range of flower-head sizes. The Berkheya species were therefore also selected so that a range of flower-head sizes, from small to large, were represented. Thus the effect of flower-head size on the herbivore communities could be investigated.

Berkheya distributions were obtained from herbarium records kept by the Botanical Research Institute in

Table 3.1 A list of Berkheya species whose flower-heads were sampled in South Africa.

Berkheya species	No. samples
B. bipinnatifida (Harv.)	13
B. decurrens (Thunb.)	11
B. heterophylla (Thunb.)	16
B. onobromoides (D.C.)	14
B. rigida (Thunb.)	14
Berkheya sp	11

Pretoria. The geographical distribution of each Berkheya species sampled was small so that the entire range could be effectively sampled. The sites where the six Berkheya species were sampled is shown in Fig. 3.1.

3.2 Sampling sites

The Berkheya species sampled in South Africa have a patchy distribution and some of the species were especially difficult to find. Populations were sampled if there were sufficient flower-heads in the appropriate stage of development. All of the sites were in disturbed areas, either along roadsides, or in fallow land.

3.3 Flower-head sampling techniques

For each site, a sample comprised between 100 and 300 mature flower-heads which were cut from the plant and placed into plastic bags. The bags were kept in a cool-box until the flower-heads could be sorted in the laboratory.

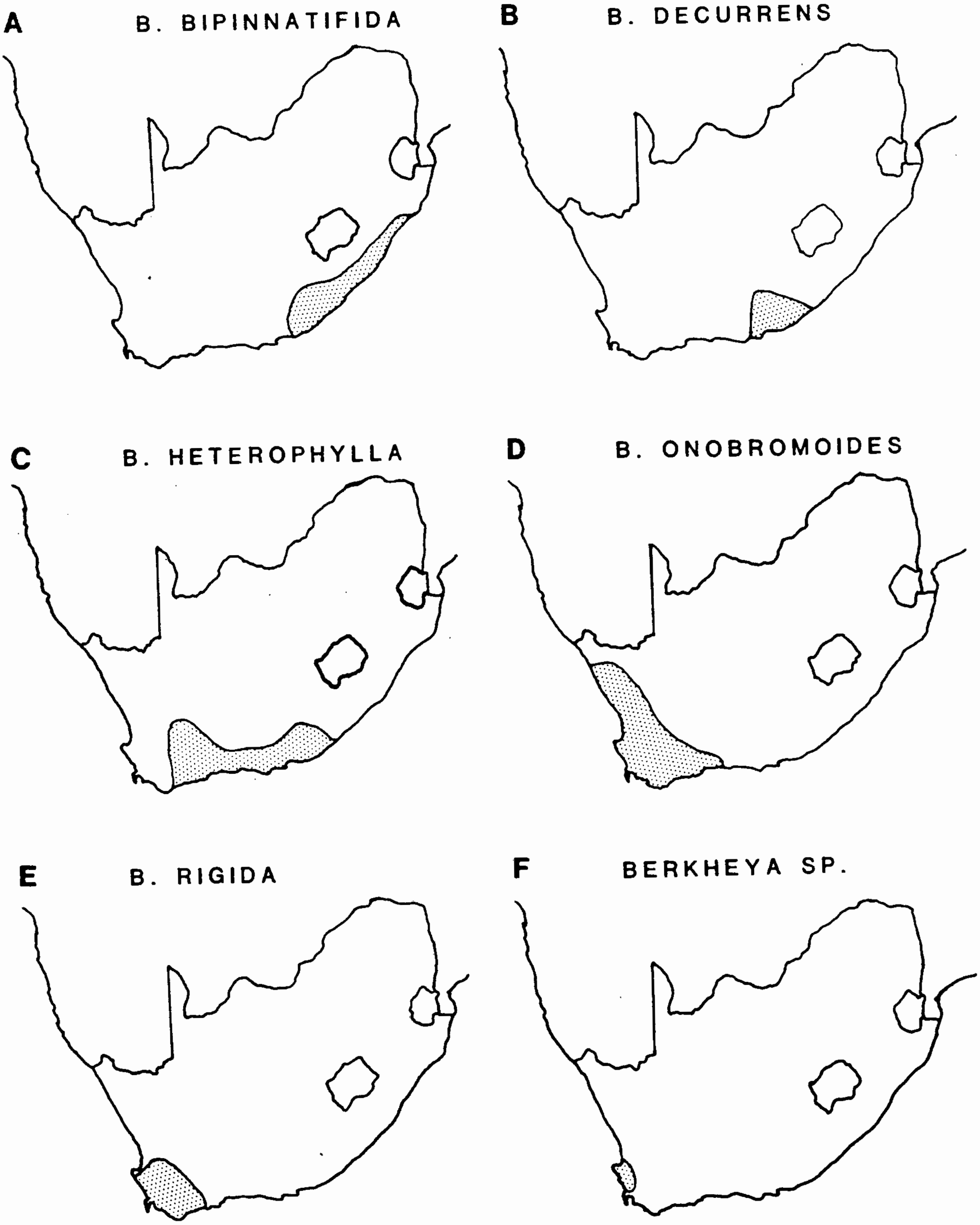


Fig. 3.1 Geographical distribution of the six Berkheya species sampled in South Africa.

At each site a herbarium specimen was collected and pressed. All the herbarium specimens were identified at the Bolus Herbarium in Cape Town to ensure that the correct plant species was sampled.

In the laboratory the flower-heads from each site were sorted into two subsamples. One subsample, consisting of a minimum of 100 flower-heads, was placed into emergence boxes made from cardboard cylinders (Fig. 3.2). Flower-heads were loosely packed into the cylinder which was then sealed. A small glass tube extended from a hole at the front of the cylinder. Emerging insects were attracted to the light and trapped in the glass tube. The insects could

Fig. 3.2 An emergence box used to collect insects as they emerged from flower-heads collected in the field.

then be easily collected from the glass tubes. Tubes were replaced every two days, or more frequently if necessary, to prevent large beetles damaging smaller insects and to prevent predation by spiders. The emergence boxes were checked for any insects that did not enter the glass tube when the contents were emptied out.

Another subsample of 25 flower-heads were frozen until they could be dissected. Frozen flower-heads were thawed and, before dissection, the diameter of each was measured across the width of the capitulum with vernier calipers. Each part of the flower-head was then carefully dissected and removed to expose any insects. All the achenes were also cut open to check for insects inside them. When insects were found, the adults were pinned and juveniles were preserved in 70% alcohol. All were labelled. Careful notes were kept of where the insects were found on the flower-heads and also the extent and characteristics of any damage caused by feeding.

After dissection, the flower-head pieces were dried in an oven at 50 °C for 48 hours and then weighed. Dry weight was recorded to obtain a measure of food resource and flower-head size. The difference in dry-weight between flower-heads that had been fed upon and those that were undamaged was used to indicate the amount of plant tissue eaten by the herbivores.

Insects obtained from the emergence boxes and dissected flower-heads were counted and sorted into morpho-types. Voucher specimens were sent for identification to the National Collection of Insects in Pretoria. Not all specimens were identified to species and some specimens could not even be identified to genus. This occurred because relatively few taxonomists work on South African insect groups, and, as no serious collecting had been done on Berkheya before, some of the species were collected for the first time and have not yet been described.

The initial morpho-typing was therefore important to determine the number of insect species. This was particularly necessary for lepidopteran species that were often represented by a single larva, that did not pupate, and that could not be formally identified.

3.4 Thistles surveyed in Europe by Zwölfer and in North America by Goeden and Ricker

Information on the insect herbivores that colonise the flower-heads of thistles native to Europe was obtained from a survey done by Zwölfer (1965) who made an extensive study of the insect herbivores of 59 thistle species (Table 3.2). Many thistle species are weeds in North America, South Africa, Australia, New Zealand and other countries (Holm et al. 1977), and the aim of Zwölfer's (1965) survey was to identify insect species suitable for the biological control of these weeds. Information about flower-head morphology was obtained from Tutin et al. (1976).

Cecidomyidae were sometimes recorded on flower-heads of thistles (Zwölfer 1965). These have been excluded from the analysis because the number of species involved is not known. Zwölfer (1984) also excluded cecidomyids from his analysis of guild structure in the flower-heads.

Six Cirsium thistle species were surveyed in California by Goeden & Ricker (1986a, 1987a, 1987b) (Table 3.3).

Table 3.2. List of Cynaroideae species, sampled by Zwölfer (1965), and used in this thesis. Continued on next page.

Species	No. samples
Arctium lappa L.	10
A. minus (Hill) Bernh.	19
A. tomentosum Mill.	5
Staelina dubia L.	2
Carduus nutans L.	90
C. defloratus L.	21
C. personatus (L.) Jacq.	16
C. acanthoides L.	32
C. crispus L.	22
C. sanctae-balmae Lois.	5
C. tenuiflorus Curt.	8
C. pycnocephalus L.	10
Cirsuim eriophorum (L.) Scop.	22
C. vulgare (Sâvi) Ten.	126
C. ferox DC.	3
C. pannonicum (L.) Gaud.	2
C. canum (L.) All.	9
C. acaule (L.) Scop.	23
C. heterophyllum (L.) Hill.	5
C. tuberosum (L.) All.	8
C. salisburgense (Willd.) G.Don.	16
C. erisithales (Jacq.) Scop.	12
C. oleraceum (L.) Scop.	42
C. spinosissimum (L.) Scop.	10
C. palustre (L.) Scop.	52
C. brachycephalum Jur.	5
C. monspessulanum All.	2
C. arvense (L.) Scop.	367
Silybum marianum (L.) Gäertn.	9
Galactites tomentosum Moench.	6
Onopordum acanthium L.	32
O. illyricum L.	5
Serratula tinctoria L.	11

Table 3.2. continued.

Species	No. samples
Centaurea jacea L.	82
C. nigrescens Willd.	9
C. nemoralis Jord.	23
C. pseudophrygia C.A. Mey.	4
C. cyanus L.	2
C. montana U.	5
C. truimfetti All.	2
C. stoebe L.	40
C. diffusa Lam.	4
C. paniculata L.	16
C. aspera L.	7
C. scabiosa L.	77
C. collina L.	4
C. calcitrapa L.	4
C. solstitialis L.	4
C. melitensis L.	2
Microlonchus salmanticus DC.	2
Carthamus lanatus L.	8
Xeranthemum annuum L.	1
Carlina vulgaris L.	30
C. corymbosa L.	2
C. acaulis L.	19
Echinops ritro L.	6
E. sphaerocephalus L.	4

Table 3.3. List of Cirsium species sampled in California by Goeden & Ricker (1986a, 1987a, 1987b).

Species	No. samples
Cirsium californicum Gray	28
C. proteanum J.T. Howell	12
C. mohavense (Green) Petrak	5
C. occidentale (Nuttall) Jepson	6
C. neomexicanum Gray	7
C. tioganum (Congdon) Petrak	4
C. nidulum (Jones) Petrak	3
C. congdonii Moore and Frankton	4
C. brevistylum Cronquist	3

Information on the flower-head herbivore species was extracted from these surveys to use in the analyses of herbivore communities.

CHAPTER 4

INSECT HERBIVORES ASSOCIATED WITH BERKHEYA FLOWER-HEADS

Abstract

1. Details about the insect herbivore species that comprised the communities present on the flower-heads of the six Berkheya species sampled in South Africa are presented.

2. Number of species present on the flower-heads of each Berkheya species were: B. bipinnatifida 9 species, B. decurrens 27 species, B. heterophylla 17 species, B. onobromoides 14 species, B. rigida 14 species and Berkheya sp 12 species. The insect taxa represented were Coleoptera, Diptera, Lepidoptera and Hemiptera.

3. The biologies of the most commonly occurring herbivore species were studied firstly to identify what kinds of guilds were present and secondly to determine what impact the herbivores had on the flower-head.

4. Three guilds were identified; external chewers, internal chewers, and sap suckers. Internal chewers caused the most visible damage to the flower-heads which was assessed by two methods. Firstly, the number of achenes eaten by each herbivore species was determined and secondly, the reduction in flower-head dry weight due to herbivore feeding was calculated. The latter method was not successful possibly because most of the flower-head parts eaten had a high water content so there was very little loss in dry weight. Resources were not limiting and none of the species of internal chewers displayed any behavioural adaptation to reduce crowding inside the flower-heads when this occurred.

5. Species packing in the herbivore communities on each Berkheya species was determined to compare firstly, the number of herbivore species in the flower-heads from each Berkheya site sampled and secondly, the proportion of flower-heads that were fed upon (percentage utilisation) at each Berkheya site sampled. Percentage utilisation reached 100% in herbivore communities on all Berkheya species except B. bipinnatifida and Berkheya sp.

A study of herbivore community structure requires diverse but detailed information about the component plant and insect herbivore species. Details about the host plants have already been covered (chapter 2) and the information required about insects on thistle flower-heads is already available.

To date, nothing has been published about any aspect of insect herbivores found on Berkheya. Lists of herbivore species collected from the flower-heads of six Berkheya species are therefore provided and the taxonomic composition of each herbivore community is compared. In addition, the biology of the most commonly occurring herbivore species is described. This information is required to place the insects into the correct guilds (Root 1973). Competition for resources in thistle flower-heads has been suggested as an important factor in the evolution of these herbivore communities (Zwölfer 1979a). Feeding damage was therefore assessed to determine what part of the flower-head was eaten by each species and to observe whether resources are limiting in Berkheya flower-heads.

The guilds found on Berkheya flower-heads are described and the guild structure of each Berkheya species is compared. Finally, the local herbivore communities of the six Berkheya species are examined and compared.

4.1 Insect herbivores found on Berkheya flower-heads

The herbivore species found in association with the flower-heads of B. bipinnatifida, B. decurrens, B. heterophylla, B. onobromoides, B. rigida and Berkheya sp are listed in Tables 4.1 to 4.6 respectively.

Berkheya decurrens flower-heads were colonised by the greatest number of herbivore species (27 species), followed by B. heterophylla (17 species), B. rigida (14 species), B. onobromoides (14 species), Berkheya sp (12 species) and B. bipinnatifida (9 species). Most of these herbivore species are associated only with the Asteraceae.

Table 4.1 A list of the herbivore species found colonising the flower-heads of Berkheya bipinnatifida. The stages collected; L, N, P and A refer to larvae, nymphs, pupae and adults. Immature stages indicated that these species bred on the flower-heads. Other biological details, like where and how they feed on the flower-head, are also provided.

Herbivore Species	Frequency (%) in collections	Stages collected	Endophagous/ ectophagous	Guild
COLEOPTERA				
Scarabaeidae				
Dichelus sp 1	8	A	ectophagous	chewer
Curculionidae				
Larinus sp 1	8	A	endopdagous	chewer
HEMIPTERA				
Pentatomidae				
Sciocoris	69	N, A	ectophagous	sap sucker
Pseudococcidae				
sp	8	N, A	ectophagous	sap sucker
Aphididae				
Brachycaudus helichrysi (Kaltenbach)	8	N, A	ectophagous	sap sucker
Anthocoridae				
sp	8	N, A	ectophagous	sap sucker
LEPIDOPTERA				
sp 1	15	L	endophagous	chewer
Tortricidae	8	L	endophagous	chewer
Geometridae	8	L	ectophagous	chewer

Table 4.2 A list of the herbivore species found colonising the flower-heads of *Berkheya decurrens*. The stages collected; L, N, P and A refer to larvae, nymphs, pupae and adults. Immature stages indicated that these species bred on the flower-heads. Other biological details, like where and how they feed on the flower-head, are also provided. Continued on next page.

Herbivore Species	Frequency (%) in collections	Stages collected	Endophagous/ ectophagous	Guild
COLEOPTERA				
Scarabaeidae				
Dichelus sp 1	9	A	ectophagous	chewer
Dichelus sp 2	9	A	ectophagous	chewer
Curculionidae				
Larinus sp 2	73	L, P, A	endophagous	chewer
Eremnus aciculaticollis Boheman	9	A	ectophagous	chewer
Platycopes sp	9	A	ectophagous	chewer
DIPTERA				
Tephritidae				
sp 1	9	L, P, A	endophagous	chewer
sp 2	9	L, P, A	endophagous	chewer
Urophora agromyzella Bezzi	9	L, P, A	endophagous	chewer
Trupanea decora (Loew)	55	L, P, A	endophagous	chewer
Chloropidae				
Epimadiza sp	36	L, P, A	endophagous	chewer
HEMIPTERA				
Pentatomidae				
Veterna sp	9	A	ectophagous	sap sucker
Andocides vittaticeps Stal	9	A	ectophagous	sap sucker
Sciocoris sp	46	N, A	ectophagous	sap sucker
Coccidae				
sp	18	N, A	ectophagous	sap sucker
Pseudococcidae	9	N, A	ectophagous	sap sucker
Aphididae				
Brachycaudus helichrysi (Kaltenbach)	27	N, A	ectophagous	sap sucker
Lygaeidae				
Nysius sp	18	N, A	ectophagous	sap sucker
Anthocoridae				
sp	27	N, A	ectophagous	sap sucker
Miridae				
sp 1	9	A	ectophagous	sap sucker
Scutelleridae				
Sphaerocoris testudogrisea de Geer	36	N, A	ectophagous	sap sucker
Phrrhocoridae	9	A	ectophagous	sap sucker

Table 4.2 continued.

Herbivore Species	Frequency (%) in collections	Stages collected	Endophagous/ ectophagous	Guild
LEPIDOPTERA				
sp 1	9	L	endophagous	chewer
sp 2	9	L	endophagous	chewer
sp 3	9	L	endophagous	chewer
sp 4	9	L	endophagous	chewer
sp 5	9	L	endophagous	chewer
Noctuidae				
Heliothis armigera (Hübner)	18	L	ectophagous	chewer

The taxonomic composition of the herbivore species found on the flower-heads of each of the Berkheya species sampled is summarised in the pie diagrams in Fig. 4.1. Four insect orders, Coleoptera, Diptera, Lepidoptera and Hemiptera were represented on five Berkheya species. Berkheya bipinnatifida, which lacked Diptera, was the exception. The proportions of the taxa differed significantly between each Berkheya species ($G = 43.73$, $P < 0.001$, R x C test of independence). However, when the B. bipinnatifida herbivore community was excluded from the analysis, the taxonomic composition of the other 5 Berkheya species did not differ significantly ($G = 2.2$, $P > 0.5$, R x C test of independence). Thus the kinds of insects and the proportions in which they occurred were similar on the five Berkheya species.

Only the curculionid, Larinus, appeared to specialise on Berkheya flower-heads. The identity of the Larinus species collected could not be determined to species level because of the uncertain state of Larinus taxonomy in southern Africa. However, an initial investigation by an

Table 4.3 A list of the herbivore species found colonising the flower-heads of Berkheya heterophylla. The stages collected; L, N, P and A refer to larvae, nymphs, pupae and adults. Immature stages indicated that these species bred on the flower-heads. Other biological details, like where and how they feed on the flower-head, are also provided.

Herbivore Species	Frequency (%) in collections	Stages collected	endophagous/ ectophagous	guild
COLEOPTERA				
Scarabaeidae				
Dichelus sp 1	6	A	ectophagous	chewer
Dichelus sp 2	6	A	ectophagous	chewer
Curculionidae				
Larinus sp 1	19	L, P, A	endophagous	chewer
Elimenistes sp	6	A	ectophagous	chewer
Chrysomelidae				
Chrysolina sp	6	L, A	ectophagous	chewer
DIPTERA				
Tephritidae				
Urophora agromyzella Bezzi	63	L, P, A	endophagous	chewer
Trupanea decora (Loew)	13	L, P, A	endophagous	chewer
HEMIPTERA				
Pentatomidae				
Sciocoris sp	75	N, A	ectophagous	sap sucker
Coccidae				
sp	6	N, A	ectophagous	sap sucker
Pseudococcidae				
sp	25	N, A	ectophagous	sap sucker
Aphididae				
Brachycaudus helichrysi (Kaltenbach)	6	N, A	ectophagous	sap sucker
Scutelleridae				
Sphaerocoris testudogrisea de Geer	19	N, A	ectophagous	sap sucker
Anthocoridae				
sp	25	N, A	ectophagous	sap sucker
LEPIDOPTERA				
sp 1	19	L	endophagous	chewer
Tortricidae				
sp	6	L, P, A	endophagous	chewer
Noctuidae				
sp 1	6	L	endophagous	chewer
sp 2	6	L	endophagous	chewer

Table 4.4 A list of the herbivore species found colonising the flower-heads of *Berkheya onobromoides*. The stages collected; L, N, P and A refer to larvae, nymphs, pupae and adults. Immature stages indicated that these species bred on the flower-heads. Other biological details, like where and how they feed on the flower-head, are also provided.

Herbivore Species	Frequency (%) in collections	Stages collected	endophagous/ ectophagous	guild
COLEOPTERA				
Chrysomelidae				
Chrysolina sp	21	L, P, A	ectophagous	chewer
Scarabaeidae				
Hopliini sp 5	7	A	ectophagous	chewer
Curculionidae				
Larinus sp 3	64	L, P, A	endophagous	chewer
DIPTERA				
Tephritidae				
Trupanea decora (Loew)	7	L, P, A	endophagous	chewer
sp 2	7	L, P, A	endophagous	chewer
HEMIPTERA				
Anthocoridae				
sp	21	N, A	ectophagous	sap sucker
Pentatomidae				
Sciocoris sp	14	N, A	ectophagous	sap sucker
Andocides vittaticeps Stl	7	A	ectophagous	sap sucker
Scutelleridae				
Sphaerocoris testudogrisea de Geer	7	A	ectophagous	sap sucker
Miridae				
sp 1	14	N, A	ectophagous	sap sucker
sp 2	50	N, A	ectophagous	sap sucker
sp 3	14	N, A	ectophagous	sap sucker
LEPIDOPTERA				
sp 6	7	L	ectophagous	chewer
Pterophoridae				
Agdistis pustulalis Walker	7	L, P, A	ectophagous	chewer

Table 4.5 A list of the herbivore species found colonising the flower-heads of Berkheya rigida. The stages collected; L, N, P and A refer to larvae, nymphs, pupae and adults. Immature stages indicated that these species bred on the flower-heads. Other biological details, like where and how they feed on the flower-head, are also provided.

Herbivore Species	Frequency (%) in collections	Stages collected	endophagous/ ectophagous	guild
COLEOPTERA				
Chrysomelidae				
Cassida coloraria Boheman	57	L, P, A	ectophagous	chewer
Scarabaeidae				
Dichelus sp 4	14	A	ectophagous	chewer
Curculionidae				
Larinus sp 1	36	L, P, A	endophagous	chewer
DIPTERA				
Tephritidae				
sp 2	7	A	endophagous	chewer
Urophora agromyzella Bezzi	29	L, P, A	endophagous	chewer
Trupanea decora	21	L, P, A	endophagous	chewer
HEMIPTERA				
Pentatomidae				
Andocides vittaticeps Stl	7	N	ectophagous	sap sucker
Sciocoris sp	57	N, A	ectophagous	sap sucker
Aphididae				
Brachycaudus helichrysi	7	N, A	ectophagous	sap sucker
Scutelleridae				
Sphaerocorris testudogrisea de Geer	7	A	ectophagous	sap sucker
Anthocoridae				
sp	57	N, A	ectophagous	sap sucker
Miridae				
sp 1	7	N, A	ectophagous	sap sucker
LEPIDOPTERA				
Pterophoridae				
Agdistis pustulalis Walker	71	L, P, A	ectophagous	chewer
Tortricidae				
sp	7	L	ectophagous	chewer

Table 4.6 A list of the herbivore species found colonising the flower-heads of Berkheya sp. The stages collected; L, N, P and A refer to larvae, nymphs, pupae and adults. Immature stages indicated that these species bred on the flower-heads. Other biological details, like where and how they feed on the flower-head, are also provided.

Herbivore Species	Frequency (%) in collections	Stages collected	endophagous/ ectophagous	guild
COLEOPTERA				
Chrysomelidae				
Cassida coloraria Boheman	18	L, A	ectophagous	chewer
Curculionidae				
Larinus sp 1	36	L, P, A	endophagous	chewer
Sciobus prob. nanus Marshall	9	A	ectophagous	chewer
DIPTERA				
Tephritidae				
Urophora agromyzella Bezzi	46	L, P, A	endophagous	chewer
Trupanea decora (Loew)	9	L, P, A	endophagous	chewer
HEMIPTERA				
Pentatomidae				
Sciocoris sp	55	N, A	ectophagous	sap sucker
Scutelleridae				
Sphaerocoris testudogrisea de Geer	18	N, A	ectophagous	sap sucker
Aphididae				
Uroleuco compositae (Theobald)	9	N, A	ectophagous	sap sucker
Coccidae				
sp	9	N, A	ectophagous	sap sucker
Miridae				
sp1	9	N, A	ectophagous	sap sucker
LEPIDOPTERA				
sp 10	9	L	endophagous	chewer
Pterophoridae				
Agdistis pustulalis Walker	27	L, P, A	ectophagous	chewer

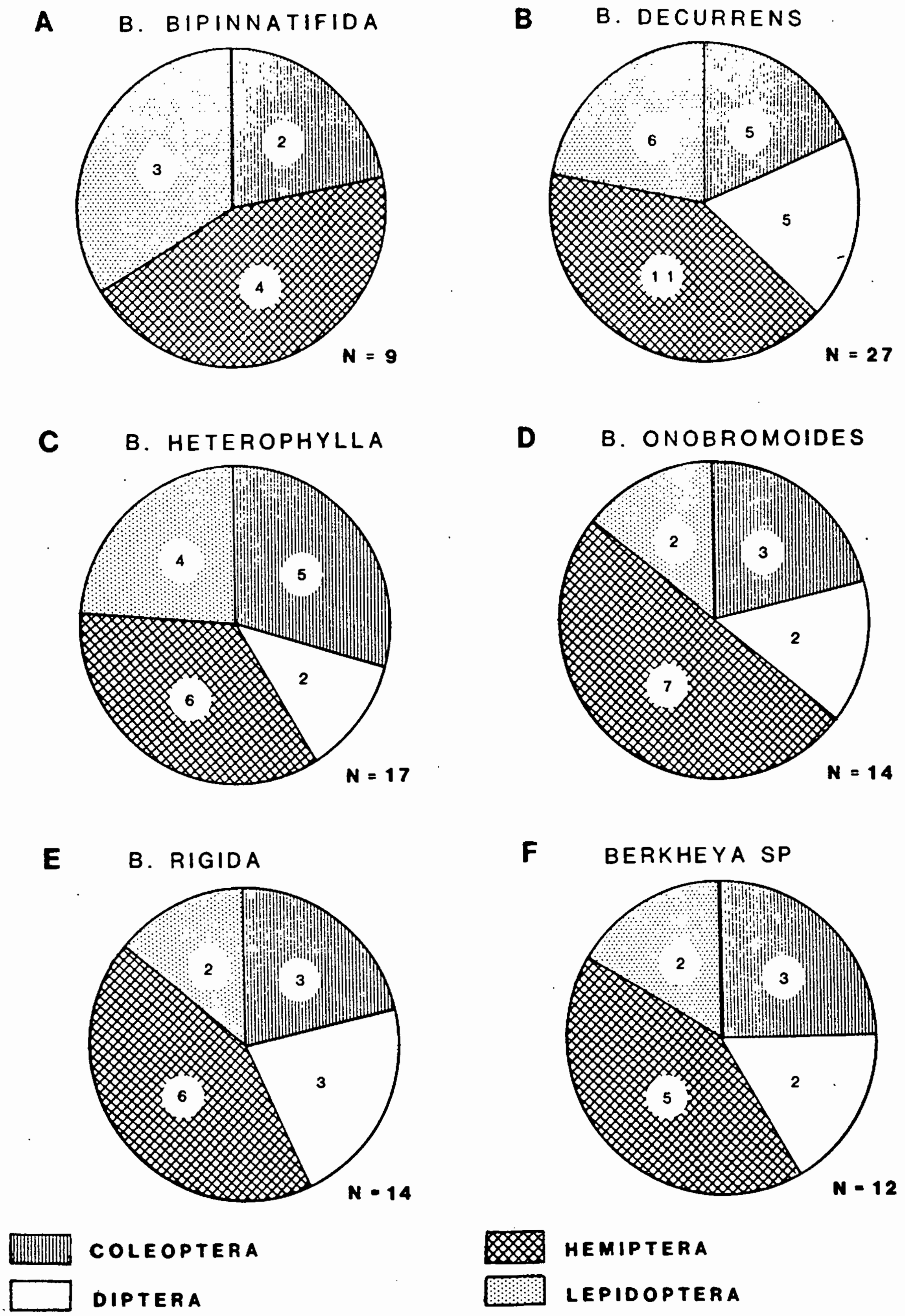


Fig. 4.1 The taxonomic composition of the herbivore communities found in *Berkheya* flower-heads. Actual species numbers are shown on the graphs and N is the total number of herbivore species.

experienced curculionid taxonomist identified three possible species; Larinus sp 1 on B. bipinnatifida, B. heterophylla, B. rigida, and Berkheya sp, Larinus sp 2 on B. decurrens and Larinus sp 3 on B. onobromoides (R. Oberprieller, pers. comm. 1988). There is no record in South Africa of Larinus feeding on any plant genus other than Berkheya.

The other herbivore species collected are generalists and are commonly found on a wide range of composite plant species. The pentatomid Sciocoris sp, was present on all six Berkheya species, and occurred more frequently than all other herbivore species in samples collected from B. bipinnatifida, B. heterophylla, and Berkheya sp. Larinus sp 2 and Larinus sp 3 were the most common herbivore species collected on B. decurrens and B. onobromoides respectively. In samples of B. rigida, the pterophorid caterpillar Agdistis pustulalis Walker was the most commonly occurring herbivore.

To learn how these herbivores live in the flower-heads, and what impact they may have on each other, the biology of the common species was studied.

4.2 Biology of the most commonly encountered herbivore species

Several aspects, relevant to this study, of the biology of the common herbivore species were studied. The life cycles were studied to observe which stages were associated with the flower-heads and which part of the flower-heads were fed upon. Some herbivores consumed a considerable portion of the flower-head. This could limit the amount of food available to other herbivores on the same flower-head and could also influence whether or not potential insect colonisers could settle or oviposit on a flower-head. For this reason, the amount of flower-head consumed by the most voracious species was determined.

4.2.1 Life cycles

(i) Larinus sp 3 (Curculionidae: Coleoptera)

The life cycles of all three Larinus species appeared to be similar so the life cycle of Larinus sp 3 is used here as an example (Fig. 4.2). The larvae fed mainly on the achenes and the receptacle but early instars sometimes also fed on the florets. The final instar larvae formed a pupal chamber from frass and chewed plant material. If the flower-head dried out completely, the wall of the pupal chamber appeared to be too hard for the adult to chew through. Moisture, possibly in the form of rain, may be necessary to soften the wall of the chamber before the weevil can emerge. Moisture may also stimulate the adult to chew out of the flower-head. Adults feed on all aerial parts of the plant. They are cryptically coloured, slow moving and keep hidden amongst the leaves. They were never seen to fly. Populations of B. onobromoides are very patchy and isolated so the weevils must fly to colonise these plants. One generation a year was normal but two generations were recorded at one site.

Larinus pupae were parasitised by Physaraia bilobata (Cameron) (Hymenoptera: Braconidae) and a eurytomid (Hymenoptera).

Fig. 4.2 The life-cycle of Larinus sp 3 in the flower-heads of B. onobromoides. (A) Egg inserted amongst the achenes and (B) larva. Continued on next page.

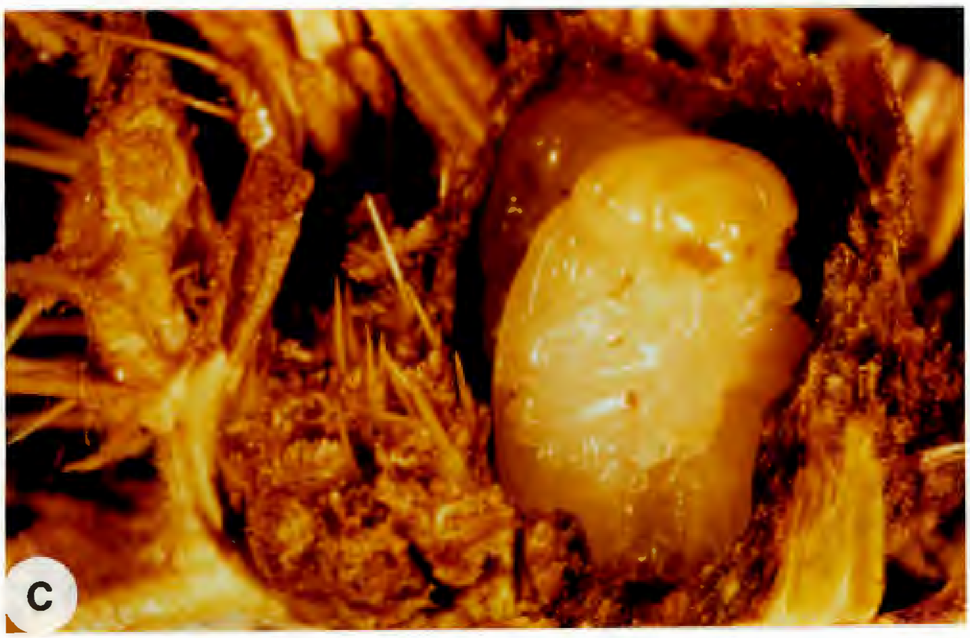


Fig. 4.2 continued. The life-cycle of Larinus sp 3 in the flower-heads of B. onobromoides; (C) pupa and (D) adult.

(ii) Urophora agromyzella Bezzi (Tephritidae: Diptera)

Eggs were laid singly in mature flower buds, possibly because developing achenes were softer and more easily penetrated than mature achenes. Each larva fed inside a single achene which it completely excavated. Achenes that contained U. agromyzella larvae showed no external sign of damage so each achene was dissected to find the larvae. Urophora species are known to be highly selective in choosing oviposition sites and are able to accurately manoeuvre their ovipositor within the flower-head (Berube & Zacharuk, 1983). For U. agromyzella to leave no external sign of their presence within the achene, the female would have to oviposit in the corolla tubes of developing florets and the young larvae would have to tunnel into the dorsal end of the achene. Alternatively, the female may use the corolla to guide the ovipositor to the achene and oviposit inside the achene. No structural gall was formed. Two generations per year appeared to occur on B. heterophylla. The second generation overwintered in the pupal stage while still inside the achene. Adults are entirely black and are about the same size as the achenes. Unlike most tephritids, the wings are clear with no markings.

Urophora agromyzella larvae and pupae were parasitised by ?Anastatus (Hymenoptera: Eupelmidae). Another urophoran that completes development entirely in on achene is U. stylata F. which attacks Cirsium vulgare flower-heads in Europe. Urophora stylata forms a gall in the achene which causes the achene to swell slightly (Redfern 1983). Not all Urophora are solitary. U. solstitialis L. is gregarious and the larvae form a multilocular gall inside the flower-head (Zwölfer 1979a).

(iii) Trupanea decora (Loew) (Tephritidae: Diptera)

Eggs were laid singly in mature buds and the young larvae fed on the florets. Mature larvae fed on the achenes and each larva excavated a small cavity among the achenes above which they formed an open ended tunnel in the florets, through which they emerged after pupating. This species does not form galls although there is a record of congeneric species in North America that is a facultative gall former (Goeden 1985).

(iv) Epimadiza sp (Chloropidae: Diptera)

Eggs were laid in mature buds and the larvae fed on achenes. Only one generation per summer was recorded. The adults were black, like U. agromyzella, but were slightly larger and the females had a short ovipositor.

(v) Sciocoris sp (Pentatomidae: Hemiptera)

This species lived externally on the flower-heads. Eggs were laid in groups within the protective fold of a bract. The eggs were sometimes parasitised by a signiphorid (Hymenoptera). Nymphs usually fed on young bracts and the adults often fed on the achenes, especially late in summer when the flower-heads dried out. Several overlapping generations occurred in a summer.

(vi) Sphaerocoris testudogrissea de Geer (Scutelleridae: Hemiptera)

The nymphs and adults fed on all parts of the flower-head. This species is a wide ranging generalist and has been collected on plant groups other than composites.

(vii) Agdistis pustulalis Walker (Pterophoridae: Lepidoptera)

Eggs were laid in the protective fold of a bract. Larvae fed on all aerial parts of the plant. On the flower-heads they chewed the surface of the bracts which caused characteristic 'windows'. If larvae were present in large numbers, the bracts and leaves were skeletonised. Pupation occurred in a protected area of the plant. On the flower-head this was usually in the protective fold of the bracts. Pupae were parasitised by a small braconid (Hymenoptera).

(viii) Cassida coloraria Boheman (Chrysomelidae: Coleoptera)

Larvae and adults grazed on the flower-heads. Sometimes larvae chewed into young flower-heads, but they usually fed externally on the bracts.

(ix) Dichelus spp (Scarabaeidae: Coleoptera)

These species are members of the Hopliini tribe, commonly called 'monkey beetles' because of their furry bodies and large hind legs. The hind legs and claws are well developed and are used to anchor and then extract themselves from composite flower-heads (Scholtz & Holm 1985).

The life-cycle is not known and larvae of the Hopliini have not been recorded but presumably they live in the soil and feed on plant roots and other vegetable matter like the larvae of many other phytophagous Scarabaeidae. The adults caused considerable damage to composite flower-heads when present in large numbers. On Berkheya flower-heads the Dichelus spp fed on the florets and grazed on the tops of the achenes.

Once the parts of the flower-head fed upon by the herbivores had been identified, the impact of herbivore feeding on the flower-heads could be determined.

4.2.2 Impact of herbivore feeding

Many of the herbivore species listed in tables 4.1 to 4.6 caused no visible damage to the flower-heads. This was either due to low numbers of the herbivore species in the community or because feeding caused no visible physical damage.

The hemipteran species are a good example of this latter group. Feeding by these sap suckers caused no noticeable stress to the flower-heads or the plants. Presumably any sap consumed by the hemipterans was replaced by the plant and the plant was able to compensate effectively. Adult Sciocoris sp fed upon achenes which could have caused them to become nonviable. Achene viability was not studied as this is a complex topic beyond the scope of this thesis.

Physical damage was caused to the flower-heads by the herbivores with mouthparts adapted for chewing. Herbivore species that occurred commonly on the Berkheya species had the potential to cause sufficient damage to flower-heads to make food a limiting factor in the community.

Species that appeared to have the greatest impact on the flower-heads were those that fed internally. The impact of the internal chewers, which occurred commonly in Berkheya flower-heads, was assessed by counting the number of achenes eaten per flower-head and by measuring the weight loss per flower-head due to feeding. This was compared to the number of achenes and the dry flower-head weight of uninfested flower-heads. Initially therefore, the mean achene complement and dry weight of uninfested flower-heads had to be determined. The flower-heads selected for this purpose showed no sign of insect feeding damage, either externally or internally.

A significant positive correlation between flower-head diameter and the number of achenes present in uninfested flower-heads was found in five of the Berkheya species sampled (Fig.4.3), although in Berkheya sp and B. rigida the correlation was low. In B. bipinnatifida the correlation was not significant (Fig.4.3a). These regression lines were used to determine the impact the insect species, that formed the guild of internal chewers, had on achene numbers. This was done by comparing the number of achenes remaining in flower-heads fed upon by the herbivores to the number of achenes that should be present in flower-heads of that size, and this estimate was provided by the regression lines.

Larinus spp reduced achene numbers per flower-head considerably (Fig. 4.4) and most of the points fall below the regression line. Sometimes more achenes were left than expected in flower-heads infested with Larinus, but this was probably mostly due to the variable number of achenes per flower-head.

The tephritid U. agromyzella also caused a reduction in achenes per flower-head in B. heterophylla and Berkheya sp (Fig. 4.5). Urophora agromyzella had little impact on achene numbers in B. rigida. Unaccountably, in these flower-heads, most of the points fall above the regression

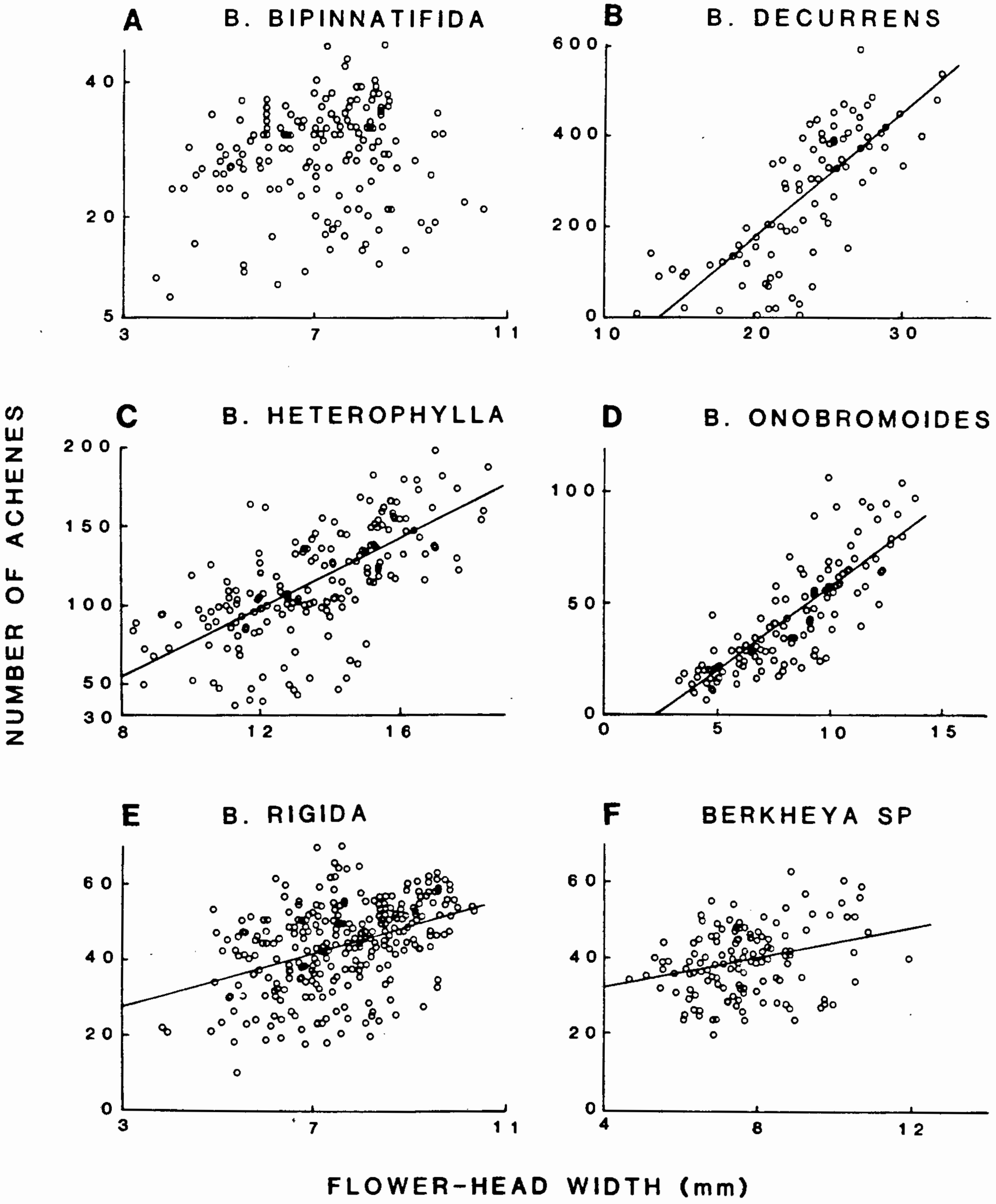


Fig. 4.3 The relationship between the number of achenes and flower-head width in uninfested flower-heads of the six Berkheya species. (A) $y = 0.77x + 23.43$, $r^2 = 0.02$, $P > 0.05$; (B) $y = 27.56x - 380.46$, $r^2 = 0.57$, $P < 0.001$; (C) $y = 10.48x - 29.1$, $r^2 = 0.45$, $P < 0.001$; (D) $y = 7.62x - 19.1$, $r^2 = 0.70$, $P < 0.001$; (E) $y = 3.61x + 16.27$, $r^2 = 0.18$, $P < 0.001$; (F) $y = 2x + 24.2$, $r^2 = 0.09$, $P < 0.001$.

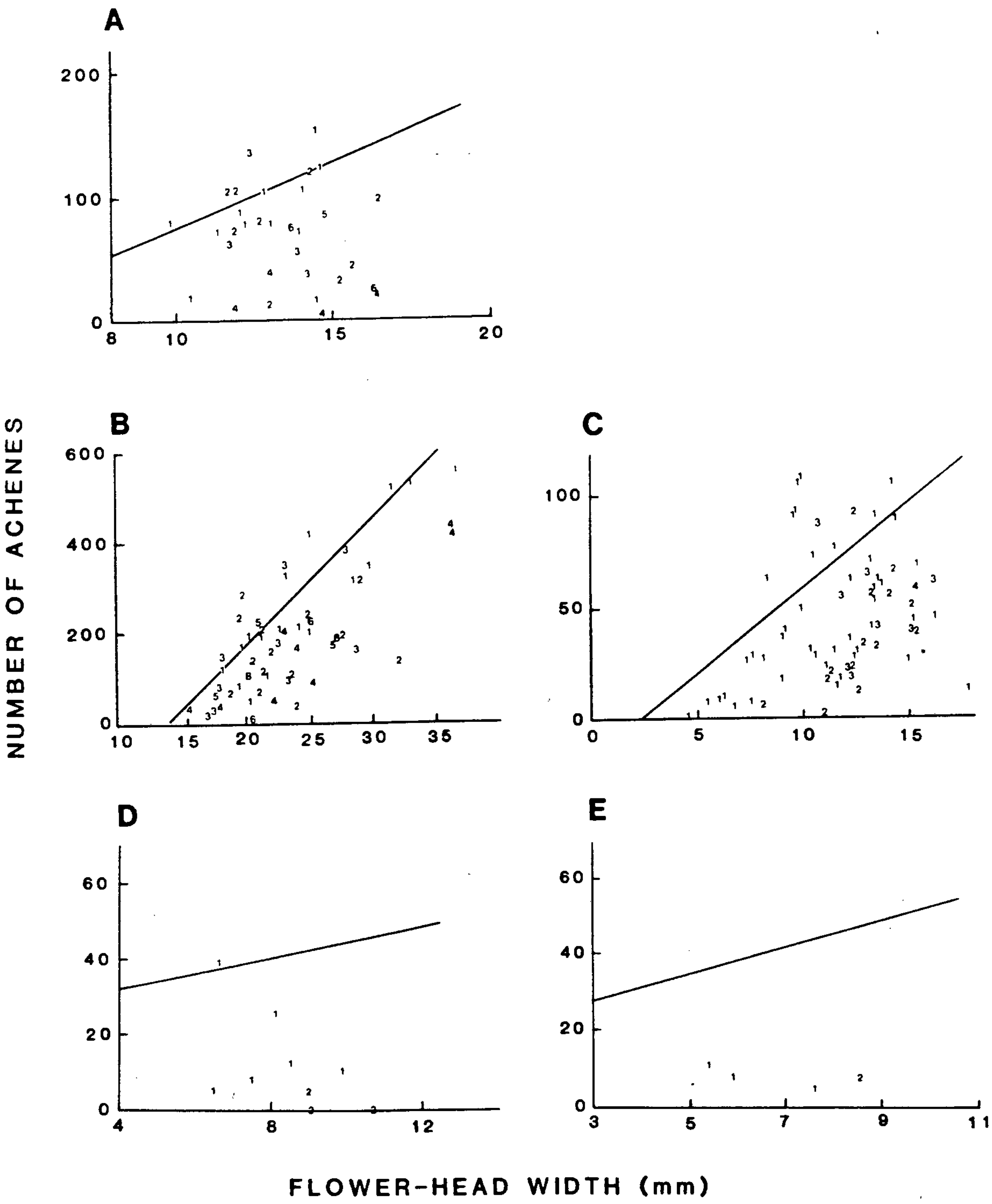


Fig. 4.4 The impact of Larinus species feeding on the number of achenes in Berkheya flower-heads; (A) B. heterophylla, (B) B. decurrens, (C) B. onobromoides, (D) Berkheya sp, (E) B. rigida. The number of Larinus individuals in each flower-head is shown. The regression lines are taken from Fig. 4.3 and represent the relationship between achene numbers and flower-head width in uninfested flower-heads.

