ARTHROPOD COMMUNITIES OF PROTEACEAE WITH SPECIAL EMPHASIS ON

PLANT-INSECT INTERACTIONS

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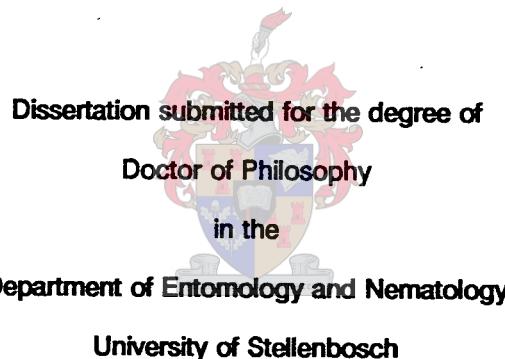
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DECLARATION

I the undersigned hereby declare that the work contained in this thesis is my own original work and has not previously in its entirety or in part been submitted at any university for a degree.

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ABSTRACT

Arthropod communities of five proteaceous species viz. *Protea repens, P. neriifolia, P.cynaroides, Leucospermum cordifolium* and *Leucadendron laureolum* were studied. A faunal list of the insects was compiled according to the feeding guilds of insects. Six phytophagous guilds were recognized: flower visitors, thrips, endophages, ectophages, sap-suckers, and ants. The guild composition, species packing and seasonal distribution for the free-living insects, spiders and other arthropods were investigated on the different plant species. The ants, flower visitors and sap-sucking species found on the plant species, were very similar, but the number of leaf chewing species common to all the plant species was low, suggesting that some species were monophagous. Insect abundance increased during the wet winter months when the plants were in flower. Of the total number of herbivores collected, flower visitors represented 69,5%, leaf feeders 14,5% and sap-suckers 16,1%. The chewers constituted 60,1% of the total herbivore biomass. Leaf damage increased with age ; young leaves were practically free of herbivore damage, while older leaves were still acceptable as food. The degree of insect damage differed amongst the plant species varying from 2% to 15%. The following leaf characteristics were investigated to determine the factors involved in defence against insect herbivory : total phenolic content, protein precipitating ability, cyanogenesis, nitrogen content, leaf toughness, woodiness and fibre content. It appears that the plant species use different mechanisms to protect their leaves. The infructescences of *Protea repens* were exploited by the larvae of four Coleoptera and four Lepidoptera species. The community structure of these phytophagous insects was determined largely by negative interactions. Various strategies are followed (e.g. niche segregation in time and space) to lessen interspecific competition.

i

EKSERP

'n Studie van die arthropood gemeenskap op vyf proteasoorte, naamlik *Protea repens, P. neriifolia, P. cynaroides, Leucospermum cordifolium* en *Leucadendron laureolum* is gedoen. 'n Faunalys van insekte volgens hul voedingsgildes is saamgestel. Die insekte is in ses fitofage gildes verdeel naamlik blombesoekers, blaaspootjies, endovoeders, ektovoeders, sapsuiers en miere. Die samestelling van die gildes, spesie-rangskikking en seisoenale verspreiding is bepaal vir die vrylewende insekte, spinnekoppe en ander arthropode. Die miere, blombesoekers en sapsuierspesies wat op die plantsoorte gevind is, is byna dieselfde, maar verskille in die blaarvoederspesies is gevind wat 'n aanduiding is dat sommige spesies monofaag mag wees. Gedurende die nat wintermaande toon die insekgetalle 'n toename. Blombesoekers verteenwoordig 69,5%, blaarvoeders 14,5% en sapsuiers 16,1% van die aantal insekherbivore wat versamel is. Die kouers vorm 60,1% van die totale herbivoor biomassa. Soos die blare verouder, neem die skade op die blare toe; jong blare toon byna geen skade nie, terwyl ouer blare steeds geskik is vir insekvoedsel. Die insekskade op die blare wissel by die verskillende plante tussen 2% en 15%. Om te bepaal watter blaareienskappe moontlik 'n rol kan speel in blaarverdediging teen insekte is die volgende ondersoek: totale fenoliese inhoud, die vermoë om proteïene te presipiteer, sianogenese, stikstofinhoud, blaartaaiheid, houtagtigheid en veselinhoud. Dit wil voorkom asof die plante verskillende meganismes gebruik om die blare te beskerm. Saadkoppe van *Protea repens* word deur vier Coleoptera en vier Lepidoptera spesies benut. Die gemeenskapstruktuur van die boorders word tot 'n groot mate bepaal deur negatiewe interaksies. Verskeie strategieë word gevolg (bv. nissegregasie in tyd en ruimte) om kompetisie tussen spesies te verminder.