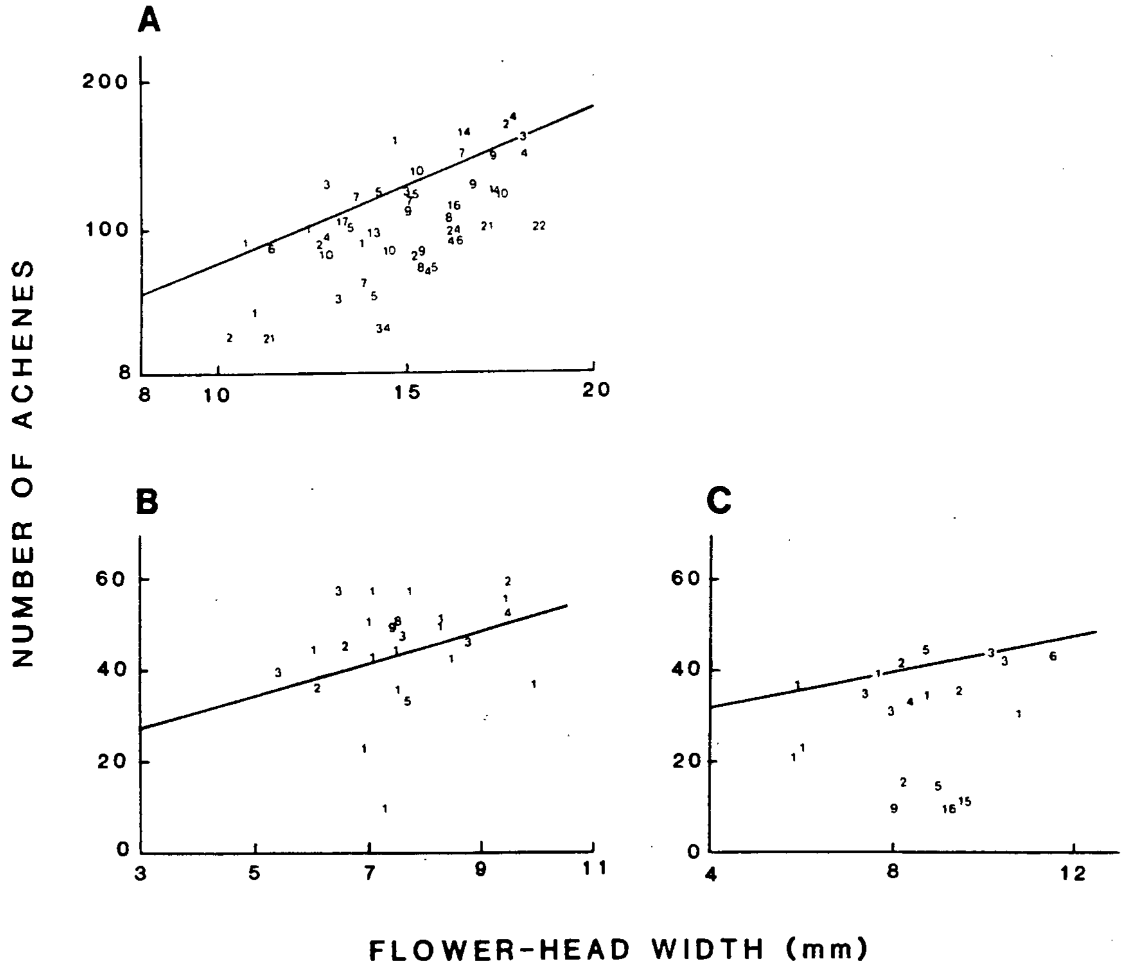


Fig. 4.5 The impact of U. agromyzella feeding on achene numbers in Berkheya flower-heads; (A) B. heterophylla, (B) B. rigida, (C) Berkheya sp. The number of U. agromyzella individuals in each flower-head is shown. The regression lines are taken from Fig. 4.3 and represent the relationship between achene numbers and flower-head width in uninfested flower-heads.

line (Fig. 4.5b). However, each U. agromyzella larva consumed the contents of one achene during its development. The number of achenes per flower-head destroyed by U. agromyzella therefore correlated exactly with the number of larvae in the flower-head.

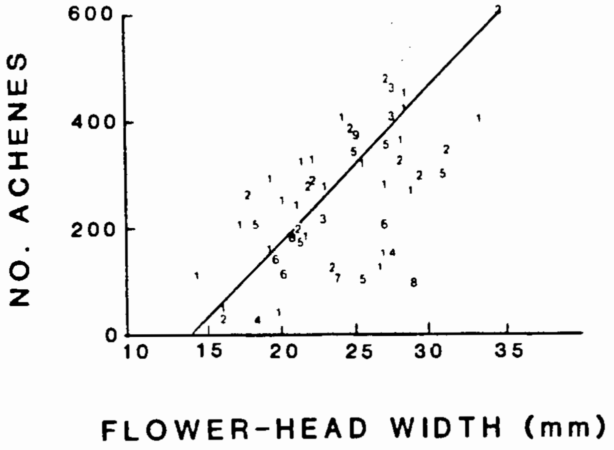


Fig. 4.6 The impact of Epimadiza sp. feeding on achene numbers in B. decurrens flower-heads. The number of U. agromyzella individuals in each flower-head is shown. The regression line is taken from Fig. 4.3 and represents the relationship between achene numbers and flower-head width in uninfested B. decurrens flower-heads.

The chloropid, Epimadiza sp, occurred only in B. decurrens flower-heads (Fig. 4.6) and caused some slight damage to the achenes. However, due to the variability in achene numbers per flower-head, some points fall above the regression line .

Trupanea decora, a tephritid, was present in low numbers on B. heterophylla, B. onobromoides, B. rigida and Berkheya sp (Tables 4.1 to 4.6) and did not occur in the samples of dissected flower-heads. Fifty-five percent of B. decurrens flower-heads were infested by T. decora (Table 4.3) but they did not have much effect on achene numbers (Fig. 4.7).

Figs 4.4 to 4.7 should, in theory, show that as more insects infest each flower-head, more achenes should be eaten. There should therefore be a negative correlation

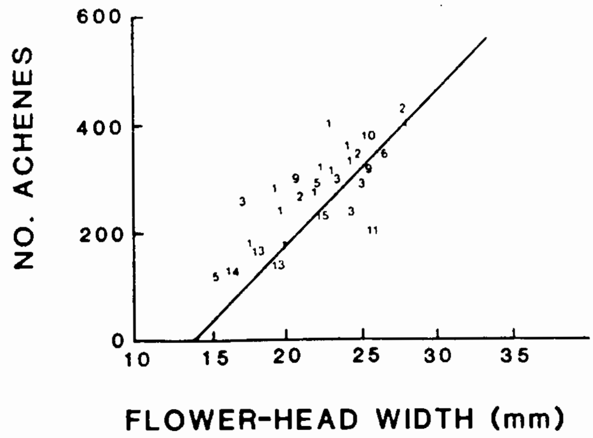


Fig. 4.7 The impact of *T. decora* feeding on achene numbers in *B. decurrens* flower-heads. The number of *T. decora* individuals in each flower-head is shown. The regression line is taken from Fig. 4.3 and represents the relationship between achene numbers and flower-head width in uninfested *B. decurrens* flower-heads.

between the number of achenes left in the flower-head, and the number of herbivores present. Table 4.7 shows that the correlations were all negative, but they were not always statistically significant. This is probably due to the the small amount of damage and the variable number of achenes per flower-head.

Dry flower-head weight was the other measure used to determine the extent of herbivore feeding damage. In uninfested flower-heads, dry weight was highly correlated with flower-head width in all *Berkheya* species (Fig. 4.8). However, when the flower-head dry weights of infested flower-heads were plotted and compared to the regression lines obtained from uninfested flower-heads (Fig. 4.8), none of the herbivore species appeared to have any significant effect on the flower-head (Fig. 4.9). It appears that the amount of plant matter eaten by the herbivores forms a negligible portion of the complete

Table 4.7 Correlation between the number of herbivores in a flower-head and the number of achenes remaining. Calculated from the residual values in Figs 4.4 to 4.7 (Spearman's rank correlation). N is the number of flower-heads. (N.S. P>0.05; * P<0.05; ** P<0.01).

Berkheya species	Herbivore species	N	r_s	P
B. decurrens	Larinus sp 2	51	-0.28	0.0466 *
	Epimadiza sp	46	-0.26	N.S.
	T. decora	29	-0.40	0.0354 *
B. heterophylla	U. agromyzella	44	-0.36	0.0184 *
	Larinus sp 1	30	-0.30	N.S.
B. onobromoides	Larinus sp 3	63	-0.38	0.0031 **
B. rigida	Larinus sp 1	4	-0.54	N.S.
	U. agromyzella	22	-0.17	N.S.
Berkheya sp	Larinus sp 1	8	-0.85	0.0253 *
	U. agromyzella	20	-0.3174	N.S.

flower-head mass. In fresh flower-heads, the receptacle and developing achenes seem to have a higher water content than the rest of the flower-head. The dry weight of these parts would therefore be proportionately lower compared to the rest of the flower-head. Flower-head dry weight was therefore not a satisfactory measure for determining the amount of herbivore feeding.

4.3 Competition for food resources

Zwölfer (1979a) has suggested that interspecific competition plays an important role in the evolution of insect herbivore communities in thistle flower-heads. Interspecific competition for limited resources has been an important corner-stone in the theory of community structure (MacArthur 1972, Cody & Diamond 1975, May 1981) despite the difficulties involved in unequivocally

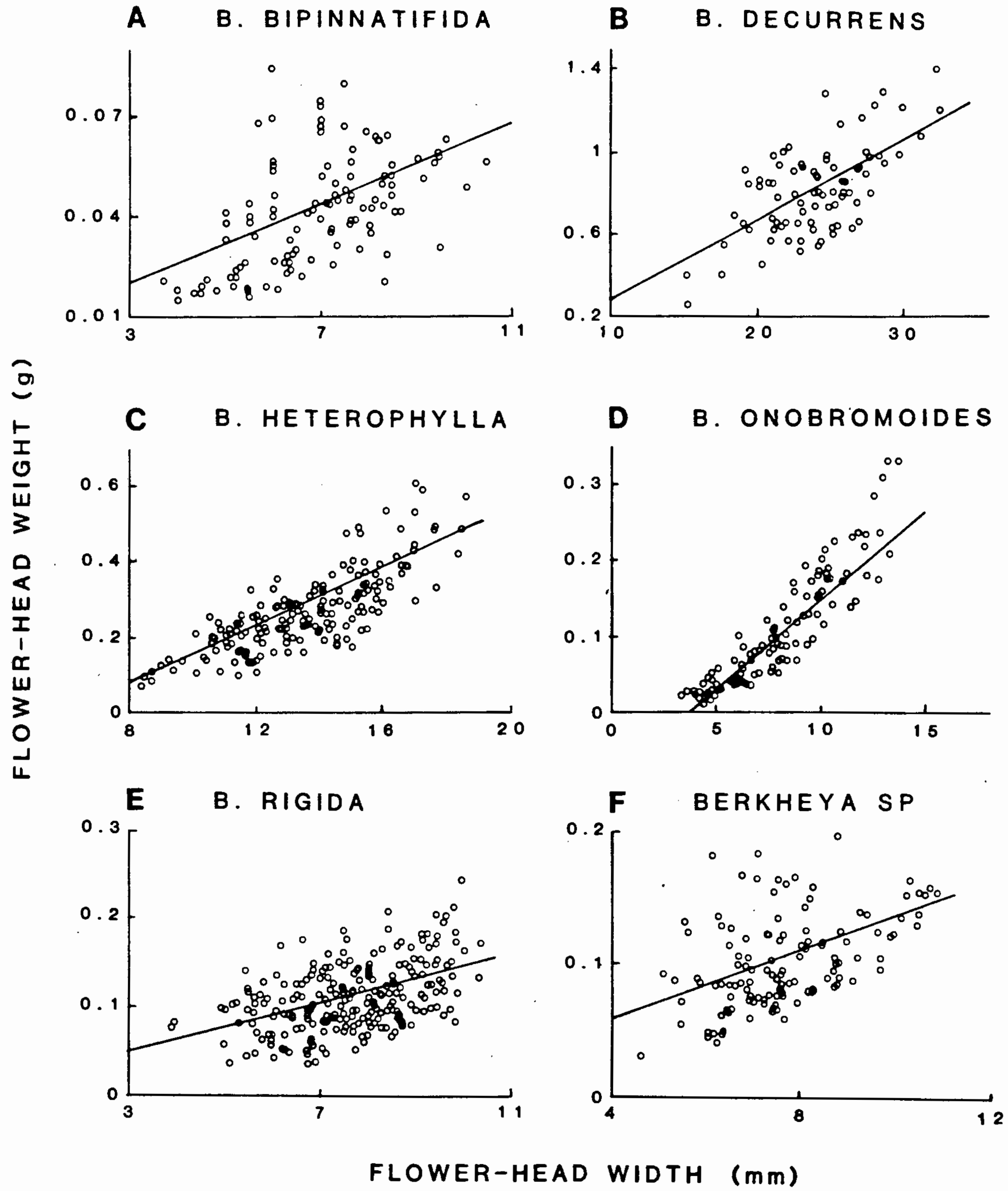


Fig. 4.8 Regressions illustrating the relationship between flower-head dry weight and flower-head width in uninfested flower-heads of the six *Berkheya* species. (A) $y = 0.006x + 0.002$, $r^2 = 0.26$, $P < 0.001$; (B) $y = 0.04x - 0.15$, $r^2 = 0.41$, $P < 0.001$; (C) $y = 0.04x - 0.23$, $r^2 = 0.63$, $P < 0.001$; (D) $y = 0.03x - 0.09$, $r^2 = 0.81$, $P < 0.001$; (E) $y = 0.01x + 0.01$, $r^2 = 0.23$, $P < 0.001$; (F) $y = 0.01x + 0.01$, $r^2 = 0.21$, $P < 0.001$.

demonstrating its importance and effects (Connell 1980). Lawton & Strong (1981) have described how unlikely it is that interspecific competition has played a role in many insect herbivore communities, where alternative hypotheses can provide successfull explanations for several patterns that could also be generated by interspecific competition. However, among known examples of interspecific competition in phytophages, Strong _et al_. (1984) listed three cases of amensalism (asymmetrical competition) in herbivore communities on thistle flower-heads demonstrated by Zwölfer (1979a). Therefore preliminary observations on the possibility of competition in _Berkheya_ flower-heads were carried out. Further experimental work, beyond the scope of the present thesis, will be required to provide more definitive answers.

Because less food may be available to insect herbivores as the flower-head becomes more crowded, it would seem to be advantageous for the herbivore species to be able to detect the presence of other herbivores in the flower-head before ovipositing. In addition, if crowding occurred commonly in the past, and if there was competition for resources, the herbivores may be expected to have evolved behaviourally to reduce crowding. Short of actually changing host plant species, which is a large evolutionary step, crowding could be reduced by spreading offspring among the available flower-heads and by ovipositing more eggs into large flower-heads. This behaviour is found in some parasitoid species that avoid superparasitism by detecting the presence of other parasitoids in a host before they oviposit and thereby prevent an over-exploitation of resources (Vinson 1976). Avoidance of oviposition sites where conspecific eggs have been laid

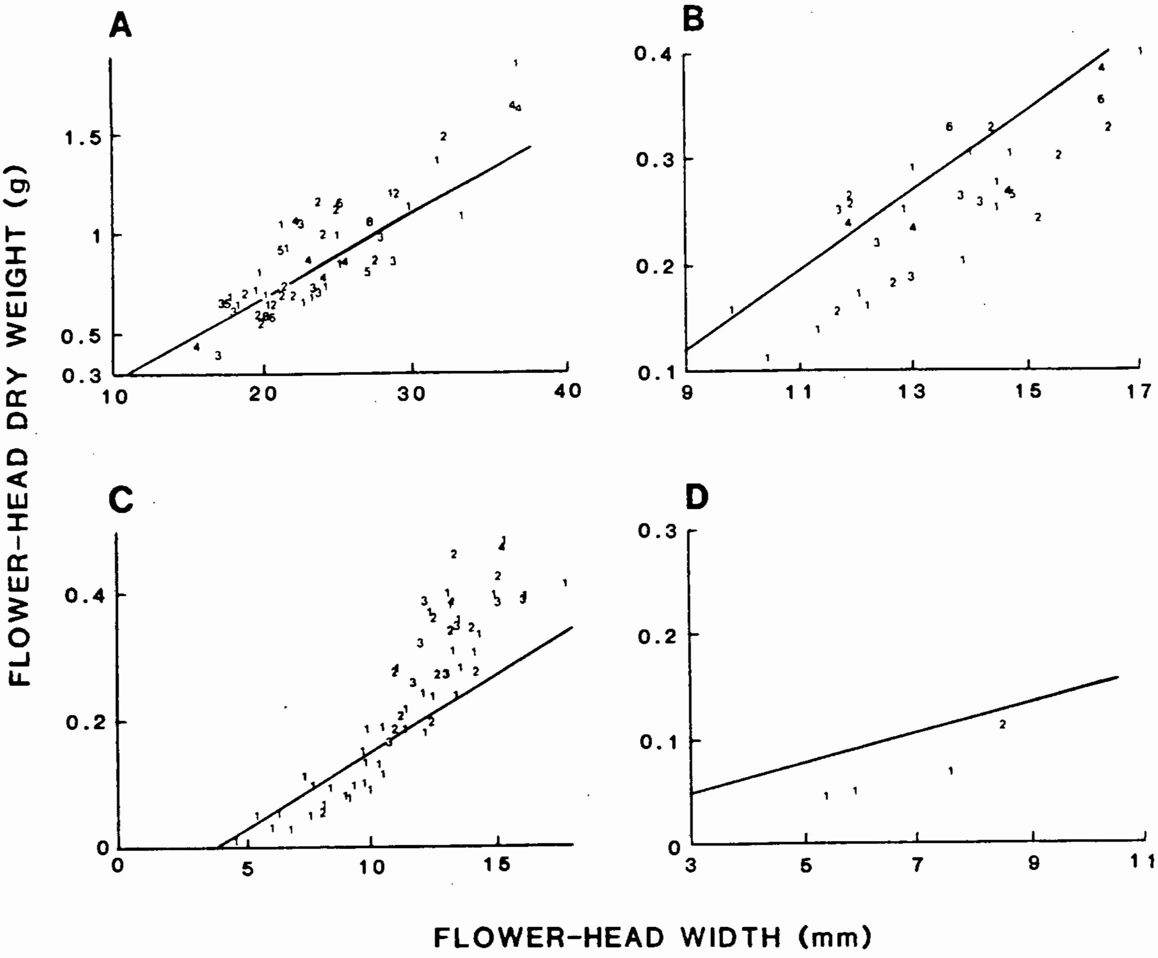


Fig. 4.9 The impact of insect herbivores on flower-head dry weight; (A) Larinus sp 2 on B. decurrens, (B) Larinus sp 1 on B. heterophylla, (C) Larinus sp 3 on B. onobromoides, (D) Larinus sp 1 on B. rigida, (E) Larinus sp 1 on Berkheya sp, (F) U. agromyzella on B. heterophylla, (G) U. agromyzella on B. rigida, (H) U. agromyzella on Berkheya sp, (I) Epimadiza sp on B. decurrens, (J) T. decora on B. decurrens. The number of individuals in each head is shown. The regression lines are taken from Fig. 4.8 and represent the relationship between flower-head dry weight and flower-head width in uninfested flower-heads. Continued on next page.

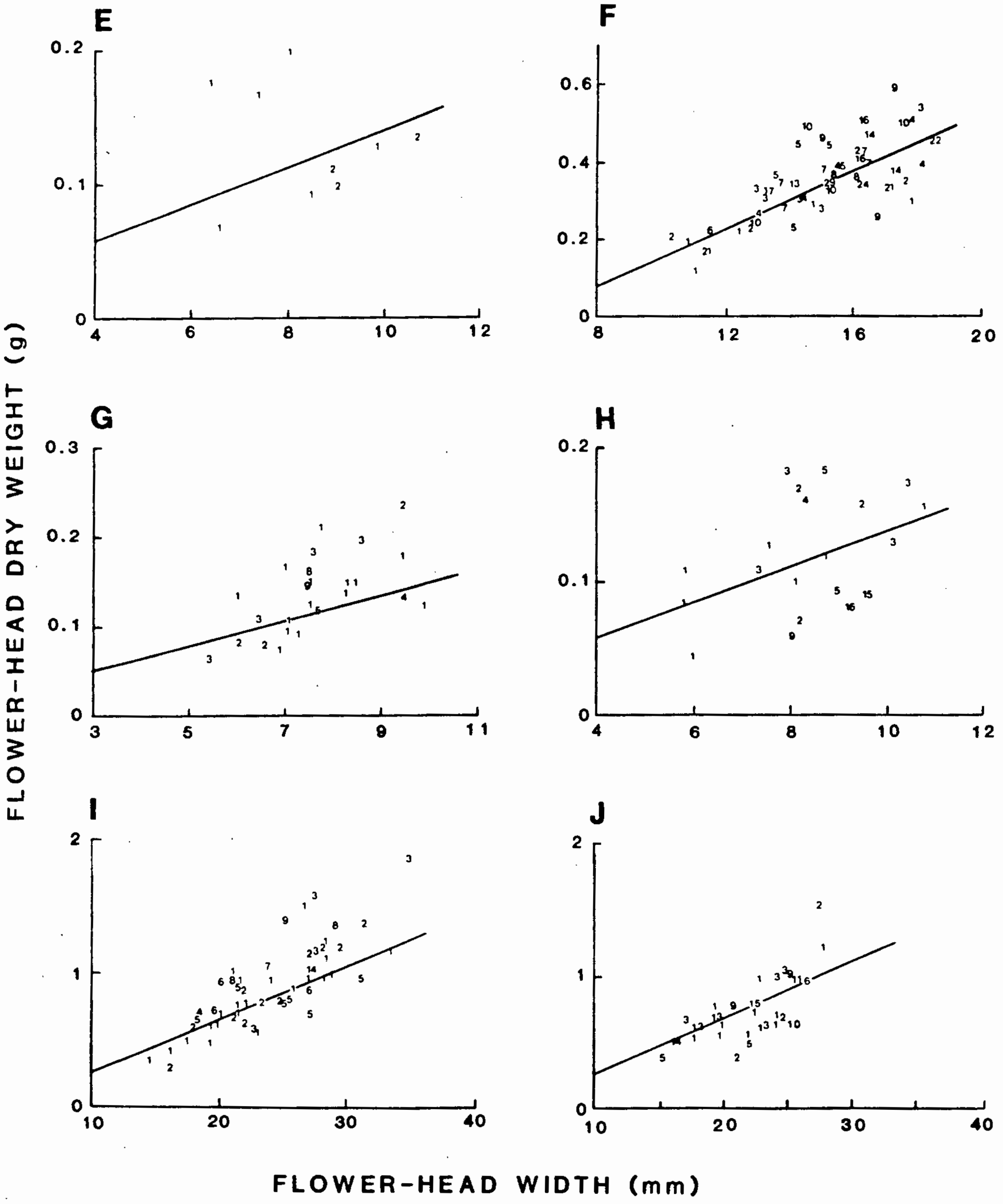


Fig. 4.9 continued.

has also been documented for many insect herbivore species (Rausher 1979, Prokopy 1981).

None of the insect herbivore species that fed inside the flower-heads showed any sign of spreading their offspring evenly among the available flower-heads. Many flower-heads were completely uninfested (eg. all the examples in Fig. 4.3), and many individuals were often crowded into a single flower-head (Fig. 4.4 to 4.7). In addition, the average number of individual insects per flower-head (infested flower-heads only) was usually low (Table 4.8). Urophora agromyzella on B. heterophylla with a mean of 10.3 individuals per flower-head, showed that crowding of up to 45 individuals could occur in a single flower-head without detrimental effects to these herbivores, because all survived and there was no reduction in adult size. Uninfested and infested flower-heads occurred together on the same plant, so differences in chemical defences, between the flower-heads, are unlikely to account for the patchy herbivore distribution. Sometimes 100% of the flower-heads were infested (Fig. 4.11) so competition may occur occasionally, but this is unlikely to be important and the reasons for this are now discussed.

Shorrocks & Rosewell (1986) developed a simulation model which shows, that on divided and ephemeral resources (like flower-heads), it is possible for several herbivore species to exploit the same type of resource, without competing, if they each have aggregated distributions. The more aggregated each herbivore species is distributed, the more probability refuges (empty flower-heads) there will be, which reduces the chance of different herbivore species encountering each other in the same flower-head.

Table 4.8 Mean numbers of individual insect herbivores per Berkheya flower-head for single species infestations. N equals the number of flower-heads, and S.E. is the standard error of the mean.

Herbivore species	B. decurrens	B. heterophylla	B. onobromoides	B. rigida	B. sp
U. agromyzella					
N	1	9	16		
Mean		10.3		2.3	4
S.E.		1.4		0.43	0.92
Min		1		1	1
Max		47		9	21
Larinus spp					
N	63	32	69	4	9
Mean	3.1	2.34	1.49	1.25	1.33
S.E.	0.33	0.26	0.09	0.22	0.16
Min	1	1	1	1	1
Max	12	6	4	2	2
T. decora					
N	29				
Mean	4.8				
S.E.	0.86				
Min	1				
Max	15				
Epimadiza					
N	52				
Mean	2.9				
S.E.	0.36				
Min	1				
Max	14				

Therefore, the likelyhood of different species competing, is reduced.

This hypothesis (Shorrocks & Rosewell 1986) was investigated using herbivore communities in B. decurrens flower-heads as an example because insect populations in these flower-heads were the most crowded. The distribution of Larinus sp 2, Epimadiza sp and T. decora, which were the most commonly occurring species that fed inside B. decurrens flower-heads, was examined. Larinus sp 2, Epimadiza sp and T. decora each occupied less than 35% of the available flower-heads, and together they left 46% of the flower-heads unoccupied (Table 4.9a). Furthermore, because these herbivore species were aggregated, and because many flower-heads were unoccupied, only 15% of flower-heads were occupied by two herbivore species and only 1% had all three herbivore species present (Table 4.9b). While Larinus sp 2, Epimadiza sp and T. decora may compete when they occur in the same flower-head, resource partitioning will not occur because the incidence of competition is relatively rare in the population (Atkinson & Shorrocks 1981, 1984, Shorrocks et al. 1984).

Generally, there was no correlation between flower-head size and the number of herbivores per flower-head (Table 4.10). Correlations occurred only in U. agromyzella on B. heterophylla and in Larinus sp 3 on B. onobromoides. These two species are the only herbivores that appeared to exhibit any behavioural ability to reduce crowding in the flower-heads because they could differentiate between large and small flower-heads (Table 4.10). Therefore, because there seems, generally, to be no behavioural adaptations to reduce crowding in the flower-heads, it appears that food resources is not usually limiting in Berkheya herbivore communities at present, and may not have been limiting in the past.

In conclusion, interspecific competition for resources, in Berkheya flower-heads, does not appear to be strong overall, but experiments are required to provide more conclusive evidence.

Table 4.9 Spatial distribution of the most common three endophagous herbivore species in *B. decurrens* flower-heads. (A) Proportion of flower-heads unoccupied by endophages. (B) Proportion of flower-heads colonised 0, 1, 2, or all 3 endophagous species. N = 210 flower-heads.

A. Endophagous species	% flower-heads not occupied	B. No. species in head	% flower-heads so occupied
Larinus sp 2	67	0	46
Epimadiza sp	71	1	38
T. decora	89	2	15
All three	46	3	1

Table 4.10 Correlation between herbivore numbers per flower-head and flower-head width (Spearman's rank correlation). N equals number of flower-heads. (* P<0.05, ** P<0.01).

Berkheya species	Herbivore species	N	r_s	P
B. decurrens	*Larinus* sp 2	57	-0.03	N.S.
	Epimadiza sp	52	0.13	N.S.
	T. decora	29	-0.04	N.S.
B. heterophylla	*Larinus* sp 1	32	0.28	N.S.
	U. agromyzella	47	0.38	0.0109 *
B. onobromoides	*Larinus* sp 3	69	0.33	0.0061 **
B. rigida	*Larinus* sp 1	4	0.78	N.S.
	U. agromyzella	25	-0.03	N.S.
Berkheya sp	*Larinus* sp 1	9	0.64	N.S.
	U. agromyzella	21	0.44	N.S.

4.4 Guild structure

Three main guilds, external chewers, internal chewers and sap suckers, were identified. Internal chewers comprise those species with chewing mouthparts who spend their immature stages inside the flower-head. Species like *Larinus* spp were classed as internal chewers, even though the adults may occasionally feed externally on the bracts. The guild structure of insect herbivore communities associated with the six Berkheya species sampled is summarised in Fig. 4.10. The guild structure of the herbivore communities in the flower-heads did not differ between each of the Berkheya species (G = 11.62, R x C test of independence, P > 0.25). Even the B. bipinnatifida community, which had a different taxonomic composition to the other Berkheya communities, had a similar guild structure. Therefore, although herbivore species composition was not the same, the method in which these insects exploited the flower-heads appears to have been similar.

4.5 Species packing

The herbivore species listed in tables 4.1 to 4.6 did not occur in each flower-head population simultaneously and the number of species may vary considerably between flower-head populations (see section 4.3). Species packing (sensu Zwölfer 1985) is a measure of the number of herbivore species that occur on the flower-heads at a particular site and represents local species richness. It was used here to compare the local species richness of the herbivore communities associated with the flower-heads of the six Berkheya species.

Table 4.11 provides a list of the average species packing for each of the Berkheya species. In all six Berkheya species sampled, at each site, the number of flower-heads infested with herbivores was directly related to the number of herbivore species present (Fig. 4.11). In B. bipinnatifida and Berkheya sp, the maximum proportion of infested flower-heads in a population was below 60% and

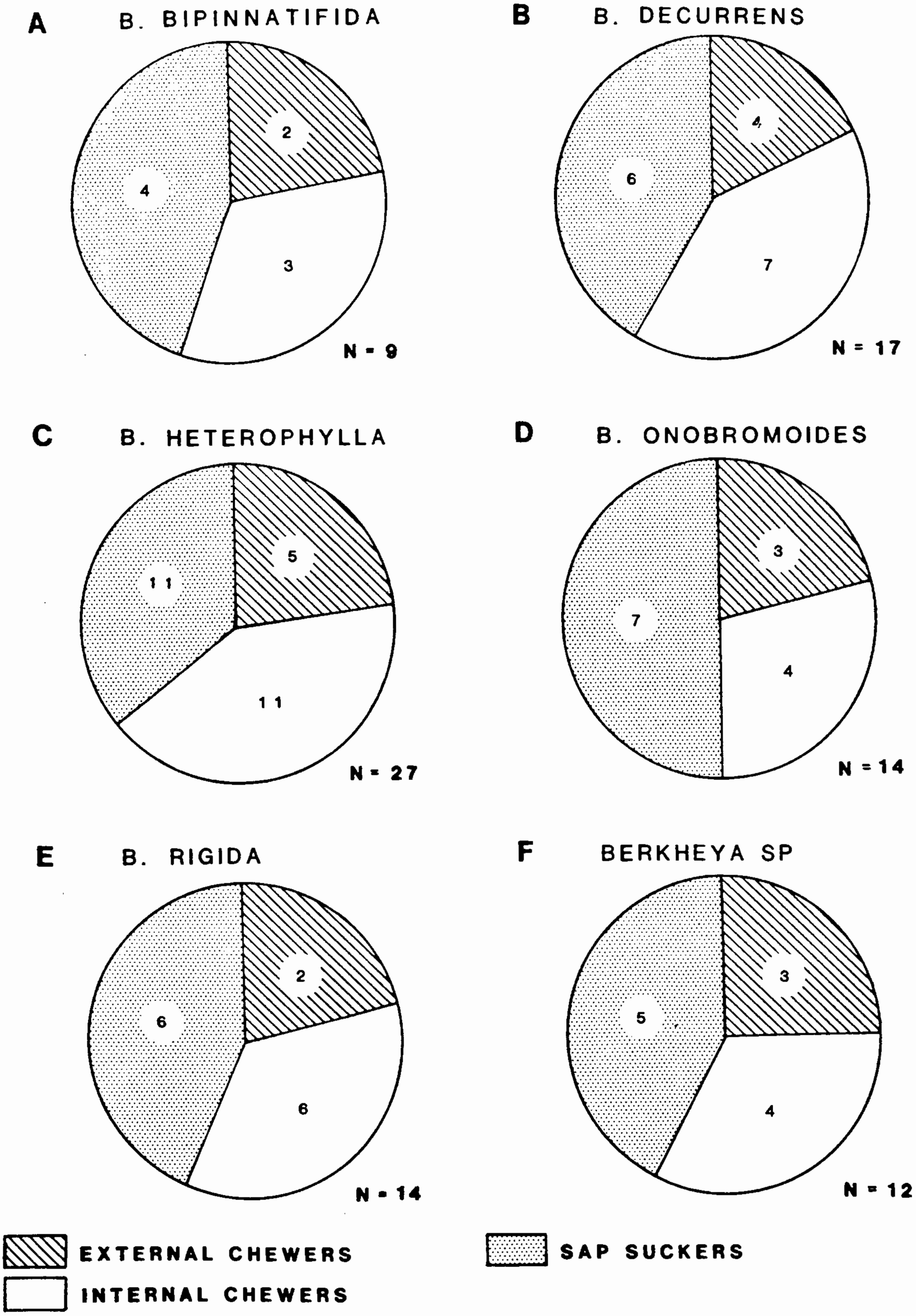


Fig. 4.10 The guild composition of the herbivore communities found in Berkheya flower-heads. Actual species numbers are shown on the graphs and **N** equals the total number of insect herbivore species.

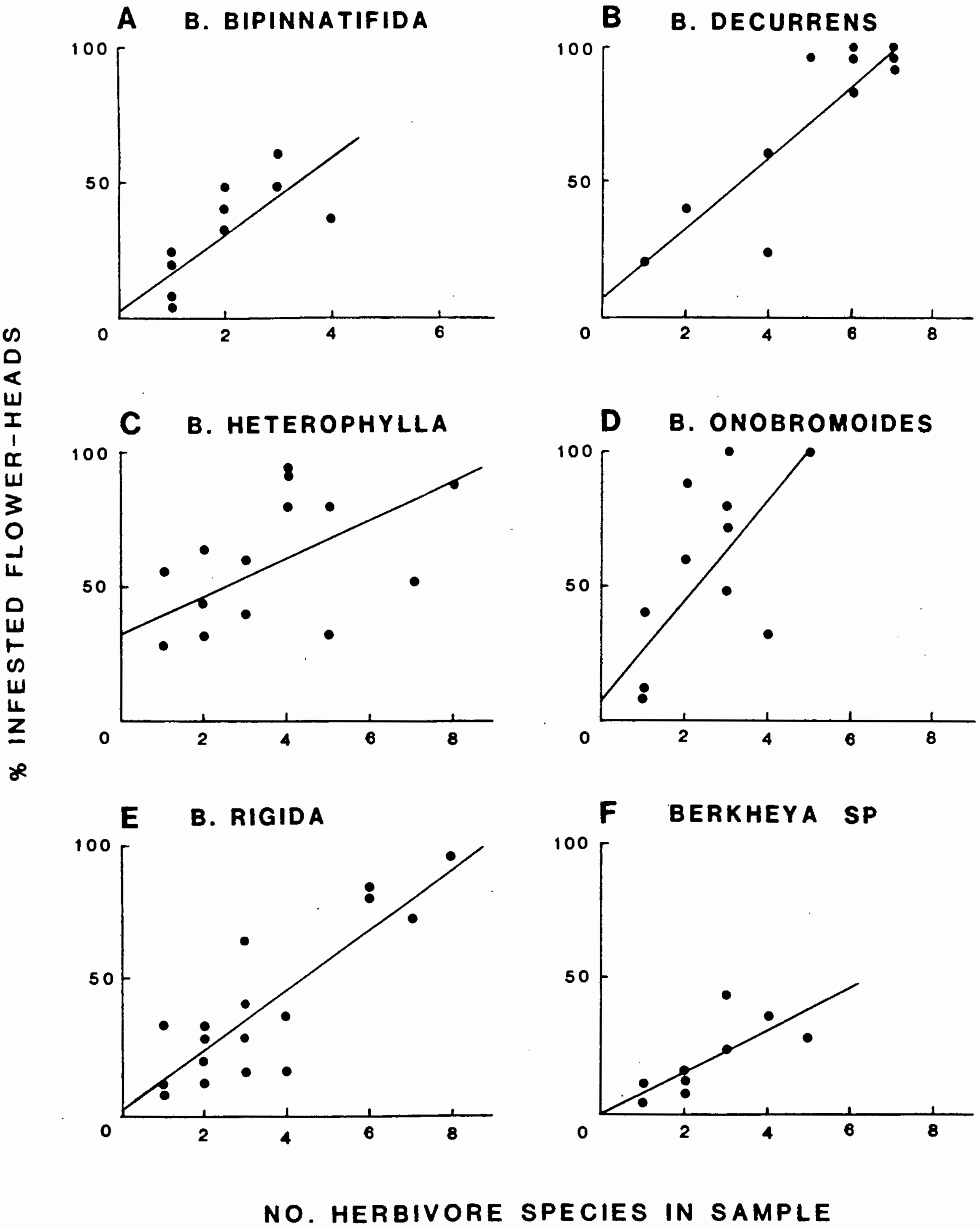


Fig. 4.11 Relationship between the number of infested flower-heads and the number of herbivore species in a particular sample.
(A) $y = 14.32x + 1.78$, $r^2 = 0.68$, $P < 0.05$; (B) $y = 13.6x + 5.4$, $r^2 = 0.78$, $P < 0.001$;
(C) $y = 7.34x + 31.91$, $r^2 = 0.35$, $P < 0.05$; (D) $y = 18.8x + 7.96$, $r^2 = 0.61$, $P < 0.05$;
(E) $y = 11.3x + 0.99$, $r^2 = 0.76$, $P < 0.001$; (F) $y = 7.92x + 0.56$, $r^2 = 0.79$, $P < 0.001$.

Table 4.11 Mean species packing of herbivores in Berkheya flower- head populations. N is number of sites sampled.

Berkheya sp	N	Mean species packing	±S.E.M.	Range
B. bipinnatifida	13	1.5	0.42	0-4
B. decurrens	11	4.5	0.69	2-7
B. heterophylla	16	4.1	0.43	0-8
B. onobromoides	14	2.7	0.59	0-6
B. rigida	14	3.1	0.27	0-8
Berkheya sp	11	2.1	0.48	0-4

50% respectively. For B. decurrens, B. heterophylla, B. onobromoides and B. rigida, some flower-head populations had from 80% to 100% infestation. Species packing of four or greater was required to achieve over 80% infestation.

Percentage flower-head utilization was lowest in B. bipinnatifida and Berkheya sp. The flower-head populations of these two Berkheya species was hardly affected by their herbivore communities because flower-head utilization was too low.

Information about the insect herbivore communities associated with Berkheya flower-heads, recorded in this chapter, are used in the analyses that follow as well as in comparisons with herbivore communities associated with thistle flower-heads.

CHAPTER 5

THE HERBIVORE COMMUNITY

Abstract

1. The insect herbivore communities that colonise the flower-heads of Berkheya, Californian thistles and European thistles were compared.

2. The total number of herbivore species varied between communities.

3. The proportion of specialist species varied between communities from 0 to 100%. A majority of specialist species over generalist species was rare in the herbivore communities and in 82% of the communities, specialist species comprised less than 40% of total species numbers.

4. The proportion of endophagous and ectophagous species in the herbivore communities also varied between communities. Generally however, herbivore communities on European thistles had a majority of endophagous species, while the herbivore communities on Berkheya and Californian thistles comprised mostly ectophagous species.

5. A comparison of taxonomic composition, using classification and ordination, showed that Coleoptera, Diptera, Hymenoptera and Lepidoptera were represented in the herbivore communities from the flower-heads of European thistles, and Coleoptera, Diptera, Hemiptera and Lepidoptera were represented in the communities from Berkheya and European thistle flower-heads. The comparison of taxonomic composition of the herbivore communities by insect orders, showed that the herbivore communities from the flower-heads of Berkheya and Californian thistles were similar. However, when the herbivore communities were compared at family and genus level, differences between these communities were noticed. Therefore, the hierarchical level at which the taxonomic composition of communities are compared can influence the outcome of the analyses.

6. Guild composition of the insect herbivore communities was also compared and analysed using classification and ordination. Four major guilds were recognised; internal chewers, external chewers, gall formers and sap suckers. The guild composition of herbivore communities from the flower-heads of Berkheya and Californian thistles were most similar to each other because each community comprised internal chewers, external chewers and sap suckers. Herbivore communities associated with the flower-heads of European thistles had a different guild composition that comprised internal chewers, external chewers and gall formers.

7. Generally, it appears that the herbivore communities associated with Berkheya and Californian thistles are similar and that the herbivore communities from both these groups differ from those associated with European thistle flower-heads.

In this chapter, five features that describe or characterise the herbivore communities from the flower-heads of Berkheya and thistles, are examined. The approach adopted here was to first compare the insect herbivore communities to identify any similarities between them, before examining the effect of host plants on these communities in later chapters. The comparison of the plant communities and analyses of plant effects are thus kept separate initially, and the influence of previous assumptions about the relationships between herbivore communities and plants is avoided.

The five aspects of the herbivore community that were examined are; (1) the total number of herbivore species that colonise the flower-heads of each plant species, (2) the proportion of specialist species to generalist species, (3) the proportion of endophagous to ectophagous species, (4) the taxonomic composition of the herbivores and (5) their guild composition.

These particular aspects together provide an accurate and descriptive picture, in numerical terms, of each community. Furthermore, they have been shown to be useful descriptive terms in other community studies (see reviews by Strong et al. 1984, and Zwölfer 1988). Throughout the chapter, comparisons are made of the herbivore communities of the flower-heads of thistles in Europe, thistles in California and Berkheya in South Africa.

5.1 Total herbivore species numbers

The total number of herbivore species that colonise the flower-heads (species richness) of a particular plant species provides the first basic description of the community. High species numbers suggest a large, and probably complex, herbivore community. A community of only one herbivore species is therefore the most simple type.

There was a large variability in the number of herbivore species found on the flower-heads of the different plant species (Table 5.1). Herbivore species numbers also varied greatly within the same plant genus. The possible reasons for this variability will be examined in the following chapters.

On some plants species, similar or identical herbivore species numbers were found but this does not imply that the characteristics of their herbivore communities are similar. The species numbers may be made up of different

Table 5.1 Mean number of insect herbivore species in communities associated with Berkheya and thistle genera. [1]European thistles, [2]Californian thistles and [3]Berkheya in South Africa.

Plant genus	No. plant species sampled	Mean no. insect species	Range
Arctium[1]	3	5.3	4 - 7
Staelina[1]	1	1	
Carduus[1]	8	9.3	1 - 36
Cirsium (Europe)[1]	16	6.2	2 - 13
Silybum[1]	1	4	
Galactites[1]	1	5	
Onopordum[1]	2	6	6 - 6
Serratula[1]	1	6	
Centaureae[1]	16	6.1	0 - 19
Microlonchus[1]	1	3	
Carthamus[1]	1	4	
Xeranthemum[1]	1	1	
Carlina[1]	3	3	1 - 4
Echinops[1]	2	1	0 - 2
Cirsium (California)[2]	9	11.6	4 - 33
Berkheya[3]	6	15.5	9 - 27

kinds of insects and the type of association between these insects and their host plant may differ. Therefore, it is necessary to inspect the communities in more detail.

5.2 Proportion of specialist herbivores

Strong et al. (1984) point out different ways in which feeding preferences are described. For example, a herbivore may be considered monophagous in one area but polyphagous over its entire range (Downey & Fuller 1961, Singer 1971, Knerer & Atwood 1973, Fox & Morrow 1981). Also, depending on the scale of comparison, feeding on one plant species, one genus or one family may all be considered monophagy (Dugdale 1975, Lawton & Schröder 1978, Holloway & Herbert 1979, Slansky 1976). Various definitions of herbivore specialization have been used with regard to insect herbivores on thistles (Table 5.2). In this thesis, a specialised herbivore is defined as one that feeds on a single plant species or on a few closely related plant species; a generalised herbivore feeds on several plant species that are not in the same genus (ie. generalists are those herbivore species that do not fit the definition of a specialist herbivore).

A specialist herbivore is committed to its host plant and changes in host range are difficult and must evolve over time (Strong et al. 1984). Generalist species are more easily able to adopt a new host plant species because they are adapted to cope with a wider range of physical and biochemical barriers to feeding.

Because specialization probably requires a long association between insect and plant to evolve, a large proportion of specialist herbivores in a community suggests an old and relatively stable association. A

Table 5.2 A list of terms used to describe the feeding preferences of herbivores associated with thistles, and their definitions.

Term	Definition	Reference
Monophagous	Feed on a single plant species	Zwölfer 1965, Lawton & Schröder 1978
Almost monophagous	Feed on a few related plants	Zwölfer 1965
Stenophagous	Feed on a small group of congeneric plants	Zwölfer 1982a
	Feed on one plant tribe	Goeden & Ricker 1986a
Oligophagous	Feed on plants in the same subtribe	Zwölfer 1965
	Feed on plants in the same tribe	Lawton & Schröder 1978
Euryphagous	Restricted to a plant tribe or family	Goeden & Ricker 1986a
Specialists	Stenophagous species	Zwölfer 1982a
	Feed on a few congeneric plants	This study
Generalists	Euryphagous species	Zwölfer 1982a
	Species that are not specialists	This study
Polyphagous	Feed on several plant orders	Zwölfer 1982a
	Feed on several plant tribes or families	Goeden & Ricker 1986a, Lawton & Schröder 1978

community comprising many generalists however is not necessarily younger than one with many specialists, but the community may be less stable. Environmental changes could cause a generalist to alter its geographical distribution so that it no longer encounters a particular plant species, and by the same mechanism other generalists could move into the area. Therefore the number and kind of generalist species, that include a particular plant species in its diet, can alter rapidly. These changes are not possible for specialist species which, in similar circumstances, could easily become extinct.

Specialised herbivores closely associated with their host plants have sometimes undergone extensive adaptive radiation along with the plant taxon (Price 1983). Larinus is an example of a diverse genus closely associated with thistles in Europe (Zwölfer et al. 1971). Another example is the cecidomid midges which are gall formers, a very specialised habit (Eastop 1973), and which form the the largest herbivore family in Britain (Price 1977, 1980).

The proportion of specialist and generalist species, that occurred on the flower-heads of Berkheya and thistles, are provided in Table 5.3. Table 5.3 shows that the proportion of specialists was very variable and ranged from 0 to 100%. Range and not standard deviation was used as a measure of variability because the distributions are not normal. A proportion of 100% specialists in the community was rare and occurred in only 6% of the communities while 82% of the communities had fewer than 40% specialists. Thus most of the herbivore community comprised generalist species.

A further point of note is the variability of specialist species numbers within each plant genus. In most genera, the proportion of specialist species in the community ranged widely from 0 to more than 50%, but in Arctium, Onopordum and Berkheya, the proportion of specialists did not differ significantly between plant species (chi-square test of heterogeneity) (Table 5.3). The mean proportion of specialists for these genera were 50, 33 and 17% respectively, so they clearly differed significantly between each other. No generalizations can be made about

Table 5.3 Number, proportion and range of specialist and generalist insect herbivores in the flower-head communities of thistles and Berkheya. [1] European thistles, [2] Californian thistles and [3] Berkheya in South Africa.

Plant genus	No. plant species sampled	Specialists mean no.	Specialists %	Generalists mean no.	Generalists %	Range Special.	Range General.
Arctium[1]	3	2.7	50	2.7	50	2 - 4	2 - 3
Staelina[1]	1	1	100	0	0		
Carduus[1]	8	1.8	19	7.5	81	0 - 5	1 - 33
Cirsium[1]	16	0.6	9	5.6	91	0 - 3	1 - 11
Silybum[1]	1	0	0	4	100		
Galactites[1]	1	0	0	5	100		
Onopordum[1]	2	2	33	4	67		
Serratula[1]	1	2	33	4	67		
Centaurea[1]	16	1.4	24	4.6	76	0 - 6	0 - 13
Michrolonchus[1]	1	2	67	1	33		
Carthamus[1]	1	1	25	3	75		
Xeranthemum[1]	1	0	0	1	100		
Carlina[1]	3	2.3	78	0.7	22	1 - 4	0 - 2
Echinops[1]	2	1	100	0	0	0 - 2	0 - 0
Cirsium[2]	9	0.3	3	11.2	97	0 - 2	4 - 33
Berkheya[3]	6	1	17	14.5	83	1 - 1	8 - 26

the proportion of specialists in the other plant genera because of the variability between plant species.

5.3 Proportion of endophagous herbivores

Flower-head inhabiting herbivores have two distinct options, they can feed either externally on or internally in the flower-head. Those that feed inside thistle and Berkheya flower-heads tend to be the soft-bodied coleopteran, dipteran and lepidopteran larvae that are protected from the external environment when inside the flower-head. Ectophagous species are more mobile and usually have other means of protection.

A complex suite of parasitoids is found attacking herbivores on thistles (Varley 1947, Redfern 1983) and on Berkheya (chapter 4), so it appears doubtful that the reason for endophagy is selection for enemy free space (Jeffries & Lawton 1984). However, the enemy free space hypothesis cannot be rejected because it may have been important originally when the herbivores first colonised the flower-heads. On Berkheya flower-heads, ectophagous species were mostly mobile, except for the scale insects (chapter 4), and few of these species were parasitised or preyed upon. The eggs of the pentatomid Sciocoris were the only stage of an ectophagous species parasitised and the only insect predators observed, during many hours of sampling, were a few coccinellids that attacked aphids. Therefore, in terms of escaping enemies, ectophagy combined with mobility appears to be more successful than endophagy. However, because their population growth is under control (Berkheya were not covered in vast numbers of ectophagous species), ectophagous species must be exposed to other mortality factors which could counteract the positive effects resulting from the paucity of predators and parasitoids. In addition, endophagy may have evolved at a time when pressure from parasitoids was relatively low.

The proportion of endophagous species in the flower-heads of each of the plant genera is presented in Table 5.4. As was the case for the proportion of specialists, variability between communities on congeneric plant species was often large (see ranges, Table 5.4). Generally, the results show that 79% of the European thistles have more the 75% endophagous species in their

Table 5.4 Number, proportion and range of endophagous and ectophagous herbivores in the flower-head communities of thistles and Berkheya. [1] European thistles, [2] Californian thistles and [3] Berkheya in South Africa.

Plant genus	No. plant species sampled	Endophages mean no.	Endophages %	Ectophages mean no.	Ectophages %	Range Endo.	Range Ecto.
Arctium[1]	3	4.3	81	1	19	4 - 5	0 - 2
Staelina[1]	1	1	100	0	0		
Carduus[1]	8	6.3	68	3	32	0 - 16	0 - 20
Cirsium[1]	16	5.7	92	0.5	8	1 - 13	0 - 3
Silybum[1]	1	4	100	0	0		
Galactites[1]	1	3	60	2	40		
Onopordum[1]	2	5	83	1	17	4 - 6	0 - 2
Serratula[1]	1	6	100	0	0		
Centaurea[1]	16	5.4	89	0.69	11	1 - 18	0 - 4
Michrolonchus[1]	1	3	100	0	0		
Carthamus[1]	1	4	100	0	0		
Xeranthemum[1]	1	1	100	0	0		
Carlina[1]	3	3	100	0	0	1 - 4	0 - 0
Echinops[1]	2	1	100	0	0	0 - 2	0 - 0
Cirsium[2]	9	3.7	32	7.9	68	1 - 7	1 - 28
Berkheya[3]	6	3	27	8	73	3 - 11	4 - 16

flower-heads. In California, 67% of the thistle species have less than 50% endophagous species, and in Berkheya all the plant species have less than 45% endophagous species.

Why are there generally fewer endophagous species in California and South Africa than in Europe? Strong et al. (1984) showed that Carduus pycnocephalus L. (Asteraceae: Carduoidaea) and Silybum marianum (L.) Gaertn. (Asteraceae: Carduoideae), introduced into North America, have fewer endophages than native thistle species. They believe this implies that endophages colonise more slowly than ectophages. A comparison of the insect herbivore communities colonising the flower-heads of two European thistle species introduced into South Africa with the herbivore communities in Berkheya flower-heads, obtained similar results (Appendix 2).

An implication of the slow recruitment of endophagous species relative to ectophagous species is that Cirsium species endemic to California and Berkheya species in South Africa may be younger, in evolutionary terms, than the thistles in Europe. It is possible that Berkheya evolved from the European Cynaroideae and are therefore a younger group (chapter 2). Also, Cirsium in North America is believed to have originated from Asia (Zwölfer 1988) and is therefore probably younger than the European Cirsium species but there are problems with this argument (see chapter 2). The relative age of the plant species may not be as important as the length of time the plants have been in North America. The herbivore - thistle association has been shorter in North America than in Europe which is the evolutionary centre of the thistles (Zwölfer 1988). Thus, the relatively lower proportions of endophages in the herbivore communities on the flower-heads of thistles and Berkheya in California and South Africa respectively, may be due to a shorter association between the herbivores and plants when compared to herbivore communities in Europe.

5.4 Taxonomic composition

Plant species may have the same number of herbivore species, the same proportion of specialists and the same proportion of endophages, but these figures provide no information about the kinds of insect species present. A comparison of the taxonomic composition of the herbivores on the flower-heads of each plant species may show important differences or similarities between herbivore communities.

Five insect orders were represented by the herbivores present in the flower-heads of thistles and Berkheya; Coleoptera, Diptera, Lepidoptera, Hemiptera and Hymenoptera (Zwölfer 1965, Goeden & Ricker 1986a, 1987a, 1987b, chapter 4). The proportion of herbivores in these orders on each plant species was variable and patterns were not easily identified.

In two earlier studies of the insect fauna on thistles, the proportions of insect orders were combined for certain plant genera, (Goeden & Ricker 1987b) and for all the Cynaroideae sampled by Zwölfer (1965) (Lawton & Schröder 1978). These authors studied the herbivores found on the entire plant and did not confine their studies to flower-heads alone. However, because of the variability in the proportion of herbivore species in each insect order, between plant species, the results for different herbivore communities should not be combined.

To avoid the problem of the variability in taxonomic composition between plant species, no attempt was made to group results for plant genera. Instead, the taxonomic composition of all the plant species were compared to each other, using ordinal techniques.

5.4.1 Classification and ordination

The technique used to analyse the taxonomic composition was firstly to draw up a similarity matrix, using the proportion of insect species in each order for each plant species. Many measures of similarity have been designed (Clifford & Stephenson 1975, Southwood 1978). The Bray-

Curtis measure is used here (Bray & Curtis 1957). A feature of the data to be analysed is that there are many zeros and transformation of the data will not alter this. Many measures of similarity take account of joint absences and may show that the communities of several plant species are similar because they lack the same herbivore species. The advantage of the Bray-Curtis measure is that it is not affected by joint absences and it also gives more weight to common groups than to rare ones (Field & McFarlane 1968).

The Bray-Curtis measure is described as

$$\delta_{jk} = \frac{\sum_{i=1}^{s} (Y_{ij} - Y_{ik})}{\sum_{i=1}^{s} (Y_{ij} + Y_{ik})}$$

where Y_{ij} = score for the ith species in the jth sample;
Y_{ik} = score for the ith species in the kth sample;
δ_{jk} = dissimilarity between jth and kth samples summed for all species (Field et al. 1982).

The similarity matrix was used to compile a dendrogram using group-average sorting. This method combines two groups together at the average level of similarity between all members of one group and all members of the other. Dendrograms have the advantage of being simple because samples (in this example herbivore communities associated with plant species) are clustered into distinct groups.

Four major disadvantages of dendrograms, listed by Field et al. (1982), and summarised here are; (1) the identity of a sample is lost once it has been placed in a group, (2) only inter-group relationships are shown, (3) two adjacent samples are not necessarily the most similar and (4) dendrograms may force a graded series into discrete classes because discontinuities tend to be over emphasized. Because of these disadvantages, Field et al. (1982) advised that another complimentary method be used in addition to the dendrogram. If the results from the two techniques agree, then they can be accepted, but if they differ then the results must be interpreted accordingly.

Multi-dimensional scaling (MDS), a method of ordination, is used here to compliment the dendrogram (Shepard 1962, Kruskal 1964, Kruskal 1977, Kruskal & Wish 1978). MDS is flexible with data that have many zero counts. This gives MDS an advantage over other techniques such as correspondence analysis and principal co-ordinates which are relatively inflexible with many zero values. The MDS plot presents the data in two dimensions and the grouping of the data can then be compared to the grouping obtained in the dendrogram.

The techniques described above are summarised in Fig. 5.1 and in the next section they are applied to the taxonomic composition of herbivores on thistle and Berkheya flower-heads.

5.4.2 Analysis of taxonomic composition

The taxonomic composition was determined from the proportion of herbivore species in each insect order. The results of this analysis are provided in the dendrogram in Fig. 5.2 and the plot in Fig. 5.3. Both the dendrogram and the plot show a similar division of the herbivore communities. Three groups 1, 2 and 3 are recognised in

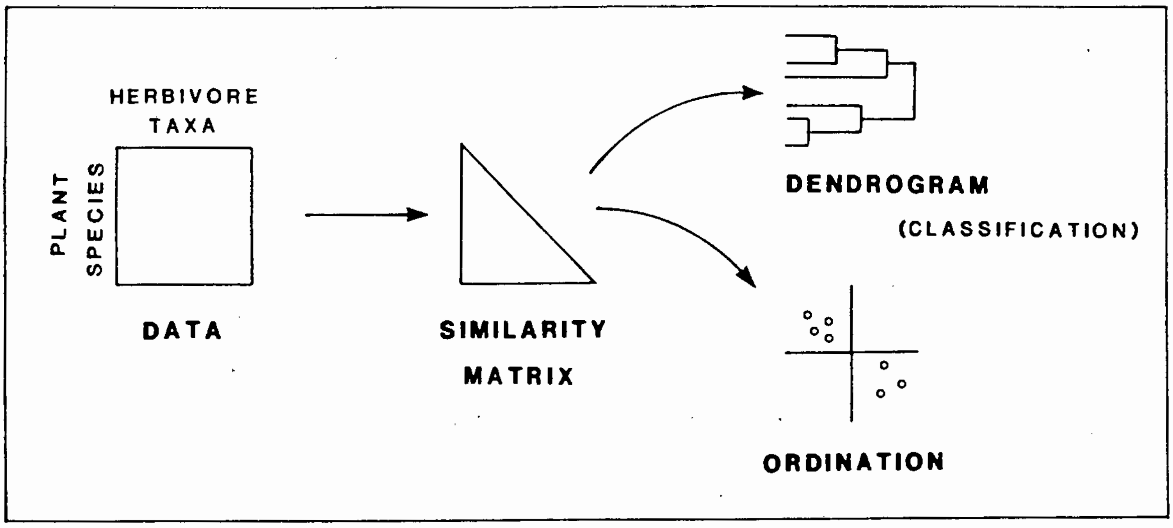


Fig. 5.1 Diagram to summarise the method used to analyse and compare the taxonomic composition of herbivore communities from thistles and Berkheya flower-heads. Adapted from Field et al. (1982).

Fig. 5.3 and were distinguished at an arbitrary similarity level of 48% shown by the broken line in Fig. 5.2.

The small group 3 comprises only two plant species, Microlonchus salmanticus DC. and Xeranthemum annuum L. These species are relatively scarce and come from smaller genera than most of the other plant species (Zwölfer 1965, chapter 2). Of more interest are the two larger groups, 1 and 2. Group 1 consists of the rest of the European thistles and also Cirsium brevistylum Cronquist (number 53) which is one of the Californian thistles (see below for why C. brevistylum is included in group 1). Group 2 consists of the rest of the Californian thistle species as well as all the Berkheya species. Goeden & Ricker (1987b) have noted that different kinds of insects are associated with thistles in California and Europe. The taxonomic composition of herbivores on thistles from California is more similar to communities on Berkheya in South Africa

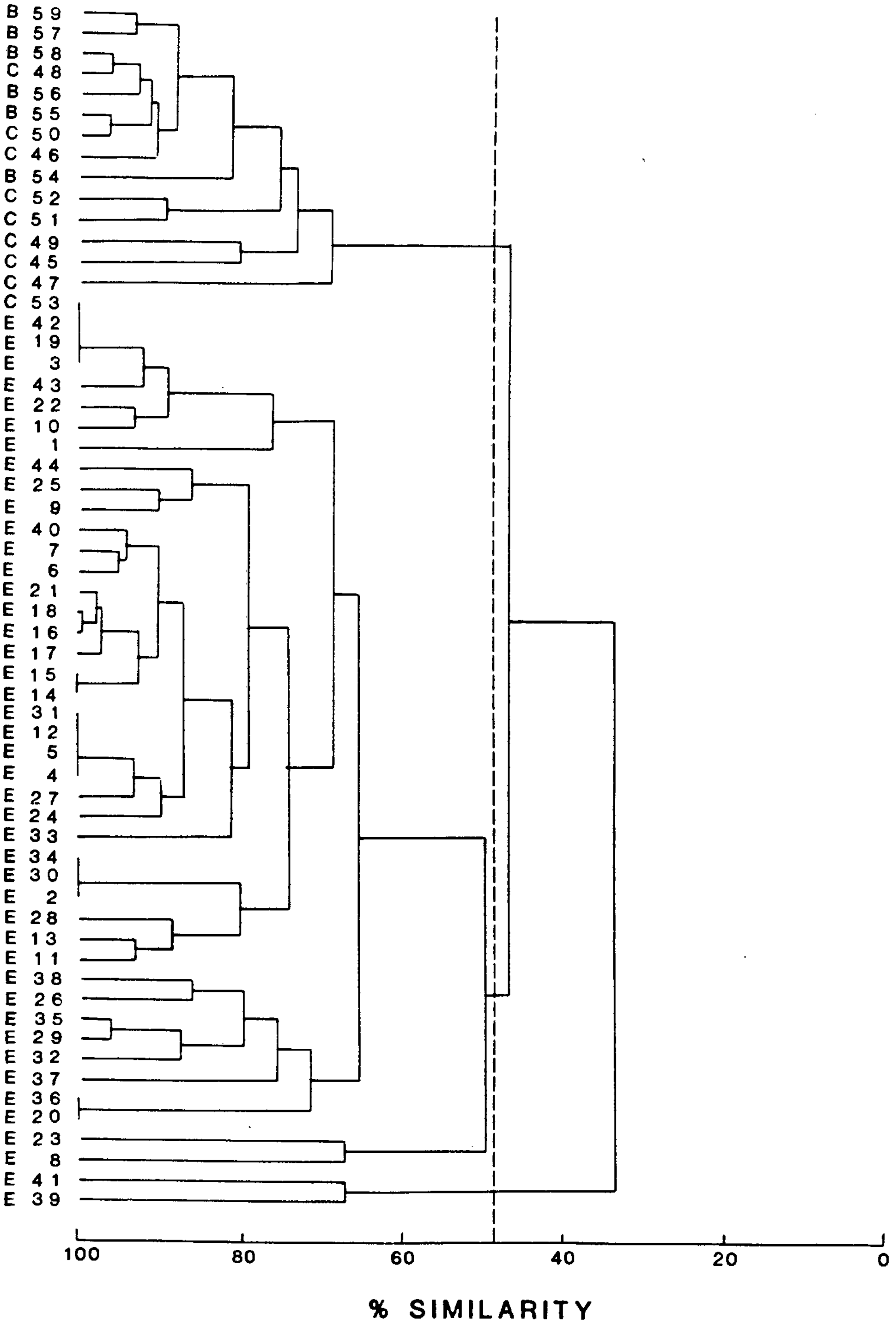


Fig. 5.2 Dendrogram showing the classification of 59 herbivore communities based on the proportion of herbivore species in each order. Three main groups are distinguished at an arbitrary similarity level of 48%. B, C and E refer to *Berkheya* in South Africa, Californian thistles, and European thistles respectively and the numbers refer to plant species: 1. *Arctium lappa*, 2. *A. minus*, 3. *A. tomentosum*, 4. *Carduus nutans*, 5. *Carduus personatus*, 6. *C. acanthoides*, 7. *C. crispus*, 8. *C. pycnocephalus*, 9. *Cirsium eriophorum*, 10. *C. vulgare*, 11. *C. pannonicum*, 12. *C. canum*, 13. *C. acaule*, 14. *C. tuberosum*, 15. *C. salisburgense*, 16. *C. eristhales*, 17. *C. oleraceum*, 18. *C. palustre*, 19. *C. brachycephalum*, 20. *C. monspessulanum*, 21. *C. arvense*, 22. *Silybum marianum*, 23. *Galactites tomentosa*, 24. *Onopordum acanthium*, 25. *Onopordum illyricum*,

Fig. 5.2 continued. 26. Serratula tinctoria, 27. Centaurea jacea 28. C. nigrescens, 29. C. nemoralis, 30. C. pseudophrygia, 31. C. montana, 32. C. stoebe, 33. C.paniculata, 34. C. aspera, 35. C. scabiosa, 36. C. collina, 37. C. calcitrapa, 38. C. solstitialis, 39. Microlonchus salmanticus, 40. Carthamus lanatus, 41. Xeranthemum annuum, 42. Carlina vulgaris, 43. C. acaulis, 44. E. ritro, 45. Cirsium californicum, 46. C. proteanum, 47. C. mohavense, 48. C. occidentale, 49. C. neomexicanum, 50. C. tioganum, 51. C. nidulum, 52. C. congdonii, 53. C. brevistylum, 54. Berkheya bipinnatifida, 55. B. heterophylla, 56. B. decurrens, 57. B. rigida, 58. Berkheya sp, 59. B. onobromoides.

than to communities on other closely related thistles in Europe.

The dendrogram in Fig. 5.2 and the plot in Fig. 5.3 do not explain what is different in the taxonomic composition of the herbivore communities in the three groups, but merely show that interesting differences exist. To determine what differences there are between the three groups, the proportions of herbivore species present in each order were compared between the groups using the Mann-Whitney U test.

There is no statistically significant difference in the proportion of Coleoptera between groups 1 and 2 (Fig. 5.4a). No Coleoptera are present in group 3. Group 1 has a larger proportion of Lepidoptera than group 2 (Fig. 5.4b), and this difference is just significant ($P < 0.05$). There are no Lepidoptera in group 3. Diptera form a much larger proportion of the herbivore community in group 1 than in group 2 ($P < 0.001$) and constitute most of the community in group 3 (Fig. 5.4c). Herbivorous Hymenoptera were present only in European thistle communities (group 1 and 3) (Fig. 5.4d), but because so few plant species had

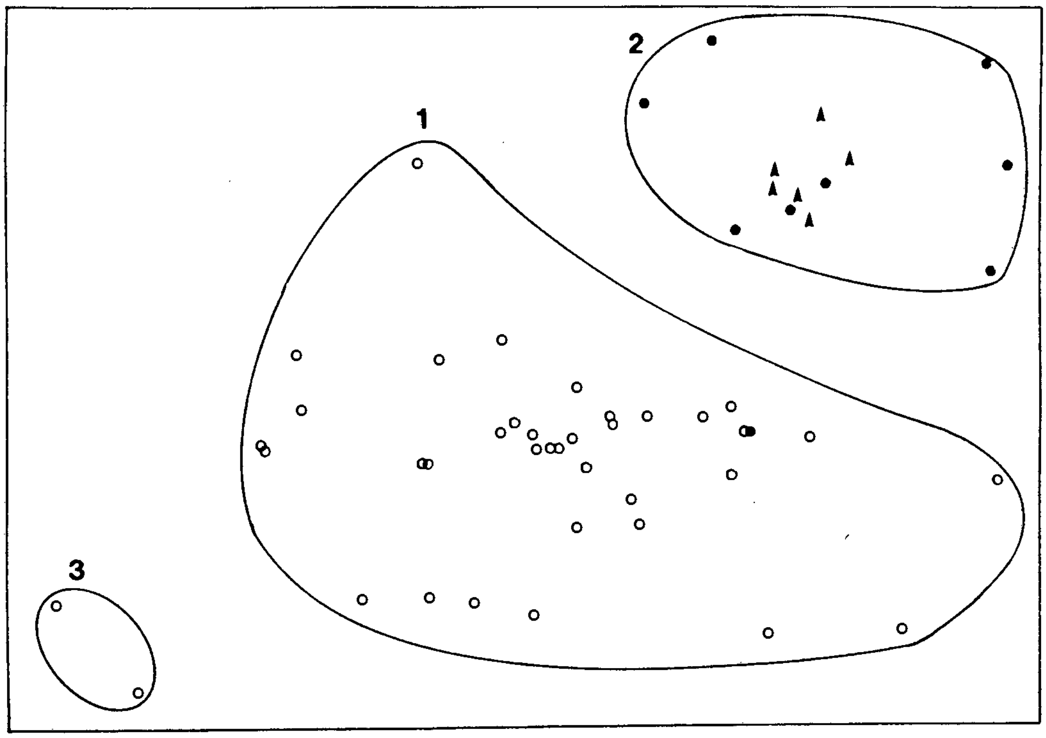
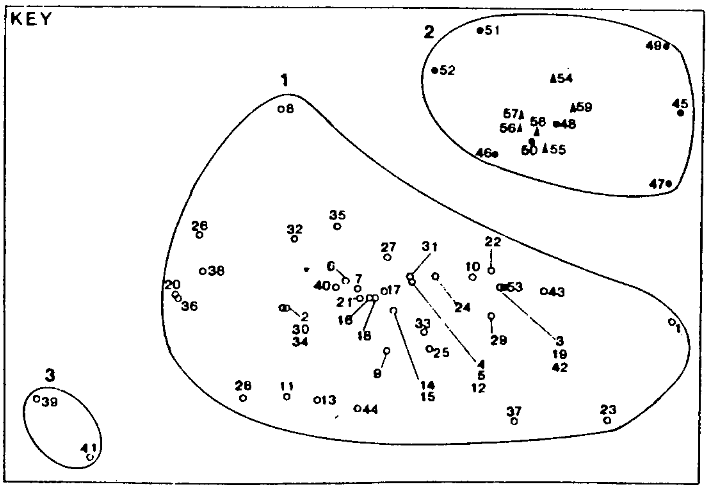


Fig. 5.3 Ordination of 59 herbivore communities based on the proportion of herbivore species in each order. Clusters 1, 2 and 3 were distinguished in the dendrogram (Fig. 5.2). Axis scales are arbitrary and are therefore not given. Open circles, closed circles and triangles represent communities from European thistles, Californian thistles and Berkheya respectively. A key to the plot is provided below. Numbers in the key refer to plant species which are listed in Fig. 5.2.



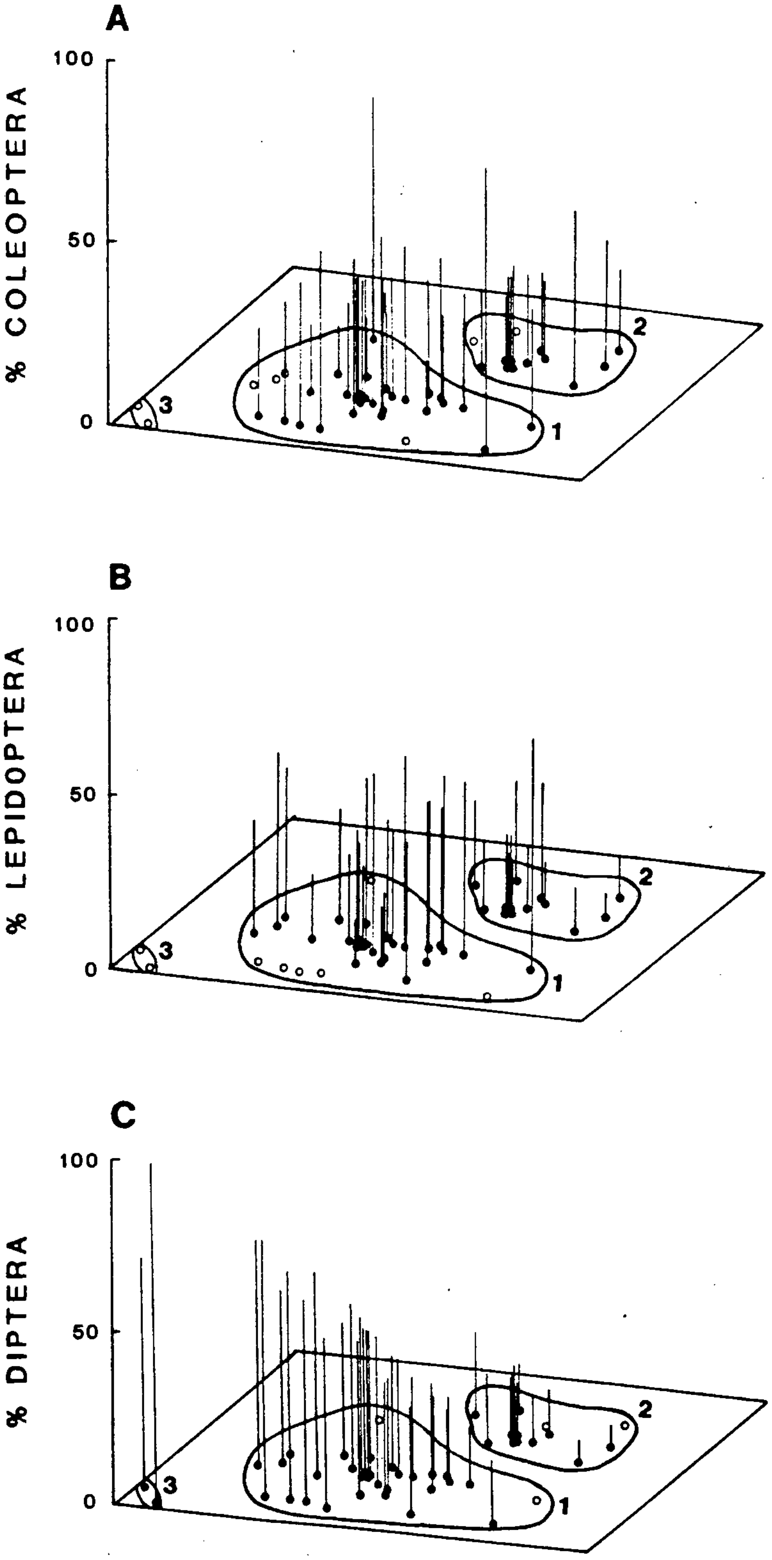


Fig. 5.4 Three dimensional replicas of the clusters 1, 2, and 3 in Fig. 5.3 that represent the proportion of the herbivore communities in each order. A. Coleoptera, B. Lepidoptera, C. Diptera, D. Hymenoptera, E. Hemiptera. Open circles show that the taxon is not represented in the community. Closed circles show that the taxon is present and the vertical lines indicate the proportion of the community comprised of the taxon. Plant species to which the symbols refer are provided in the key to Fig. 5.3. Continued on next page.

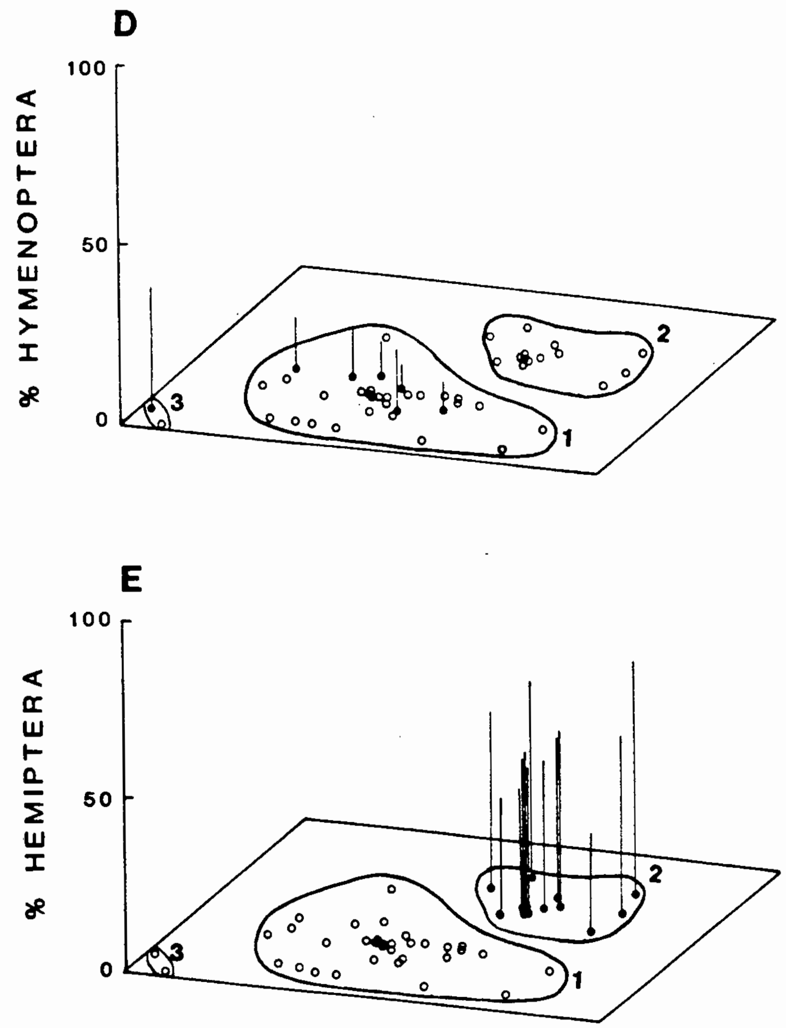


Fig. 5.4 continued.

Hymenoptera present (seven plant species), and because they formed a low proportion of the herbivore community in these plant species (< 20% except for one community in group 3 which had < 40% Hymenoptera), there was no statistically significant difference between groups 1 and 2 ($P > 0.05$). However, this difference is of biological significance. The last taxon examined was the Hemiptera which were present only in group 2 (Fig. 5.4e).

The reason that the plant species were split into three main groups (Fig. 5.3) now becomes apparent. Herbivore communities on plants in group 1 (European thistles) comprised mainly Coleoptera, Lepidoptera and Diptera with a small number of Hymenoptera. In group 2 (Berkheya and Californian thistles) the herbivore communities consisted mainly of Coleoptera and Hemiptera with fewer Lepidoptera and Diptera. Herbivore communities in group 3 were comprised almost entirely of Diptera. The inclusion of the herbivore community from C. brevistylum, a Californian thistle, in group 1 is exceptional and this is because it did not have any Hemiptera, which were present in all other Californian thistles in group 2, and it therefore had more in common with the communities from European thistles in group 1.

The possible reasons for these differences are discussed in later chapters.

5.4.3 Taxonomic hierarchies

Taxonomic composition can be examined at different hierarchical levels; phylum, class, order, family, genus and species. Obviously, the results obtained from an analysis of taxonomic composition will differ depending upon the level at which the community is looked at. In this study, for example, if the communities are compared at the level of class Insecta or higher, then all the communities will be found to have the same taxonomic composition.

The herbivore communities have already been shown to exhibit significant differences at ordinal level and the differences are expected to become more obvious if the analysis is continued to species level. To determine how the interpretation of the taxonomic composition changes when the analysis is done at different hierarchical levels, taxonomic composition was examined at family and genus level. An analysis at the species level was not done because at this level all the herbivore communities would differ from each other.

5.4.3.1 Family level

Taxonomic composition at the family level was analysed using the proportion of herbivore species present in each family.

Four groups were distinguished in Fig. 5.5 at the line drawn arbitrarily at 35% similarity. These groups were plotted in Fig. 5.6. The dendrogram and the plot show a similar division of the herbivore communities. The results differ from the comparison at ordinal level in two main ways. Firstly, the herbivore communities of the European thistles are all in one group (group 1). Secondly, the communities on Berkheya and the Californian thistles now show sufficient differences to separate them (groups 2 and 3 (Californian thistles), and group 4 (Berkheya)). The herbivore communities in group 3 are from C. brevistylum and Cirsium congdonii Moore and Frankton.

5.4.3.2 Genus level

Many of the insect genera present in the herbivore communities comprised only one species, so the analysis of taxonomic composition at genus level was done according to presence or absence of the genus and not according to proportional representation. The results of the analysis

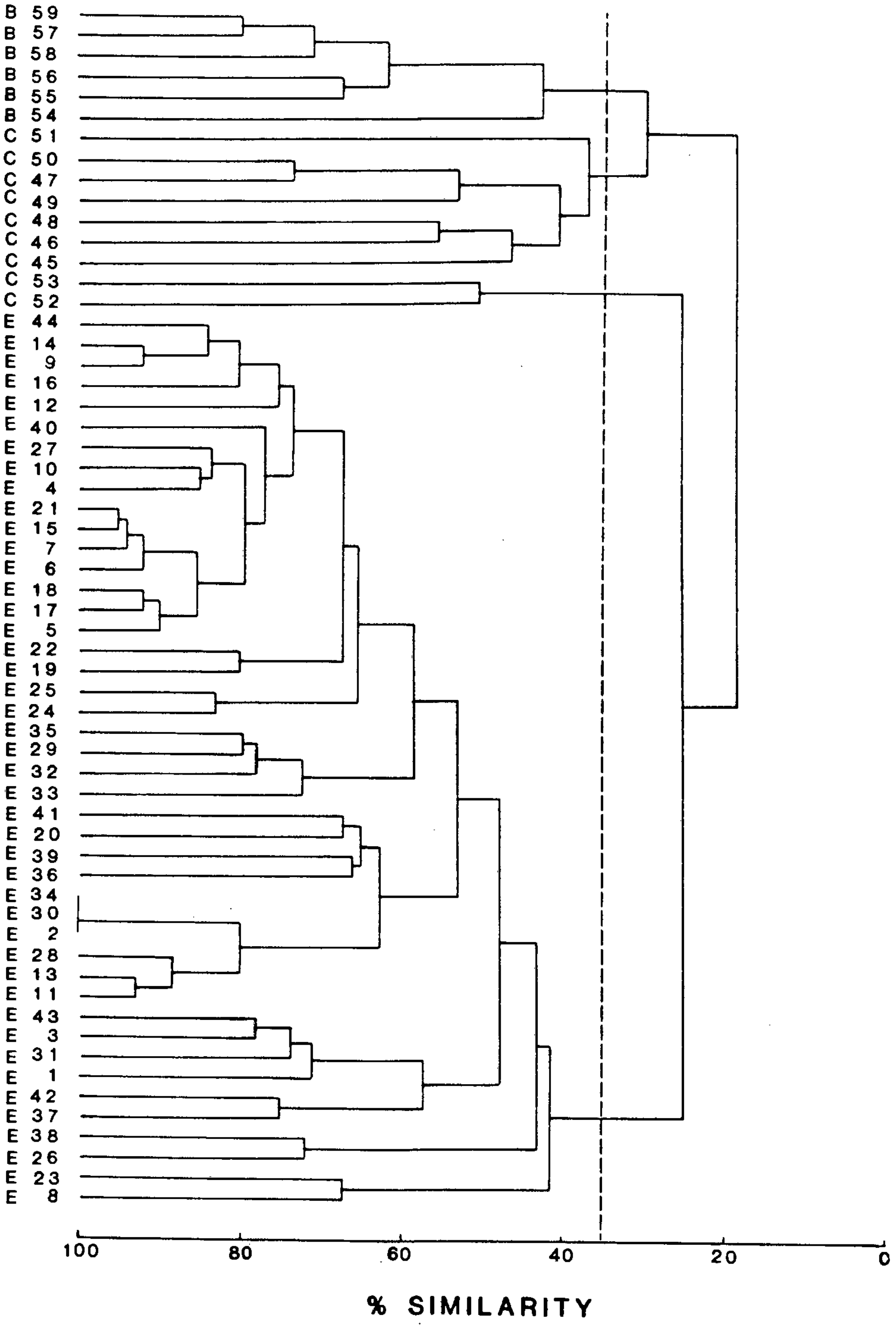


Fig. 5.5 Dendrogram showing the classification of 59 herbivore communities based on the proportion of herbivore species in each family. Four main groups are distinguished at an arbitrary similarity level of 35%. B, C, and E refer to Berkheya, Californian thistles and European thistles respectively. See legend to Fig. 5.2 for a key to the numbers which refer to the plant species.

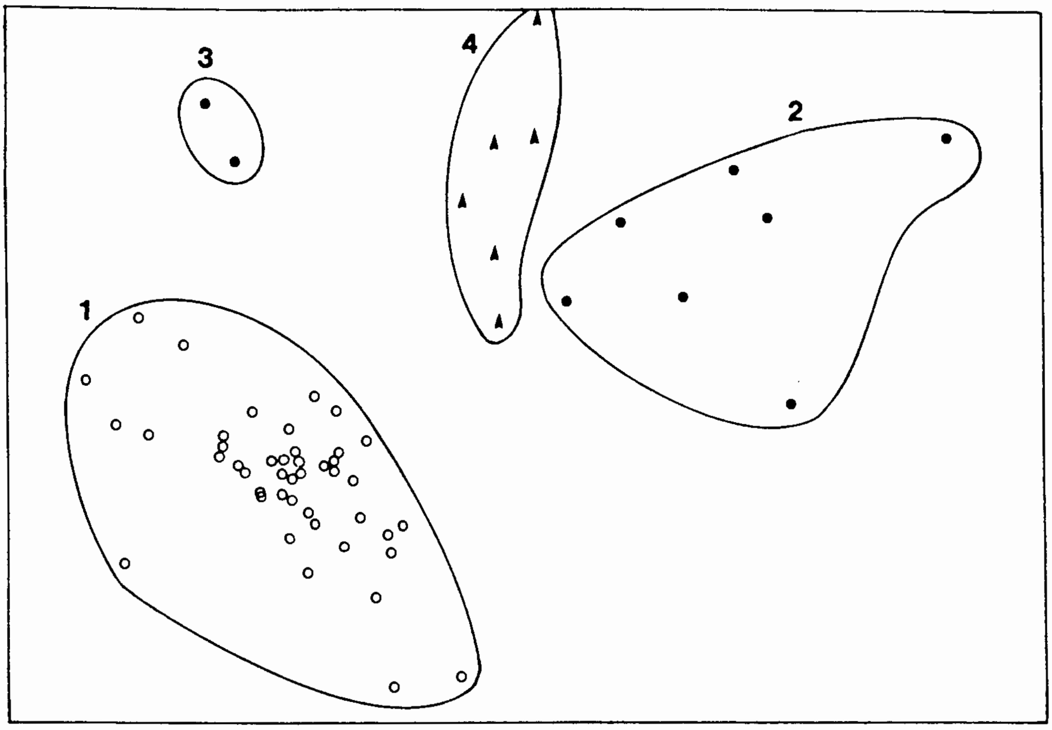
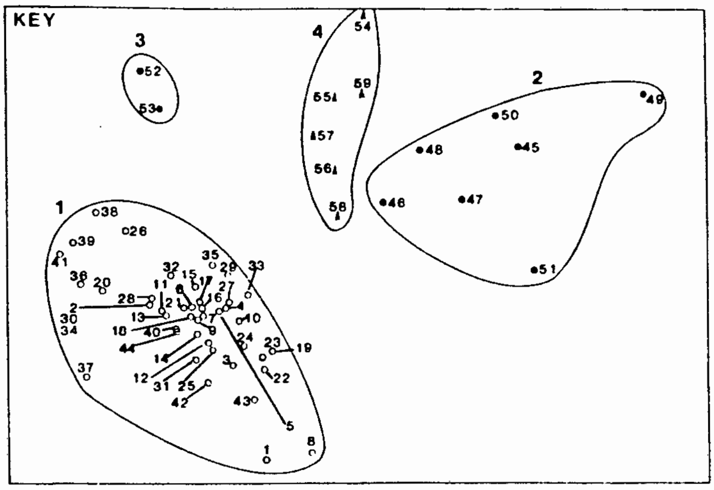


Fig. 5.6 Ordination of 59 herbivore communities based on the proportion of herbivore species in each family. Clusters **1**, **2**, **3** and **4** were distinguished in the dendrogram (Fig. 5.5). Axis scales are arbitrary and are therefore not given. Open circles, closed circles and triangles represent communities from European thistles, Californian thistles and Berkheya respectively. A key to the plot is provided below. Numbers in the key refer to the plant species which are listed in Fig. 5.2.



of the taxonomic composition of the herbivore communities at genus level is given in the dendrogram in Fig. 5.7 and the plot in Fig. 5.8. Similar divisions of the herbivore communities are shown in the dendrogram and the plot. Three groups can be distinguished at 18% similarity taken from the dendrogram (Fig. 5.7).

What is significant is that the herbivore communities on European thistles, Californian thistles and Berkheya each fall into different groups, 1, 2, and 3 respectively (Fig. 5.8). There is much variation, between European thistles, in the taxonomic composition of their herbivore communities. However the plot, obtained by MDS, illustrates that in spite of their differences, herbivore communities on European thistles have more in common with each other than with communities on the other plant species.

At the genus level, the herbivore communities on Berkheya had more in common with communities on European thistles than with communities on Californian thistles (Fig. 5.7). Yet, at the ordinal level, herbivore communities on Berkheya and Californian thistles were shown to be very similar (Figs 5.2 & 5.3). The reason for this change was that the analysis became more detailed from the ordinal to the genus level, so the differences between the herbivore communities became more marked. Table 5.5 shows how the average percentage similarity of the herbivore communities within plant groups generally decreased as the analysis became more detailed and the differences between the communities became clear.

At the ordinal level Berkheya and Californian thistles had the Hemiptera in common (Fig. 5.4e). However, the kinds of hemipteran species on the two plant groups were very

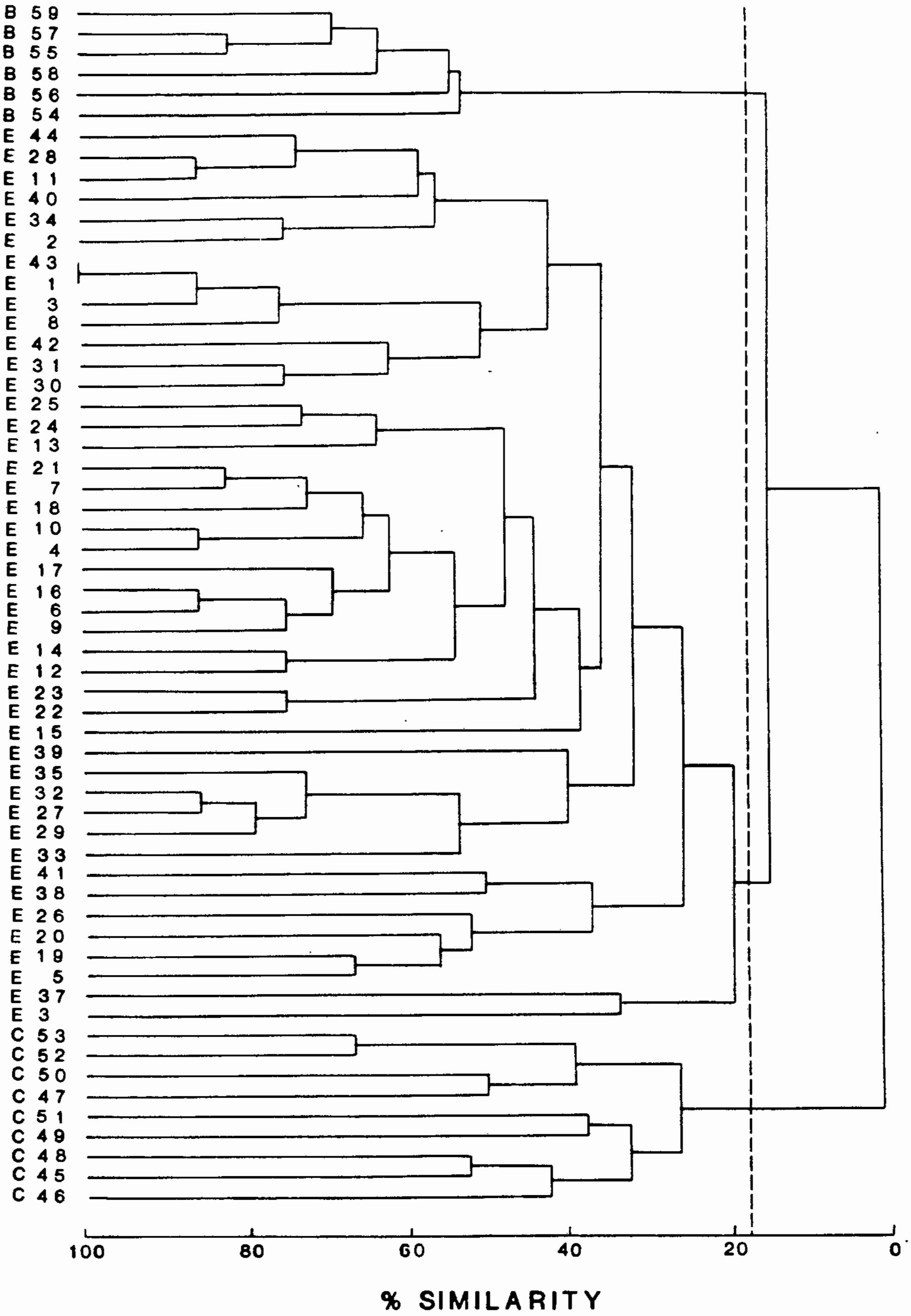


Fig. 5.7 Dendrogram showing the classification of 59 herbivore communities based on the presence or absence of each genus. Three main groups were distinguished at an arbitrary similarity level of 18%. The letters B, C and E refer to Berkheya, Californian thistles and European thistles respectively. See legend to Fig. 5.2 for a key to the numbers which refer to the plant species.

different, therefore at the genus level these herbivore communities appear to be different (Fig. 5.8). Herbivore communities on *Berkheya* have two genera in common with communities on European thistles, *Larinus* and *Urophora*. This would explain why, at the genus level, *Berkheya* herbivore communities appear more similar to herbivore communities found on European thistles than to those present on Californian thistles.

The presence of *Larinus* and *Urophora* in *Berkheya* flowerheads is of special interest because these genera are also found on European thistles. This subject will be commented on in more detail in the next section.

What this analysis shows is that an investigation of taxonomic composition can arrive at conflicting results. An analysis of taxonomic composition should be done on two levels. Firstly, the highest hierarchical level at which the communities differentiate (ordinal level in this example) and secondly, at the genus or species level. An analysis at the highest hierarchical level will provide a general view of major trends and patterns in the communities. At the species level, more detailed patterns emerge which may reflect slight differences between the host plant species. Patterns which may occur in analyses between these two levels may be artifacts of the classification system. These patterns will be affected by whether the taxonomists working on the relevant insect groups were 'splitters' (split existing taxa into several new taxa) or 'lumpers' (combine several related taxa into one group).