PREFACE

This study was conducted as part of a comprehensive research program on indigenous plants.

The work was done under research facets :

GS 24 31/20/1/2 ; Bio-ecological studies of insects on Proteas,
GS 24 31/20/2/1 ; Taxonomic studies of insects on Proteas
GS 24 31/20/2/2 ; Taxonomic studies of mites on Proteas.

This program forms part of the work of the Fynbos Research Unit at Elsenburg Stellenbosch, a subdivision of the Vegetable and Ornamental Plant Research Institute.
The manuscript is comprised of the following chapters:

Phytophagous insect fauna of five Proteaceae in the south-western Cape Province, South Africa (Coetzee 1989a).

Spider communities of five proteaceous species in the fynbos biome, south-western Cape (Coetzee 1989b).

Guild composition, species packing and seasonal distribution of the arthropod communities on five proteaceous species (Coetzee 1989c).

The insect herbivore guild and its effect on the foliage of five proteaceous species of the Cape fynbos (Coetzee 1989d).

Antiherbivore mechanisms of the foliage of five proteaceous species in the Cape fynbos (Coetzee 1989e).

Coexistence and resource utilization of larval Coleoptera and Lepidoptera in the infructescence of *Protea repens* (Proteaceae) (Coetzee 1989f).

In this manuscript references to chapters will be as indicated as brackets above. Each chapter has been prepared for publication.

iii

ACKNOWLEDGEMENTS

iv

CONTENTS

1

INTRODUCTION

The family Proteaceae is an important component of the Cape flora or fynbos (Taylor 1978 ; Bond & Goldblatt 1984) and because of the beauty of its flowers and foliage, many species are universally utilized commercially. In an attempt to contribute to the understanding of the structure and functioning of the plant family, various botanists studied the Proteaceae intensively, especially during the last decade; taxonomy (Rourke 1972; 1980; Williams 1972), phenology (McDonald 1985), germination (Van Staden 1978; Brits 1986; 1987) and general ecology (Bond 1984; 1985; Manders 1986; Midgley 1987; Bond 1988 ; Le Maitre 1988).

Information on interaction between the Proteaceae and arthropods has until now been restricted to fragmentary studies on pests (Gess 1968; Myburgh *et al.* 1973; Myburgh *et al.* 1974; Myburgh & Rust 1975 a,b; Coetzee 1986), seed dispersal (Bond & Slingsby 1983), pollination (Coetzee & Giliomee 1985) and seed predation (Coetzee & Giliomee 1987 a,b). These studies indicated that insects could have an effect on the distribution and abundance of the Proteaceae.

In an attempt to gain more insight into the organizing force of protea-arthropod interactions, certain associations between the Proteaceae and arthropods were investigated. The family Proteaceae is represented by *ca.* 369 species (Bond & Goldblatt 1984) in the south-western Cape. To make the study feasible and practicable, the project was restricted to five ecologically and economically important proteaceous species viz.*Protea repens* (L.)L., *P. neriifolia* R.Br., *P. cynaroides* (L.)L., *Leucospermum cordifolium* (Salisb. ex Knight) Fourcade and *Leucadendron laureolum* (Lamarck) Fourcade.

They were chosen on the following criteria: they represent dominant species of the three important genera *Protea, Leucospermum* and *Leucadendron*, have a relatively wide distribution area, and are of commercial value. For information on the plants taxonomic characteristics and distributionof the plant species, see Coetzee (1989a).

2

The main aim of the study was to determine the impact of herbivores on the selected Proteaceae and to investigate plant defence mechanisms. This information would not only be useful in the protection of commercially grown proteas but would also contribute to our knowledge of insect-plant interactions in the fynbos and thus to fynbos ecology in general. The results of the study are presented in the following six chapters which have been or will be submitted as papers to recognized scientific journals.