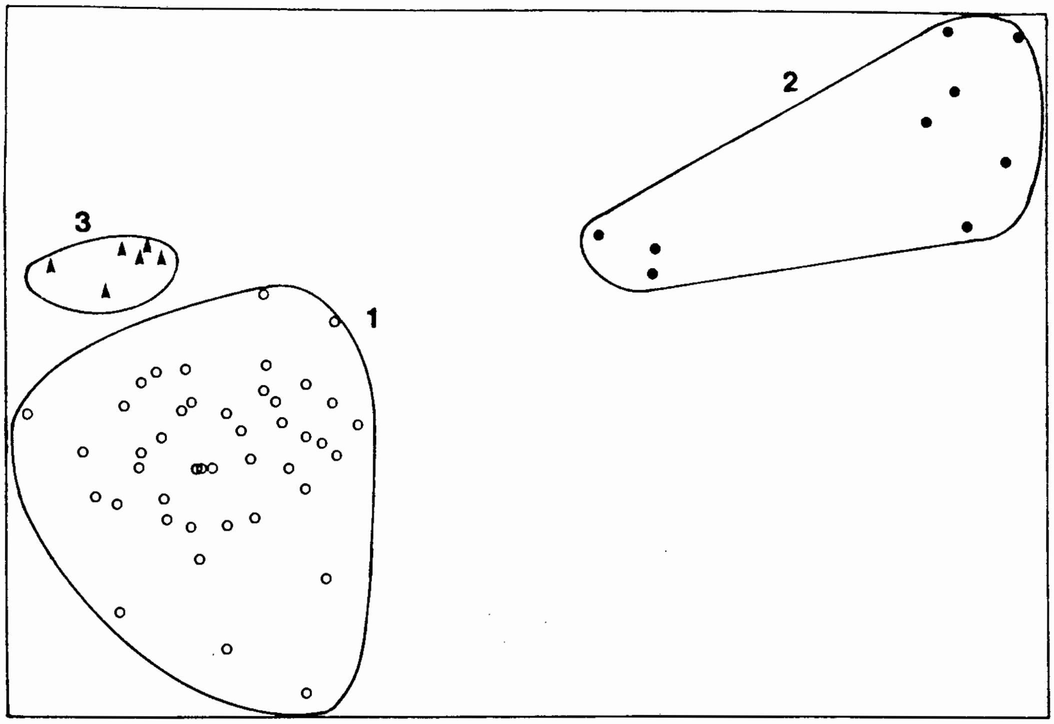


Fig. 5.8 Ordination of 59 herbivore communities based on the presence or absence of each genus. Clusters 1, 2 and 3 were distinguished in the dendrogram (Fig. 5.7). Axis scales are arbitrary and are therefore not given. Open circles, closed circles and triangles represent communities from European thistles, Californian thistles and Berkheya respectively. A key to the plot is provided below. Numbers in the key refer to the plant species which are listed in Fig. 5.2.

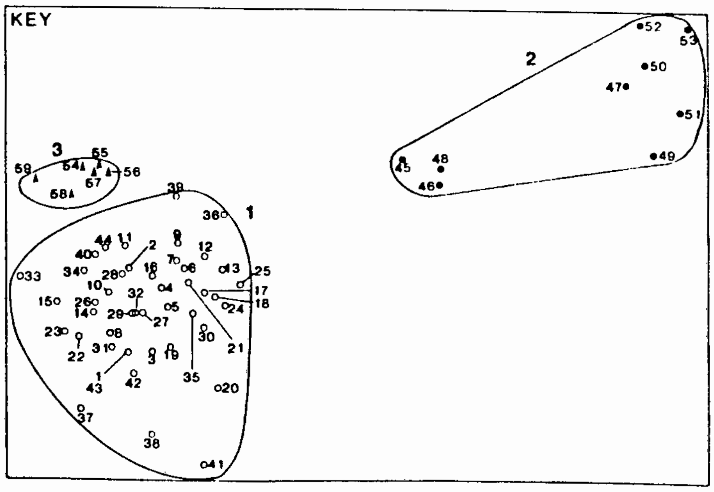


Table 5.5 The taxonomic level of analysis and the similarity of herbivore communities from the flower-heads of European thistles, Californian thistles and Berkheya. Similarity levels are taken from the dendrograms in Figs. 5.2, 5.5 and 5.7.

	% Similarity within Plant Group		
Level of comparison	European Thistles	Californian Thistles	Berkheya
Class	100	100	100
Order	49	67	81
Family	41	37	42
Genus	19	27	53

5.4.4 Larinus and Urophora

The occurrence of Larinus and Urophora in Berkheya flower-heads is of interest because these genera are closely associated with thistles in Europe.

The taxonomy of Larinus in southern Africa is preliminary and requires revision to sort out this group. Initially it was believed that each of the six Berkheya species sampled could be attacked by a different Larinus species (Appendix 1). Subsequently, Mr. R.L. Oberprieller, a taxonomist, of curculionid beetles, at the National Collection of Insects in Pretoria, made a preliminary study of the Larinus collected on the Berkheya. Five possible Larinus species were recognised. Larinus sp 1 which occurred on B. bipinnatifida, B. heterophylla, B. rigida and Berkheya sp; Larinus sp 2 which occurred on B. decurrens and Larinus sp 3 which occurred on B. onobromoides (Tables 4.1 to 4.6). The other two species, Larinus sp 4 and sp 5 came from incidental collections on B. barbata and B. carduoides respectively, in the western Cape.

The close evolutionary association of *Larinus* with thistles in Europe is well documented (Zwölfer *et al*. 1971, Zwölfer 1988). It is therefore remarkable that, in addition to its association with thistles, *Larinus* appears to have diversified in a similar association with *Berkheya* in southern Africa.

How did the association between *Larinus* and *Berkheya* evolve? This is difficult to answer because the association is obviously well developed and its origins are now probably obscured. One explanation is that *Larinus* was possibly already associated with the group of plants that split off from the Carduoideae in Europe and formed the *Berkheya* genus. Several collections in South Africa on two thistle species introduced from Europe, *Carduus macrocephalus* Desf. and *Cirsium vulgare*, found no *Larinus* species (Appendix 2). Apparently the *Larinus* species on *Berkheya* have not been able to colonise European thistles. Thistle and *Berkheya* populations are often intermingled so that *Larinus* species have had every opportunity to colonise the thistles.

Members of the genus *Larinus* found on *Berkheya* may have been separated from their parent group in Europe for long enough to be distinct from the European group. If this is correct it may be legitimate to place *Larinus* from South Africa in a separate subgenus or even in a new genus. However, this may result in a circular argument, because if *Larinus* on *Berkheya* were renamed, there would no longer be this interesting association between one insect herbivore genus and two taxonomically different and geographically separate plant groups.

The tephritid *Urophora agromyzella* was the only *Urophora* species found on the *Berkheya* species sampled. Records kept at the National Collection of Insects in Pretoria indicate that *U. agromyzella* is a generalist which has been recorded from other distantly related composite species. These records also show that other *Urophora* species have been recorded from the Asteraceae, therefore this genus is not confined to *Berkheya* in southern Africa. Moreover, species of *Urophora* have been found associated with Asteraceae other than thistles, in southern California (Goeden 1987).

The Palaearctic genus *Larinus* is divided into four subgenera. Thus it is possible that the *Larinus* on *Berkheya* in Southern Africa may fall into a new subgenus, or they may be part of an existing subgenus. Taxonomists are also not certain about the composition of the *Urophora*. The American species may be transferred to other genera (Steyskal 1979) and there may be sufficient differences to separate the Afrotropical species from the Palaearctic species. I am grateful to Dr P. Harris for this information. (Added after examination).

5.5 Guild composition

An ecological guild, defined by Root (1973), is a group of species that exploits the same resource in a similar way. Guilds provide an indication of the functional organisation in a community.

According to Simberloff (1976, 1978), guild composition is a crude method in which to classify a community. However, here its purpose is to aid in the comparison of communities and, together with the other aspects examined in this chapter, to help describe the communities. Several researchers have found the guild concept useful for similar purposes (Lawton 1982, Moran & Southwood 1982).

The guild composition of herbivores that feed on thistle flower-heads has been studied by Zwölfer (1985, 1988). Zwölfer (1988) identified three guilds, which he called trophic strategies, in the herbivore communities. The first trophic strategy consists of herbivore species that attack the flower-head buds and which may form galls. Species that oviposit and feed on maturing flower-heads form the second strategy and the third strategy comprises mobile polyphagous species that are usually phytophagous but which may become carnivores if they encounter other insects.

The disadvantage of these groupings is that they are rather widely defined and a precise knowledge of the biology of each herbivore species is required to place them into the correct guild. In addition, species may fit into more than one guild. This system in not ideal for use in a comparison with guilds on Berkheya because additional guilds are present on Berkheya that may overlap with those described by Zwölfer (1988).

In this study of guild composition, four major guilds are recognised. Chewing species have been divided into two guilds; internal chewers which feed inside the flower-head and external chewers which feed on the outside of the flower-head. The other two guilds are sap suckers and gall formers. Gall formers are defined here as species that form definite structural galls. Zwölfer (1985) includes species, in the guild of gall formers, that do not form structural galls but are able to channel additional assimilates into the flower-heads. This is a wide definition of a gall former and many sap sucking hemipterans like aphids may also fall into this category. In another study of the guild structure of thistle insect communities by Lawton & Schröder (1978), only species that formed structural galls were included in this guild. In this study, the most commonly used definition of a gall former is applied, thus only those species that form structural galls are placed in this guild.

The data were analysed in the same way as the taxonomic composition was examined, with the aid of classification and multi-dimensional scaling. The proportion of herbivore species in each guild was used in the analysis. Unlike the taxonomic composition, there is no problem of hierarchical differences when the guild composition is examined.

At the 60% level of similarity, herbivore communities associated with the plant species were divided into three groups (Fig. 5.9). These groups are plotted in Fig. 5.10. A similar division of the herbivore communities was obtained from the dendrogram and the plot. The small group 3 comprised only the Microlonchus salmanticus herbivore community. Group 1 consisted almost entirely of communities on European thistles. The thistle Cirsium brevistylum, a species found in California, was also present in this group. Group 2 comprised the remainder of the Californian thistles and all the communities from the Berkheya species.

Note that the composition of the three groups in Fig. 5.10 is almost identical to the grouping obtained from the analysis of taxonomic composition by orders (Fig. 5.3). Guild composition is not merely a reflection of taxonomic composition by orders. Coleoptera and Lepidoptera were present in the guilds of external chewers and internal chewers, and Diptera were present in the guilds of internal chewers and gall formers. Species of herbivorous Hymenoptera (gall formers) and Hemiptera (sap suckers) were the only taxa restricted to certain guilds (Zwölfer 1965, 1988, Goeden & Ricker 1987b, chapter 4). The guild composition of herbivores from Berkheya and Californian thistles were most alike and they differed substantially from the guild composition found in European thistles. The herbivore community from C. brevistylum falls into group 1 and not group 2 with the other Californian thistles because it had more in common with the other communities in group 1, and because it lacked a guild of sap suckers which was present in all communities in group 2. It is interesting to note that 19 communities on European thistles had the same guild structure, but this was

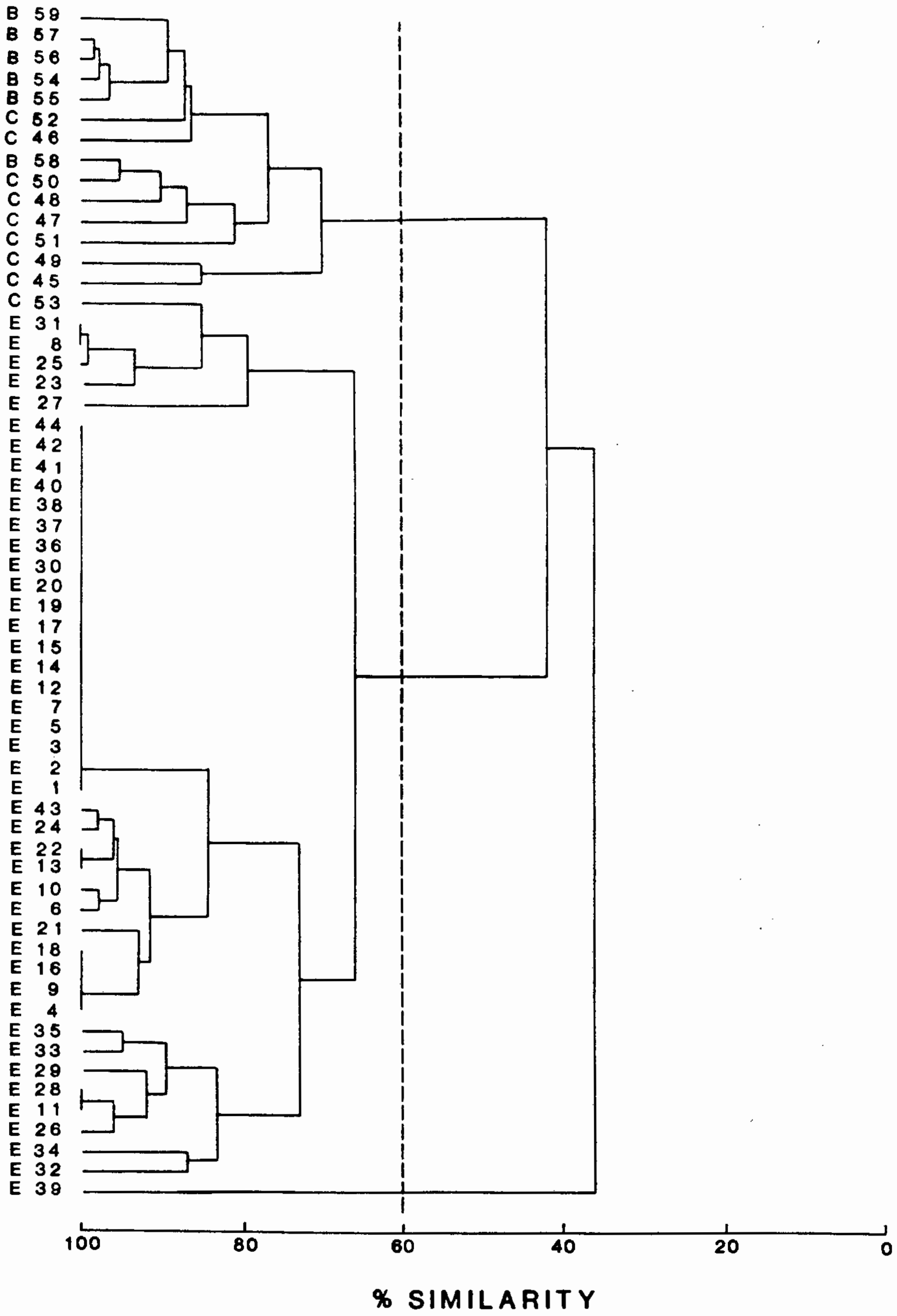


Fig. 5.9 Dendrogram showing the classification of 59 herbivore communities based on the proportion of herbivore species in each guild. Three main groups were distinguished at an arbitrary similarity level of 60%. The letters B, C and E refer to <u>Berkheya</u>, Californian thistles and European thistles respectively. See legend to Fig. 5.2 for a key to the numbers which refer to the plant species.

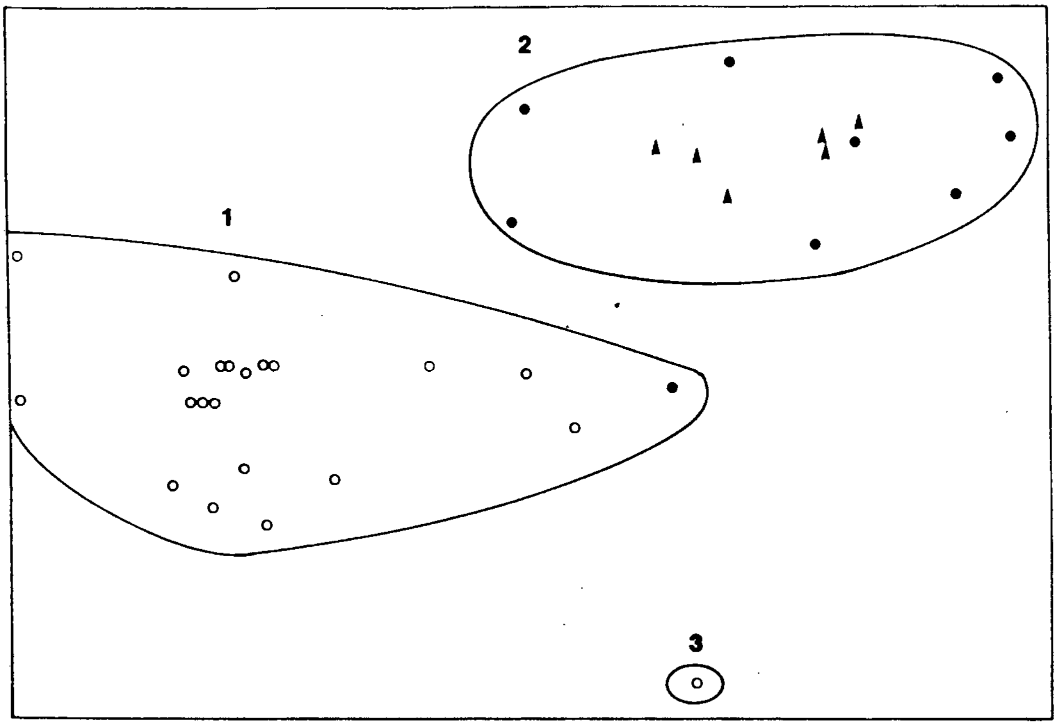
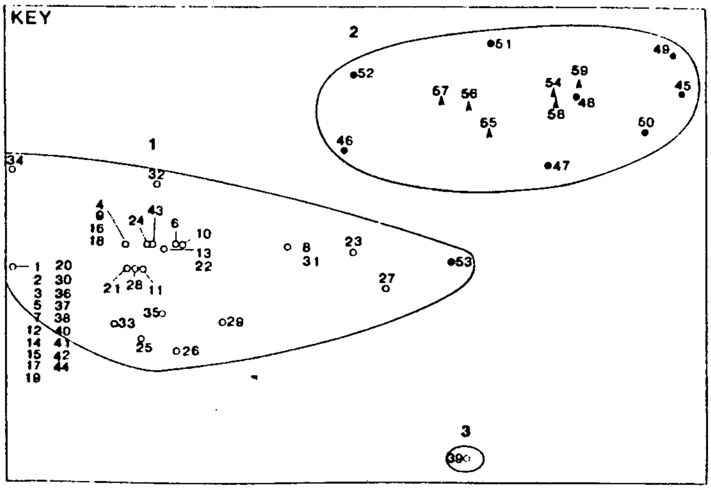


Fig. 5.10 Ordination of 59 herbivore communities based on the proportion of herbivore species in each guild. Clusters 1, 2 and 3 were distinguished in the dendrogram (Fig. 5.9). Axis scales are arbitrary and are therefore not given. Open circles, closed circles and triangles represent communities from European thistles, Californian thistles and Berkheya respectively. A key to the plot is provided below. Numbers in the key refer to the plant species which are listed in Fig. 5.2.



because they comprised only endophagous chewers (Fig.5.9). The other guilds were absent.

To identify why the herbivore communities have grouped together in this way, the proportions of herbivore species in each guild have been compared between the groups using the Mann-Whitney U test. Endophagous chewers formed a significantly larger proportion of the community in group 1 (European thistles) than in group 2 (Berkheya and Californian thistles) (P<0.0001) (Fig. 5.11a). Ectophagous chewers formed a larger proportion of the herbivore community in group 2 (Berkheya and Californian thistles) compared to group 1 (European thistles) (P<0.001) (Fig. 5.11b). A marked difference between group 1 and 2, was the presence of sap suckers in group 2 (Berkheya and Californian thistles) and their absence from group 1 (European thistles) (Fig. 5.11c).

The absence of a guild of sap sucking insects from the flower-heads of European thistles is remarkable, especially as hemipterans were often recorded on other aerial parts of these plants (Zwölfer 1965). Lawton & Schröder (1978) analysed the guild composition of the European thistles, using Zwölfer's (1965) data, and they looked at all the herbivores from the entire plant. The guild of sap sucking insects formed 11% of the entire herbivore community on European thistles. The sap sucking guild is much smaller on European thistles than on Berkheya and thistles in California, but even this does not account for their absence from the flower-heads. One possibility is that Zwölfer (1965) was selective in his sampling, and for some reason ignored Hemiptera on the flower-heads. However, Zwölfer himself (pers. comm.) remarked about the large number of Hemiptera found on flower-heads of Berkheya in South Africa, pointing out how

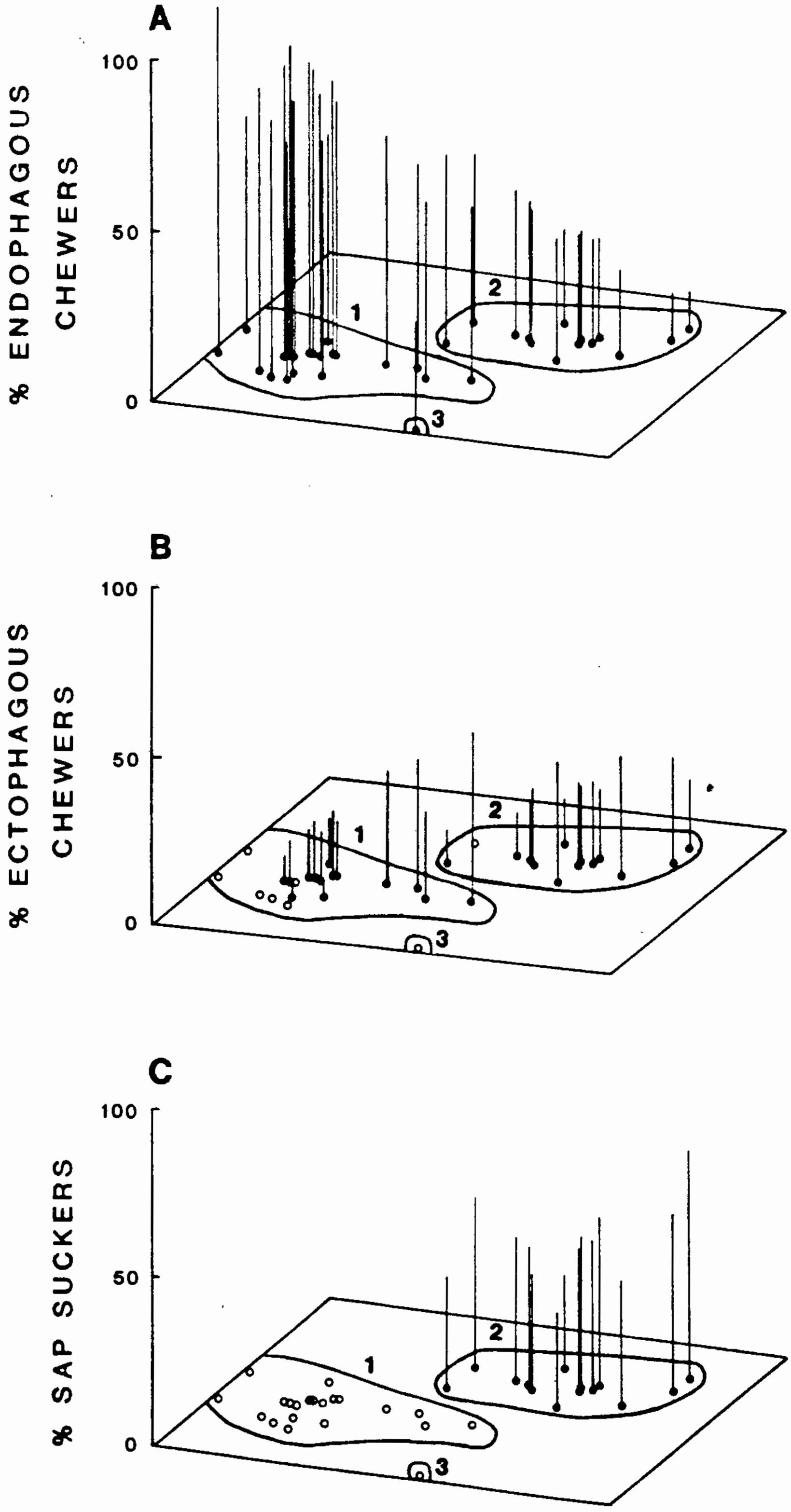


Fig. 5.11 Three dimensional replicas of the clusters 1, 2 and 3 in Fig. 5.10 that represent the proportion of species in the herbivore communities in each guild. A. Endophagous chewers, B. Ectophagous chewers, C. Sap suckers, D. Gall formers. Open circles show that the guild is not represented in the community. Closed circles show that the guild is present and the vertical lines indicate the proportion of the community that comprises the guild. A key to the plot is provided below Fig 5.11. Numbers in the key refer to the plant species which are listed in Fig. 5.2.

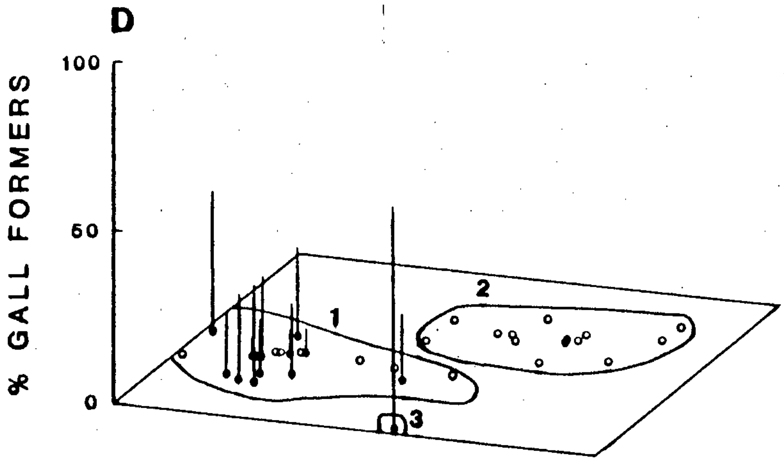


Fig. 5.11 continued.

different this was to the situation in Europe.

Hemiptera have been found on the flower-heads of C. pycnocephalus and S. marianum in Europe by Goeden (1974, 1976). However, the Hemiptera formed a smaller proportion of the flower-head herbivore communities on these two European thistles than is found on Californian thistles and Berkheya. Thus it appears that Hemiptera are not common members of the flower-head communities of European thistles. Current research by CSIRO entomologists in Europe will probably clarify this issue (Goeden, pers comm). I am grateful to Prof. Goeden for drawing my attention to his work at examination.

The last guild comprised the species that form structural galls. These species occurred in a few herbivore communities in group 1 (European thistles) and formed a large proportion of the community in group 3 (M. salmanticus) (Fig. 5.11d). No gall forming species were present in the herbivore communities of Californian thistles and Berkheya. Because gall formers are relatively rare in group 1, a comparison of groups 1 (European thistles) and 2 (Berkheya and Californian thistles) showed only a slight significant difference between them ($P < 0.05$, Mann-Whitney U test).

Clearly, there are large differences between the herbivore communities of European thistle flower-heads and Berkheya and Californian thistle flower-heads. The variation in guild composition of herbivore communities within groups illustrates the differences in the herbivore communities of sympatric, closely related plants. Differences between graphs may show the effect of different host plant distributions and different host plant taxa. These effects will be examined in the next chapter. Also of interest is the similarity between the communities on Berkheya and Californian thistle flower-heads that needs to be investigated in more detail.

Lawton (1982) discussed the concept of vacant niches. His study of the herbivore communities on bracken throughout the world showed that many niches, that were filled in some areas, were empty in other areas. Data for communities on Berkheya and thistle flower-heads also suggest that there are unexploited niches. Zwölfer (1979a) has proposed that competition for resources is responsible for structuring communities in thistle flower-heads. However, the presence of vacant niches on thistle flower-heads suggests that competition may not be of major importance in structuring the communities, a conclusion that matches the preliminary analysis of interspecific competition in section 4.3.

There is a problem when applying the vacant niche hypothesis to communities on Berkheya and thistle flower-heads. Lawton's (1982) study was on a single plant species, bracken fern. This study concerns many plant species, thus differences in plant secondary compounds and small differences in flower-head structure may account for the differences in guild composition. However, major differences in guild composition were observed between closely related thistle species, where biochemical and morphological differences between their flower-heads were likely to be minimal, as well as between distantly related plants from a variety of taxa. In addition, the communities on Berkheya and those on Californian thistles had a similar guild composition, even though these plants are not closely related. Therefore, there appears to be vacant niches on Berkheya and thistle flower-heads.

The taxonomic composition of the herbivore communities varied between each other, but, at the ordinal level, the communities from Berkheya and Californian thistle flower-heads were similar to each other. These communities differed from those on European thistles because of the larger proportions of Lepidoptera and Diptera in the latter group. In addition, phytophagous Hymenoptera were found only in some communities on European thistles while Hemiptera were present in the communities on Berkheya and Californian thistles only.

An interesting similarity between communities on Berkheya and European thistle flower-heads, was the association of Larinus and Urophora with both groups. The presence of Larinus and their diversity on Berkheya is even more remarkable considering the close association of this genus with the European thistles.

The guild composition of the flower-head communities also varied widely but several communities on European thistles had the same guild structure. The communities from Berkheya and Californian thistles had very similar guilds. They differed from the guild composition found in communities on European thistles mainly because the latter group had a larger proportion of endophagous chewers and some communities had gall formers. A major difference was that sap suckers were found associated with flower-heads only in communities from Berkheya and Californian thistles, even though they are present on other parts of the plant in European thistles. Differences in guild composition between these groups also indicate that empty niches are available.

The possible effects of host plant range on the herbivore communities are now examined in chapter 6 to determine whether plant range can account for any of the herbivore community characteristics observed.

CHAPTER 6

EFFECT OF PLANT RANGE AND DISTRIBUTION ON HERBIVORE COMMUNITIES

Abstract

1. The effect of host plant range and distribution on the insect herbivore communities from the flower-heads of Berkheya, Californian thistles and European thistles was examined. The range of the host plants is not known accurately, but widespread plants were sampled more frequently than rare plants, thus sampling frequency correlated roughly with plant range.

2. Plant range accounted for 43% of the variability in total herbivore species numbers from all herbivore communities. However, when considered separately, species richness in communities from Berkheya and Californian flower-heads were greater than in communities from European thistles with corresponding ranges. Plant range accounted for 55% and 61% of the variability in herbivore species numbers in communities from Berkheya and Californian thistles and from European thistles respectively.

3. Plant range correlated with specialist herbivore species numbers only in communities from European thistles. However, in communities on Berkheya and Californian thistles, generalist species numbers accrued more rapidly, with increasing plant range, than did communities from European thistles. Generally, in communities from European thistles, the proportion of specialist species in the community was highest in thistles with a small range, but generalist species were more common in communities from widely distributed thistles. Generalist species were always more common than specialist species in herbivore communities from Berkheya and Californian thistles.

4. Plant range accounted for 60% and 17% of the variability in endophagous and ectophagous species numbers respectively, in herbivore communities from the flower-heads of European thistles. In communities from Berkheya and Californian thistles, plant range accounted for 53% of the variability of ectophagous species numbers, but showed no relationship with endophagous species numbers.

5. In herbivore communities from Californian thistles, the number of Coleoptera, Lepidoptera and Diptera species correlated with plant range, but not the number of phytophagous Hymenoptera. The number of Coleoptera and Hemiptera species in communities from Berkheya and Californian thistles correlated with plant range.

6. The number of herbivore species in the three guilds associated with European thistle flower-heads correlated with plant range. However, in communities from Berkheya and Californian thistles, only the number of endophagous chewers and sap suckers were influenced by plant range.

7. Species packing correlated with plant range in communities from Berkheya and Californian thistles.

This chapter examines the effect that host plant range has on various aspects of the insect herbivore communities from the flower-heads of Berkheya, Californian thistles and European thistles.

6.1 Total number of herbivore species

The species richness of herbivore communities associated with thistle and Berkheya flower-heads was variable (section 5.1). Previous studies have shown that sampling frequency accounted for 74% of the variability in herbivore species richness on thistles in Europe (Lawton & Schröder 1978) and for 74% of the variability in herbivore species richness on the flower-heads only, of thistles in Europe (Zwölfer 1982a). The species-accrual rate of the flower-heads and of the entire thistle plant was the same.

In this study, sampling frequency accounted for 43% of the variability in herbivore species numbers on the flower-heads of European thistles, Californian thistles and Berkheya (Fig. 6.1). Herbivore species richness was higher on the flower-heads of Berkheya and Californian thistles than on the flower-heads of European thistles that had been sampled a similar number of times. Separate regression lines for these two groups illustrate this clearly (Fig. 6.2). Sampling frequency explained 55% of the variability in species richness on Berkheya and Californian thistles and 61% of the variability of species richness on European thistles. The slopes of these two regression lines are statistically significantly different ($t_{(2),68} = 2.39$, $P<0.05$). Herbivores accrued slightly faster per unit sampling effort on Berkheya and Californian thistle flower-heads than on European thistle flower-heads. The obvious conclusion to be drawn, is that

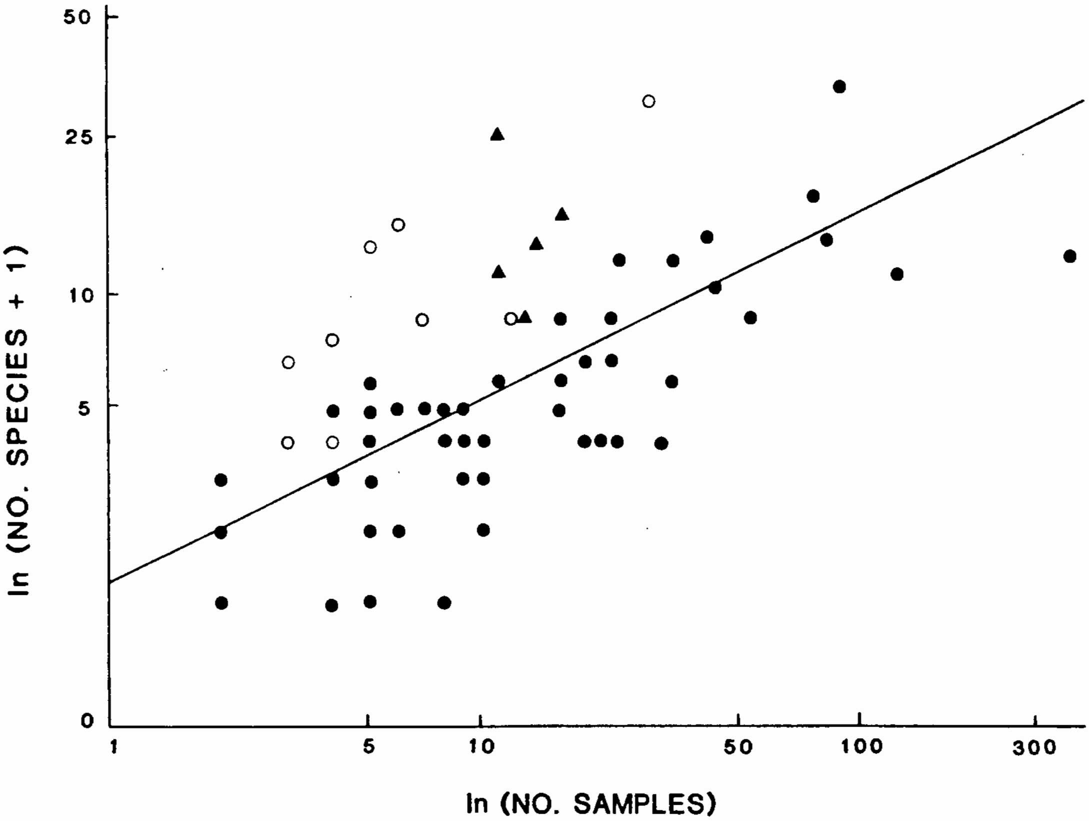


Fig. 6.1 Relationship between number of sites sampled and number of insect herbivores recorded on various species of Berkheya (triangles), Californian thistles (open circles) and European thistles (closed circles); $\ln y = 0.45 \ln x + 0.84$, $r^2 = 0.43$, $P < 0.001$.

more herbivore species colonised the flower-heads in South Africa and California than in Europe. In addition, the effect of the geographical distribution of host plants is illustrated (Fig. 6.2), because species richness differed depending on the region where the plants grow. Possibly similar conditions prevail in California and South Africa to account for the similar herbivore accrual rates.

What role did host plant range play in this relationship? The true geographical area covered by each thistle and Berkheya species is not accurately known. Even if the

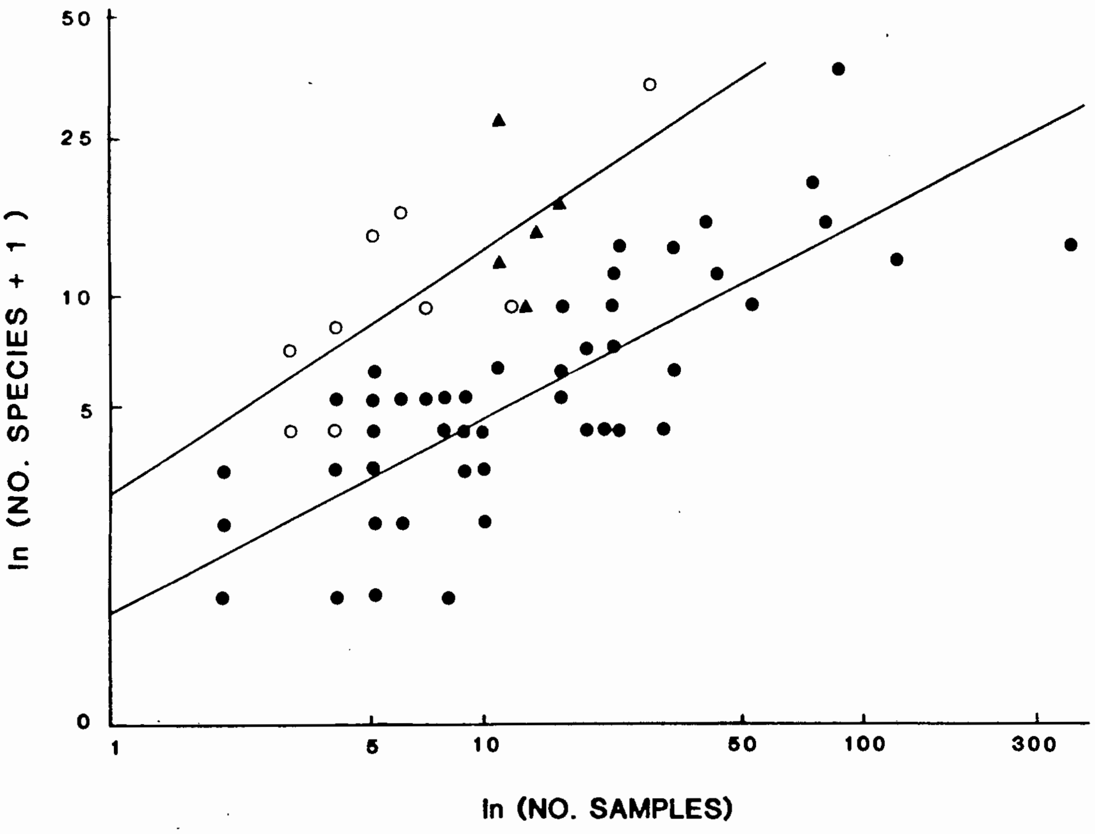


Fig. 6.2 Relationship between number of sites sampled and number of insect herbivores recorded on species of *Berkheya* (triangles) and Californian thistles (open circles), ln y = 0.59 ln x + 1.26, r^2 = 0.55, $P < 0.001$, and on European thistles (closed circles) ln y = 0.46 ln x + 0.62, r^2 = 0.61, $P < 0.001$.

ranges were known, plants are often distributed unevenly within their range so that a widespread plant may be relatively scarce. Lawton & Schröder (1978) and Goeden & Ricker (1987b) interpreted sampling frequency to reflect

the distribution and abundance of the plant. Thus, widespread and common plants were assumed to have been sampled more frequently than scarce plants with a smaller range.

Lawton & Schröder (1978) argued that this interpretation was reasonable, with respect to Zwölfer's (1965) data, because firstly, sampling frequency did correlate roughly with the plants' geographical range. Secondly, Zwölfer's (1965) data fitted the regression ln S = ln A (r^2 = 0.74) better than S = ln A (r^2 =0.40) (where S is number of species and A is area), which, according to May (1975), demonstrates that the area-effect, and not sampling effort is what is represented by the regression. The relationship illustrated in Fig. 6.1 provides a better fit (r^2 = 0.43) than for a S ln A regression (r^2 = 0.33) and therefore also appears to represent the effect of plant range rather than sampling frequency.

Results reported here differ considerably from those of Zwölfer (1982a) who obtained a correlation coefficient of 0.74 for the regression of total species richness for herbivores in flower-heads on the log number of populations sampled. Zwölfer (1982a) used 20 years of accumulated information, including much unpublished data, on the insect herbivores associated with 65 species of thistles found in Europe in his analyses, so his data are more reliable than that used in this study. Differences in the data used for the analyses would account for the lower correlation coefficient obtained here (r^2=0.61, Fig. 6.1). The more detailed study of species richness, by Zwölfer (1982a), explained more of the variability in herbivore species numbers associated with European thistle flower-heads than was accounted for by the analysis in this study.

Better correlation coefficients, of 0.91, 0.68 and 0.72, were achieved when separate regressions were plotted for three European thistle genera, Carduus, Cirsium and Centaurea (Fig. 6.3). The slopes of these three regression lines all differed significantly from each

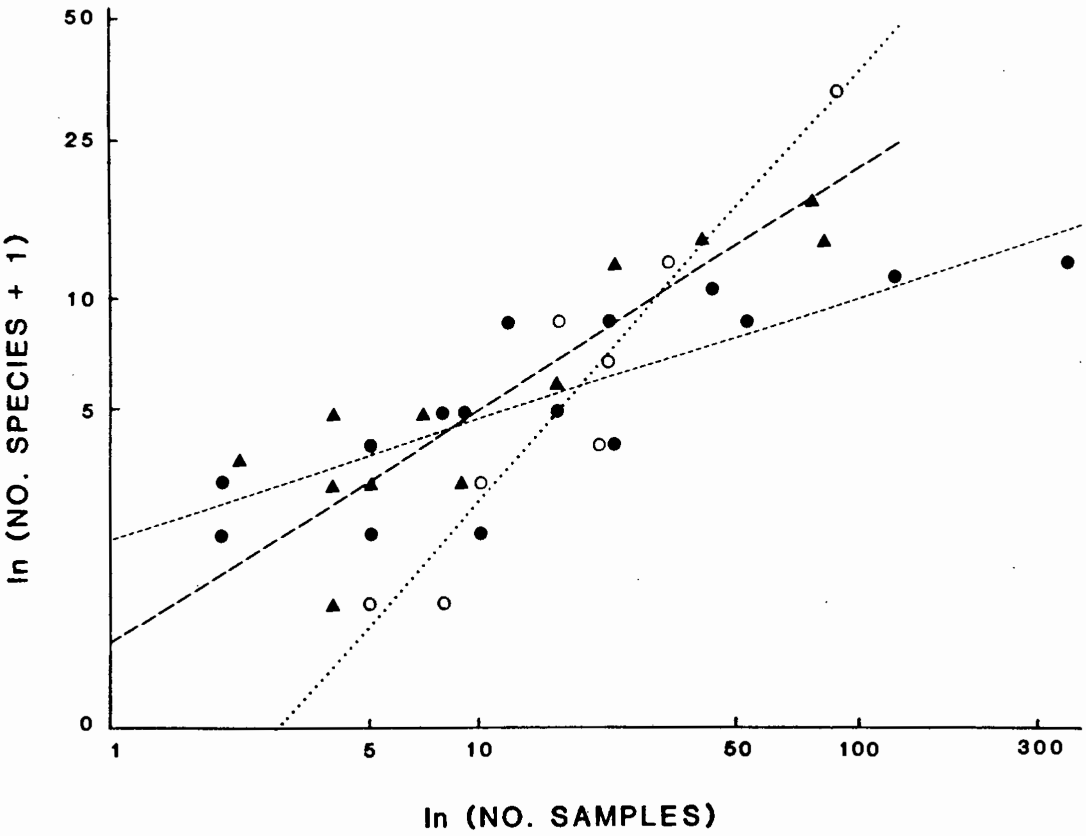


Fig. 6.3 Relationship between the number of sites sampled and the number of herbivore species in the flower-heads of <u>Carduus</u> (open circles, dotted line), $\ln y = 1.05 \ln x - 1.14$, $r^2 = 0.90$, $P < 0.001$, $N = 8$; <u>Centaurea</u> (triangles, long dashes), $\ln y = 0.58 \ln x + 0.44$, $r^2 = 0.72$, $P < 0.001$, $N = 16$; <u>Cirsium</u> (closed circles, short dashes), $\ln y = 0.30 \ln x + 1.05$, $r^2 = 0.68$, $P < 0.001$, $N = 16$.

other (Table 6.1). This shows that the effect of plant range on herbivore species numbers varied greatly between the genera of European thistles. The regression in Fig. 6.2, for European thistles, is not valid when applied to a plant group, like the three genera in Fig. 6.3. Regressions obtained from specific thistle groups cannot be related to all the European Carduoideae and vice versa. This should be considered when regressions obtained from large plant groups are used to describe species accrual rates on specific groups of plants.

Table 6.1 Statistical comparison of regression slopes in Fig. 6.3.

	Carduus	*Cirsium*
Centaurea	$t = 7.12$ $P < 0.001$	$t = 5.20$ $P < 0.001$
Cirsium	$t = 16.27$ $P < 0.001$	

6.2 Specialist and generalist species

On European thistle flower-heads, the number of specialist species increased with plant range (sampling effort), but on *Berkheya* and Californian thistle flower-heads, no correlation between the number of specialist species and plant range was found (Fig. 6.4). A higher accrual rate was produced by generalist species on all three groups of plants (Fig. 6.5). Zwölfer (1982a) obtained similar results for herbivore communities associated with European thistle flower-heads. Thus, generalist species were mainly responsible for the species-area relationship on European thistles (Figs 6.1) and were solely responsible for this relationship in the case of *Berkheya* and Californian thistles (Fig. 6.2) because there was no correlation between plant range and specialist species numbers on these two latter groups. In addition, because there were more generalist species on the flower-heads of *Berkheya* and Californian thistles than on the flower-heads of European thistles, the total species richness was higher on the *Berkheya* and Californian thistles.

Because the number of generalist species increased more rapidly with sampling frequency than specialist species numbers, the proportion of specialist to generalist

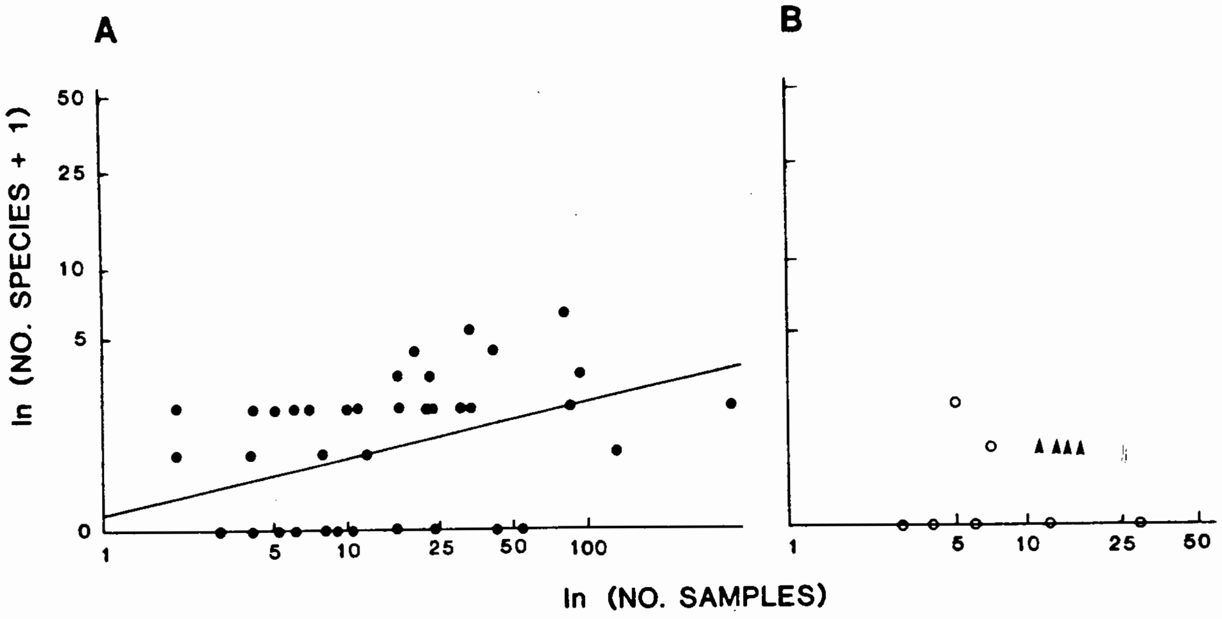


Fig. 6.4 Relationship between the number of sites sampled and the number of specialist herbivore species in the flower-heads of (A) European thistles, $\ln y = 0.22 \ln x + 0.14$, $r^2 = 0.2$, $P < 0.001$ and (B) Berkheya (triangles) and Californian thistles (open circles), $\ln y = 0.2 \ln x - 0.02$, $r^2 = 0.12$, $P > 0.05$.

species changed with plant range. Fig. 6.6a shows how, on European thistles, the proportion of specialist species decreased as plant range (number of samples) increased, and also illustrates the corresponding increase in the proportion of generalist species. Proportions were variable when few insect species were present, and meaningless if species richness is one, so the data were grouped according to sampling frequency to avoid this effect. Lawton & Schröder (1978) used a similar technique. Thistles sampled on only a few occasions (equivalent to thistles with small ranges) generally had a large proportion of specialist species.

Similar trends were not observed in communities on <u>Berkheya</u> and Californian thistles (Fig. 6.6b) where the

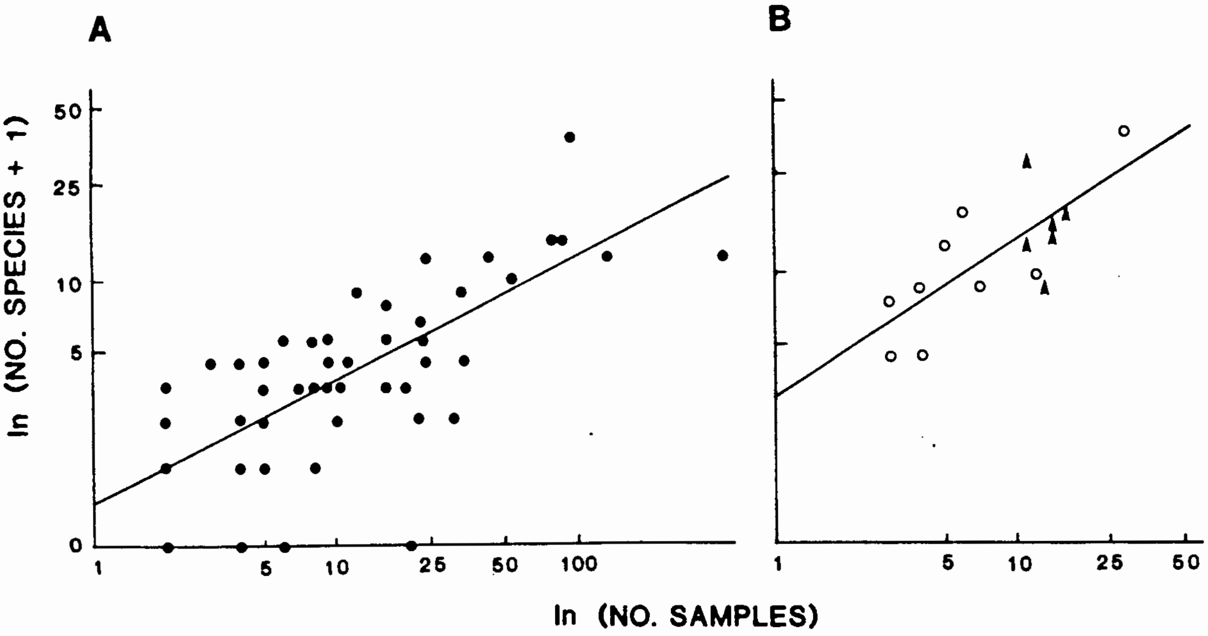


Fig. 6.5 Relationship between the number of sites sampled and the number of generalist species in the flower-heads of (A) European thistles, $\ln y = 0.46 \ln x + 0.37$, $r^2 = 0.52$, $P < 0.001$, and (B) *Berkheya* (triangles) and Californian thistles (open circles), $\ln y = 0.59 \ln x + 1.25$, $r^2 = 0.55$, $P < 0.005$.

proportion of specialist species remained low, even on plants with small ranges.

Lawton & Schröder (1978) divided the herbivore communities, collected from the entire thistle plant, into monophages, oligophages and polyphages, (see Table 5.2 for definitions). They showed that the proportion of polyphages increased with plant range, and the proportion of oligophages decreased correspondingly. The proportion of monophagous species remained constant. These findings concur with the results reported above, if the different definitions of feeding preferences are considered.

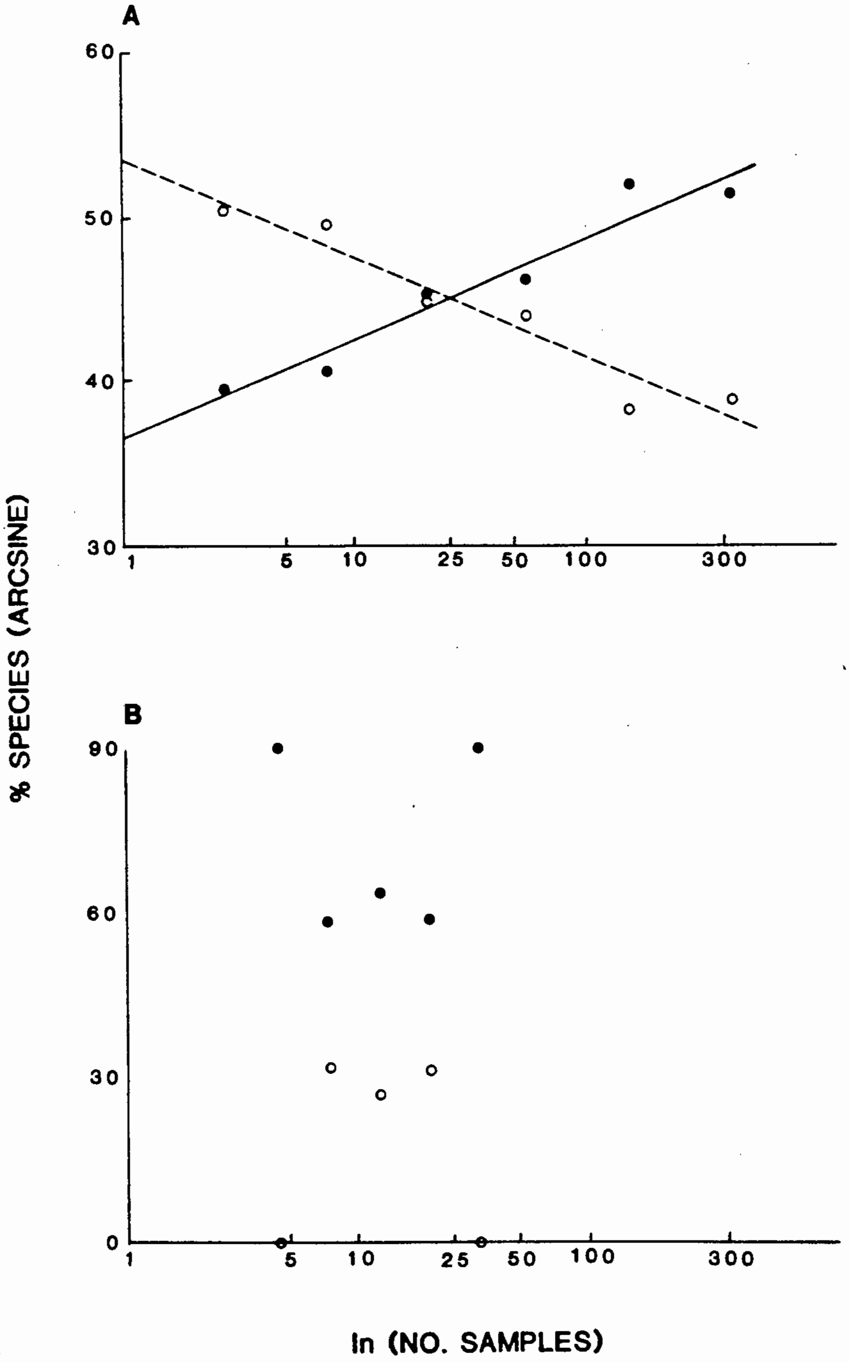


Fig. 6.6 Relationship between the number of sites sampled and the proportion of specialist (open circles, broken line) and generalist (closed circles, solid line) herbivore species in the flower-heads of (A) European thistles; specialists, ln y = -2.66x + 53.55, $r^2 = 0.93$, $P < 0.01$; generalists ln y = 2.66x + 36.45, $r^2 = 0.93$, $P < 0.01$, and (B) *Berkheya* and Californian thistles; specialists, ln y = -0.09x + 18.18, $r^2 = 0$, $P > 0.05$; generalists, ln y 0.09x + 71.81, $r^2 = 0$, $P > 0.05$. Proportions are expressed as the arcsine transformation.

6.3 Endophagous and Ectophagous species

The proportion of endophages to ectophages is of interest because, after comparative studies on introduced and native thistles, Goeden & Ricker (1986b, 1987b) suggested that young insect-plant associations are characterised by a high proportion of ectophages (see also Appendix 2).

In herbivore communities from European thistle flower-heads, plant range (number of samples) explained 60% of the variation in the number of endophage species (Fig. 6.7a), but only 17% of the variation of ectophages (Fig. 6.8a). In Berkheya and Californian thistles, ectophage numbers did increase with sampling frequency (Fig. 6.8b) while endophages showed no trend (Fig. 6.7b).

In the herbivore communities on the flower-heads of European thistles, endophagous species accrued more rapidly than ectophagous species, with an increase in plant range (equivalent to sampling frequency). European thistles with a wide distribution therefore had more endophage species than ectophages but on Berkheya and Californian thistles the converse was true. However, when the proportions of endophages and ectophages were compared at increasing sampling frequencies, no change was observed (Fig. 6.9). Data were grouped together to avoid the variability of proportions at low sampling frequencies. In communities on European thistles, more endophagous than ectophagous species were present. Communities on Berkheya and Californian thistles generally had more ectophagous than endophagous species.

The results presented in this section show that plant range could affect the number of endo- and ectophagous species, and may have accounted for much of the variability in proportions observed in Table 5.4. The

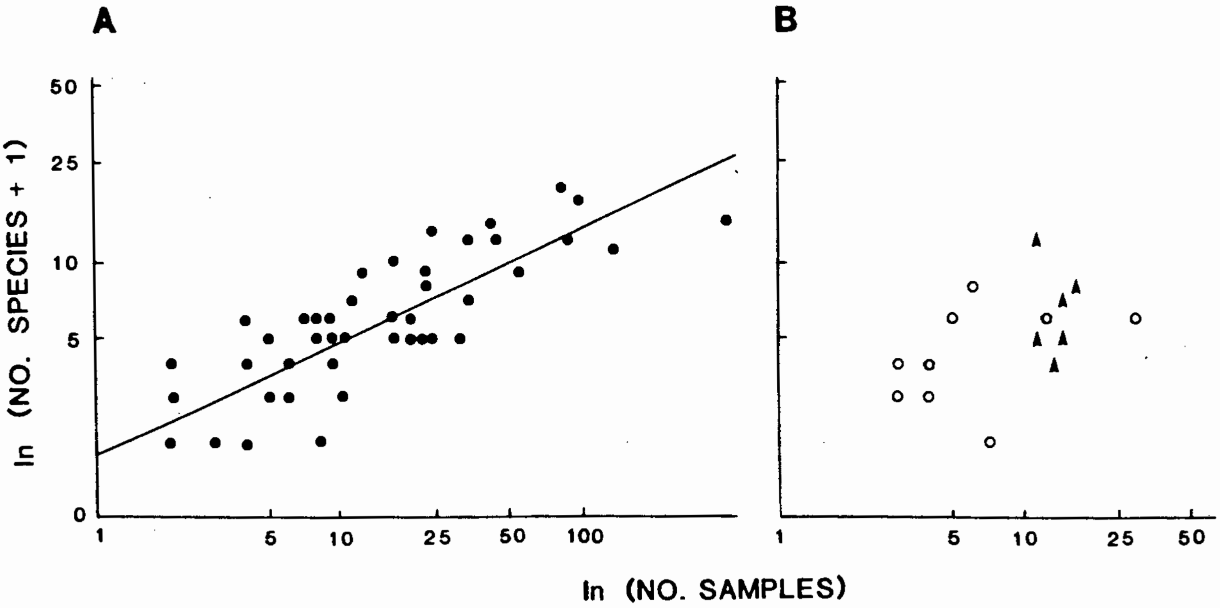


Fig. 6.7 Relationship between the number of sites sampled and the number of endophagous species in the flower-heads of (A) European thistles, ln y = 0.44 ln x + 0.56, $r^2 = 0.60$, $P < 0.001$, and (B) Berkheya (triangles) and Californian thistles (open circles), ln y = 0.33 x + 0.93, $r^2 = 0.24$, $P > 0.05$.

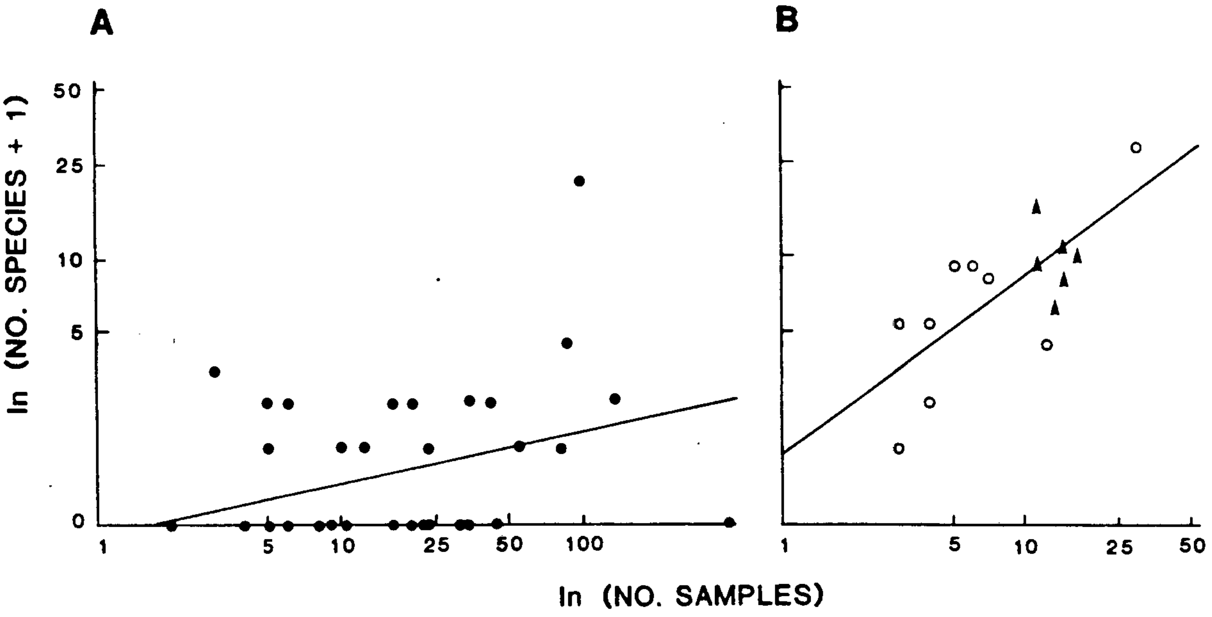


Fig. 6.8 Relationship between the number of sites sampled and the number of ectophagous species in the flower-heads of (A) European thistles, $\ln y = 0.20 \ln x - 0.1$, $r^2 = 0.17$, $P < 0.005$, and (B) Berkheya (triangles) and Californian thistles (open circles), $\ln y = 0.70 \ln x + 0.62$, $r^2 = 0.53$, $P < 0.005$.

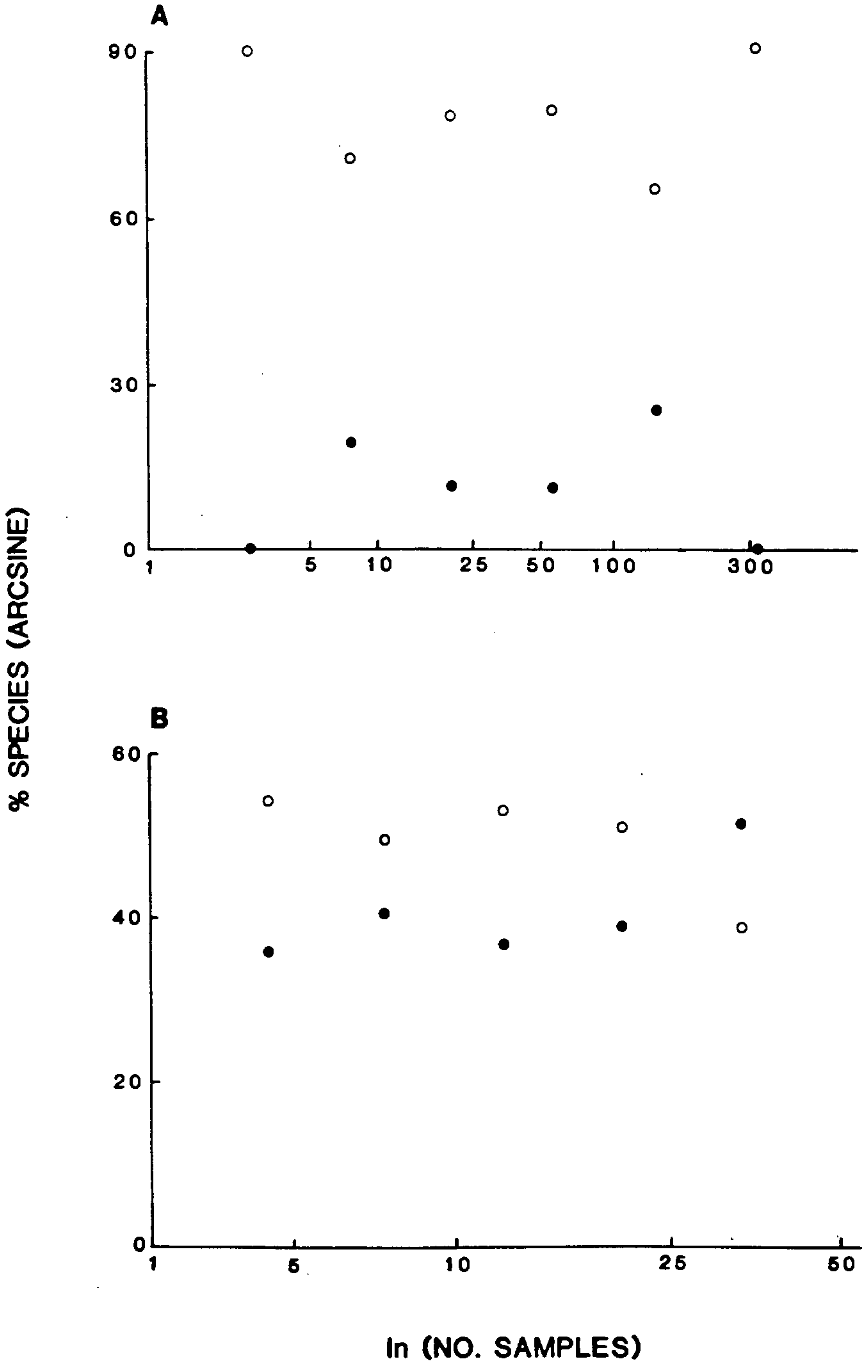


Fig. 6.9 Relationship between the number of sites sampled and the proportion of endophagous (open circles) and ectophagous (closed circles) species in the flower-heads of (A) European thistles; endophages, $\ln y = -0.49 \ln x + 80.5$, $r^2 = 0.008$, $P > 0.05$; ectophages, $\ln y = 0.49 \ln x + 9.50$, $r^2 = 0.008$, $P > 0.05$, and (B) *Berkheya* and Californian thistles; endophages, $\ln y = -5.97 \ln x + 64.19$, $r^2 = 0.56$, $P > 0.05$; ectophages, $\ln y = 5.97 \ln x + 25.82$, $r^2 = 0.56$, $P > 0.05$. Proportions are expressed as the arcsine transformation.

effect of geographical distribution was also noticeable because the effect of plant range differed between Europe, and California and South Africa.

6.4 Taxonomic composition

Plant range was expected to affect the number of insect herbivore species in each order, because more species were found on widespread plants.

On the flower-heads of European thistles, the number of species of Coleoptera, Lepidoptera and Diptera correlated with plant range (sampling frequency) (Table 6.2). The number of phytophagous Hymenoptera species remained low and was not correlated with plant range. On the flower-heads of Berkheya and Californian thistles, species numbers in Coleoptera and Hemiptera correlated positively with plant range (sampling frequency) but species numbers in Lepidoptera and Diptera showed no significant correlation (Table 6.2). The insect orders in which no statistically significant correlations were found usually formed only a small proportion of the communities (see Fig. 5.4).

Geographic differences between the herbivore communities of thistles and Berkheya were noted in section 5.4. At the ordinal level, the taxonomic composition of Berkheya and Californian thistles were most alike. At the genus level, communities on Berkheya flower-heads were more similar to communities on European thistles than to those on Californian thistles. Two types of differences were noted between herbivore communities from different geographic areas. Firstly, the taxa present on the flower-heads were not the same in each area, even when the comparison is made at the ordinal level (section 5.4).

Table 6.2 Correlation of herbivore species numbers with sampling frequency for each insect order present (Spearman's rank correlation) (*** P<0.001, * P<0.05).

Order	Number of plant species sampled	r_s
<u>European thistles</u>		
Coleoptera	57	0.69 ***
Lepidoptera	57	0.66 ***
Diptera	57	0.68 ***
Hymenoptera	57	0.26
<u>Berkheya</u> and <u>Californian thistles</u>		
Coleoptera	15	0.62 *
Lepidoptera	15	0.33
Diptera	15	0.05
Hemiptera	15	0.65 *

Secondly, those taxa that were common to each region often occurred in different proportions in the herbivore community (Table 6.2).

6.5 Guild Composition

The number of insect herbivore species in the three guilds present on the flower-heads of European thistles, endophagous chewers, ectophagous chewers and gall formers all correlated with plant range (sampling frequency) (Table 6.3).

Although the guild of gall formers correlated significantly with plant range (Table 6.3), only a few species of European thistles were colonised by this guild (section 5.5). Lawton & Schröder (1978), using Zwölfer's (1965) data based on collections from the entire thistle

Table 6.3 Correlation of herbivore species numbers with sampling frequency for each guild (Spearmans's rank correlation) (*** P<0.001, ** P<0.05).

Guild	Number of plant species sampled	r_s
European thistles		
Endophagous chewers	57	0.87 ***
Ectophagous chewers	57	0.36 **
Gall formers	57	0.65 ***
Berkheya and Californian thistles		
Endophagous chewers	15	0.63 *
Ectophagous chewers	15	0.40
Sap suckers	15	0.65 *

plant, showed that the proportion of gall formers increased with plant abundance (sampling frequency). They argued that because the gall forming guild is specialised, colonisation is slow and is more likely on widespread plants. Results from herbivore communities associated with just the flower-heads of European thistles support their hypothesis.

A different situation was noted in the herbivore guilds associated with the flower-heads of Berkheya and Californian thistles. The number of endophagous chewers and sap suckers correlated with plant range (sampling frequency) but the number of ectophagous chewers showed no correlation with plant range (Table 6.3).

As noted in the previous chapter (section 5.5) the guilds on Berkheya and Californian thistles were similar, and both differed considerably from the guild composition of

European thistles. No gall formers were present on the flower-heads of *Berkheya* and Californian thistles.

There are three possible causes of this deficiency; (1) if no gall forming insect species are present in California and southern Africa, the gall forming habit would first have to evolve. This is clearly more difficult than a simple host shift by extant gall formers already present in the area; (2) the plant range of the plant species in these areas may be too small (ie. the degree of exposure to potential colonists is too low); and (3) *Berkheya* and Californian thistles may be much younger, in evolutionary terms, than European thistles. Therefore, the available gall formers, if present, require more time to colonise the potential host plant species.

The first two hypotheses are manifestly incorrect, firstly because gall formers are present on Asteraceae in California and southern Africa (Munro 1926, Harnett & Abrahamson 1979, Goeden 1988) and I have found two stem galls on *B. bipinnatifida* caused by unidentified tephritids (parasitised as pupae). Secondly, several of the European thistles, that had a gall forming guild in their flower-heads, were sampled on fewer occasions than the *Berkheya* and some Californian thistles (eg. *Cirsium pannonicum* (L.) Gaud., *Centaurea cyanus* L. and *Microlonchus salmanticus* were all sampled on only two occasions in Europe by Zwölfer (1965) and gall formers were found in the flower-heads). Therefore, in Europe at least, plants with small ranges comparable to some of the rarer *Berkheya* have accumulated gall formers.

One explanation remains: the absence of gall formers from the flower-heads of *Berkheya* and Californian *Cirsium*, is because there has not been sufficient time for this association to evolve. There is evidence to suggest that

Berkheya and Californian thistles are younger than European thistles, in evolutionary terms, because the former two groups probably arose from parent stock in the European thistles (see chapter 2). The stem galls found on B. bipinnatifida may be the first host shift by a gall former onto Berkheya. Lawton & Schröder (1978) have also suggested that gall formers are slower to colonise plants than less specialised guilds. More Berkheya species need to be sampled to provide stronger support for this hypothesis. (Of course, other explanations may also exist for an absence of gall formers on Berkheya and thistles in California. For example, there may be physiological or biochemical reasons why these plants cannot produce galls. These arguments are not very convincing.)

In section 5.5, differences in guild composition were noted in the herbivore communities associated with plants that were geographically separate. The guild composition of communities on Cirsium thistles in California differed markedly from the guild composition of communities on thistles in Europe, including congeneric species. However, remarkable similarities were noted in the guild composition of herbivores in Californian thistles and Berkheya.

The geographic isolation of Californian thistles from European thistles can explain the differences in their guild and taxonomic composition (section 6.4). But, the communities on Berkheya are isolated geographically and taxonomically from Californian thistles, yet their herbivore communities had a similar guild composition.

6.6 Species packing

Herbivore communities on the flower-heads of Berkheya and Californian thistles showed a positive relationship between average species packing and the number of samples collected (Fig. 6.10). This indicated that the more widespread plants tended to have larger local herbivore communities. The regression for species packing in Californian thistles only was not significant (Goeden &

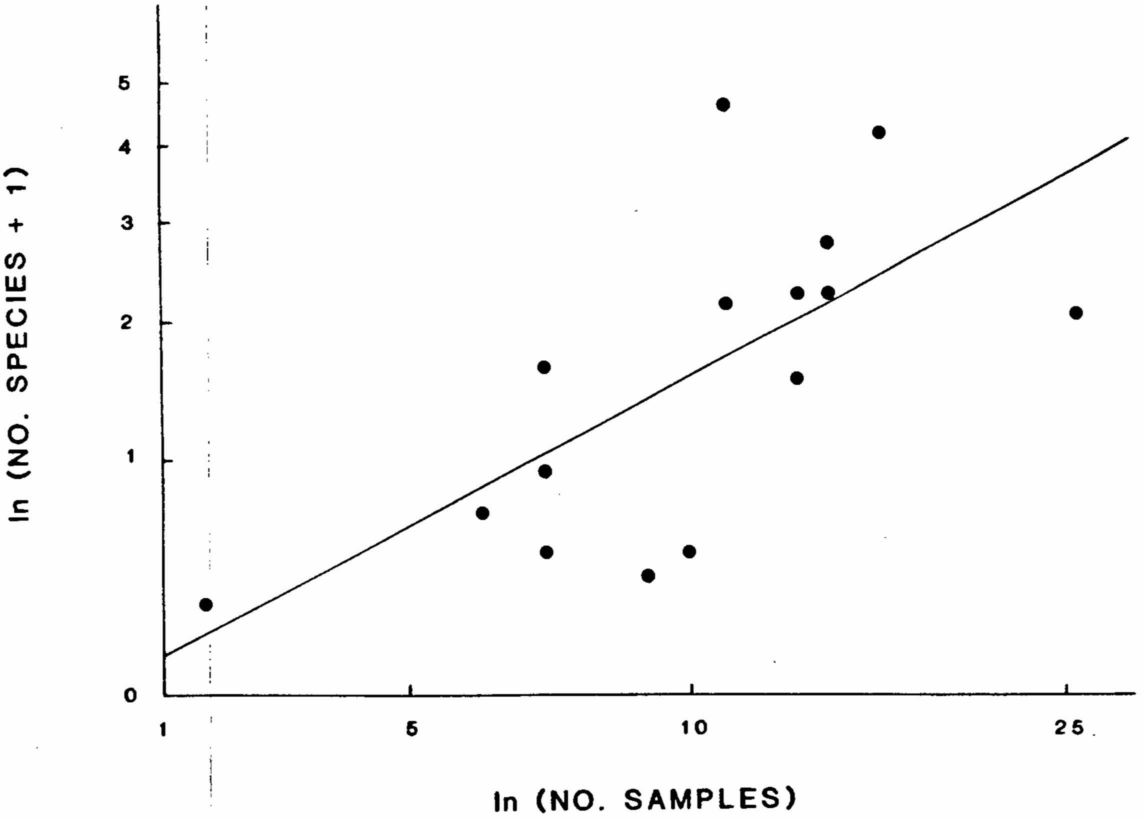


Fig. 6.10 Relationship between the number of sites sampled and mean species packing (number of species per flower-head population) for herbivore communities from Berkheya and Californian thistles, $\ln y = 0.61 \ln x - 0.48$, $r^2 = 0.45$, $P < 0.01$.

Ricker 1987b) so the communities on Berkheya flower-heads were responsible for the significant regression in Fig. 6.10.

In the herbivore communities on European thistles, no relationship between species packing and sampling frequency was found (Zwölfer 1982a). However, Zwölfer (1982a) did find, that for some widespread thistle species, the relationship between species packing and resource utilization (proportion of flower-heads attacked at any one site) differed among different geographic regions. Zwölfer (1987) showed that in Centaurea solstitialis L., species packing was highest at the plants' presumed evolutionary centre, in Greece. Therefore, species packing is usually highest in the area that the plant species has colonised for the longest time.

Information on average species packing was available for only a few European thistle species (Zwölfer 1979a). Of these, the highest average species packing was 3.68 ± 1.36 (mean ± SE), which was found in flower-heads of Centaurea maculosa Lam. Two Berkheya species, B. decurrens, and B. heterophylla had a higher average species packing of 4.5 ± 0.4 and 4.1 ± 0.5 (mean ± SE) respectively. Cirsium proteanum had the highest average species packing in the group of Californian thistles of 2.2 ± 0.3 (mean ± SE). Average species packing was lowest in the Californian thistles.

Results reported in this chapter are summarised in Table 6.4. Intensity of sampling, equivalent to host plant range, has had a marked effect on the herbivore communities associated with the flower-heads of Berkheya and thistles and accounted for most of the variability in

Table 6.4 Summary of the effect of host plant range on the insect herbivore communities. Correlation coefficients are in brackets. Letters C and E refer to California and Europe respectively.

Herbivore community	Plant taxa *Berkheya* & *Cirsium* (C)	 Cynaroideae (E)
No. species	increases ($r^2=0.55$)	increases ($r^2=0.61$)
No. specialists	none	increases ($r^2=0.12$)
No. generalists	increases ($r^2=0.55$)	increases ($r^2=0.52$)
No. endophages	none	increases ($r^2=0.60$)
No. ectophages	increases ($r^2=0.53$)	increases ($r^2=0.17$)
Taxa	increase in Coleoptera ($r_s=0.62$) Hemiptera ($r_s=0.65$)	increase in Coleoptera ($r_s=0.69$) Lepidoptera ($r_s=0.66$) Diptera ($r_s=0.68$)
Guilds	increase in endophages ($r_s=0.63$) sap suckers ($r_s=0.65$)	increase in endophages ($r_s=0.87$) ectophages ($r_s=0.36$) gall formers ($r_s=0.65$)

herbivore species numbers between communities on different plant species. Herbivore species numbers are also expected to be influenced by flower-head size and this is investigated in the next chapter.

CHAPTER 7

EFFECT OF FLOWER-HEAD SIZE ON HERBIVORE COMMUNITIES

Abstract

1. The gross morphology of the flower-heads of Berkheya and thistles is similar but the mean flower-head size differs between plant species. Therefore the effect of flower-head size on the insect herbivore communities from Berkheya and European thistles was determined. No accurate information was available on flower-head sizes of the Californian thistles so they were excluded from the analyses.

2. Flower-head size accounted for 86% of the variation in herbivore species numbers on Berkheya, but there was no such relationship on European thistles, even when the thistle genera were compared separately.

3. Specialist species numbers did not correlate with flower-head size, but in Berkeya, 89% of the variability of generalist species numbers was accounted for by the flower-head size.

4. Endophagous species numbers correlated with flower-head size only in the Centaurea and ectophagous species numbers correlated with flower-head size in Carduus and Cirsium.

5. Taxonomic and guild composition of the herbivore communities was generally little affected by flower-head size.

6. In Berkheya flower-heads, some herbivore species that were members of the guild of endophagous chewers showed a direct relationship between their body size, measured by dry weight, and the mean flower-head size of the Berkheya species they colonised. Larinus body length was also shown to be influenced slightly by the size of the flower-head in which they developed and by the amount of crowding inside the flower-head.

7. Species packing correlated with flower-head size in Berkheya, but not in European thistles.

Several studies have shown that the architectural complexity of a plant can affect the number of insect herbivore species that colonise it (Lawton & Schröder 1977, 1978, Strong & Levin 1979, Moran 1980, Neuvonen & Niemela 1981, Niemela et al. 1982). Two components of architectural complexity are the size of the plant and the variety of plant structures (Southwood et al. 1979, Lawton 1983a, Strong et al. 1984). A corollary of the architectural complexity hypothesis is that morphologically similar plants should support similar numbers of insect herbivore species. The flower-heads of Berkheya and thistles are morphologically similar and they were therefore expected to be able to support similar kinds and numbers of herbivore species. However, between the plant species many different sizes of flower-heads are found, so the effect of flower-head size on the herbivore communities was determined. Information on flower-head size was available for only Berkheya and European thistle flower-heads so communities on Californian thistles were excluded from the analysis (Turner 1977, chapter 4). Flower-head diameter was taken to represent flower-head size.

7.1 Total number of herbivore species

The effect of flower-head diameter was determined on the total number of herbivore species, the number of specialist and generalist species, and the number of endophagous and ectophagous species. The correlation coefficients resulting from this analysis are presented in Table 7.1.

No relationship between flower-head diameter and total species numbers was found on the herbivore communities of all the European thistles and Berkheya combined. This is clearly illustrated in Fig. 7.1. Zwölfer (1982a, 1987) also found no significant relationship.

In the previous section, analyses of communities on plant genera often gave different results to analyses of communities on entire plant groups (eg. European thistles). Separate analyses of the major plant genera showed that in Berkheya there was a statistically significant correlation between flower-head size and herbivore species numbers (Fig. 7.2) with size accounting

Table 7.1 Correlation coefficients from regressions of herbivore species richness on flower-head diameter (* $P<0.05$, ** $P<0.01$). N is the number of plant species sampled. See text for further explanation.

		Correlation Coefficients (r^2)				
Genus	N	Tot. species numbers	No. spec. spp	No. gen. spp	No. endo.	No. ecto.
All	60	0.001	0.01	0.001	0.006	0.003
Carduus	8	0.1	0.23	0.30	0.12	0.50 *
Cirsium (E)	16	0.01	0.01	0.02	0.005	0.33 *
Centaurea	16	0.23	0.08	0.23	0.27 *	0.08
Berkheya	6	0.86 **	0	0.89 **	0.43	0.62

for 86% of the variation in herbivore species numbers in Berkheya. Note that in Fig. 6.1, the number of samples collected on Berkheya species varied very little, and there is, in fact, no relationship for this genus, between sampling effort and herbivore species richness. The scatter in Berkheya species illustrated in Fig. 6.1 appears to be largely explained by differences in flower-head size. No correlation was found in Carduus, Cirsium and Centaurea (Table 7.1).

No relationship was found between flower-head diameter and the number of specialist species, but in Berkheya, the number of generalist species did correlate with flower-head size (Table 7.1 and Fig. 7.3). So, on Berkheya flower-heads, much of the variation in the number of generalist species, noted in Fig. 6.5 and not accounted for by the species area relationship, may be explained by flower-head size.

The number of endophagous species was generally not correlated with flower-head size (Table 7.1). The

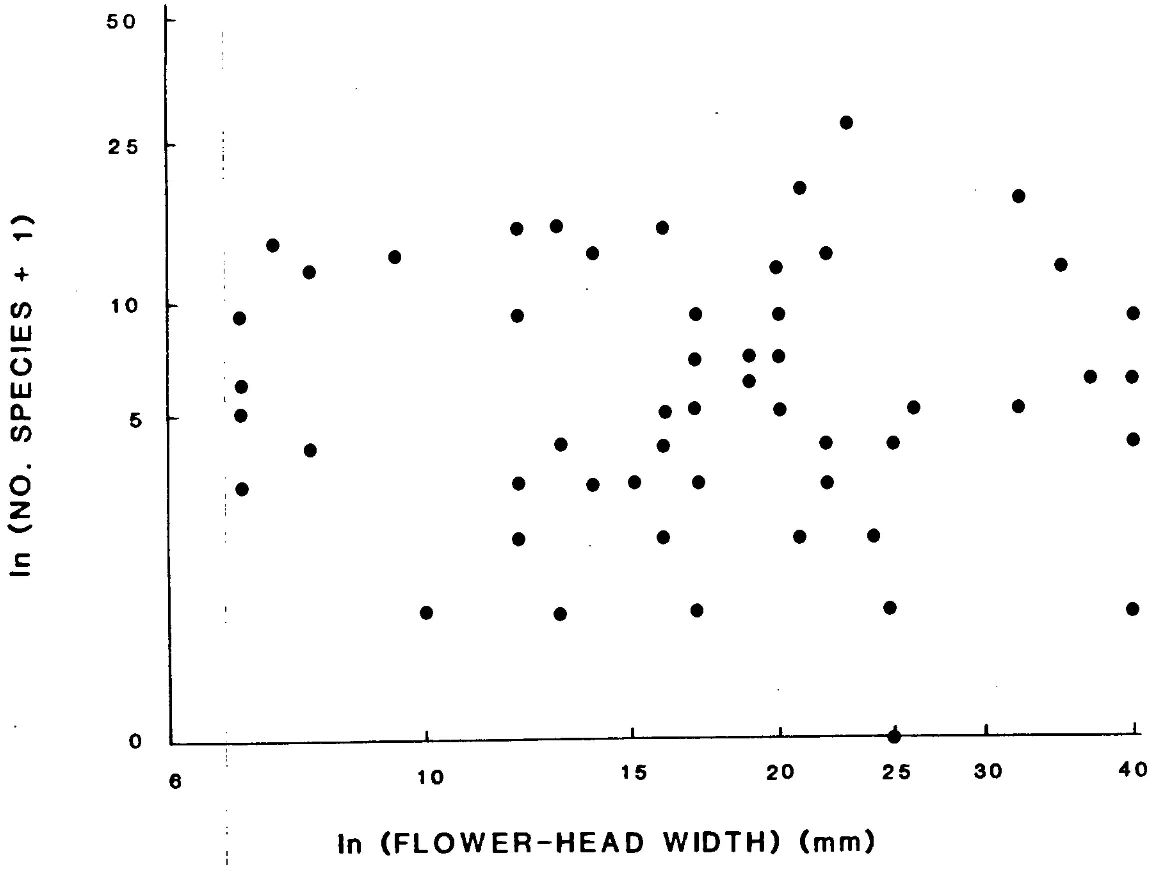


Fig. 7.1 Relationship between flower-head width and the number of herbivore species in each community on Berkheya species and European thistles, $\ln y = 0.05 \ln x + 1.68$, $r^2 = 0.001$, $P > 0.05$.

exception to this was in the genus Centaurea where a correlation was found (Fig. 7.4). In Carduus and Cirsium, the number of ectophagous species correlated with flower-head size (Fig. 7.5a and b). However, in Carduus, the relationship was strongly influenced by the single outlying point (Fig. 7.5a), and if this point is removed the correlation is not statistically significant.

These results further point to the problem of analysing data from higher taxonomic groups. Significant trends are missed because the herbivore communities on different

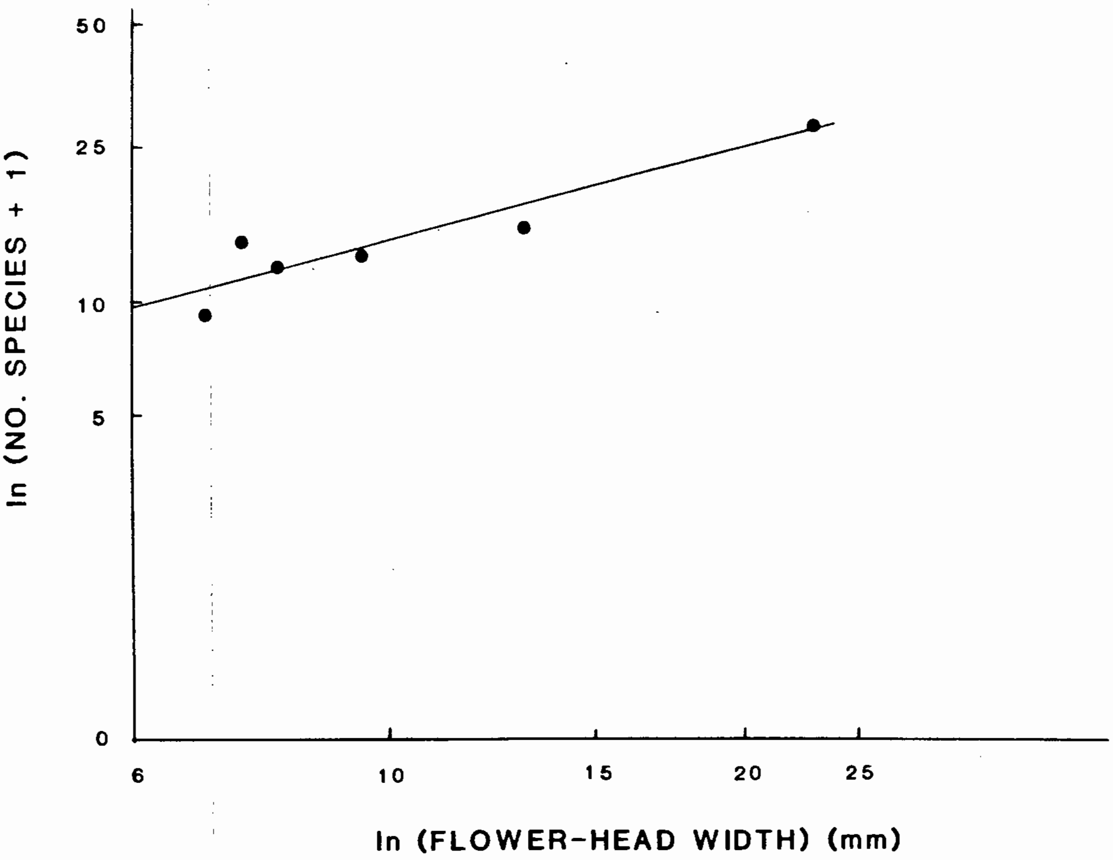


Fig. 7.2 Relationship between flower-head width and the number of herbivore species in communities from the flower-heads of Berkheya species. $\ln y = 0.7 \ln x + 1.09$, $r^2 = 0.86$, $P < 0.01$.

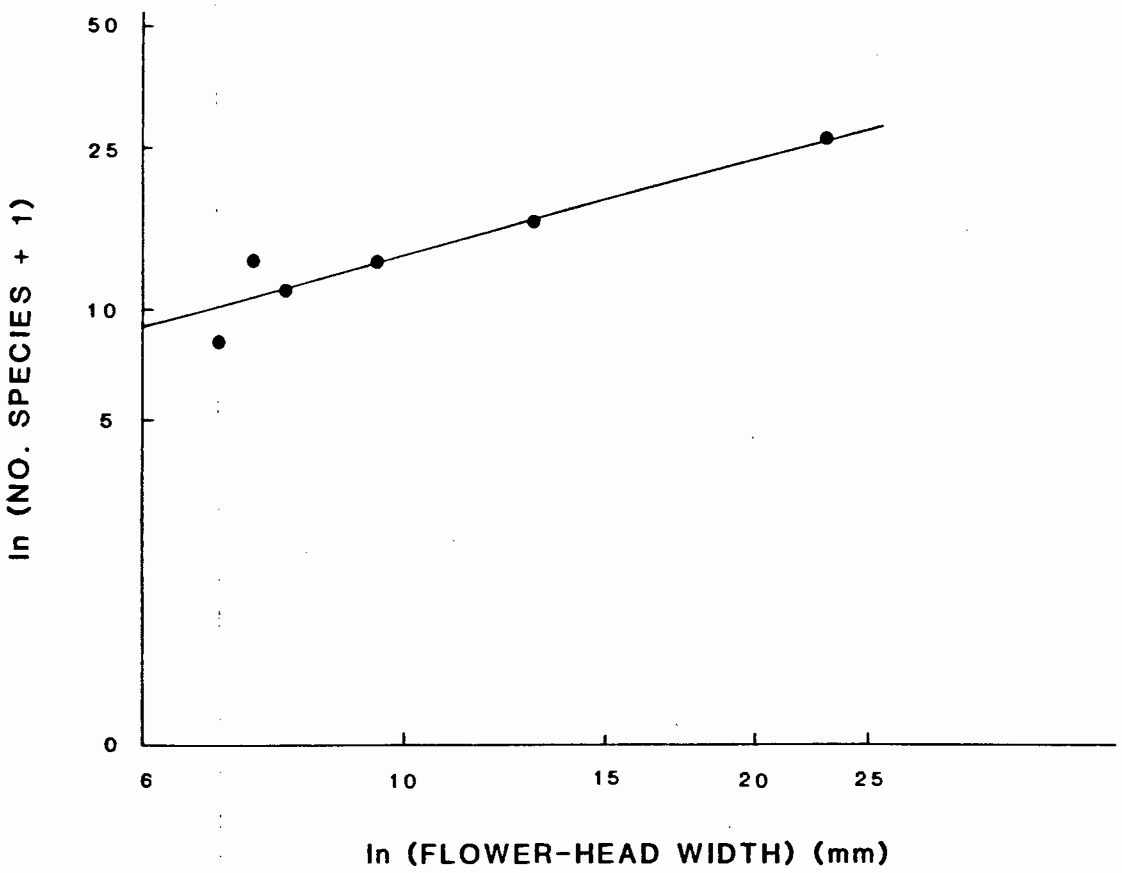


Fig. 7.3 Relationship between flower-head width and the number of generalist herbivore species in communities from the flower-heads of Berkheya species, $\ln y = 0.77 \ln x + 0.89$, $r^2 = 0.89$, $P < 0.01$.

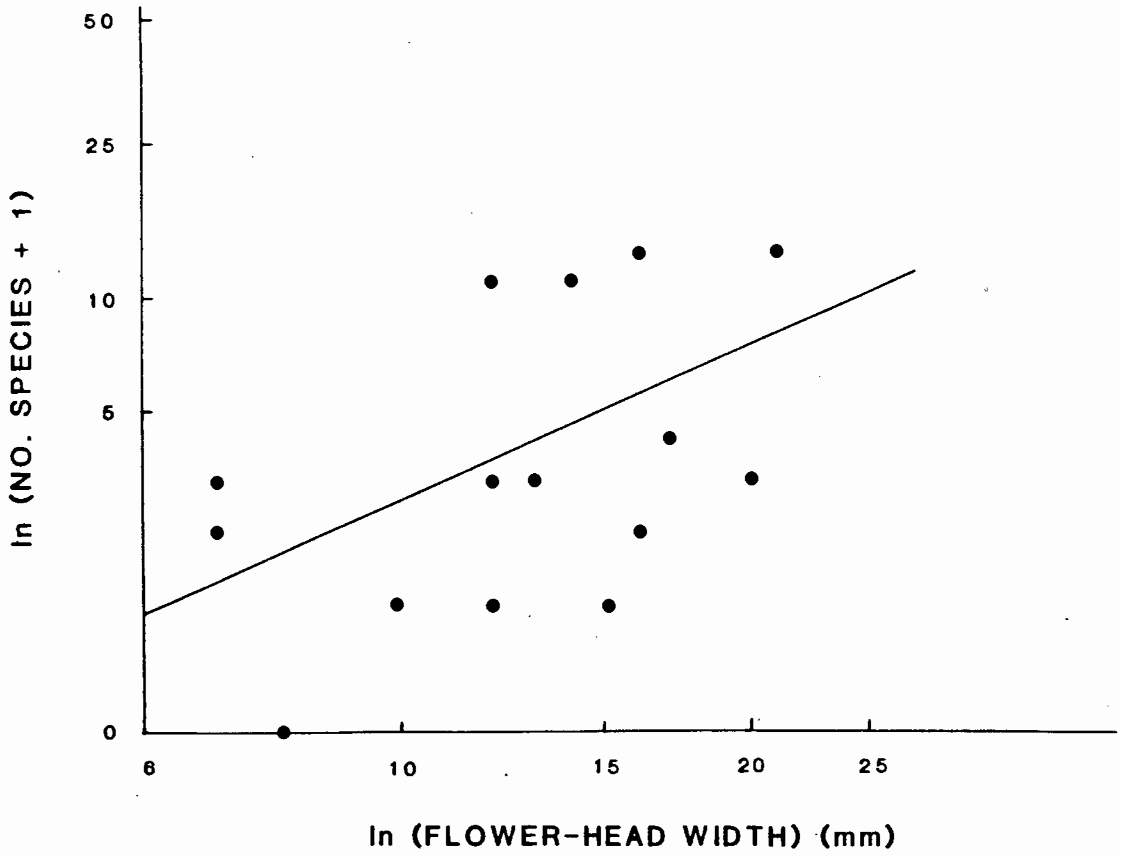


Fig. 7.4 Relationship between flower-head width and the number of endophagous species in communities from the flower-heads of Centaurea species.