Phytophagous insect fauna of five Proteaceae in the south-western Cape Province, South Africa (Coetzee 1989a).

Spider communities of five proteaceous species in the fynbos biome, south-western Cape (Coetzee 1989b).

Guild composition, species packing and seasonal distribution of the arthropod communities on five proteaceous species (Coetzee 1989c).

The insect herbivore guild and its effect on the foliage of five proteaceous species of the Cape fynbos (Coetzee 1989d).

Antiherbivore mechanisms of the foliage of five proteaceous species in the Cape fynbos (Coetzee 1989e).

Coexistence and resource utilization of larval Coleoptera and Lepidoptera in the infructescence of *Protea repens* (Proteaceae) (Coetzee 1989f).

3

MATERIALS AND METHODS

A. Study areas

The study sites were situated in the fynbos vegetation of the south-western Cape. For information on collecting sites and grid reference see Table 1a and 1b.

TABLE 1a   Study sites for the arthropod communities and the effect on the host plants of the five Proteaceae.

HOST PLANT	FAUNA LIST	SPIDER GUILD	ARTHROPOD GUILD	HERBIVORE GUILD	LEAF DAMAGE	LEAF ASSAYS	INFRUCTESCENCES DAMAGE AND INSECT GUILD
P. repens							
Swartboskloof, Jonkershoek	*	*	*	*	*	*	*
Jan Marais Nature reserve	*	*	*				*
Stellenbosch mountain	*						*
Helderfontein, Stellenbosch	*					*	
Tygerhoek, Riviersonderend	*						
Protea Heights, Devon Valley	*						
P. neriifolia							
Swartboskloof, Jonkershoek	*	*	*	*	*		
Helderfontein, Stellenbosch	*					*	
Tygerhoek, Riviersonderend	*						
Protea Heights, Devon Valley	*	*	*				
P. cynaroides							
Riviersonderend mountain	*	*	*	*	*		
Jan Marais Nature reserve	*						
Tygerhoek, Riviersonderend	*						
Protea Heights, Devon Valley	*	*	*		*		
L. cordifolium							
Houwhoek mountain, Grabouw	*	*	*	*	*		
Helderfontein, Stellenbosch	*	*	*			*	
Tygerhoek, Riviersonderend	*						
L. laureolum							
Houwhoek mountains Grabouw	*	*	*	*	*		
Helderfontein, Stellenbosch	*	*	*			*	
Jan Marais Nature reserve	*						

4

TABLE 1b   Grid references for study sites of the Arthropod communities of five Proteaceae
                plant species

HOST PLANT	GRID	
P. repens		
Swartboskloof, Jonkershoek	33°58'41"E	18°57'08"S
Jan Marais Nature reserve, Stellenbosch	33°55'52"E	18°52'35"S
Stellenbosch mountain, Stellenbosch	33°58'21"E	18°52'48"S
Helderfontein, Stellenbosch	33°54'58"E	18°52'19"S
Tygerhoek, Riviersonderend	34°08'52"E	19°54'09"S
Protea Heights, Devon Valley	33°54'16"E	18°49'27"S
P. neriifolia		
Swartboskloof, Jonkershoek	33°58'41"E	18°57'08"S
Helderfontein, Stellenbosch	33°54'58"E	18°52'19"S
Tygerhoek, Riviersonderend	34°08'52"E	19°54'09"S
Protea Heights, Devon Valley	33°54'16"E	18°49'27"S
P. cynaroides		
Riviersonderend mountain	34°08'08"E	19°53'56"S
Jan Marais Nature reserve, Stellenbosch	33°55'52"E	18°52'35"S
Tygerhoek, Riviersonderend	34°08'52"E	19°54'09"S
Protea Heights, Devon Valley	33°54'16"E	18°49'27"S
L. cordifolium		
Houwhoek mountain, Grabouw	34°12'31"E	19°09'27"S
Helderfontein, Stellenbosch	33°54'58"E	18°52'19"S
Tygerhoek, Riviersonderend	34°08'52"E	19°54'09"S
L. laureolum		
Houwhoek mountain, Grabouw	34°13'00"E	19°11'17"S
Helderfontein, Stellenbosch	33°54'58"E	18°52'19"S
Jan Marais Nature reserve, Stellenbosch	33°55'52"E	18°52'35"S