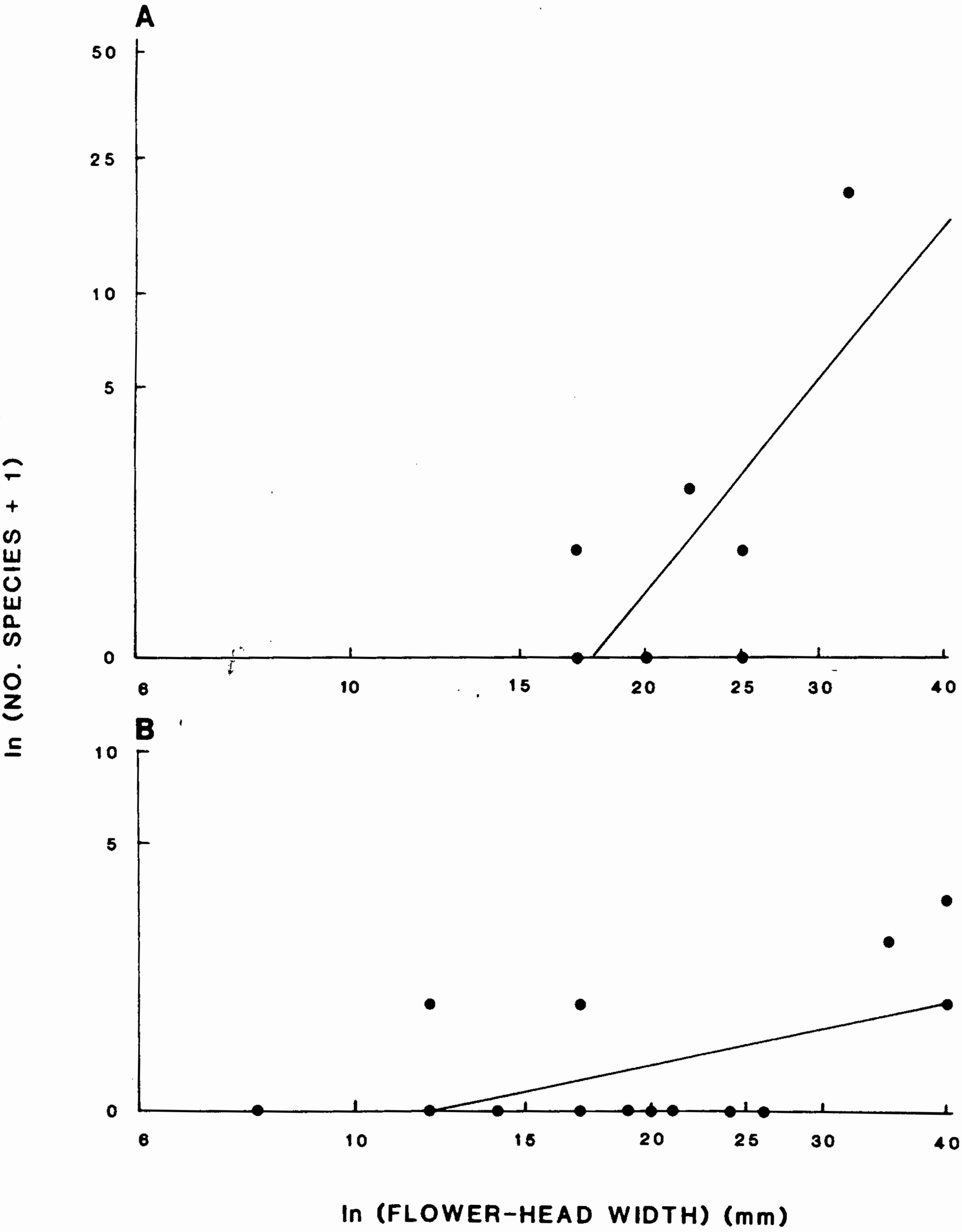


Fig. 7.5 Relationship between flower-head width and the number of ectophagous species in communities from the flower-heads of (A) *Carduus* species, $\ln y = 3.41 \ln x - 9.8$, $r^2 = 0.50$, $P < 0.05$, and (B) *Cirsium* species, $\ln y = 0.59 \ln x - 1.46$, $r^2 = 0.33$, $P < 0.05$.

plant genera may not be affected in the same way or to the same extent. Thus, although the herbivore communities from plant tribes or families together may show no relationship when tested against certain variables, communities on smaller plant groups, like genera, may show a significant relationship.

7.2 Taxonomic and guild composition

The taxonomic composition of the herbivore communities was analysed to determine whether the number of species in any particular insect taxon was influenced by flower-head size. The results, presented in Table 7.2, show statisticallly significant correlations only for the number of dipteran species in Centaurea flower-heads and the number of coleopteran species in Berkheya flower-heads.

Guild composition was analysed in the same way. Only the number of species in the guild of ectophagous chewers in Berkheya correlated with flower-head size (Table 7.3). When species numbers in guilds do not correlate with flower-head size, there are two implications. Firstly, there may be no pressure to fill the 'vacant space' in larger flower-heads. Secondly, the insects present in large flower-heads may be larger than insects in smaller flower-heads so that there is no vacant space. In herbivore communities where species numbers increase with flower-head size, similar sized insects should be present in flower-heads of varying size. This hypothesis is investigated in the following section.

Table 7.2 Correlation of herbivore species numbers in each insect order present in the herbivore communities, with flower-head diameter (Spearman's rank correlation) (* $P<0.05$). N is the number of plant species sampled.

		Correlation Coefficients (r_s)				
Genus	N	Coleop.	Lepidop.	Diptera	Hymenop.	Hemip.
Carduus	8	0.22	0.26	0.56		
Cirsium (E)	16	0.41	-0.27	-0.02		
Centaurea	16	0.38	0.28	0.60 *	0.15	
Berkheya	6	0.93 *	0.58	0.58		0.81

Table 7.3 Correlation of herbivore species numbers in each guild present in the flower-head communities, with flower-head diameter (Spearman's rank correlation) (* $P<0.05$). N is the number of plant species sampled.

		Correlation Coefficients (r_s)			
Genus	N	Endophages	Ectophages	Gall formers	Sap. suckers
Carduus	8	0.38	0.45	0.08	
Cirsium (E)	16	-0.07	0.44	-0.09	
Centaurea	16	0.44	0.26	0.33	
Berkheya	6	0.81	0.97 *		0.81

7.3 Effect of flower-head size on herbivore size

The number of herbivore species on *Berkheya* flower-heads increased directly with flower-head size (Fig. 7.2). Therefore, an increase in herbivore body size with flower-head size was not expected.

Most of the herbivore species commonly found on Berkheya species with small flower-heads were also found on species with large flower-heads (Table 4.1 to 4.6). Only two herbivore species, Larinus sp 1 and Epimadiza sp, occured exclusively on B. decurrens which had relatively large flower-heads. The size of these herbivore species was compared to other herbivore species in similar taxa and guilds that were found in Berkheya species with smaller flower-heads than B. decurrens.

The comparison of herbivore size was made by weighing oven-dried specimens. The results show that in comparisons involving two pairs of herbivores in similar taxa and guilds, species were significantly smaller if collected from a Berkheya species with small flower-heads than from a Berkheya species with large flower-heads (Table 7.4). There is therefore a hint that insect size is influenced by flower-head size. However, a comparison between Epimadiza sp and U. agromyzella is probably not strictly correct because the species are taxonomically unrelated and do have slightly different habits. Moreover, the latter species also occurs in B. decurrens flower-heads. In general, therefore, because most of the herbivore species on Berkheya were generalists, and many were common to all Berkheya species sampled, the hypothesis that herbivore size increases with flower-head size did not hold true. Only in one pair of species in the genus Larinus was a larger species present in larger flower-heads.

The size of specialist species in the genus Larinus on Berkheya was also affected by flower-head size in another way. Larinus size was calculated from the distance between the anterior edge of the compound eye and the posterior tip of the elytra, added to the distance between the tip of the rostrum and the anterior edge of the

Table 7.4 Comparison the size (mean dry weight ± SE) of some insect herbivores from Berkheya species with different sized flower-heads. N is the number of herbivores weighed.

		Mean Dry Weight (g)	
		B. heterophylla	B. decurrens
Species	N	(small flower-heads)	(large flower-heads)
Larinus sp1	20		$9.6 \times 10^{-3} \pm 5.1 \times 10^{-4}$
Larinus sp2	20	$3.9 \times 10^{-3} \pm 4.5 \times 10^{-4}$	
		$t = 9.68$	$P<0.001$
Epimadiza sp	20		$2.4 \times 10^{-4} \pm 1.5 \times 10^{-5}$
U. agromyzella	20	$1.5 \times 10^{-4} \pm 9.1 \times 10^{-6}$	
		$t = 4.82$	$P<0.001$

compound eye. Larinus sp 2 showed a very slight tendency to be longer at maturity if they developed in large B. decurrens flower-heads than in small flower-heads (Fig. 7.6). In addition, crowding of Larinus sp 2 in B. decurrens flower-heads had a slight negative effect on body size (Fig. 7.7).

The phenomenon, of herbivore size being related to flower-head size, is more characteristic of the European thistles (Zwölfer 1982a, 1987) and is not confined to specialist species. Zwölfer (1987) showed that ovipositor length in Terellia and Urophora, and rostrum length in Larinus is related to the size of their host plants flower-heads. Both these structures are used to place eggs inside the flower-head. It is doubtful that the length of the ovipositor and rostrum are strictly functional adaptations with the larger structures required for oviposition in

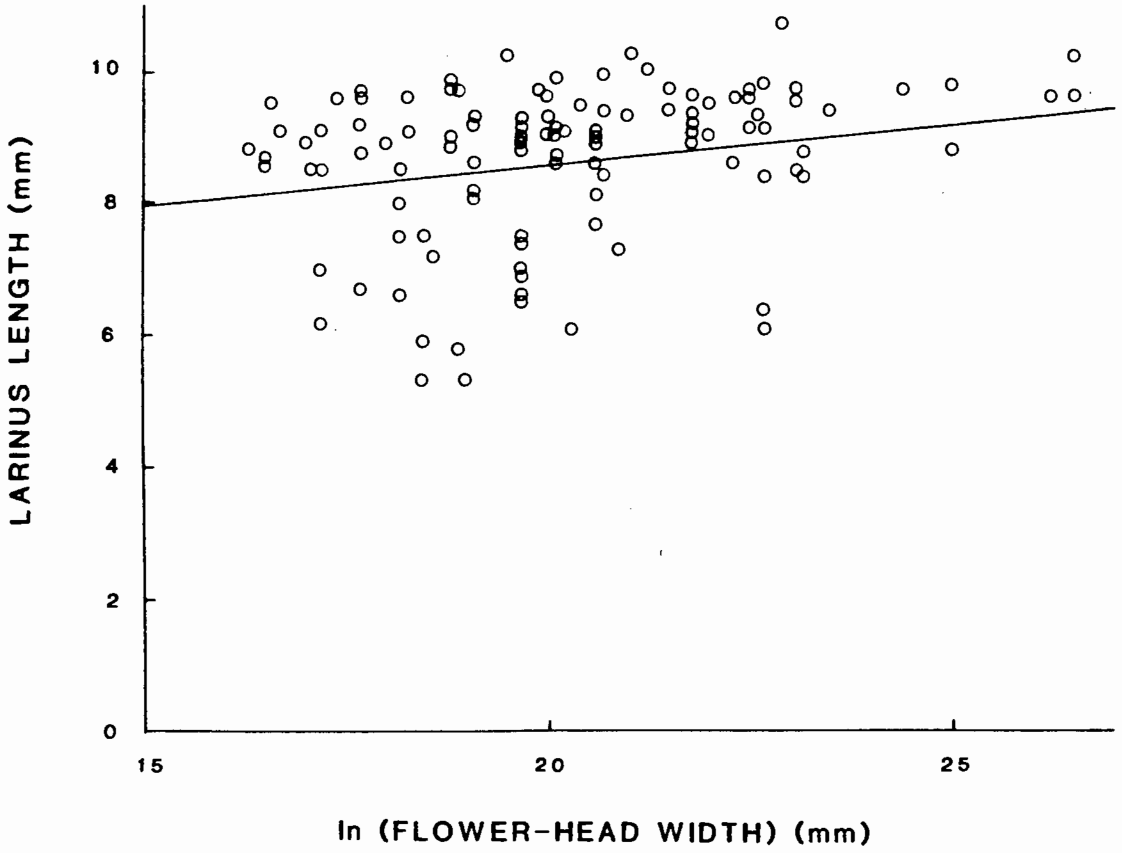


Fig. 7.6 Relationship between the width of B. decurrens flower-heads and the body length of Larinus sp 3, $y = 0.12x + 6.18$, $r^2 = 0.06$, $P < 0.01$.

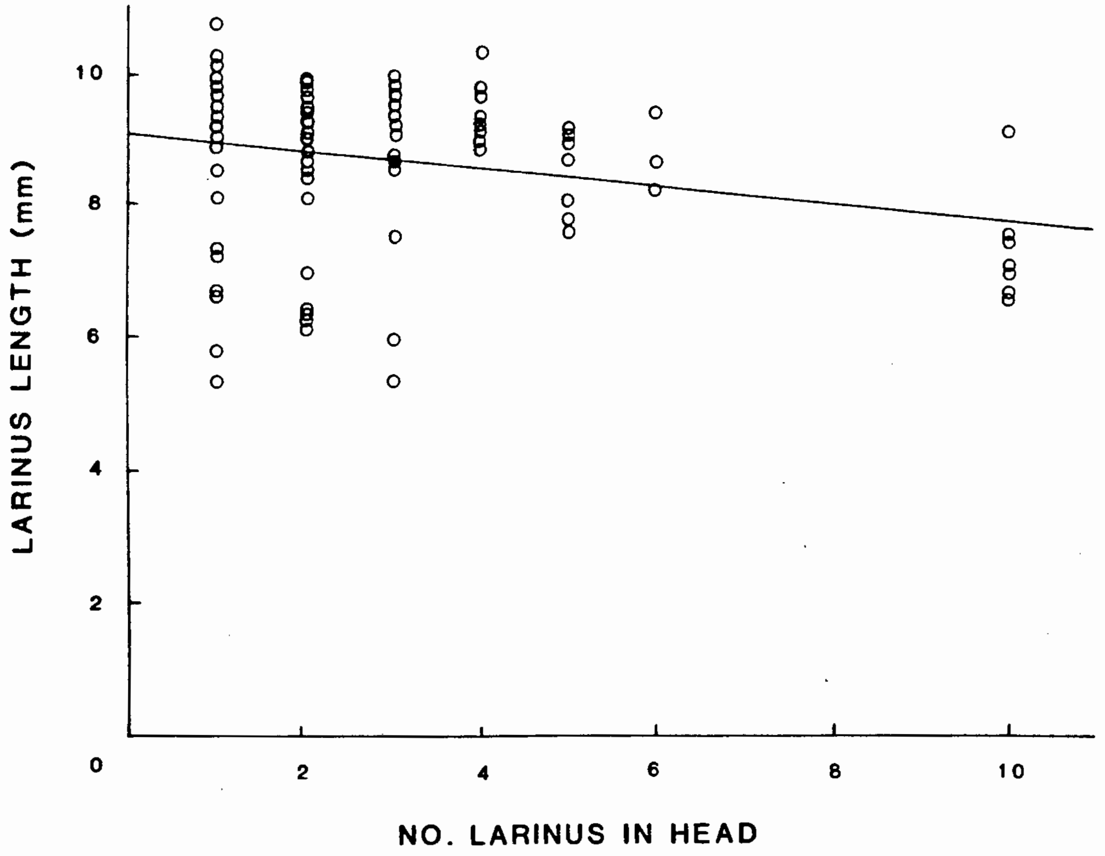


Fig. 7.7 Relationship between the number of Larinus sp 2 in a B. decurrens flower-head and their body length at maturity, $y = -0.14x + 9.11$, $r^2 = 0.09$, $P < 0.01$.

large flower-heads. Rather, the length of the ovipositor and rostrum are probably incidental effects of the relationship between body size and flower-head size.

7.4 Species packing

In Berkheya, species packing correlated positively with flower-head diameter (Fig. 7.8). This is in contrast to

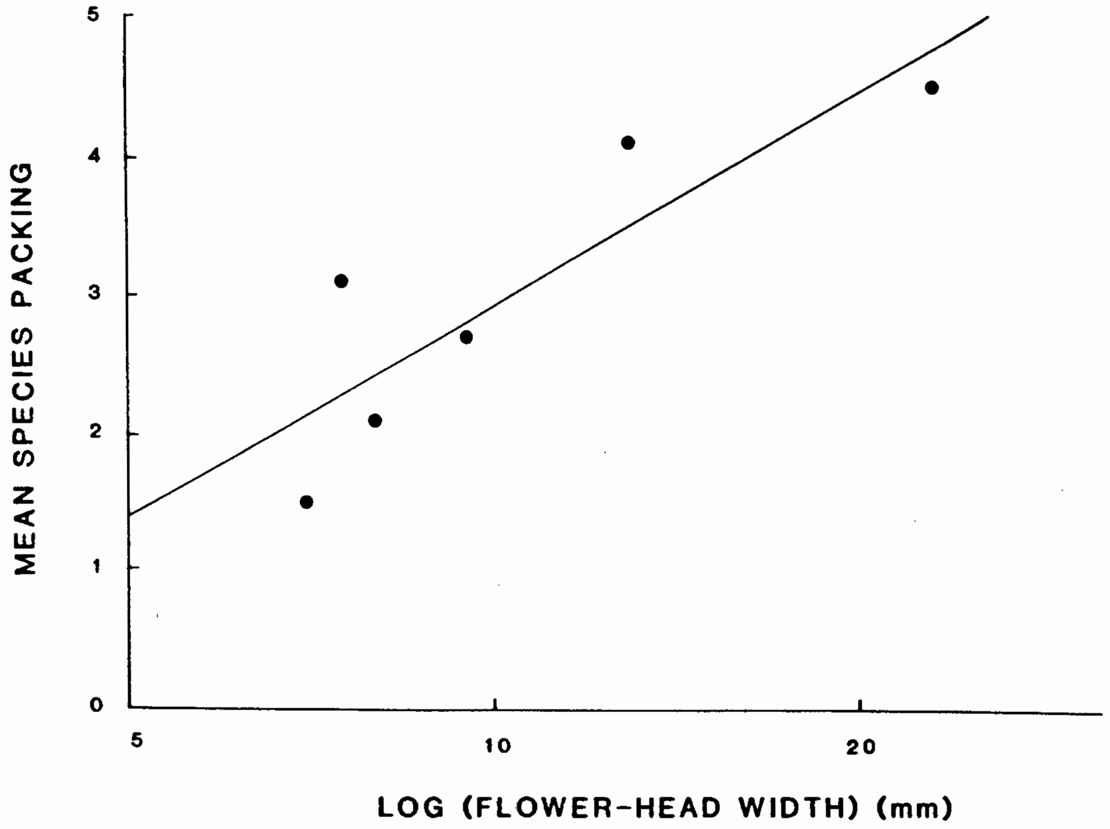


Fig. 7.8 Relationship between the mean flower-head width of six Berkheya species and the mean species packing in each Berkheya species, $y = 5.1x - 2.17$, $r^2 = 0.76$, $P < 0.05$.

European thistles where species packing was not correlated with flower-head size (Zwölfer 1987). This is probably because species richness in European thistles did not correlate with flower-head size either (Zwölfer 1982a, 1987). Again, the possible cause of this may be the general correlation of herbivore size with flower-head diameter in many herbivore species from European thistles.

The results reported in this chapter are summarised in Table 7.5. Most of the variability in herbivore species numbers in the herbivore communities associated with Berkheya flower-heads was explained by flower-head size. No such relationship was found in herbivore communities associated with the flower-heads of European thistles, but the size of some of their herbivore species was related to flower-head size (Zwölfer 1987). In the next chapter the effect of taxonomic isolation of the host plant on the insect herbivore communities is examined.

Table 7.5 Summary of the effects of flower-head size on the insect herbivore communities associated with *Berkheya* and European thistles. Correlation coefficients are in brackets. Letters E refers to Europe.

Herbivore community	Plant taxa			
	Berkheya	*Carduus*	*Centaurea*	*Cirsium* (E)
No. species	increases (r^2=0.86)	none	none	none
No. specialists	none	none	none	none
No. generalists	increases (r^2=0.89)	none	none	none
No. endophages	none	none	increases (r^2=0.27)	none
No. ectophages	none	increases (r^2=0.50)	none	increases (r^2=0.33)
Taxa	increase in Coleoptera (r_s=0.93)	none	increase in Diptera (r_s=0.60)	none
Guilds	increase in ectophages (r_s=0.97)	none	none	none

CHAPTER 8

THE EFFECT OF HOST PLANT TAXONOMIC ISOLATION ON THE INSECT HERBIVORE COMMUNITIES

Abstract

1. The effect of taxonomic isolation of the host plants on the insect herbivore communities associated with the flower-heads of Berkheya, Californian thistles and European thistles was investigated.

2. Regression analyses seldom gave statistically significant results because some plant species, that were not taxonomically isolated, were colonised by few herbivore species because they had small ranges, and some were colonised by many herbivore species because they had larger ranges (estimated by sampling frequency). Therefore a different technique was devised to identify biologically significant relationships.

3. Herbivore species numbers were highest in communities from plant species that were members of large genera with over 40 congenerics.

4. Specialist species numbers were not influenced by taxonomic isolation, but generalist species numbers were highest in communities associated with plants that had more than 40 congeneric species in the same region.

5. Taxonomic isolation had more effect on the number of ectophagous species than on endophagous species numbers. Only communities associated with plants which had more than 40 sympatric congenerics comprised more than 7 endophagous species and more than 3 ectophagous species.

6. Taxonomic and guild composition of the communities was influenced by taxonomic isolation because herbivorous Hymenoptera (taxon) and gall formers (guild) tended to be restricted to certain plant subtribes and genera.

In theory, plants that are taxonomically isolated or are toxic are expected to have relatively fewer herbivore species that feed on them (Strong et al. 1984). Conversely, plants that have many close relatives are expected to be fed upon by more herbivore species because host 'switches' over evolutionary time are are presumably easier between closely related and biochemically similar plant species (Futuyma 1976). The herbivore communities of Berkheya and thistle flower-heads are now examined to test this hypothesis.

Taxonomic isolation is measured by the number of congeneric species in the same geographic region. The fewer the number of congeneric species, the more 'isolated' the host plant.

8.1 Total herbivore species numbers

The regression of the number of herbivore species on taxonomic isolation of the host plants, for Berkheya and all thistles, is not statistically significant (Fig. 8.1). This concurs with the results of Zwölfer (1982a, 1987) in his analysis of the flower-head communities of European thistles. The regression (Fig. 8.1) is not statistically significant because although many of the herbivore communities from plant species in the larger genera have the largest number of herbivore species, several members of the large plant genera also have few herbivores species.

Apparently the species-area effect (ie. widespread plants support more species) complicated the association between number of herbivores and the size of the plant genus. There was variability in the number of herbivore species in communities associated with large plant genera because the host plant species extended over different sized geographic ranges. Therefore, insect herbivore communities on plant species from large genera that had small ranges comprised few insect herbivore species, but communities on widespread plant species from large genera had a higher species richness. One method used to avoid the species-area effect is to plot the residuals from the

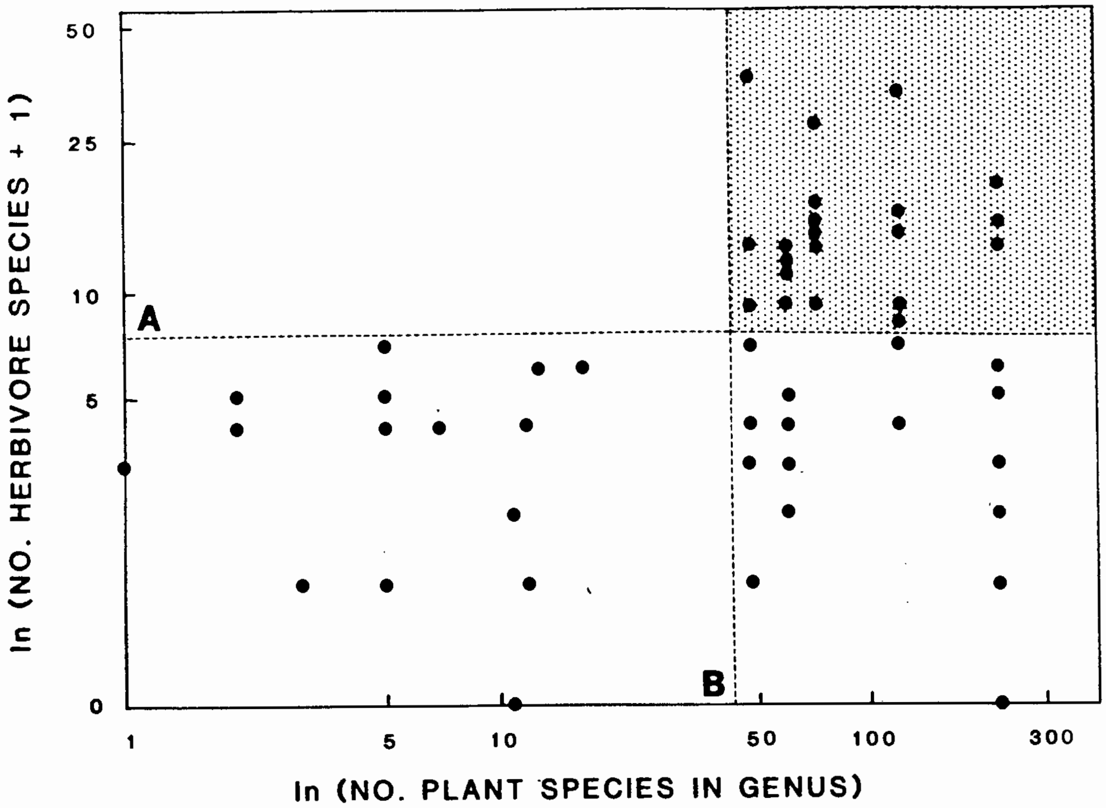


Fig. 8.1 Relationship between taxonomic isolation of the host plant (number of congeneric species in the same area) and the species richness of the flower-head herbivore communities $\ln y = 0.13 \ln x + 1.35$, $r^2 = 0.05$, $P > 0.05$. See text for further explanation.

species-area curve against the number of species in the plant genus (Lawton & Schröder 1978). However, the use of this technique has failed to identify statistically significant relationships between the number of herbivore species on European thistles and the number of plant species in the genus (Lawton & Schröder 1978). Moreover, it cannot be used for either Berkheya or the Californian thistles alone, because only a single genus was sampled in each region.

It is possible to take the residuals from Fig. 6.1 and plot this against the number of sympatric species in the genus (sympatric here means 'within Europe', 'within California' and 'within southern Africa'). This analysis differs from that of Lawton & Schröder (1978) because it uses only flower-head herbivores and the data from Berkheya and Californian thistles are added. The regression is not statistically significant (Table 8.1).

An alternative way of doing the analysis is visual in Fig. 6.1. A horizontal line A was drawn across the graph (Fig. 8.1) at a point just above the maximum number of herbivore species in the communities from the smaller plant genera (ie. those with fewer than 40 sympatric congenerics). The large plant genera (> 40 species) were divided from the small genera (< 40 species) by a vertical line B. The position of line B was selected because there is an obvious rapid increase in herbivore numbers to the right of its position (Fig. 8.1).

Table 8.1 Regressions of residuals from the species-area relationship, with the number of sympatric plant species in the genus. Data from herbivore communities on all plant groups sampled were included. See text for further explanation. (* P<0.05).

Herbivore species	Slope	Y intercept	r^2
All species	0.08	-0.33	0.04
Specialists	-0.08	0.32	0.04
Generalists	0.17	-0.65	0.10 *
Endophages	0.02	-0.09	0.01
Ectophages	0.14	-0.54	0.04

The points on the graph now illustrate some interesting facts. Points that fall in the shaded area, in the upper right quadrate formed by the intersection of lines A and B, represent all the plant species inhabited by more than 8 herbivore species (Fig. 8.1). These plants come from relatively large genera of over 40 species. Thus, only plant species which have more than 40 congeneric relatives in the same geographical region, were inhabited by more than 8 insect herbivore species.

8.2 Specialist and generalist species

A regression between the residual values from the species-area relationship in Fig. 6.4 (number of generalist species on sampling frequency) and the number of sympatric plant species in the genus was not significant. The number of specialist species was not influenced by the size of the genus in which the host plant is a member (Table 8.1). When the number of generalist species is analysed in a similar way (residuals taken from Fig. 6.5), this relationship is significant (Table 8.1), although only 10% of the variability in generalist species numbers is accounted for.

These graphs were also analysed using the method described above (section 8.1) which confirmed the above results. In Fig. 8.2a, only two points are in the shaded area which indicates that the number of specialist species was not affected by the number of congeneric plant species. Many points fall into the shaded area in Fig. 8.2b. These points represent herbivore communities on plant species from the larger genera that have more than five generalist species. Therefore, the number of generalist species was influenced by the size of the plant genus but the number

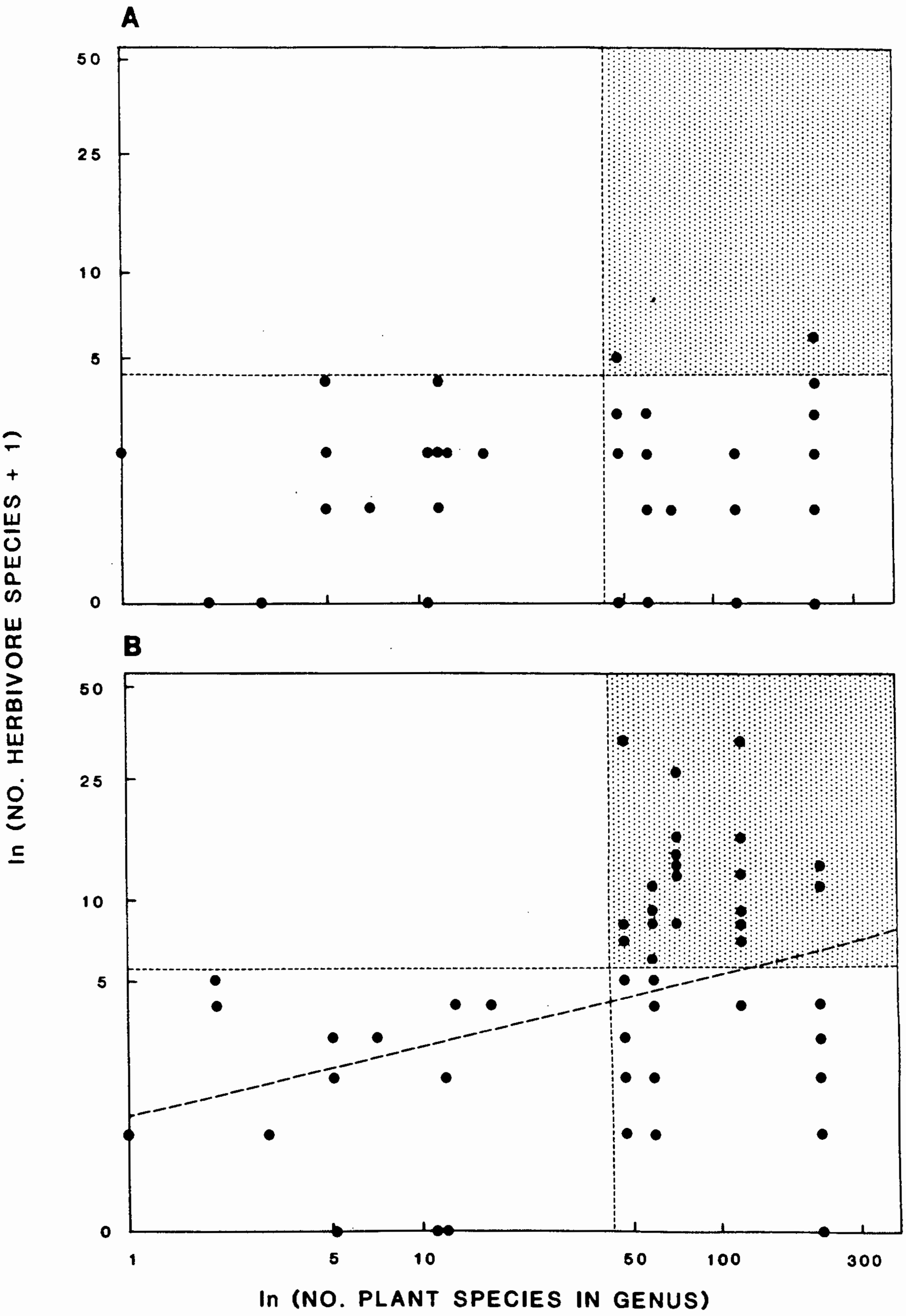


Fig. 8.2 Relationship between taxonomic isolation of the host plant (number of congeneric species in the same area) and the number of (A) specialist herbivore species, $\ln y = -0.08 \ln x + 0.82$, $r^2 = 0.02$, $P > 0.05$, and (B) generalist herbivore species, $\ln y = 0.21 \ln x + 0.82$, $r^2 = 0.11$, $P < 0.01$. See text for further explanation.

of specialist species was not affected. Plant species that had less than 40 congeneric species did not accumulate many generalist species. The supposed biochemical similarity between closely related plants did not appear to enhance the accrual of specialist herbivore species in the communities.

All six Berkheya species and eight of the nine Californian thistle species fall into the shaded area (Fig. 8.2b). Clearly, the number of congeneric plant species was an important reason for the many generalist species associated with the insect herbivore communities on plants in these two geographic regions.

8.3 Endophagous and ectophagous species

Regressions between residuals from the species-area relationships for endophagous and ectophagous species (Figs 6.7 and 6.8 respectively) and the number of sympatric plant species in the genus showed no statistically significant relationships (Table 8.1). However a regression between the number of endophagous species in the community and the taxonomic isolation of the host plant was statistically significant (Fig. 8.3a). Only 12% of the variation in endophagous species numbers was accounted for by the regression. The shaded area in Fig. 8.3a shows more clearly that communities on plants with over 40 congenerics were the only ones to have more than seven endophagous species.

A regression shows no relationship between the number of ectophagous species and the size of the plant genus (Fig. 8.3b). But the points in the shaded area show that communities in plants with over 40 congenerics were the

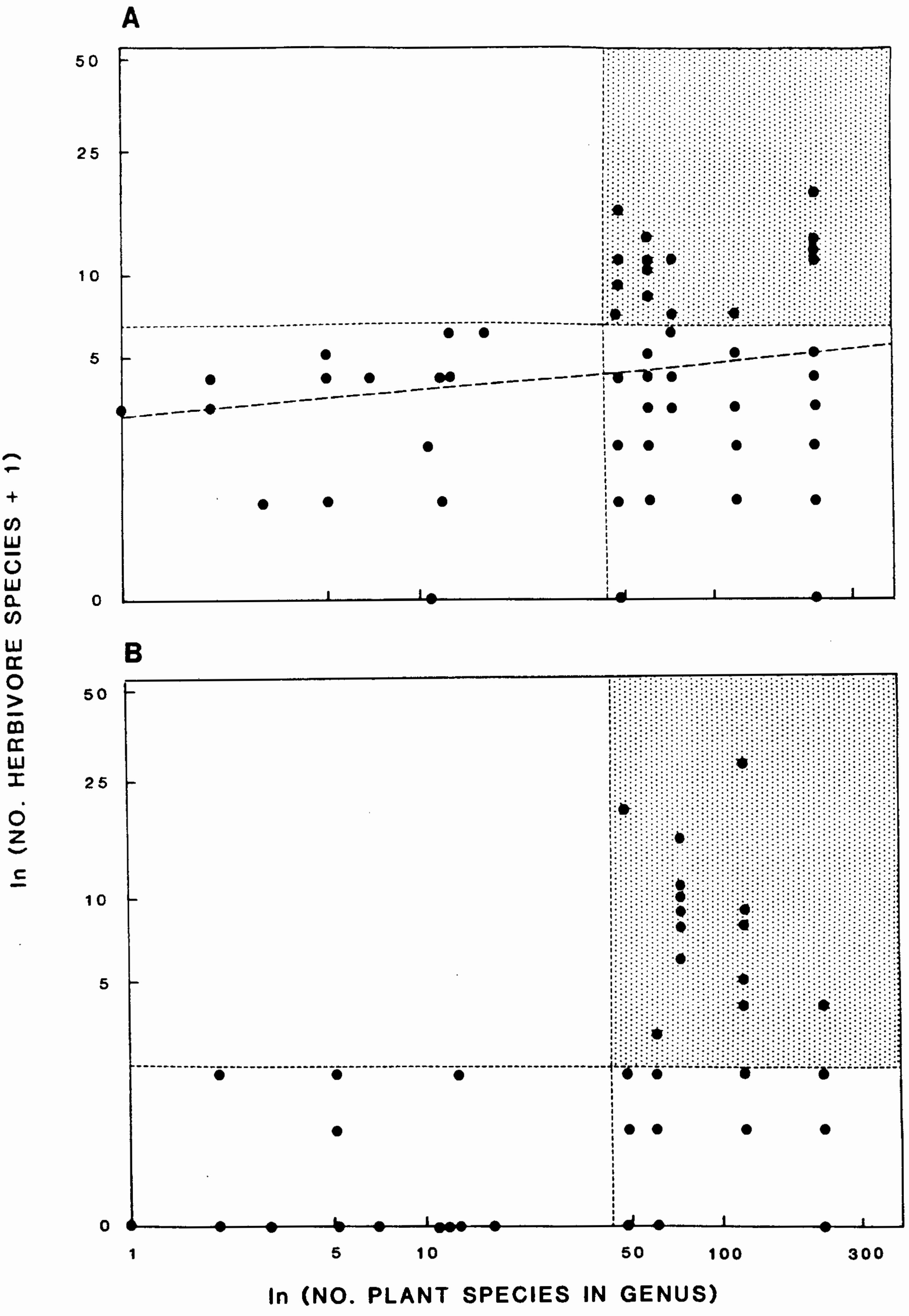


Fig. 8.3 Relationship between taxonomic isolation of the host plant (number of congeneric species in the same area) and the number of (A) endophagous species, $\ln y = 0.08 \ln x + 1.32$, $r^2 = 0.12$, $P < 0.01$, and (B) ectophagous species, $\ln y = 0.15 \ln x + 0.11$, $r^2 = 0.05$, $P > 0.05$. See text for further explanation.

only communities to be colonised by more than three ectophagous species.

8.4 Effect of host plant taxonomy on taxonomic composition

An analysis of the effect of taxonomic isolation of the host plants on the taxonomic composition of the the herbivore communities on Berkheya and European and Californian thistles, depends at which hierarchical level of the plant classification system the comparison is done. This is similar to the analysis of herbivore taxonomic composition, in chapter 5, where the results depended upon whether the herbivore communities were compared by orders, families or genera. In this section, the taxonomic composition of the herbivore communities was examined, firstly in the three separate plant groups from South Africa, California and Europe, secondly in these groups divided into their sub-tribes and thirdly when divided into genera. In each example, the herbivore communities were compared by determining the proportion of species in each insect order present in the community.

The plant groups from the different geographic regions were the Carduoideae in Europe that were sampled by Zwölfer (1965), the Carduoideae in California that were sampled by Goeden & Ricker (1986a, 1987a, 1987b) and the Arctoteae in South Africa sampled during this study. Fig. 8.4a shows that the herbivore communities of Carduoideae (California) and Arctoteae were most similar (data from all herbivore communities in each region were grouped together). Both differed markedly from Carduoideae

(Europe) herbivore communities because the two former groups lacked Hymenoptera and the latter group lacked Hemiptera.

Only one plant genus was sampled in South Africa (Berkheya) and in California (Cirsium) respectively (Goeden & Ricker, 1986a, 1987a, 1987b, chapter 4). Therefore the taxonomic composition of the communities from these plants did not differ when the plant species were grouped according to region (Fig. 8.4a), sub-tribe (Fig. 8.4b) and genus (Fig.8.4c). The Carduoideae sampled in Europe by Zwölfer (1965) comprised several subtribes and genera (see Fig. 2.8).

The taxonomic composition of herbivore communities on the subtribes differed (Fig. 8.4b). The Echinopinae had the least diversity with only two insect orders present. Of the European group, the highest herbivore diversity was found in herbivore communities on the Centaureinae which had four insect orders present. It was also the only subtribe to have phytophagous Hymenoptera.

The taxonomic composition of the herbivore communities was compared between plant genera in Fig. 8.4c and there were marked differences between the communities on the European genera. It was therefore interesting that the herbivores on Cirsium in California and on Berkheya were so similar, especially when the geographic isolation and taxonomic differences of these two plant groups were considered. Also of interest was the phytophagous Hymenoptera which were confined to the Centaurea. An incorrect impression, that all thistles are fed upon by phytophagous Hymenoptera, can be gained from grouped information, as in Fig. 8.4a. In addition, the taxonomic composition of the herbivore communities of the Carduoideae in Europe (Fig.

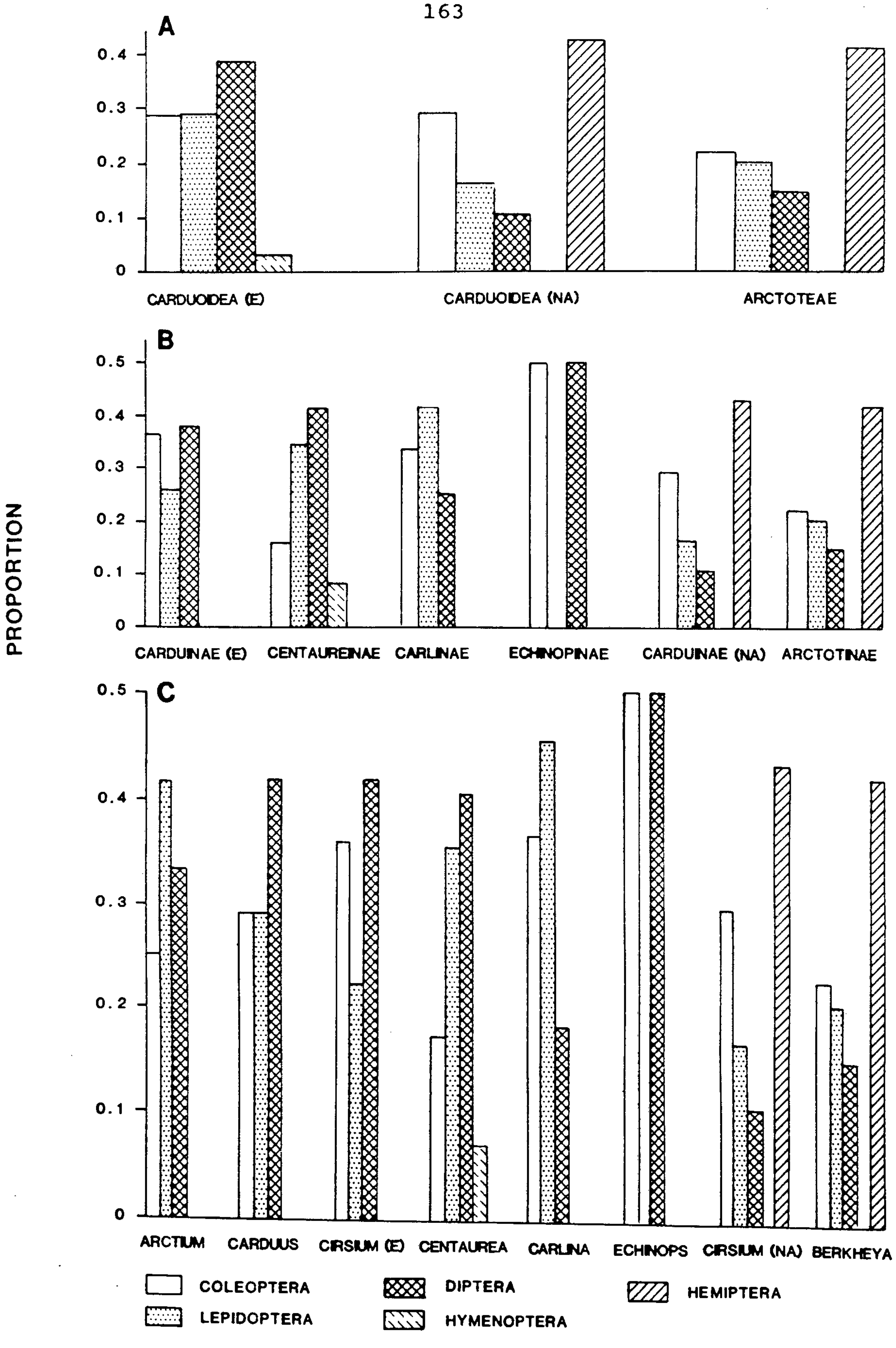


Fig. 8.4 Taxonomic composition, analysed by the proportion of herbivore species in each order, of the herbivore communities associated with the flower-heads of Berkheya, Californian thistles (NA = North America/California) and European thistles (E = Europe). Guild composition is shown for the combined herbivore communities from (A) the three plant groups (Berkheya, Californian thistles and European thistles), (B) plant subtribes and (C) plant genera.

8.4a) was not a good indicator of what the communities were actually like on the individual plant species (Fig. 5.4), nor on the plant genera (Fig. 8.4c). Even the herbivore communities on plant genera within the same subtribe were not similar (Figs 8.4b and 8.4c). These results are consistant with a similar analysis done by Zwölfer (1988) but he compared the taxonomic composition of the herbivore communities associated with all the aerial parts of the thistles.

The effect of plant taxa on the composition of insect taxa in the herbivore communities is clear. Coleoptera and Diptera were the only insect taxa present in communities from all the plant species, although they made up different proportions of each community. The phytophagous Hymenoptera were restricted to the Centaurea and were not present on Californian thistles nor Berkheya, and Lepidoptera were not found on Echinops. Taxonomic isolation can therefore have the effect of restricting insect herbivore taxa to certain plant groups. These differences should allow the taxonomic composition of herbivore communities to provide information about the phylogeny of the plant species with which they are associated. Zwölfer (1988) suggested that the genus Larinus, species of which occur on nearly all the thistle species in Europe, could provide an indication of the phylogenetic relationships of their host plants. Morphological and electrophoretical studies have already illustrated that this is a possibility (Herbst 1987 cited by Zwölfer 1988, Zwölfer et al. 1971).

8.5 Effect of host plant taxonomy on guild composition

The effect of host plant taxonomy on the guild composition of the herbivore communities was analysed in the same way as the effect of host plant taxonomy on the taxonomic composition on the herbivore communities was analysed. Fig. 8.5a shows that the guilds of sap suckers and gall formers were restricted to certain geographical regions. Endophagous chewers formed the largest guild in communities from each subtribe in Europe and sap suckers formed the largest guild in California and South Africa. However, when the European thistles were divided into their subtribes, the taxonomic composition of the herbivore communities associated with each subtribe were different (Fig. 8.5b). Gall formers were found only in communities on Carduinae (Europe) and Centaureinae. Even more differences between herbivore communities became apparent when the composition of guilds in plant genera were examined (Fig. 8.5c).

Because the only genera sampled in California and South Africa were Cirsium and Berkheya respectively, there was no change in guild composition at different hierarchical levels (Fig. 8.5a,b,c). Similar guilds were present in communities on Berkheya in South Africa and Cirsium in California. The only difference was that in communities on Berkheya flower-heads, endophagous chewers formed a larger proportion of the community than ectophagous chewers, while on Cirsium in California, the proportions were the same (Fig. 8.5c).

Differences in the guild and taxonomic composition of communities associated with the flower-heads of plants from different geographic regions may be due to the

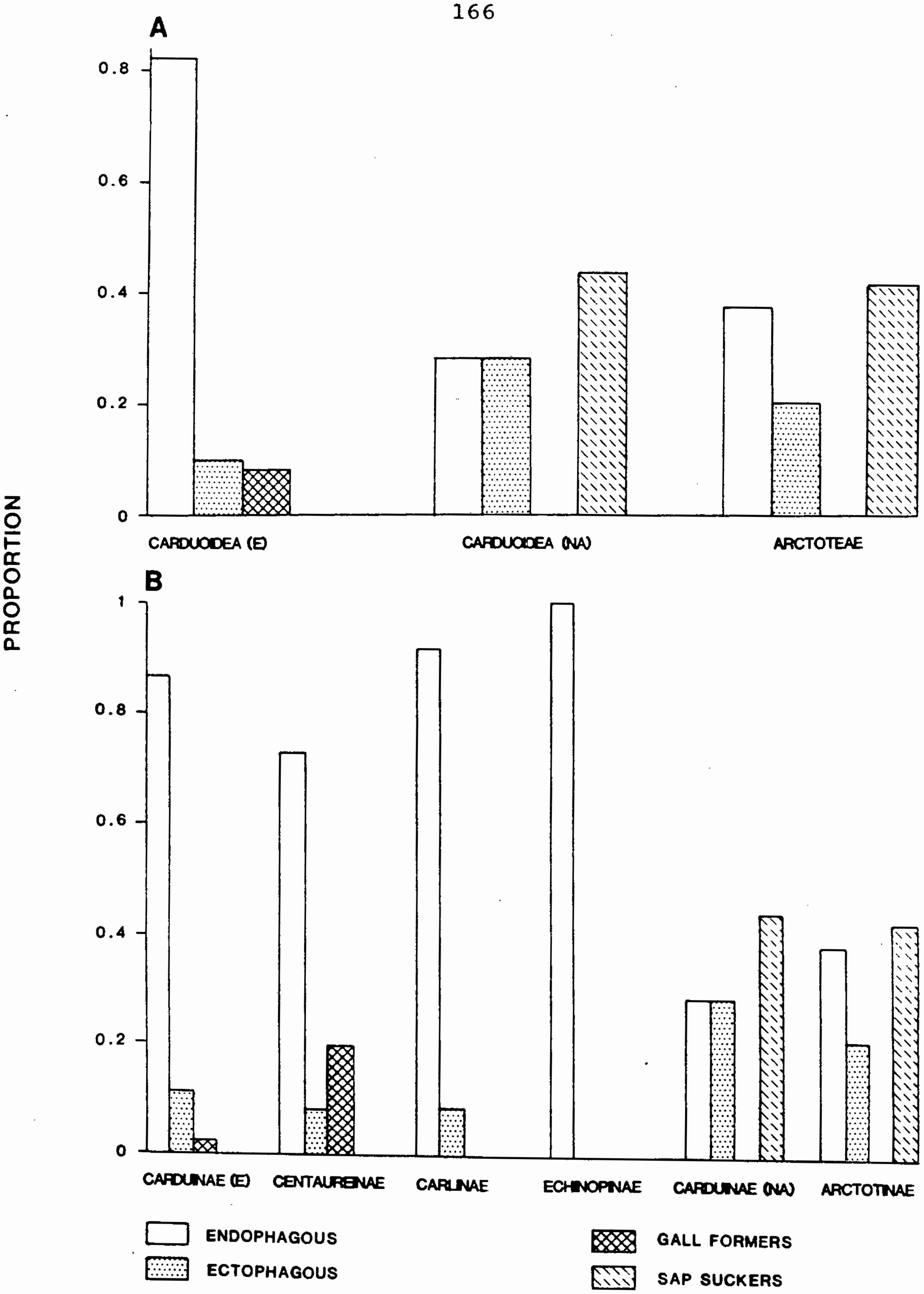


Fig. 8.5 Guild composition, analysed by the proportion of herbivore species in each guild, of the herbivore communities associated with the flower-heads of Berkheya, Californian thistles (NA = North America/California) and European thistles (E = Europe). Guild composition is shown for the combined herbivore communities from (A) the three plant groups (Berkheya, Californian thistles and European thistles), (B) plant subtribes and (C) plant genera. Continued on next page.

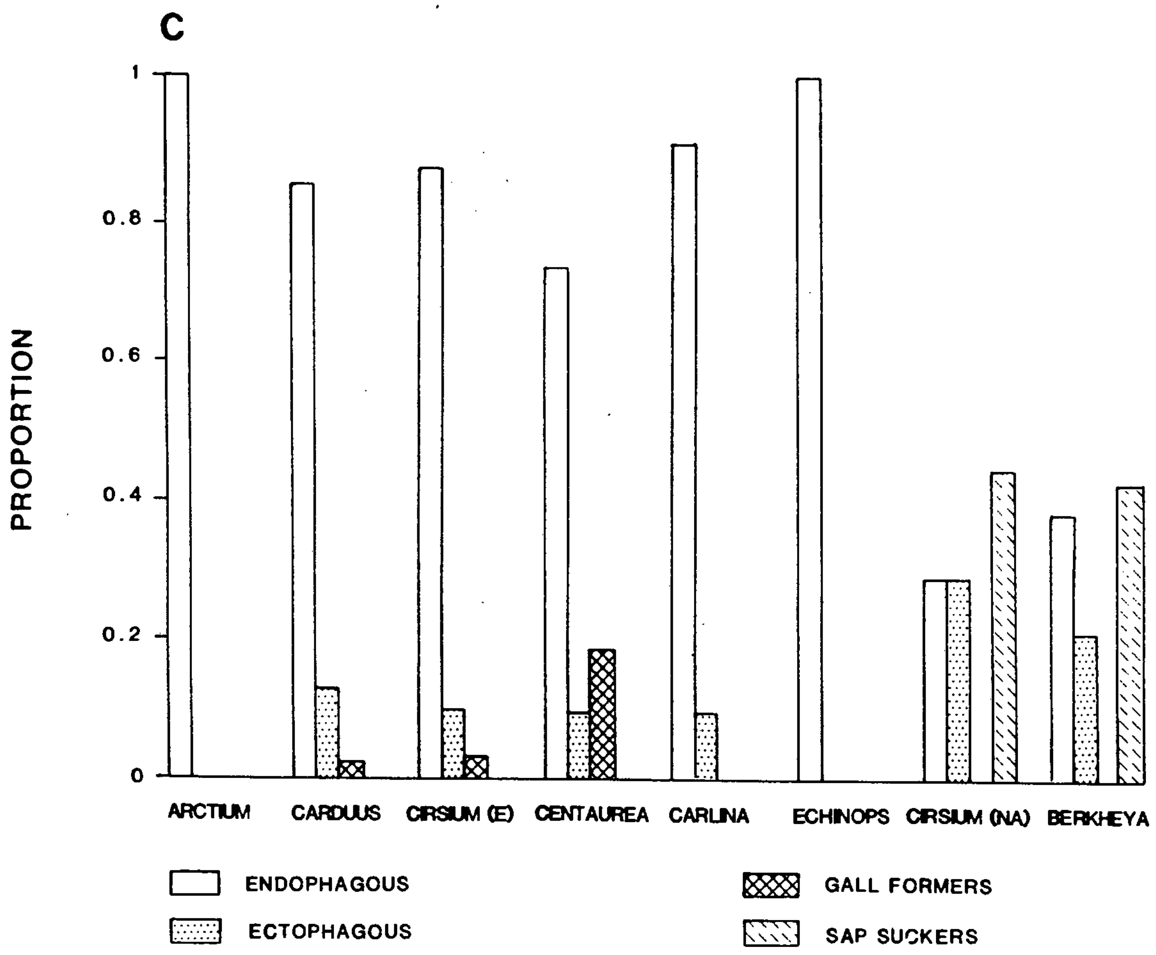


Fig. 8.5 continued.

availability of different 'pools' of potential colonisers in each area. For some reason, the 'pool' of colonisers in California and South Africa were similar which resulted in the communities in these areas accruing similar kinds of herbivore species. This will be discussed in more detail in the general discussion.

The results presented in this chapter are summarised in Table 8.2. Host plant taxonomic isolation has been shown to affect the accrual of generalist herbivore species and also the movement of insect taxa and guilds between plant species.

Table 8.2 Summary of the effects of host-plant taxonomic isolation on the insect herbivore communities associated with the flower-heads of Berkheya, Californian thistles and European thistles. See text for explanation.

	Plant taxa	
Herbivore community	Less than 40 congenerics	More than 40 congenerics
No. species	all < 8 species	57% > 8 species
No. specialists	all < 5 species	5% > 4 species
No. generalists	all < 6 species	62% > 5 species
No. endophages	all < 7 species	41% > 6 species
No. ectophages	all < 3 species	56% > 2 species

CHAPTER 9

GENERAL DISCUSSION

Initially in this chapter, the main points in this thesis are synthesised and discussed. Then the evolution of insect herbivore communities in the flower-heads of Berkheya and thistles and the effect of different herbivore species pools is discussed.

9.1 A synthesis of host-plant effects on the herbivore communities in the flower-heads of Berkheya and thistles

The effects of host plant range, flower-head structure and taxonomic isolation on the insect herbivore community in the flower-heads of Berkheya and thistles were examined from five perspectives: (1) total species numbers, (2) proportion of specialist and generalist species, (3) proportion of endophagous and ectophagous species, (4) taxonomic composition and (5) guild composition.

9.1.1 Number of herbivore species

Insect species numbers varied considerably between the insect herbivore communities associated with the flower-heads of different Berkheya and thistle species (Table 5.1). More than 50% of this variability was explained by sampling frequency (Fig. 6.2), which, in the thistles, corresponded roughly with plant range (Lawton & Schröder 1978). More herbivore species were present in and on the flower-heads of Berkheya and Californian thistles than on

European thistles that had a similar range. Moreover, the number of species accumulated more rapidly, with increasing plant range, in herbivore communities from Berkheya and Californian thistles than in communities from European thistles.

A possible explanation for this phenomenon is that the density of insect herbivore species in the regions as a whole was greater in California and South Africa than in Europe. This could mean that more habitats are covered by the plants, per unit area (habitat heterogeneity hypothesis (Williams 1964)), in South Africa and California than in Europe. However, this would mean that there were more habitats, per unit area, in California and South Africa than in Europe, a suggestion that would be difficult to elucidate. However, the number of insect herbivore species available need not be related to habitat heterogeneity and the encounter frequency hypothesis would then be important. Even closely related thistle genera in Europe accumulated insect herbivore species at different frequencies (Fig. 6.3). Presumably these thistle genera, Carduus, Centaurea and Cirsium, were encountered by similar numbers of herbivore species per unit area, but for some reason, successful colonisation occurred more frequently in certain thistle genera. However, if the thistle species within a genus were themselves generalists, and occurred in more habitats than thistles in another genus, which had more specific habitat requirements, then the plant genera would be expected to accumulate herbivores at different frequencies.

These differences in herbivore accrual frequencies may also be linked to plant quality. Certain plant taxa may be more difficult to colonise than others if they possess novel biochemical or mechanical defences that are usually associated with taxonomically isolated taxa (Janzen 1968, 1973, Lawton & Price 1979). Taxonomically isolated plants are expected to be colonised more slowly because the unadapted insect herbivores cannot cope with their unusual biochemical defences (Connor et al. 1980, Moran & Southwood 1982, Southwood et al. 1982). Thus taxonomically isolated plants are expected to have impoverished faunas (Strong et al. 1984). The species richness of herbivore communities from Carduus, Centaurea and Cirsium species in Europe are not depauperate when compared to communities on other thistles in Europe. Nor are these plant genera taxonomically isolated because each has more than 40 sympatric congenerics. The most parsimonious explanation to account for differences in herbivore accrual frequencies between insect herbivore communities on Carduus, Centaurea and Cirsium, is that these genera are each slightly different, possibly in their secondary compounds. This hypothesis can be tested by experiments to determine whether the thistle genus with the lowest herbivore accrual frequency is indeed the least palatable to insect herbivores. There are many difficulties in interpreting the results of such analyses. For example, a study by Wratten et al. (1981) of the palatability of leaves from nine species of British trees found that the least palatable trees supported the largest numbers of herbivore species. However, Wratten et al. (1981) measured palatability with snails, which may be less sensitive to secondary compounds than insect herbivores.

The differences in species richness found in the herbivore communities in the flower-heads of Carduus, Centaurea and Cirsium demonstrates how slight taxonomic differences between plant groups can lead to differences between their associated herbivore communities. However, this does not explain why the species richness of herbivore communities from Berkheya and Californian thistle flower-heads, two allopatric and very distantly related plant taxa, are similar and this will be discussed further in a later section.

9.1.2 Specialist and generalist species

In insect herbivore communities from the flower-heads of European thistles, the number of specialist and generalist species correlated positively with host plant range but the number of generalist species accrued more rapidly than specialist species (Figs 6.4 and 6.5). In herbivore communities from the flower-heads of Berkheya and Californian thistles, the number of specialist species was not related to plant range, but the number of generalist species did correlate with plant range. Because of the different accrual frequencies, in the herbivore communities on European thistle flower-heads, there was a change in the proportion of specialist species which ranged from more than 50% in communities associated with thistle species with small ranges, to less than 40% in thistle species with large ranges. These results are consistent with the hypothesis that the recruitment of specialist species, like gall formers and miners, is much slower than for generalist species (Lawton & Schröder 1978, Lawton & Price 1979, Strong 1979, Kogan 1981).

Herbivore communities in Berkheya flower-heads were the only communities in which species numbers, and generalist species numbers in particular, increased with flower-head size (Fig. 7.3). In herbivore communities on European thistles, several monophagous and oligophagous species, especially in the genera Larinus, Urophora, and Terellia, showed a preference for host plants which had flower-heads that corresponded to their body size ie. small herbivore species colonised thistle species with small flower-heads and large herbivore species colonised thistle species with large flower-heads (Zwölfer 1982a, 1987).

Specialist species numbers were not influenced by taxonomic isolation of the host plant (Fig. 8.2a). However, more generalist species were found on plant species with many sympatric congeneric species than on plant species that were taxonomically isolated (Fig. 8.2b). Obviously, host shifts by generalist herbivore species are simpler because they are generalists and can contend with a variety of secondary compounds. Specialist species, by definition, cannot change host plants easily.

The role of plant secondary compounds in the evolution of host specificity in insect herbivores has received much attention (Ehrlich & Raven 1964, Feeny 1976, Levins & MacArthur 1969, Cates 1980, Rhoades & Cates 1976, Futuyma et al. 1984, Dethier 1954, Bernays & Chapman 1978, Thompson 1982, 1986). Factors other than plant secondary compounds are also considered to be important in the evolution of herbivore specialisation, for example, morphological adaptations by herbivores (Kennedy 1986, Lee et al. 1986), behavioural adaptations (Wiklund 1982, Futuyma 1983), and pressure from natural enemies (Gilbert & Singer 1975, Smiley 1978, Lawton 1978, Smiley & Wisdom 1985). At present there is much debate about the relative importance of different selective pressures with some researchers placing emphasis on the role of plant secondary compounds (egs Ehrlich & Murphy 1988, Shultz 1988, Thompson 1988) while others emphasise the role of natural enemies (Bernays & Graham 1988).

Bernays & Moran (in press) have suggested a scheme for the evolution of herbivore specialisation. In essence, specialist species are supposed to evolve gradually from generalist species. Specialisation is meant to occur in response to intense mortality factors (natural enemies and possibly weather), so that plant species where the highest mortality occurs are avoided by the herbivores in favour of those plant species where mortality factors are lowest. As the herbivore becomes more specialised, so do their natural enemies which can use host plant secondary compounds to locate the herbivores. Some support for this scheme of Bernays & Moran (in press) is provided by Larinus species that specialise on Berkheya flower-heads. These Larinus species are parasitised by the braconid P. bilobata which has itself specialised, and parasitises only Larinus species associated with Berkheya flower-heads (J.S. Donaldson pers. comm.). Unfortunately, the parasitoids of the other herbivore species could not be determined, so it is not possible to know whether these parasitoids of herbivore generalists are themselves generalists as predicted by Bernays & Moran (in press).

9.1.3 Endophagous and ectophagous species

Generally, herbivore communities from the flower-heads of European thistles had a larger proportion of endophagous species than was found in the communities from Berkheya and Californian thistles (Fig. 6.9). This was partly because the accrual of endophagous species was higher, per unit area of plant range, in communities from European thistles, than in those from Berkheya and Californian thistles (Fig. 6.7). The recruitment of ectophagous species was greater in communities from Berkheya and

Californian thistles than in those from European thistles (Fig. 6.8).

Taxonomic isolation of the host plant also appeared to affect the number of endophagous and ectophagous species. Insect herbivore communities that had many endophagous or ectophagous species were all from plant species that had more than 40 congeneric species (Fig. 8.3).

These results did not suggest an obvious reason for the differences between the communities from European thistles and those from Berkheya and Californian thistles. One possible, but not very compelling reason, might be that endophagous species were favoured in Europe because the climate is more severe than that found in California and South Africa which have warmer climates; ectophagous species may be more vulnerable to harsher environmental conditions. For example, ectophagous species, like Hemiptera, were present on the other vegetative parts of the European thistles (Zwölfer 1965), but they formed only a small proportion of the insect herbivore community (Lawton & Schröder 1978).

9.1.4 Taxonomic and guild composition

The most obvious differences between the insect herbivore communities from the flower-heads of Berkheya, Californian thistles and European thistles was in the kinds of insects in the communities and in the way these insects utilised the flower-heads. Generally, the herbivore communities from Berkheya and Californian thistles were most similar to each other and both were different from the herbivore communities on European thistle flower-heads. The most noticeable differences were the absence of Hemiptera, Hymenoptera and gall formers, were most affected by these secondary plant compounds, and had more restricted plant ranges.

When the insect genera that comprised the herbivore communities were compared, the communities from Berkheya and European thistles had more in common with each other than with communities from Californian thistles. This was due to Larinus and Urophora that were present in communities from Berkheya and Californian thistles. These genera, especially Larinus, provide additional evidence for the hypothesis that Berkheya evolved from the European thistles (see chapter 2 and chapter 5).

Plants have clearly had considerable effects on the insect herbivore communities from the flower-heads of Berkheya and thistles. In the next section these aspects are examined to determine how they may have influenced the evolution of these herbivore communities.

9.2 Evolution of the insect herbivore communities in the flower-heads of Berkheya and thistles

According to Zwölfer (1979a), competition is a major evolutionary driving force in thistle flower-head herbivore communities. He identified two types of strategies by which insect herbivores survive in thistle flower-heads; by avoiding competition or by maximising their competitive capacity. Competition could be avoided by utilising different niches (Zwölfer 1979a), by selecting different host plant species (Zwölfer 1985), or by altering the time of larval development (see table 3 in Zwölfer 1979a). An insect's competitive ability could be maximised by specialising to exploit the resource more efficiently, eg. Urophora solstitialis may prevent competition by destroying surplus food (Zwölfer 1979a).

Connell (1980) discussed the difficulties involved in identifying where competition has been important in structuring the community. There are several difficulties in identifying competition as a selective pressure in the evolution of the herbivore communities on thistles.

Firstly, niche differentiation is not sufficient to show that competition has occurred (Connell 1980) and herbivore species may exploit different niches or colonise flower-heads at different times simply because they are different species. In herbivore communities on Berkheya flower-heads, interspecific competition is unlikely to occur. A study of the main endophagous species in B. decurrens flower-heads showed that because these herbivore species have an aggregated distribution, the chance of them competing for food is reduced, even though they share the same resource (chapter 4). These results can be related to the simulation model of Shorrocks & Rosewell (1986) which predicts that the guild size can be increased if the species (they used drosophilids as an example) living on a divided and ephemeral resource have an aggregated distribution. The aggregated distribution reduces the chance that the species might encounter the same resource, especially if much of the resource is unexploited. Alternative hypotheses other than competition, like 'enemy free space' may also explain phenomena often attributed to interspecific competition (Askew 1961, Gilbert & Singer 1975, Lawton & Strong 1981, Jeffries & Lawton 1984).

Secondly, there are many empty niches present in the herbivore flower-head communities of European thistles (chapter 5) (Lawton 1982). The flower-heads of Berkheya, Californian thistles and European thistles are morphologically similar and therefore present approximately the same number of niches to insect herbivores. The guild of sap suckers is not part of the European thistle communities, and the guild of external chewers comprises few species on European thistles (chapter 5). A similar situation was found in the herbivore community of bracken fern where several empty niches exist in communities from many regions around the world (Lawton 1982).

Thirdly, the species-area recruitment curve (Fig. 6.1) suggests that the flower-heads of most of the European thistles can still be colonised by more herbivore species. It is not competition for resources that is excluding colonisers, rather it is because these thistles have small ranges and are encountered by fewer potential colonisers. This hypothesis is consistent with the pool-exhaustion model of Lawton & Strong (1981) which would suggest that if the plant species expanded their range, more herbivore species would colonise them. . Thistle species with small ranges can still support more herbivore species but the pool of potential colonists within their range has been exhausted.

If competition was important in the evolution of Berkheya and thistle flower-head communities, then similar communities should have evolved in California, Europe and South Africa, but no convergence has occurred. Bracken fern again provides an instructive example (Lawton 1982, 1983b). There was no evidence for strong competition for resources, between herbivore species, in Berkheya flower-heads, nor is there any indication that competition occurred in the past (chapter 4), although this was not tested critically (Connell 1980). The results presented in this thesis provide support for the importance of species pools in the evolution of herbivore communities. The three groups studied were in three different geographic regions and each region had its own pool of potential colonisers. The species in these pools differed between the regions, which probably accounts for the differences between the communities.

Why were the communities on Berkheya and Californian thistles so similar? As discussed before, this question is difficult to answer. A possible explanation may be the large number of generalist species found in these communities. Generalists can colonise easily and can immigrate from a large range of distantly related or unrelated plant species. The insect herbivore communities on the flower-heads of European thistles comprised more specialist species and fewer generalist species (chapter 6). Specialist species are slow to colonise new host plant species and appear unable to switch host plants easily (chapter 8). The higher diversity of thistles in Europe than thistles in California and Arctoteae (Berkheya) in South Africa (Fig. 2.8) may explain why specialist herbivore species are more common in herbivore communities in Europe.

The relative scarcity of specialist species in the herbivore communities associated with the flower-heads of Berkheya and Californian thistles, when compared to the communities associated with European thistle flower-heads, suggests that the two former groups are younger in evolutionary terms than the European thistles and that their herbivore communities are also younger. This hypothesis is supported by the taxonomy and the distribution of the plants (chapter 2). However, Larinus has diversified in association with Berkheya in South principles examined in this thesis were, the effect, on herbivore communities, of host plant range (chapter 6), host plant architectural complexity (chapter 7), and host plant taxonomic isolation (chapter 8). Each principle influences community structure, but the relative 'strength' of the effects of these principles differs between herbivore communities. Even within herbivore communities, the effects were not constant and the relationship between plant range and the number of species in each insect order and guild is an example (Tables 6.5 and 6.6). Host plant effects were not constant, and only certain orders and guilds in herbivore communities associated with some plant genera were affected. Another example is flower-head size which correlated with herbivore species numbers only in communities associated with Berkheya. Thus, while it is possible to predict what may influence a herbivore community, it is not yet possible to predict to what extent a community will be affected.

This study has clearly indicated that it is not possible to predict accurately what herbivore communities will look like on plants in a particular area, based on knowledge from communities on similar plants in another area. This is because of differences in the species pools of potential colonisers between the two areas. Thus, the host plant-effects play a role in moulding the herbivore community, but the species pool of herbivore colonisers influences the final outcome of the interaction between insect herbivores and their host plants.

SUMMARY

1. The influence of the range, architectural complexity and taxonomic diversity of *Berkheya* and thistles on their insect herbivore communities associated with the flower-heads of these plants was investigated.

2. *Berkheya* and thistles are morphologically similar to each other. Geographical, morphological and biochemical evidence suggests that *Berkheya* evolved from the thistles indigenous to Europe.

3. The flower-heads of *Berkheya* species, *B. bipinnatifida*, *B. decurrens*, *B. heterophylla*, *B. onobromoides*, *B. rigida* and *Berkheya* sp were sampled in South Africa to identify their insect herbivores. Information on the insect herbviores associated with the flower-heads of European thistles and Californian thistles were obtained from the literature.

4. Number of insect herbivore species present on the flower-heads of each *Berkheya* species were: *B. heterophylla* 17 species, *B. onomobromoides* 14 species, *B. rigida* 14 species and *Berkheya* sp 12 species. The insect taxa represented were Coleoptera, Diptera, Lepidoptera and Hemiptera.

5. The guilds that were identified are external chewers, internal chewers and sap suckers. Internal chewers caused the most visible damage to the flower-heads but food did not appear to be a limiting factor in the communities. Interspecific competition did not appear to be important either because many 'refuges' were empty, each herbivore species tended to be aggregated and different herbivore

species co-occurred in less than 15% of the available flower-heads.

6. The insect herbivore communities that colonise the flower-heads of Berkheya, Californian thistles and European thistles were compared. A comparison of taxonomic composition, using classification and ordination, showed that Coleoptera, Diptera, Hymenoptera and Lepidoptera were represented in the herbivore communities from the flower-heads of European thistles. Coleoptera, Diptera, Hemiptera and Lepidoptera were represented in the communities from Berkheya and Californian thistle flower-heads.

7. The guild composition of herbivore communities from the flower-heads of Berkheya and Californian thistles were similar because each community comprised internal chewers, external chewers and sap suckers. Herbivore communities associated with the flower-heads of European thistles had a different guild composition that comprised internal chewers, external chewers and gall formers.

8. Plant range accounted for 43% of the variability in total herbivore species numbers from all herbivore communities. Species richness in communities from Berkheya and Californian thistle flower-heads was greater than in communities from European thistles with corresponding ranges.

9. Plant range was found to correlate with the proportion of specialist, generalist, endophage and ectophage species but the strength of these correlations differed between herbivore communities.

10. Flower-head size explained 86% of the variation in herbivore species numbers of Berkheya, but there was no such relationships on European thistles.

11. According to regression analyses, taxanomic isolation of the host plants had little effect on the insect herbivore communities. However, herbivore species numbers were highest in communities from plant genera with over 40 congenerics. Generalist species numbers were most affected by taxonomic isolation of the host plant.

12. Generally, the herbivore communities associated with Berkheya and Californian thistles were similar and differed from herbivore communities associated with European thistles.

13. Insect herbivore communities taken from plant tribes or families together may show no relationships when tested against certain variables, but communities on smaller plant groups, like genera, may show a significant relationship.

14. Plant range, architectural complexity and taxonomic isolation of the host plant all had an effect on the herbivore communities. However, host plant effects were not constant and the amount that each herbivore community was influenced differed widely between communities and between geographical regions.

REFERENCES

Askew, R.R. 1961. On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. Transactions of the Society for British Entomology. 14: 237-268.

Atkinson, W.D. & Shorrocks, B. 1981. Competition on a divided and ephemeral resource: a simulation model. Journal of Animal Ecology, 50: 461-471.

Atkinson, W.D. & Shorrocks, B. 1984. Aggregation of larval Diptera over discrete and ephemeral breeding sites: the implications for coexistence. American Naturalist, 124: 336-351.

Auerbach, M.J. & Hendrix, S.D. 1980. Insect-fern interactions: macrolepidopteran utilization and species-area association. Ecological Entomology, 5: 99-104.

Bentham, G. 1873. Notes on the classification, history and geographical distribution of Compositae. Journal of the Linnean Society, Botany, 13: 335-577.

Berenbaum, M. 1981. Effects of linear furanocoumarins on an adapted specialist insect (Papilio polyxenes). Ecological Entomology, 6: 345-351.

Bernays, E.A. & Chapman, R.F. 1978. Plant chemistry and acridoid feeding behaviour. In: Coevolution of Plants and Animals, pp. 100-141. Ed. J.B. Harborne. Academic Press, New York.

Bernays, E. & Graham, M. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology, 69: 886-892.

Bernays, E.A. & Moran, V.C. In press. Biological attributes of plant-feeding insects used to control alien weeds. In: Principles and Application of Biological Control. Ed. T.W. Fisher. UC Press, California.

Boldt, P.E. & DeLoach, C.J. 1985. Evaluating Rhinocyllus conicus (Coleoptera: Curculionidae) on Silybum marianum (Compositae) in Texas. Proceedings of the 6th International Symposium on Biological Control of Weeds, Vancouver, Canada, 1984, pp. 417-422. Ed. E.S. Delfosse. Agriculture, Canada, Ottawa.

Boldt, P.E., Kok, L.T. 1982. Bibliography of Rhinocyllus conicus Froel. (Col.: Curculionidae), an introduced weevil for the biological control of Carduus and Silybum thistles. Annals of the Entomological Society of America, 28: 355-358.

Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs, 27: 325-349.

Cameron, R.A.D. & Redfern, M. 1974. A simple study in ecological energetics using a gall-fly and its insect parasites. Journal of Biological Education, 8: 75-82.

Carlquist, A. 1976. Tribal interrelationships and phylogeny of the Asteraceae. Aliso, 8: 465-492.

Cates, R.G. 1980. Feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores: the effect of resource abundance and plant chemistry. Oecologia, 46: 22-31.

Claridge, M.F. & Wilson, M.R. 1981. Host plant associations, diversity and species-area relationships of mesophyll-feeding leafhoppers of trees and shrubs in Britain. Ecological Entomology, 6: 217-238.

Claridge, M.F. & Wilson, M.R. 1982. Insect herbivore guilds and species-area relationships: leafminers on British trees. Ecological Entomology, 7: 19-30.

Clifford, H.T. & Stephenson, W. 1975. An Introduction to Numerical Classification, Academic Press, New York.

Cody, M.L. & Diamond, J.M. (eds) 1975. Ecology and Evolution of Communities. Belknap press, Cambridge, Mass.

Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos, 35: 131-138.

Connor, E.F., Faeth, S.H., Simberloff, D. & Opler, P.A. 1980. Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. Ecological Entomology, 5: 205-211.

Connor, E.F. & McCoy, E.D. 1979. The statistics and biology of the species area relationship. American Naturalist, 113: 791-833.

Cornell, H.V. & Washburn, J.O. 1979. Evolution of the richness-area correlation for cynipid gall wasps on oak trees: a comparison of two geographic areas. Evolution, 33: 257-274.

Cronquist, A. 1955. Phylogeny and taxonomy of the Compositae. American Midland Naturalist, 53: 478-511.

Davis, D.R. 1967. A revision of the moths of the subfamily Prodoxinae (Lepidoptera: Incurvariidae). Bulletin-United States National Museum, 255: 1-170.

Dethier, V.G. 1954. Evolution of feeding preferences in phytophagous insects. Evolution, 8: 33-54.

Dittrich, M. 1977. Cynareae - systematic review. In: The Biology and Chemistry of the Compositae, II, pp 943-959. Eds Heywood, V.H., Harbourne, J.B. and Turner, B.L. Academic Press, London.

Downey, J.C. & Fuller, W.C. 1961. Variation in Plebejus icariodes (Lycaenidae). I. Foodplant specificity. Journal of the Lepidopteran Society, 15: 34-42.

Dugdale, J.S. 1975. The insects in relation to plants. In: Biogeography and Ecology in New Zealand, pp. 561-589. Ed. G. Kuschel. Monographiae Biologicae 27. Junk, The Hague.

Eastop, V.F. 1973. Deductions from the present day host plants of aphids and related species. Symposium of the Royal Entomological Society of London, 6: 157-177.

Ehrlich, P.R. & Murphy, D.D. 1988. Plant chemistry and host range in insect herbivores. Ecology, 69: 908-909.

Ehrlich, P.R. & Raven, P.H. 1964. Butterflies and plants: a study in coevolution. Evolution, 18: 586-608.

Feeny, P. 1976. Plant apparency and chemical defense. Recent Advances in Phytochemistry, 10: 1-40. Coevoultion, ed. J.B. Harbourne, pp. 163-206. Academic Press, London.

Field, J.G., Clarke, K.R. and Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series, 8: 37-52.

Field, J.G. & McFarlane, G. 1968. Numerical methods in marine ecology. I. A quantitative similarity analysis of rocky shore samples in False Bay, South Africa. Zoologia Africana., 3: 119-138.

Fox, L.R. & Morrow, P.A. 1981. Specialization: species property or local phenomenon? Science, 211: 887-893.

Futuyma, D.J. 1976. Food plant specialization and environmental predictability in Lepidoptera. American Naturalist, 110: 285-292.

Futuyma, D.J 1983. Evolutionary interactions among herbivorous insects and plants. In: Coevolution, pp. 207-231. Eds D.J. Futuyma & M. Slatkin. Sinauer, Sunderland, Massachusetts, USA.

Futuyma, D.J., Cort, R.F. & van Noordwijk, I. 1984. Adaptations to host plants in the fall cankerworm (Alsophila pometaria) and its bearing on the evolution of host affiliation in phytophagous insects. American Naturalist, 123: 287-296.

Gibbs Russell, G.E. (ed.) 1984. List of species of southern african plants. Memoirs of the Botanical Survey of South Africa, 48. Department of Agriculture, South Africa.

Gilbert, L.E. & Singer, M.C. 1975. Butterfly ecology. Annual Review of Ecology and Systematics, 6: 365-397.

Goeden, R.D. 1978. Initial analysis of Rhinocyllus conicus (Froelich) (Col.: Curculionidae) as an introduced natural enemy of milk thistle, Silybum marianum (L.) (Gaertner), and Italian thistle, Carduus pycnocephalus L., in southern California. In: Biological Control of Thistles in the Genus Carduus in the United States, ed. K.E. Frick, pp. 39-50. Stoneville, Miss: USDA.

Goeden, R.D. 1985. Host-plant relations of Trupanea spp. (Diptera: Tephritidae) in southern California. Proceedings of the Entomological Society of Washington, 87: 564-571.

Goeden, R.D. 1987. Host-plant relations of native Urophora spp. (Diptera: Tephritidae) in southern California. Proceedings of the Entomological Society of Washington, 89: 269-274.

Goeden, R.D. 1988. Gall formation by the capitulum-infesting fruitfly, Tephritis stigmatica (Diptera:

Tephritidae). Proceedings of the Entomological Society of Washington, 90: 37-43.

Goeden, R.D. & Ricker, D.W. 1977. Establishment of Rhinocyllus conicus (Col.: Curculionidae) on milk thistle in southern California. Weed Science, 25: 288-292.

Goeden, R.D. & Ricker, D.W. 1978. Establishment of Rhinocyllus conicus (Col.: Curculionidae) on Italian thistle in southern California. Environmental Entomology, 7: 787-789.

Goeden, R.D. & Ricker, D.W. 1986a. Phytophagous insect faunas of the two most common native Cirsium thistles, C. californicum and C. proteanum, in southern California. Annals of the Entomological Society of America, 79: 953-62.

Goeden, R.D. & Ricker, D.W. 1986b. Phytophagous insect faunas of two introduced Cirsium thistles, C. ochrocentrum and C. vulgare, in southern California. Annals of the Entomological Society of America, 79: 945-952.

Goeden, R.D. & Ricker, D.W. 1987a. Phytophagous insect faunas of the native thistles, Cirsium brevistylum, Cirsium congdonii, Cirsium occidentale, and Cirsium tioganum, in southern California. Annals of the Entomological Society of America, 80: 152-160.

Goeden, R.D. & Ricker, D.W. 1987b. Phytophagous insect faunas of native Cirsium thistles, C. mohavense, C. neomexicanum and C. nidulum, in the Mojave desert of southern California. Annals of the Entomological Society of America, 80: 161-175.

Goeden, R.D., Ricker, D.W. & Muller, H. 1987. Introduction, recovery, and limited establishment of Coleophora klimeschiella (Lepidoptera: Coleophoridae) on Russian thistles, Salsola australis, in southern California. Environmental Entomology, 16: 1027-1029.

Harnett, D.C. & Abrahamson, W.G. 1979. The effects of stem gall insects on life history patterns in Solidago canadensis. Ecology, 60: 910-917.

Harris, P. 1980. Establishment of Urophora affinis (Frfld.) and Urophora quadrifasciata (Meig.) (Diptera: Tephritidae) in Canada for the biological control of diffuse and spotted knapweed. Zeitschrift für Angewandte Entomologie, 89: 504-514.

Harris, P. 1986. Biological control of weeds. Fortschritte der Zoologie, 32: 123-138.

Herbst, J. 1987. Allozymanalyse bei der Gattung Larinus Germ. (Col. Curculionidae) als Hinweis auf Koevolution mit der Wirtspflanzen-Tribus Cardueae (Asteraceae). Verhandlungen Deutschen Zoologischen Gesellschaft, in press.

Heywood, Z.H. (ed.) 1978. Flowering Plants of the World. Oxford University Press, Oxford.

Holloway, J.D. & Herbert, P.D.N. 1979. Ecological and taxonomic trends in macrolepidopteran host plant selection. Biological Journal of the Linnean Society, 11: 229-251.

Holm, L.G., Plucknett, D.L., Pancho, J.V. & Herberger, J.P. 1977. The Worlds Worst Weeds, The University Press of Hawaii, Honolulu.

Howell, J.T. 1960. Cirsium. In: An illustrated flora of the Pacific states, 4: 514-538. Eds L.R. Abrams & R.S. Ferris. Stanford University, Stanford, California.

Janzen, D.H. 1968. Host plants as islands in evolutionary and contemporary time. American Naturalist, 102: 592-595.

Janzen, D.H. 1973. Host plants as islands. II. Competition in evolutionary and contemporary time. American Naturalist, 107: 786-790.

Jeffries, M.J. & Lawton, J.H. 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society, 23: 269-286.

Julien, M.H. 1982. Biological Control of Weeds. A World Catalogue of Agents and their Target Weeds. Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Kennedy, C.E.J. 1986. Attachment may be a basis for specialization in oak aphids. Ecological Entomology, 11: 291-300.

Knerer, G. & Atwood, C.E. 1973. Diprionid sawflies: polymorphism and speciation. Science, 179: 1090-1099.

Kogan, M. 1981. Dynamics of insect adaptations to soybean: impact of integrated pest management. Environmental Entomology, 10: 363-371.

Kok, L.T. & Pienkowski, R.L. 1985. Biological control of musk thistle by Rhinocyllus conicus Froel. (Col.: Curculionidae) in Virginia from 1969 to 1980. Proceedings of the 6th International Symposium on the Biological Control of Weeds, Vancouver, Canada, 1984, pp. 433-438. Ed. E.S. Delfosse. Agriculture Canada, Ottawa.

Kok, L.T. & Surles, W.W. 1975. Successful biocontrol of musk thistle by an introduced weevil, Rhinocyllus conicus. Environmental Entomology, 4: 1025-1027.

Kruskal, J.B. 1964. Multidimensional scaling by optimising goodness of fit to a non-metric hypothesis. Psychometrica, 29: 1-27.

Kruskal, J.B. 1977. Multidimensional scaling and other methods for discovering structure. In: Statistical Methods for Digital Computers. Eds Enslein, Ralston & Wilf. John Wiley, New York.

Kruskal, J.B. & Wish, M. 1978. Multidimensional Scaling, Sage Publications, Beverly Hills, California.

Lalonde, R.G. & Shorthouse, J.D. 1984. Developmental morphology of the gall of Urophora cardui (Diptera: Tephritidae) in the stems of Canada thistle (Cirsium arvense). Canadian Journal of Botany, 62: 1372-1384.

Lawton, J.H. 1976. The structure of the arthropod community on bracken. Botanical Journal of the Linnean Society, 73: 187-216.

Lawton, J.H. 1982. Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. Journal of Animal Ecology, 51: 573-595.

Lawton, J.H. 1983a. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology, 28: 23-29.

Lawton, J.H. 1983b. Non-competitive populations, non-convergent comunities, and vacant niches: the herbivores on bracken. In: A New Ecology: Novel Approaches to Interactive Systems. Eds P.W. Price, C.N. Slobodchikoff & W.S. Gaud. John Wiley & Sons, New York.

Lawton, J.H. & Price, P.W. 1979. Species richness of parasites on hosts: agromyzid flies on the British Umbelliferae. Journal of Animal Ecology, 48: 619-637.

Lawton, J.H. 1978. Host-plant influences on insect diversity: the effects of space and time. Symposium of the Royal Entomological Society London, 9: 105-125.

Lawton, J.H. & Schröder, D. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature (London), 265: 137-140.

Lawton, J.H. & Schröder, D. 1978. Some observations on the structure of phytophagous insect communities: the implications for biological control. Proceedings of the IVth International Symposium on Biological Control of Weeds, Gainesville, Florida, pp. 57-73. University of Florida.

Lawton, J.H. & Strong, D.R.Jr. 1981. Community patterns and competition in folivorous insects. American Naturalist, 118: 317-338.

Lee, Y.I., Kogan, M. & Larsen, J.R. 1986. Attachment of the potato leafhopper to soybean plant surfaces as affected by morphology of the pretarsus. Entomologia Experimentalis et Applicata, 42: 101-108.

Lessing, C.F. 1832. Synopsis generum Compositarum. Berolini.

Levins, R. & MacArthur, R.H. 1969. A hypothesis to explain the incidence of monophagy. Ecology, 50: 910-911.

MacArthur, R.H. 1972. Geographical Ecology. Patterns in the Distribution of Species. Harper & Row, New York.

Maw, M.G. (ed.) 1984. Biological Control of Weeds (1984). An Update of Julien's World Catalogue of Agents and their Target Weeds. Agriculture Canada, Regina, Saskatchewan.

May, R.M. (ed.) 1981. Theoretical Ecology. Blackwell Scientific Publications, Oxford.

May, R.M. 1975. Deterministic models with chaotic dynamics. Nature, (London), 256: 165-166.

Moore, R.J. & Frankton, C. 1974. The Thistles of Canada, Monograph No. 10, Canada Department of Agriculture, Ottawa.

Moran, V.C. 1980. Interactions between phytophagous insects and their Opuntia hosts. Ecological Entomology, 5: 153-164.

Moran, V.C. & Southwood, T.R.E. 1982. The guild composition of arthropod communities in trees. Journal of Animal Ecology, 51: 289-306.

Munro, H.K. 1926. Biological notes on the South African Trypaneidae (Trypetidae: Fruit-flies). II. Entomological Memoir, Department of Agriculture, Union of South Africa, 5: 17-40.

Neuvonen, S. & Niemela, P. 1981. Species richness of macrolepidoptera on Finnish trees and shrubs. Oecologia, 51: 364-370.

Niemela, P., Tahvainen, J., Sorjonen, J., Hokkanen, T. & Neuvonen, S. 1982. The influence of host plant growth form and phenology on the life strategies of Finnish macrolepidopterous larvae. Oikos, 39: 164-170.

Norlindh, T. 1977. Arctoteae - systematic review. In: The Biology and Chemistry of the Compositae, pp. 943-

959. Eds V.H. Heywood, J.B. Harborne, & B.L. Turner. Academic Press, London.

Price, P.W. 1977. General concepts on the evolutionary biology of parasites. Evolution, 31: 405-420.

Price, P.W. 1980. Evolutionary Biology of Parasites. Princeton University Press, Princeton, New Jersey.

Price, P.W. 1983. Alternative paradigms in community ecology. In: A New Ecology: Novel approaches to interactive Systems, pp. 353-383. Eds P.W. Price, C.N. Slobodchikoff & W.S. Gaud. John Wiley & Sons, New York.

Prokopy, R.J. 1981. Epideictic pheromones influencing spacing patterns of phytophagous insects. In: Semiochemicals: Their Role in Pest Control. Eds, D.A. Norlund, R.L. Jones & W.J. Lewis. John Wiley & Sons, New York.

Rausher, M.D. 1979. Egg recognition: its advantage to a butterfly. Animal Behaviour, 27: 1034-1040.

Redfern, M. 1983. Insects and Thistles. Cambridge University Press, Cambridge.

Redfern, M. & Cameron, R.A.D. 1985. Density and survival of Urophora stylata (Diptera: Tephritidae) on Cirsium vulgare (Compositae) in relation to flower head and gall size. Proceedings of the 6th International Symposium on Biological Control of Weeds, Vancouver, Canada, 1984, pp. 453-477. Ed. E.S. Delfosse, Agriculture Canada, Ottawa.

Rey, J.R. 1981. Ecological biogeography of arthropods on Spartina islands in northwest Florida. Ecological Monographs, 51: 237-265.

Rhoades, D.F. & Cates, R.G. 1976. Towards a general theory of plant antiherbivore chemistry. Recent Advances in Phytochemistry, 10: 168-213.

Root, R.B. 1973. Organisation of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). Ecological Monographs, 43: 95-124.

Scholtz, C.H. & Holm, E. (eds) 1985. Insects of Southern Africa. Butterworths, Durban.

Schröder, D. 1980. The biological control of thistles. Biocontrol News and Information, 1: 9-26.

Schultz, J.C. 1988. Many factors influence the evolution of herbivore diets, but plant chemistry is central. Ecology, 69: 896-897.

Seifert, R.P. & Seifert, F.H. 1976. A community matrix analysis of Heliconia insect communities. American Naturalist, 110: 461-483.

Seifert, R.P. & Seifert, F.H. 1979. A Heliconia insect community in a Venezuelan cloud forest. Ecology, 60: 462-467.

Shepard, R.N. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. Psychometrica, 27: 125-140.

Shorrocks, B. & Rosewell, J. 1986. Guild size in drosophilids: a simulation model. Journal of Animal Ecology, 55: 527-541.

Shorrocks, B., Rosewell, J., Edwards, K. & Atkinson, W.D. 1984. Interspecific competition is not a major organizing force in many insect communities. Nature, (London), 310: 310-312.

Simberloff, D.S. 1976. Experimental zoogeography of islands: Effects of island size. Ecology, 57: 629-648.

Simberloff, D.S. 1978. Colonisation of islands by insects: immigration, extinction and diversity. Symposium of the Royal Entomological Society of London, 9: 139-153.

Singer, M.C. 1971. Evolution of food-plant preference in the butterfly Euphydryas editha. Evolution, 25:383-389.

Slansky, F. Jr 1976. Phagism relationships among butterflies. Journal of the New York Entomological Society, 84: 91-105.

Smiley, J.T. 1978. Plant chemistry and the evolution of host specificity: new evidence from Heliconius and Passiflora. Science, 201: 745-747.

Smiley, J.T. & Wisdom, C.S. 1985. Determinants of growth rate on chemically heterogenous host plants by specialist insects. Biochemical Systematics and Ecology, 13: 305-312.

Southwood, T.R.E. 1960. The abundance of the Hawaiian trees and the number of their associated insect species. Proceedings of the Hawaiian entomological Society, 17: 299-303.

Southwood, T.R.E. 1961a. The numbers of species of insect associated with various trees. Journal of Animal Ecology, 30: 1-8.

Southwood, T.R.E. 1961b. The evolution of the insect-host tree relationship - a new approach. Proceedings of the XIth International Congress on Entomology, Vienna 1960, pp. 651-654.

Southwood, T.R.E. 1978. Ecological Methods. Second edition. John Wiley & Sons, New York.

Southwood, T.R.E., Brown, V.K. and Reader, P.M. 1979. The relationships of plant and insect diversities in succession. Biological Journal of the Linnean Society, 12: 327-348.

Southwood, T.R.E., Moran, V.C. & Kennedy, C.E.J. 1982. The richness, abundance and biomass of the arthropod communities on trees. Journal of Animal Ecology, 51: 635-649.

Steck, G.J. 1984. Chaetstomella undosa (Diptera: Tephritidae) biology, ecology and larval description. Annals of the Entomological Society of America, 77: 669-678.