5

B. Sample of plants.

Ten plants were sampled each month for inflorescence and infructescence insects, while free-living arthropods were collected from four plants of each species each month. Sampford's (1962) line transect method was used to select the plants. This entailed taking parallel transects at random from the middle of the area. Plants closest to the transect were sampled at 10 m intervals. Care was taken not to sample the same plant in successive collection trips.

C. Collecting methods for arthropods

i) Free-living arthropods

This study was confined to arthropods associated with the parts of the plant above ground. To collect the free-living arthropods, two methods were used viz. "knock-down" and "beating" methods. A sheet 1 x 1m (1m²) or 0.5 x 0.5 (0.25m²), depending on the growth form of the plants, was placed under each plant sampled. Each plant was then sprayed for four seconds with an aerosol formulation of dichlorvos (Insectigas^R). All insects falling onto the sheet within five minutes of spraying were collected. The beating method entailed dislodging insects from a total of 50 branches from 10 plants by beating the branches with a rod until all insects had dropped off.

ii) Inflorescence arthropods

To determine which arthropods were found in the inflorescences, samples of inflorescences (with 50 to 80% of the florets open) were collected at random, placed in plastic bags and the arthropods killed with ethyl-acetate. Inflorescences were dissected and all arthropods collected.

iii) Arthropods in the infructescences

Arthropods inhabiting the infructescences were collected by picking infructescences of different flowering seasons, using Lombaard's (1971) approach to distinguish between infructescences of different flowering seasons on the same plant. All specimens were sorted into morphospecies, classified and an accession number allocated to each morphotype. Samples were sent to taxonomists for identification. Voucher specimens are housed in the collection of the Fynbos Research Unit of the Vegetable and Ornamental Plant Research Institute (V.O.P.R.I.) at Elsenburg, Stellenbosch.

6

D. Plant materials

The expected proportion of leaf removed was calculated as a statistical expectancy (see Coetzee 1989d).

To determine which defence mechanisms the leaves of proteaceous species have developed, certain characteristics were investigated, viz. total phenolic content, protein precipitating ability, the cyanogenic ability and sclerophyllous characteristics such as leaf toughness, woodiness, nitrogen content and fibre content (Coetzee 1989e).

E. Duration of project

Checklists for the phytophagous insect fauna (Coetzee 1989a) were compiled from data collected from 1984 until 1986. This material was compared and supplemented with records from the collection of Proteaceae insects housed in the collection of the Fynbos Research Unit of the V.O.P.R.I. at Elsenburg. The survey to study the spider communities (Coetzee 1989b) and arthropod guild composition (Coetzee 1989c) started in January 1985 and ended in December 1985. Measurements of the extent of leaf damage (Coetzee 1989d) started during 1985 with the initiation of the main growth cycles on the different plant species, and continued until the cohort of leaves were 21 months old. Collection of leaf material for all antiherbivore mechanism assays (Coetzee 1989e) commenced in September 1986 and ended in January 1988. Infructescences of *Protea repens* were collected from November 1981 until April 1986 to gather data on the insect guild in the infructescences (Coetzee 1989f).

7

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8

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9

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10

CHAPTER 1

PHYTOPHAGOUS INSECT FAUNA OF FIVE PROTEACEAE IN THE SOUTH-WESTERN CAPE PROVINCE,SOUTH AFRICA

ABSTRACT

Checklists based on the collection of the insects from five proteaceous species (*Protea repens*, *P. neriifolia*, *P. cynaroides*, *Leucospermum cordifolium* and Leucadendron laureolum) are presented. A short description of each host plant's distribution and phenology is also provided. Faunal lists were compiled according to feeding guilds of insects. The following guilds were recognized: flower visitors (includes all insects found in the inflorescences feeding on nectar and pollen), thrips (in inflorescences and also on the rest of the plant), endophages (borers and leaf miners), ectophages (leaf/surface chewers), sap-suckers (sub-divided into ectophyric and sedentary sap-suckers) and ants (not truly phytophagous, but occasionally feeding on nectar).