Strong, D.R. Jr 1977. Insect species richness: hispine beetles on Heliconia latispatha. Ecology, 58: 573-582.

Strong, D.R. Jr 1979. Biogeographic dynamics of insect-host plant communities. Annual Review of Entomology, 24: 89-119.

Strong, D.R., Lawton, J.H. and Southwood, T.R.E. 1984. Insects on Plants. Community Patterns and Mechanism. Blackwell Scientific Publications, Oxford, London.

Strong, D.R. & Levin, D.A. 1979. Species richness of plant parasites and growth form of their hosts. American Naturalist, 114: 1-22.

Thompson, J.N. 1978. Within-patch structure and dynamics in *Pastinaca sativa* and resource availability to a specialized herbivore. Ecology, 59: 443-448.

Thompson, J.N. 1982. Interaction and Coevolution, John Wiley & Sons, New York.

Thompson, J.N. 1986. Patterns in coevolution. In: Patterns in Coevolution, pp. 119-143. Eds A.R. Stone & D.L. Hawksworth. Clarendon, Oxford.

Thompson, J.N. 1988. Coevolution and alternative hypotheses on insect/plant interactions. Ecology, 69: 893-895.

Turner, B.L. 1977. Fossil history and geography. In: The Biology and Chemistry of the Compositae, pp. 21-39. Eds V.H. Heywood, J.B. Harborne, & B.L. Turner. Academic Press, London.

Tutin, T.G., Heywood, V.H., Burgess, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. and Webb, D.A. (eds). 1976. Flora Europaea, 4. Plantaginaceae to

Compositae (and Rubiaceae). Cambridge University Press, Cambridge. 505 pp.

Valadon, L.R.G. 1977. Arctoteae and Calenduleae - chemical review. In: The Biology and Chemistry of the Compositae, eds, V.H. Heywood, J.B. Harborne, B.L. Turner, pp. 989-998. London: Academic, 1189 pp.

Varley, G.C. 1947. The natural control of the population balance of the knapweed gall-fly (Urophora jaceana). Journal of Animal Ecology, 16: 139-187.

Vinson, S.B. 1976. Host selection by insect parasitoids. Annual Review of Entomology, 21: 109-133.

Wagenitz, G. 1976. Systematics and phylogeny of the Compositae (Asteraceae). Plant Systematics and Evolution, 125: 29-46.

Wiklund, C. 1982. Generalist vs. specialist utilization of host plants among butterflies. In Proceedings of the Fifth International Symposium on Insect-Plant Relationships, pp. 181-191. Eds J.H. Visser & A.K. Minks. Pudoc, Wageningen, The Netherlands.

Williams, C.B. 1964. Patterns in the Balance of Nature, Academic Press, New York.

Wratten, S.D., Goddard, P. & Edwards, P.J. 1981. British trees and insects: the role of palatibility. American Naturalist, 118: 916-919.

Zwölfer, H. 1965. Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) in Europe. Commonwealth Institute of Biological Control. Technical Bulletin, 6: 81-153.

Zwölfer, H. 1979a. Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls. Symposium on Population Ecolology, Mainz, 1978. Fortschritte Zoologie. 25: 331-352.

Zwölfer, H. 1979b. Alternative Wettbewerbsstrategien bei koexistierenden Eurytoma-Arten (Hymenoptera: Eurytomidae). Verhhandlungen der Deutschen Zoologischen Gesellschaft, 72: 256.

Zwölfer, H. 1980. Distelblütenköpfe als ökologische Kleinsysteme: Konkurrenz und Koexistenz in Phytophagenkomplexen. Mitteilungen der Deutschen Gessellschaft fuer Allgemeine Angewandte Entomologie., 2: 21-37.

Zwölfer, H. 1982a. Patterns and driving forces in the evolution of plant-insect systems. Proceedings of the Fifth International Symposium on Insect-Plant Relationships, pp. 287-296. Ed. J.H. Visser, A.K. Minks. Pudoc, Wageningen, The Netherlands.

Zwölfer, H. 1982b. Das Verbreitungsareal der Bohrfliege Urophora cardui L. (Dipt.: Trypetidae) als Hinweis auf die ursprünglichen Habitate der Ackerdistel Cirsium arvense (L.), Verhandlungen Deutschen Zoologischen Gesellschaft, 75: 298.

Zwölfer, H. 1984. Zur geographischen Differenzierung von Wirtspflanzenspektren bei phytophagen Insekten. Verh. 10te Int. Symp. Entomofaun. Mitteleur., Budapest, 1983, pp. 1-4. State Museum of Natural History, Budapest.

Zwölfer, H. 1985. Insects and thistle heads: resource utilization and guild structure. Proceedings of the 6th International Symposium on Biololgical Control of Weeds, Vancouver, Canada, 1984, pp. 407-416. Ed. E.S. Delfosse. Agriculture Canada, Ottawa.

Zwölfer, H. 1986. Insektenkomplexe and Distein-ein Modell für die Selbstorganisation ökologischer Kleinsysteme. In: Selbstorganisation-Zur Bedeutung eines neuen disziplinenübergreifenden Paradigmas für die Einzelwissenchaften, pp. 181-217. Eds A. Dress, H. Hendrichs & G. Kuppers. Piper-Verlag, Munich.

Zwölfer, H. 1987. Species richness, species packing, and evolution in insect plant systems. Ecological Studies, 61: 301-319.

Zwölfer, H. 1988. Evolutionary and ecological relationships of the insect fauna of the insect fauna of thistles. Annual Review of Entomology, 33: 103-122.

Zwölfer, H., Frick, K.E. & Andres, L.A. 1971. A study of the host plant relationships of European members of the genus Larinus (Col.: Curculionidae). Technical Bulletin of the Commonwealth Institute of Biological Control. 13: 97-143.

REFERENCES
(added after examination)

Goeden, R.D. 1974. Comparative survey of the phytophagous insect faunas of Italian thistle, Carduus pycnocephalus in southern California and southern Europe relative to biological weed control. Environmental Entomology, 5: 345-474.

Goeden, R.D. 1976. The Palearctic insect fauna of milk thistle, Silybum marianum, as a source of biological control agents for California. Environmental Entomology, 5: 345-353.

Moore, R.J. & Frankton, C. 1963. Cytotaxonomic notes on some Cirsium species of the western United States. Canadian Journal of Botany, 41: 1553-1567.

Steyskal, G.C. 1979. Taxonomic studies on fruit flies of the genus Urophora (Diptera : Tephritidae). Entomological Society of Washington.

Unruh, T.R. & Goeden, R.D. 1987. Electrophoresis helps to identify which race of the introduced weevil, Rhinocyllus conicus (Coleoptera: Curculionidae), has transferred to two native southern California thistles. Environmental Entomology, 16: 979-983.

APPENDIX 1

"Proc. VII Int. Symp. Biol. Contr. Weeds, 6-11 March 1988, Rome, Italy. Delfosse, E.S. (ed. Ist. Sper. Patol. Veg. (MPAF) (1988)"

A Comparison Between the Flower-Head Insect Communities of South African Berkheya and European Cynareae.

M.M. CLARK

Zoology Department, University of Cape Town, Rondebosch
7700, South Africa.

ABSTRACT

Plant morphological complexity is known to correlate, positively, with the number of insect herbivore species on individual plant species. Morphologically similar plant species are therefore expected to support similar numbers of herbivore species. To test this hypothesis, the insect herbivore communities feeding on the flower-heads of six Berkheya species, indigenous to South Africa, were compared to communities previously sampled on Cynareae species in Europe. The composite genus Berkheya, in the tribe Arctoteae, is morphologically similar to the tribe Cynareae, and is in the same family. Also, both Berkheya and Cynareae have species that are weeds. The survey showed that Berkheya flower-heads were colonised by more herbivore species than flower-heads of Cynareae with a similar geographical range. Numbers of generalist species correlated positively with the geographical range of the host plant species, but the number of specialist species colonising flower-heads followed no pattern and could therefore not be predicted. The taxonomic composition of the herbivore species on Berkheya and Cynareae differed significantly, but two insect genera,

appears to have diversified in association with Berkheya in southern Africa as it has on Cynareae in Europe. Larinus species are recommended for the biological control of Berkheya weeds because of their specificity. Significant differences in guild structure between the two groups was also observed. These differences in the herbivore communities appear to be due to their exposure to different herbivore species pools, as a result of their geographical separation.

INTRODUCTION

Flower-heads of thistles in the tribe Cynareae (Compositae) have a characteristic morphology and are easily recognised. In southern Africa, the genus Berkheya Ehrh. (Compositae) has a remarkably similar morphology to the Cynareae, and its species are also commonly known as "thistles". Berkheya is part of a separate composite tribe, the Arctoteae, which is almost entirely endemic to Africa (Norlindh 1977). A few Cynareae species are native while some other species are introduced in sub-saharan Africa, but most species are restricted to the Palaearctic region (Zwölfer 1988).

The morphological similarity of these two "thistle" groups, which are separated geographically, provides an opportunity to test current ecological theory about the influence of plant architecture on insect herbivore diversity. Lawton & Schröder (1977) proposed that as plants increase in size and structural complexity, so they support increasingly more diverse insect herbivore communities. Several examples demonstrate this relationship (Lawton 1983). A corollary of this hypothesis, is that morphologically similar plants should support similar numbers of insect herbivore species. The flower-heads of Berkheya thistles from southern Africa and of Cynareae thistles from Europe, which have similar geographical ranges, are therefore expected to support similar numbers of insect herbivore species.

Cynareae and Berkheya flower-heads, when closely examined, have some slight differences which may be used to differentiate between very similar species. However, on a larger scale they appear similar, with many structures characteristic of composite flower-heads in common (Fig. 1).

The herbivore communities of Berkheya and Cynareae were compared initially by determining the total number of herbivore species on each plant species so that the main similarities and differences between the communities could be identified. Then, to examine the herbivore communities in more detail, their taxonomic composition and guild structure was compared.

MATERIALS AND METHODS

Mature flower-heads were collected from six Berkheya species (B. bipinnatifida (Harv.), B. decurrens (Thunb.), B. heterophylla (Thunb.), B. onobromoides (DC.), B. sp and B. rigida (Thunb.)) found in the western and eastern Cape Province of South Africa. Flower-heads collected at each site were divided into two groups; one group was placed into an emergence box, the other group was frozen and dissected later. In the emergence boxes, adult insects, which had emerged from the flower-heads, were attracted by light to a tube at one end of the box where they could be collected. The flower head dissections provided more specific information about feeding preferences.

Zwölfer (1965) collected accurate data on the herbivores of 59 Cynareae species during a comprehensive survey of Europe for potential biological control agents. Information about the flower head herbivores was extracted from this survey and used in the comparison with Berkheya insect communities.

RESULTS AND DISCUSSION

Total herbivore species numbers

Flower-heads of Berkheya have more herbivore species than Cynareae flower-heads which have been sampled a similar number of times (Fig. 2). Sampling frequency was used because no accurate information is available on the geographical range of the European Cynareae. According to Lawton & Schröder (1978), in their analysis of Zwölfer's (1965) data, in this example sampling frequency of the Cynareae does correlate with geographical range. Estimates of the area sampled for each Cynareae species, obtained from Zwölfer (1965), showed that those Cynareae sampled a similar number of times to the Berkheya species, had similar geographical ranges. The comparison of herbivore numbers could therefore be made using sampling frequency and not geographical range.

The larger number of herbivore species on Berkheya flower-heads is because there are more generalist species on these plants than on the Cynareae (Fig. 3). The number of generalist species increased positively with the number of samples collected. Few specialist species attacked the flower-heads of either group and the number of species did not correlate with sampling frequency (Fig.4). Each Berkheya species sampled had only one specialist herbivore species and numbers of specialist species on the Cynareae varied from nil to six.

Taxonomic composition

There are major differences in the herbivore taxa found on Berkheya and on Cynareae (Table 1). No Hemiptera were recorded on Cynareae flower-heads, although they were found on the stems and leaves (Zwölfer 1965). No phytophagous Hymenoptera were found on Berkheya flower heads, but three species were recorded from six Cynareae species. In addition, the proportions of the taxa differed between plant genera within the Cynareae.

Two genera, Larinus (Coleoptera: Curculionidae) and Urophora (Diptera: Trypetidae), occurred in both Berkheya and Cynareae flower-heads. The taxonomy of Larinus in southern Africa requires revision, but initial observations suggest that each of the six Berkheya species sampled is attacked by a different Larinus species. The close evolutionary association of Larinus with the Cynareae in Europe is already well documented (Zwölfer et al. 1971; Zwölfer 1988). It is therefore remarkable that, in addition to its association with the Cynareae, Larinus appears to have diversified in a similar association with Berkheya in southern Africa. A survey of other Berkheya species will show the extent of this association. Urophora agromyzella Bezzi is the only Urophora species found on the Berkheya species sampled. Records kept at the National Collection of Insects, Pretoria, indicate that U. agromyzella is a generalist and has been recorded from other distantly related composite species. These records also show that other Urophora species have been recorded from the Compositae, therefor this genus is not confined to Berkheya.

Guilds

Feeding preferences of insect herbivore species on Berkheya and on Cynareae flower-heads differed significantly (Fig. 5). Because no Hemiptera attack Cynareae flower heads they have no sap-sucking insects, a guild that comprises 18.2% of the herbivore species on Berkheya. The specialist gall forming species did not occur on Berkheya and this may reflect the low number of specialist feeders on this genus.

Each Berkheya species has only one species of internal chewer (Larinus) and external chewers and suckers form a large proportion of the herbivore species on these plants (Fig. 5). Strong et al. (1984) suggested that endophagous miners and gall formers colonise at a slower rate than external chewing and sucking species. If Strong et al. (1984) are correct, then the herbivore community on Berkheya may be younger, in evolutionary terms, than on Cynareae. The Arctoteae are closely related to the Cynareae and were previously included in this tribe (Norlindh 1977).

The Arctoteae are not as diversified as the Cynareae with about 194 species (Norlindh 1977) compared to about 2175 species (Tutin et al. 1976) respectively, which may mean that the Arctoteae is a younger group. However, it may also mean that there are fewer specialist species on Berkheya because the pool of potential colonisers is smaller in the Arctoteae than in the Cynareae.

CONCLUSIONS

Herbivore communities of Berkheya and Cynareae flower heads differed significantly, in spite of the morphological similarity of the flower heads. However, the hypothesis that morphologically similar flower-heads have similar insect herbivore communities does hold for herbivore communities within each group (Berkheya and Cynareae) which showed closer affinities. The main differences between these groups may be due to their geographical separation. The effect of the different numbers of plant species and the different habitats found in each area would have a major effect on the herbivore species pool available for colonisation.

Because the number of specialist species colonising flower-heads followed no pattern, it is not possible for biological control workers to predict specialist species numbers in advance to help with their planning. Larinus species appear to be the only good candidates for the biological control of Berkheya species that are weeds because of their close association with this plant genus.

ACKNOWLEDGEMENTS

I thank JH Hoffmann, VC Moran and JK Scott for their comments on the manuscript. This project was funded by the CSIR.

REFERENCES

Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. Ann. Rev. Ent. 28:23-9.

Lawton, J.H. and Schröder, D. 1978. Some observations on the structure of phytophagous insect communities: the implications for biological control. Proc. IV Int. Symp.Biol. Contr. Weeds, 30 August-2 September 1976, Gainsville, Florida. Freeman, T.E. (ed.). Univ. Florida, pp 57-73.

Norlindh, T. 1977. Arctoteae - systematic review. In: The Biology and Chemistry of the Compositae. II. Heywood, V.H., Harbourne, J.B. and Turner, B.L., (eds). Academic Press, London. pp 943-959.

Strong, D.R., Lawton, J.H. and Southwood, T.R.E. 1984. Insects on Plants. Community patterns and Mechanism. Blackwell Scientific Publications, Oxford. 313 p.

Tutin, T.G., Heywood, V.H., Burgess, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. and Webb, D.A. (eds). 1976. Flora Europaea. Volume 4. Plantaginaceae to Compositae (and Rubiaceae). Cambridge University Press, Cambridge. pp 505.

Zwölfer, H. 1965. Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) in Europe. Techn. Bull. Commonw. Inst. Biol. Control. 6:81-154.

Zwölfer, H. 1988. Evolutionary and ecological relationships of the insect fauna of thistles. A. Rev. Ent. 33:in press.

Zwölfer H., Frick, K.E. and Andres, L.A. 1971. A study of the host plant relationships of European members of the genus Larinus (Col.: Curculionidae). Commonw Inst. Biol. Control Techn. Bull. 13:97-143.

Table 1

Taxonomic composition of phytophagous insects that attack the flower-heads of Berkheya and selected genera of the Cynareae. Proportions are given in parentheses below the number of species.

	Number of species in each taxon				
Plant genus	Coleoptera	Lepidoptera	Diptera	Hemiptera	Hymenoptera
Berkheya	10	18	7	14	0
(6 species)	(0.20)	(0.37)	(0.14)	(0.29)	(0)
Arctium	1	3	3	0	0
(3 species)	(0.14)	(0.43)	(0.43)	(0)	(0)
Carduus	7	7	10	0	0
(8 species)	(0.29)	(0.29)	(0.42)	(0)	(0)
Cirsium	7	7	12	0	0
(15 species)	(0.27)	(0.27)	(0.46)	(0)	(0)
Onopordum	5	2	2	0	0
(2 species)	(0.56)	(0.22)	(0.22)	(0)	(0)
Centaurea	7	13	12	0	2
(16 species)	(0.21)	(0.38)	(0.35)	(0)	(0.06)
Carlina	2	4	1	0	0
(3 species)	(0.29)	(0.57)	(0.14)	(0)	(0)
Echinops	1	0	0	0	0
(2 species)	(1)	(0)	(0)	(0)	(0)

Fig. 1. A generalised cross section through the flower head of a Berkheya (A) and a Cirsium (B).

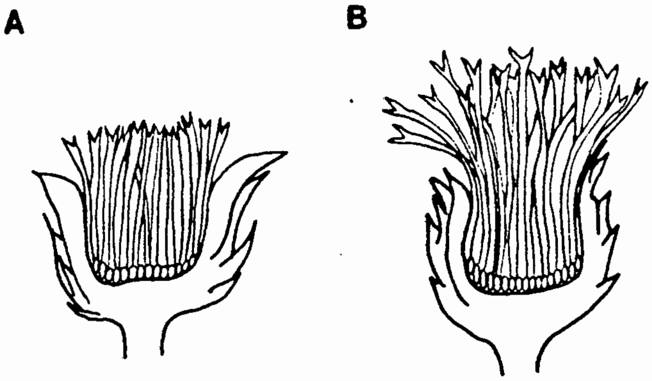


Fig. 2. Relationship between number of sites sampled and number of insect herbivores recorded on various species of Berkheya (open circles) and Cynareae (closed circles).

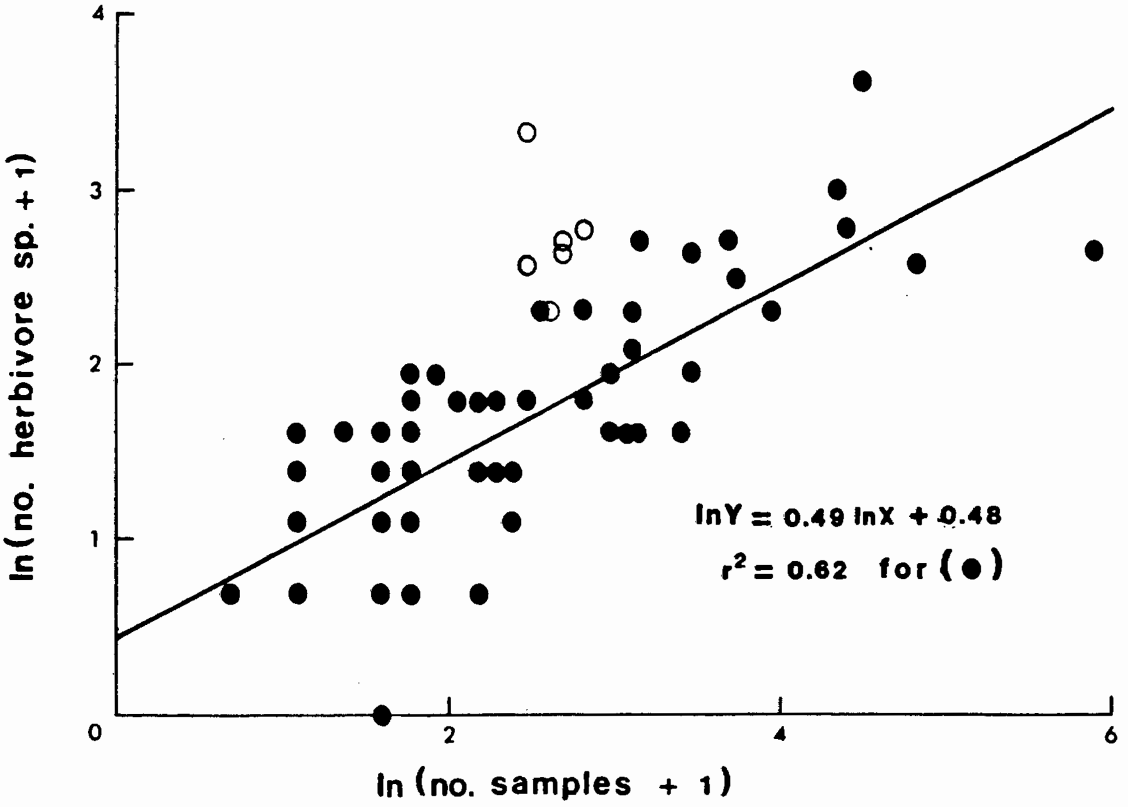


Fig. 3. Relationship between the number of sites sampled and the number of generalist herbivore species recorded on various species of Berkheya (open circles) and Cynareae (closed circles).

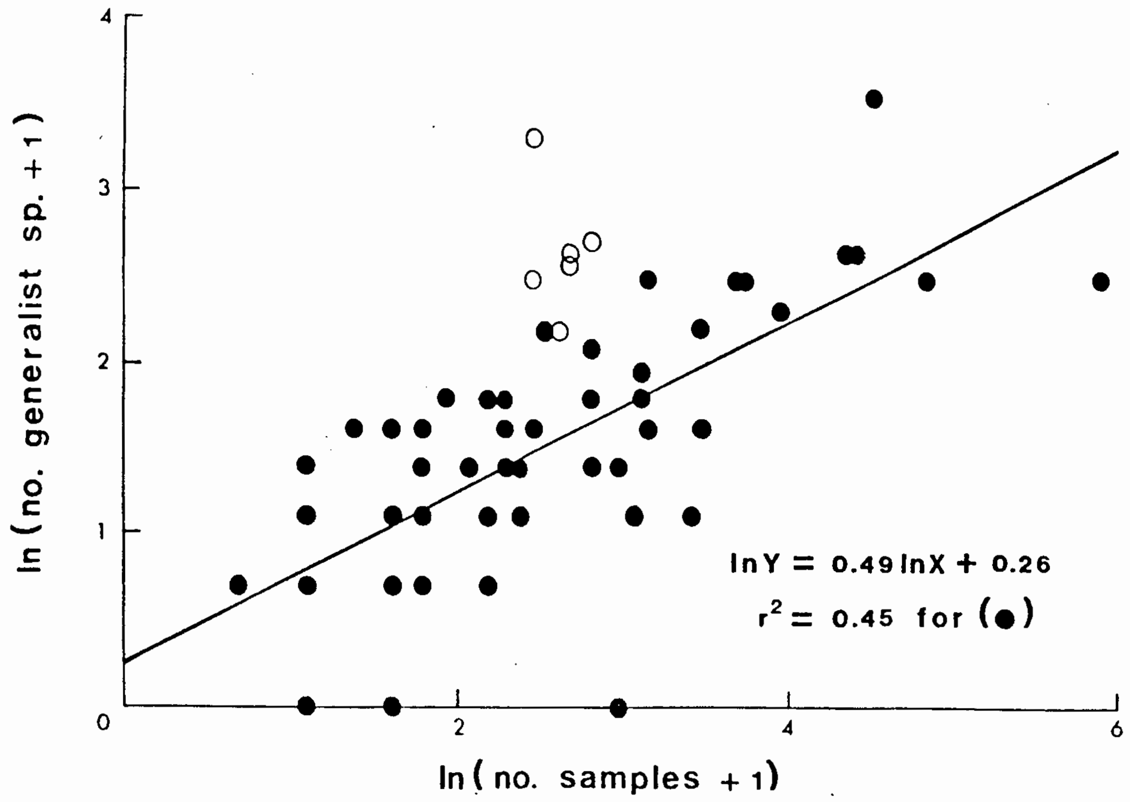


Fig. 4. Relationship between the number of sites sampled and the number of specialist herbivore species recorded on various species of Berkheya (open circles) and Cynareae (closed circles).

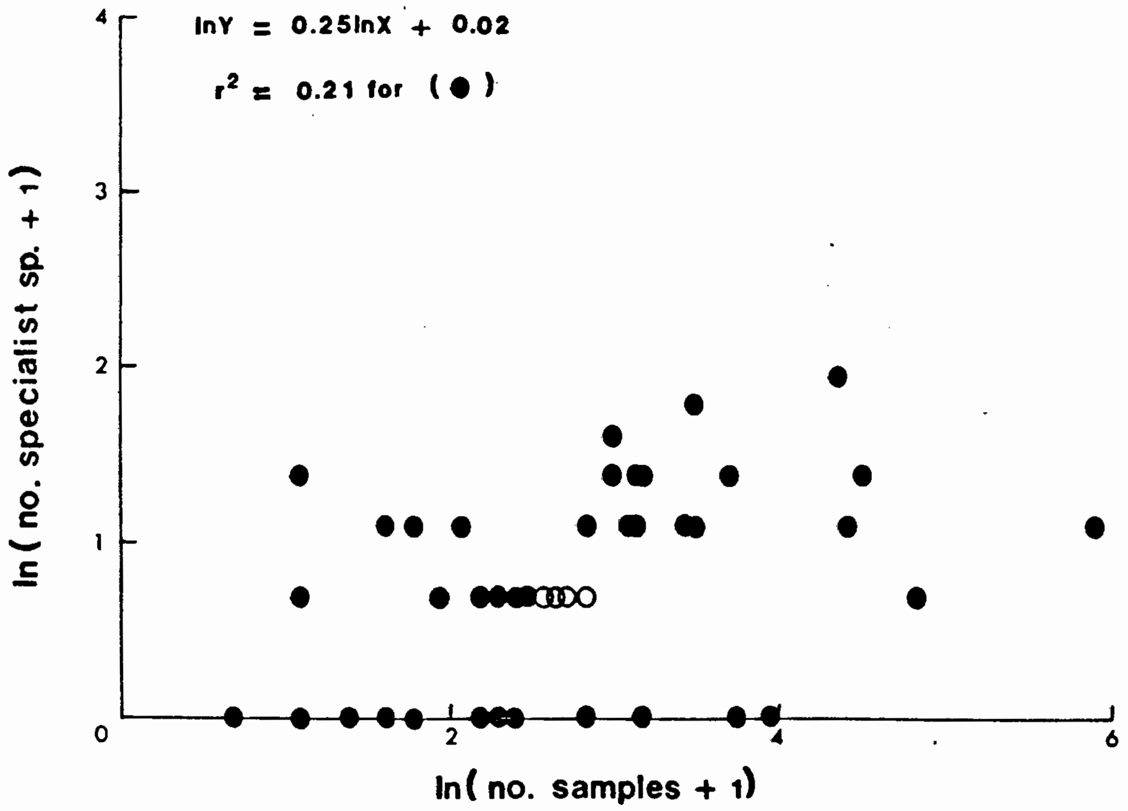
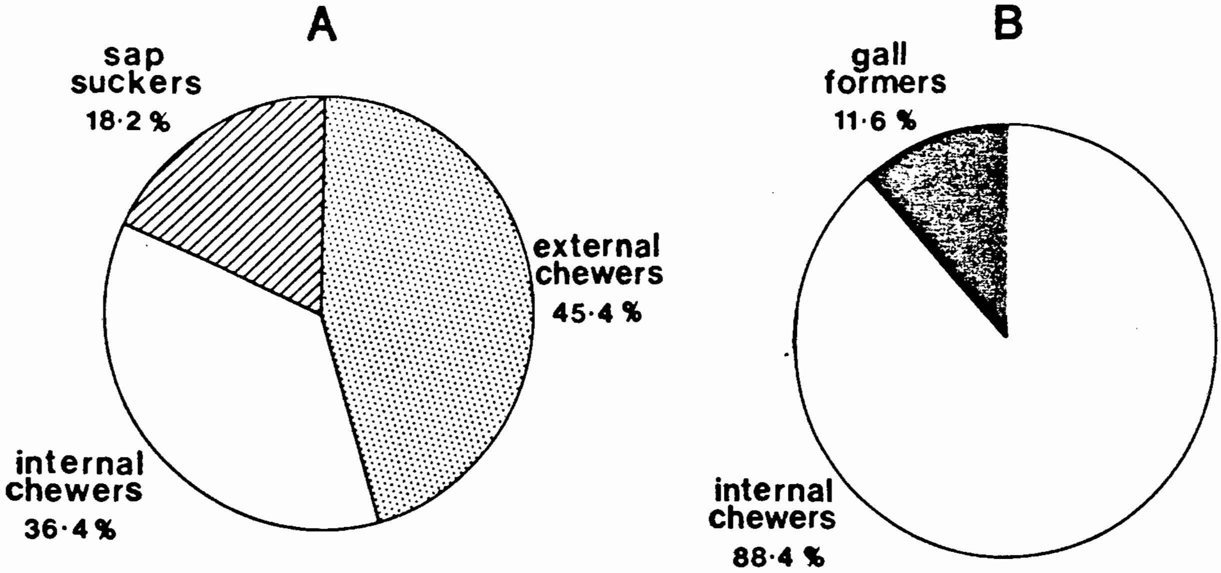


Fig. 5. Pie diagrams showing the relative proportions of the major guilds of herbivorous insects that attack the flower-heads of (A) <u>Berkheya</u> and (B) Cynareae.



APPENDIX 2

A comparison between the herbivore communities associated with the flower-heads of thistles introduced into South Africa, Berkheya endemic to South Africa and thistles endemic to Europe.

Abstract

1. Insect herbivore communities associated with introduced plant species differ markedly from the communities associated with these plants in their natural range. Herbivore communities associated with the flower-heads of two thistles, Carduus macrocephalus and Cirsium vulgare, introduced into South Africa, were compared to herbivore flower-head communities associated with Berkheya in South Africa, and with C. macrocephalus and C. vulgare in Europe.

2. Flower-heads of C. macrocephalus and C. vulgare were each sampled at 10 different sites in the eastern Cape.

3. Communities associated with the flower-heads of C. macrocephalus and C. vulgare in South Africa both comprised 14 generalist herbivore species, 10 of which also occurred on Berkheya flower-heads.

4. Total species richness was higher in the thistles introduced into South Africa than in the flower-heads of these thistles in their natural European range.

5. Communities from the introduced thistles comprised no specialist herbivore species. Proportion of endophagous species was lowest in communities from introduced thistles.

6. The pool of herbivore species in South Africa had a noticeable influence on the taxonomic and guild composition of communities on introduced thistles in South Africa. Communities on introduced thistles were colonised by Hemiptera which also formed the sap-sucking guild. Hemiptera are not present on the flower-heads of thistle species in their natural range in Europe.

Introduction

When plants are introduced into new regions they usually accumulate insect species different to those that colonise them in areas where they are endemic (Strong et al. 1984). Thus the insect herbivore communities associated with a plant species in its native region and in its region of introduction differ considerably. This has been demonstrated in several species of herbaceous plants which are endemic to Europe and that have been introduced into California (Goeden & Ricker 1968, Goeden 1971, 1974, Goeden & Ricker 1986a). Several studies on crop plants have also shown that the number and kinds of insect colonists differs markedly between continents (Entwistle 1972, Bournier 1977, Strong et al. 1977, Chiang 1978, Kogan 1981). This trend does not occur on all introduced plant species. Opuntia cacti introduced into southern Africa have not recruited any African insects although they have been present for more than 100 years, probably because they are taxonomically very different from native South African plants (Moran 1980).

Goeden (1971, 1974) noted specific differences between the insect herbivore communities on introduced thistles in California and on conspecific thistles in Europe where they are endemic. The insect herbivore communities on introduced thistles comprised a smaller proportion of endophagous insect species and a larger proportion of polyphagous species than the communities on endemic thistles in Europe. According to Strong et al. (1984), these data suggest that the evolution or accrual of endophagous and specialist insect species takes much longer than ectophagous and generalist species.

The aim of this study was to determine how the insect herbivore communities associated with the flower-heads of introduced thistle species compared with the communities on endemic plants that occurred sympatrically in the area of introduction. This would show to what extent the insect communities on introduced plants are influenced by the available pool of phytophagous insects. In South Africa there are no endemic thistle species (chapter 2), so the insect herbivore communities associated with Berkheya were used for this comparison. The herbivore communities on

Berkheya are generally similar to those found on thistles endemic to California (chapters 5, 6, 7 and 8) and they provide a general indication of the pool of potential herbivores available to colonise composites in South Africa.

Flower-heads from two species of thistles introduced into South Africa from Europe, Carduus macrocephalus Desf. and Cirsium vulgare (Sâvi) Ten., were sampled and their insect herbivore communities were compared to those associated with Berkheya species that are endemic to South Africa. To determine to what extent the herbivore communities of the introduced thistles were influenced by the available herbivore species pool, the herbivore communities associated with these two thistle species in Europe, sampled by Zwölfer (1965), were included in the study.

Materials and Methods

Records obtained from the herbarium of the Botanical Research Institute in Pretoria, showed that C. vulgare is found throughout South Africa, but that C. macrocephalus occurs only in the eastern Cape (Fig. 1). Ten samples were collected from C. macrocephalus and C. vulgare at different sites in the eastern Cape at . The techniques used to sample the flower-heads were identical to those described in chapter 3.

Grouped data were used for Berkheya when their herbivore communities were compared to those associated with thistle flower-heads. This data grouped the communities from B. decurrens, B. heterophylla, B. onobromoides, B. rigida and Berkheya sp (Tables 4.2 to 4.6). Grouping this data was valid because their communities were statistically similar to each other (chapter 4).

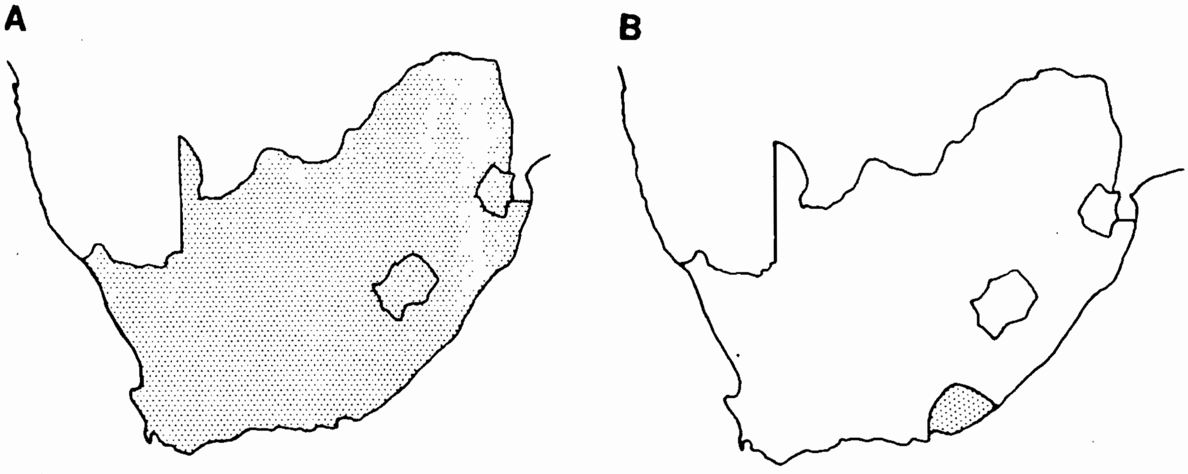


Fig. 1 Shaded areas show the distribution of (A) Cirsium vulgare and (B) Carduus macrocephalus in South Africa.

Results and Discussion

The insect herbivore species found in association with the flower-heads of C. macrocephalus and C. vulgare in the eastern Cape are listed in Tables 1 and 2 respectively. The flower-heads of both thistle species were colonised by fourteen insect herbivore species. On C. macrocephalus, 70% of the herbivore species occurred rarely in samples and on C. vulgare 60% occurred rarely. All of the herbivore species that occurred were generalists.

Insect species that were common to the flower-heads of the thistles and Berkheya in South Africa were; Brachycaudus helichrysi (Kaltenbach) (Aphididae: Hemiptera), Eremnus (Curculionidae: Coleoptera), Heliothis armigera (Hübner) (Noctuidae: Lepidoptera), Sphaerocoris

Table 1 A list of the herbivore species found colonising the flower-heads of *Carduus macrocephalus* The stages collected; L, N, P and A refer to larvae, nymphs, pupae and adults. Immature stages indicated that these species bred on the flower-heads. Other biological details, like where and how they feed on the flower-head, are also provided. (R - species collected in less than 25% of samples; O - species collected in 25 to 50% of samples.)

Herbivore Species	Frequency (%) in collections	Stages collected	endophagous/ ectophagous	guild
COLEOPTERA				
Curculionidae				
Eremnus sp	R	A	ectophagous	chewer
DIPTERA				
Tephritidae				
sp 1	R	A,P,A	endophagous	chewer
Stratiomyidae				
sp	R	L,P,A	endophagous	chewer
HEMIPTERA				
Pentatomidae				
Sciocoris sp	O	N,A	ectophagous	sap sucker
sp 3	R	A	ectophagous	sap sucker
Scutelleridae				
Sphaerocoris testudogrisea	O	N,A	ectophagous	sap sucker
Anthocoridae				
sp	O	N,A	ectophagous	sap sucker
Miridae				
sp 4	R	A	ectophagous	sap sucker
LEPIDOPTERA				
sp 4	R	L	ectophagous	chewer
sp 6	R	L	ectophagous	chewer
sp 7	R	L	ectophagous	chewer
sp 8	R	L	ectophagous	chewer
sp 9	R	L	ectophagous	chewer
Noctuidae				
Heliothis armigera	O	L	ectophagous	chewer

Table 2 A list of the herbivore species found colonising the flower-heads of *Cirsium vulgare* The stages collected; L, N, P and A refer to larvae, nymphs, pupae and adults. Immature stages indicated that these species bred on the flower-heads. Other biological details, like where and how they feed on the flower-head, are also provided. (R - species collected in less than 25% of samples; O - species collected in 25 to 50% of samples; C - species collected in more than 50% of samples.)

Herbivore Species	Frequency (%) in collections	Stages collected	endophagous/ ectophagous	guild
COLEOPTERA				
Scarabaeidae				
Dichelus sp 2	R	A	ectophagous	chewer
Dichelus sp 3	R	A	ectophagous	chewer
DIPTERA				
Tephritidae				
Craspedoxantha marginalis (Wiedemann)	R	L,P,A	ectophagous	chewer
HEMIPTERA				
Pentatomidae				
Sciocoris sp	O	N,A	ectophagous	sap sucker
Pseudococcidae				
sp	R	N,A	ectophagous	sap sucker
Aphididae				
Brachycaudus helichrysi	O	N,A	ectophagous	sap sucker
Lygaeidae				
Nysius sp	O	N,A	ectophagous	sap sucker
Scutelleridae				
Sphaerocoris testudogrisea	C	N,A	ectophagous	sap sucker
Anthocoridae				
sp	O	N,A	ectophagous	sap sucker
Pentatomidae				
sp	R	A	ectophagous	sap sucker
Cercopidae				
sp	R	A	ectophagous	sap sucker
LEPIDOPTERA				
sp 6	R	L	endophagous	chewer
Tortricidae				
sp	R	L	endophagous	chewer
Noctuidae				
Heliothis armigera	R	L	ectophagous	chewer

testudogrissea de Geer (Scutelleridae: Hemiptera), Sciocoris sp (Pentatomidae: Hemiptera), Veterna sp (Pentatomidae: Hemiptera), Dichelus sp 2 (Scarabaeidae: Coleoptera), and Lepidoptera sp 4 and sp 6. The tephritid, Craspedoxantha marginalis (Wiedemann), which colonised C. vulgare flower-heads in the eastern Cape, has been recorded from Berkheya latifolia Wood et Evans, and also several other species of Asteraceae in South Africa (Friedburg 1985).

More insect herbivore species colonised the flower-heads of introduced thistles in South Africa than the flower-heads of thistles endemic to Europe. Similar results were obtained for insect herbivore communities on the flower-heads of introduced thistles in California, sampled by Goeden & Ricker (1986a). Carduus pycnocephalus comprised 14 species in California where it is introduced, but only 3 species in Europe where it is endemic (Zwölfer 1965, Goeden 1974) even though C. pycnocephalus was sampled 10 times in both regions.

No specialist herbivore species occurred in the flower-heads of C. macrocephalus and C. vulgare introduced into South Africa even though specialists occurred in the flower-heads of these species in Europe (Table 1). Herbivore communities associated with the flower-heads of thistles introduced into California also lacked specialist species (Goeden & Ricker 1986a). However, the absence of specialist species from the herbivore communities of introduced thistles is not unusual because the communities associated with the flower-heads of several Cirsium species endemic to California lacked specialist herbivores (Goeden & Ricker 1986b, 1987a, 1987b). Moreover, the herbivore communities associated with the flower-heads of of several other European thistles, sampled in their native European distribution, also lacked specialist herbivore species (Zwölfer 1965) (see Fig. 6.4). Thus, while the absence of specialist species from introduced thistles appears to indicate that colonisation or evolution by specialist herbivore species is slower than by generalist species (Strong *et al*. 1984), this condition is not uncommon in communities on endemic thistles.

Endophagous species comprised a smaller proportion of the herbivore communities associated with the flower-heads of introduced thistles in South Africa than on these thistle species in their native region or on *Berkheya* in South Africa (Table 3). This is consistent with the collective results of Goeden (1971, 1974, 1976) and Goeden & Ricker (1986a). Endophagous herbivore species do appear to take longer to colonise or evolve than ectophagous species (Strong *et al*. 1984).

The effect of the local pool of herbivore species on the herbivore communities of introduced thistles in South Africa was most noticeable when the taxonomic and guild composition of their herbivore communities was examined. The communities associated with the flower-heads of *C. macrocephalus* and *C. vulgare* in Europe did not have any Hemiptera. However, Hemiptera comprised a large proportion of the communities on these thistles in South Africa (Table 4). Hemiptera were also common in the herbivore communities associated with the flower-heads of *Berkheya* in South Africa. Because the guild of sap suckers is comprised entirely of Hemiptera, a comparison of guild composition provided similar results (Table 5). A similar situation was found also in the communities of insect herbivores associated with the flower-heads of thistles introduced into California from Europe. The communities on the thistles introduced into California comprised many hemipteran species (Goeden 1971, 1974, Goeden & Ricker

Table 3 A comparison of the proportion of specialist species and endophagous species in the flower-head herbivore communities from thistle species introduced into South Africa and endemic in Europe (*C. macrocephalus* and *C. vulgare*), and *Berkheya* spp.

	South Africa			Europe	
Herbivores	*Berkheya*	*C. macro.*	*C. vulgare*	*C. macro.*	*C. vulgare*
% Specialists	5.8	0	0	18.7	8.3
% Endophages	47.2	14.3	14.3	88.8	28.7

Table 4 A comparison of the proportion each insect taxon represented in the flower-head herbivore communities from thistle species introduced into South Africa and endemic in Europe (*C. macrocephalus* and *C. vulgare*), and *Berkheya* spp.

	South Africa			Europe	
Herbivores	*Berkheya*	*C. macro.*	*C. vulgare*	*C. macro.*	*C. vulgare*
% Coleoptera	23.4	7.1	14.3	33.3	33.3
% Diptera	17.8	14.3	7.1	33.3	41.7
% Lepidoptera	17.8	42.9	21.4	33.4	25.0
% Hemiptera	41.0	35.7	57.1	0	0

Table 5 A comparison of the proportion each guild represented in the flower-head herbivore communities from thistle species introduced into South Africa and endemic in Europe (*C. macrocephalus* and *C. vulgare*), and *Berkheya* spp.

	South Africa			Europe	
Herbivores	*Berkheya*	*C. macro.*	*C. vulgare*	*C. macro.*	*C. vulgare*
% endophagous chewers	47.2	14.3	21.4	88.8	83.3
% ectophagous chewers	11.8	50.0	21.5	11.2	18.7
% sap suckers	41.0	35.7	57.1	0	0

1986a). In their native distribution, no Hemiptera were associated with the flower-heads of these thistles (Zwölfer 1965) but the flower-heads of endemic Californian thistles are colonised by Hemiptera (Goeden & Ricker 1986b, 1987a, 1987b). Therefore, the taxonomic and guild composition of the herbivore communities from introduced thistles are more similar to herbivore communities associated with similar endemic plants in the same area as the introduced thistles, than to the communities associated with these thistle species in their original distribution.

Conclusions

The local pool of herbivore species influenced the kinds of insect taxa and guilds that colonised the flower-heads of *C. macrocephalus* and *C. vulgare* introduced into South Africa. No specialist species colonised the flower-heads of the introduced thistles, but this does not necessarily imply that the community is young in evolutionary terms, because the flower-heads of many thistles endemic to Europe were not colonised by specialist species. The aquisition of endophagous species did appear to take longer than ectophagous species and this is consistent with the conclusions of Strong *et al*. (1984).

References

Bournier, A. 1977. Grape insects. _Annual Review of Entomology_, 22: 355-376.

Chiang, H.C. 1978. Pest management in corn. _Annual Review of Entomology_, 23: 101-123.

Entwistle, P.F. 1972. _Pests of Cocoa_. Longmans, London.

Freidberg, A. 1985. The genus _Craspedoxantha_ Bezzi (Diptera: Tephritidae: Terelliinae). _Annals of the Natal Museum_, 27: 183-206.

Goeden, R.D. 1971. The phytophagous insect fauna of milk thistle in southern California. _Journal of Economic Entomology_, 64: 1101-1104.

Goeden, R.D. 1974. Comparative survey of the phytophagous insect faunas of Italian thistle, _Carduus pycnocephalus_, in southern California and southern Europe relative to biological weed control. _Environmental Entomology_, 3: 464-474.

Goeden, R.D. 1976. The Palearctic insect fauna of milk thistle, _Silybum marianum_, as a source of biological control agents for California. _Environmental Entomology_, 5: 345-353.

Goeden, R.D. & Ricker, D.W. 1968. The phytophagous insect fauna of Russian thistle (_Salsola kali_ var. _tenuifolia_) in southern California.

Goeden, R.D. & Ricker, D.W. 1986a. Phytophagous insect faunas of the two most common native _Cirsium_ thistles, _C. californicum_ and _C. proteanum_, in southern California. Annals of the Entomological Society of America, 79: 953-62.

Goeden, R.D. & Ricker, D.W. 1986b. Phytophagous insect faunas of two introduced Cirsium thistles, C. ochrocentrum and C. vulgare, in southern California. Annals of the Entomological Society of America, 79: 945-952.

Goeden, R.D. & Ricker, D.W. 1987a. Phytophagous insect faunas of the native thistles, Cirsium brevistylum, Cirsium congdonii, Cirsium occidentale, and Cirsium tioganum, in southern California. Annals of the Entomological Society of America, 80: 152-160.

Goeden, R.D. & Ricker, D.W. 1987b. Phytophagous insect faunas of native Cirsium thistles, C. mohavense, C. neomexicanum and C. nidulum, in the Mojave desert of southern California. Annals of the Entomological Society of America, 80: 161-175.

Kogan, M. 1981. Dynamics of insect adaptations to soybean: impact of integrated pest management. Environmental Entomology, 10: 363-371.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984. Insects on Plants. Community Patterns and Mechanisms. Blackwell Scientific Publications, Oxford, London.

Strong, D.R. Jr, McCoy, E.D. & Rey, J.R. 1977. Time and the number of herbivore species: the pests of sugarcane. Ecology, 58: 167-175.

Zwölfer, H. 1965. Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) in Europe. Commonwealth Institute of Biological Control. Technical Bulletin, 6: 81-153.