Keywords: Phytophagous insects, faunal list, Proteaceae, fynbos

11

INTRODUCTION

The Proteaceae of southern Africa include an array of structurally diverse plant forms ranging from sprawling shrubs to trees, and are widely distributed in southern Africa (Fig. 1). They serve as hosts for many insect species, some of which have only recently been described (Gagné 1983; Oberprieler 1988). Although insects on some species of this family have been studied (Gess 1968; Myburgh *et al.* 1973; Myburgh *et al.* 1974; Myburgh & Rust 1975 a, b; Coetzee & Giliomee 1987 a, b), a comprehensive account of all the phytophagous insects on a particular plant species in the fynbos has never been given. In a first attempt to list the insect fauna of a proteaceous species, Coetzee & Latsky (1986) compiled a faunal list of insects collected on *Protea repens*. This study has now been extended to include phytophagous insects associated not only with *P. repens*, but also with four other species viz. *P. neriifolia, P. cynaroides, Leucospermum cordifolium and Leucadendron laureolum.* Such faunal lists are important in determining which insects are host specific and which are polyphagous and will also help to determine whether the insect fauna matches the floral diversity of the Cape Flora. They also allow for comparison of the feeding guild composition of the various species.

Faunal lists are usually compiled according to taxonomic groups, but since our main interest is in insect-plant associations, and taxonomically diverse groups can belong to similar feeding guilds, the insects documented here are grouped according to feeding guilds as proposed by Southwood (1982).

The phytophagous guild includes all insects feeding on live plant material, as well as those feeding on nectar and pollen. The guilds have been divided into flower visitors, thrips, endophages, ectophages and sapsuckers.

Flower visitors include all insects found in the inflorescence, feeding on nectar and pollen. Included in this group are flower visitors that also feed on the inner involucral bracts of the inflorescence, as well as on the nectar. Thrips (order Thysanoptera) are not only found in the inflorescences but also on the rest of the plant as ectophytic insects. Due to their unique feeding mechanism, they are regarded as a distinct group in this study. Borers and leaf miners comprise the endophagous sub-guild, whereas surface or leaf chewers comprise the sub-guild ectophagous insects. The sub-guild sap-suckers, all belonging to the order

12
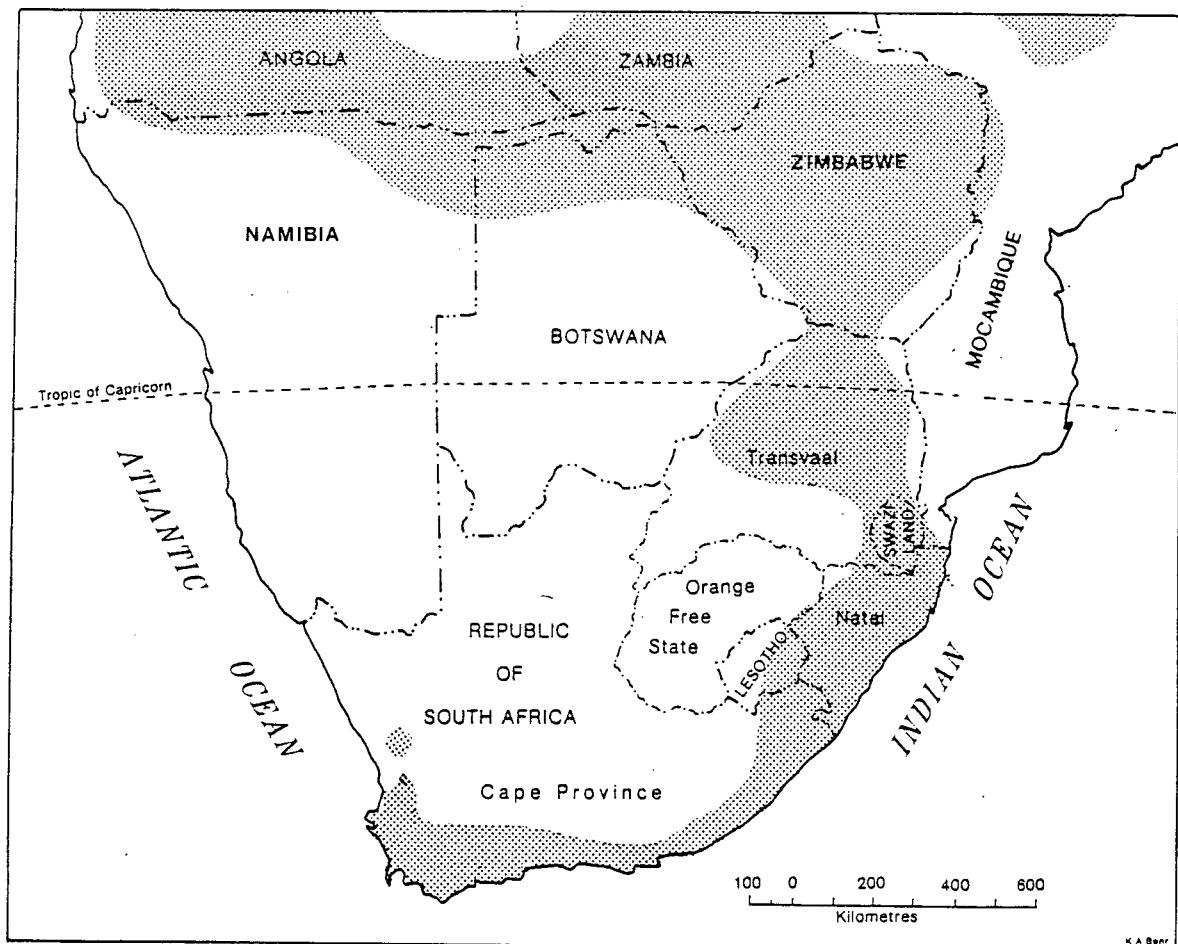
Fig. 1 Distribution of the Proteaceae in southern Africa (after Rourke 1980).

The phytophagous guild includes insects that also use the plant as a host to complete their whole life cycle, or only part of it. Chance visitors on the plant, however, are not regarded as part of the phytophagous guild. Ants (Formicidae) are not considered truly phytophagous since they take nectar only occasionally having other feeding habits also, and are regarded as a distinct group in this study.

13

DISTRIBUTION AND PHENOLOGY OF THE HOST PLANTS

Protea repens (L.) L

P. repens is one of the most common and widespread protea species in the fynbos, and is widely distributed in the Cape Province (Fig. 2). It is usually found from sea-level to 600 m above sea-level, but in the drier interior it can occur up to altitudes of 1500 m. *P. repens* forms colonies either in dense, vigorous stands or in association with other large shrublike proteas (Rourke 1980). The extent of such stands can be affected by the presence of other plant species, frequency of fires and other factors such as agricultural encroachment.
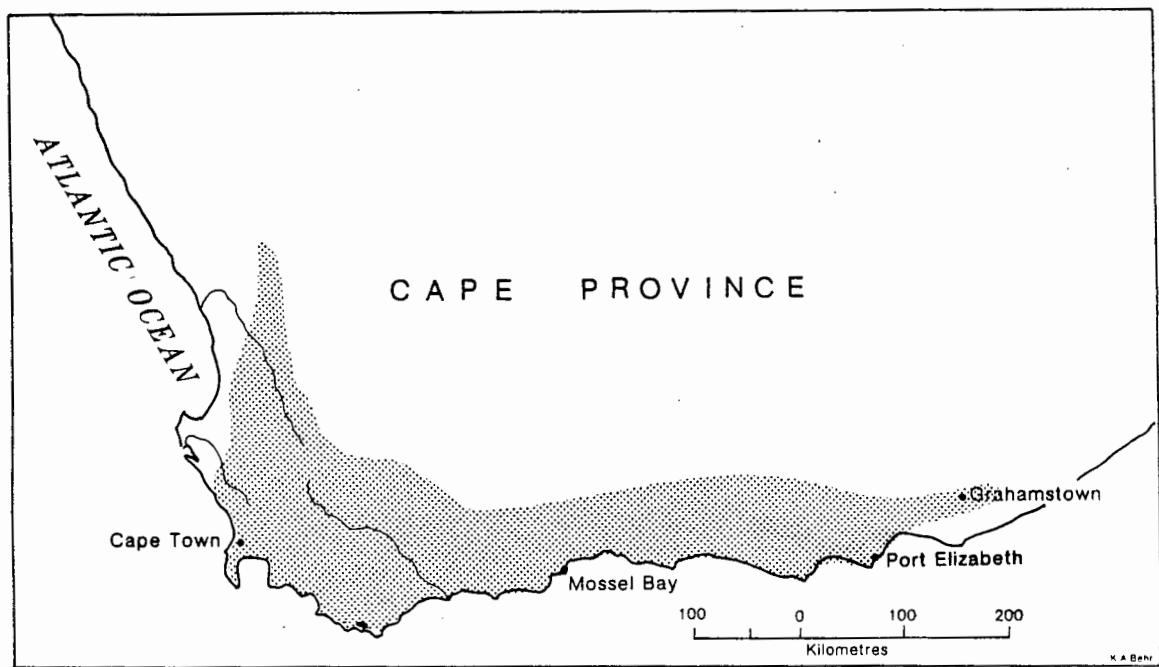
Fig. 2   Distribution of *Protea repens* (L.) L. (after Rourke, 1980)

P. repens plants develop into shrubs 2.0 to 4,5 m tall with a crown width of up to 5 m (Rourke 1980). Vegetative buds are initiated from July to October and start growing from August the following year, with the peak of the main growth cycle in September. If the shoots develop a terminal reproductive bud, the vegetative bud will continue growing beyond the reproductive bud (G. Jacobs personal communication). The slender shoots which do not form reproductive buds continue growing. These flushes can be distinguished from the main cycle by comparing the distance between the hypsophylls, the main cycle having the greatest distance between whorls of hypsophylls. Reproductive buds on thicker shoots are initiated after shoot elongation has been completed. Early initiated flower-buds are inhibited so that the flowering period synchronizes with the flower buds initiated later. Flowering takes place 12 months after initiation of buds.

Leaves are fully grown within 30 days after shoot-elongation. The leaves of *P. repens* are hairless, and linear-spatulate to inverse ablanceolate in shape (Rourke 1980). The average surface area of the leaves is 670 mm^2. Abscission started approximately 21 months after shoot growth stoped and reached its peak between November and January (Mitchell & Coley 1987). The vegetative growth cycle is practically uniform throughout the range of *P. repens* (Rourke 1980). The leaves dry out completely before abscission. Although the vegetative growth cycles of *P. repens* are uniform in all the areas, the flowering periods differ. The south-western Cape varieties flower between May and October, while those of the eastern Cape Province flower between September and March. The inflorescence of *P. repens* consists of individual florets, grouped together and surrounded by creamy-white to red inner involucral bracts. These are hard and shiny, with a sticky texture as a result of resin exuded on the outside of the bracts. Anthesis of florets commences with the outer florets and progresses inward. During this process the perianth segments containing the anthers drop away from the style, and the pollen adheres to the pollen presenter, which forms the upper part of the style. The inflorescence remains open for 10 to 14 days and then closes, due to the adaxial movement of the bracts (Coetzee & Giliomee 1985) to form an infructescence with achenes (hereafter called seeds). Fertile seeds take about six months to mature. *P. repens* infructescences can remain closed for many years, but can open by means of hygroscopic mechanisms after the death of the involucral receptacle. Involucral receptacle death can be the result of mechanical damage (Rourke 1980), fire damage (Jordaan 1949) or insect damage (Coetzee & Giliomee 1987 a, b).

15

Protea neriifolia R. Br.

P. neriifolia is found in a few isolated patches on the southern slopes of the Klein Winterhoek Mountain range, and scattered eastward from Jonkershoek to Port Elizabeth (Fig. 3). The plants grow in soil of Table Mountain sandstone origin or granite (Rourke 1980). The stands are generally found on south- facing slopes, from sea level to an altitude of 1300 m. As shown in Fig. 3, *P. neriifolia* is widely distributed, but in low-lying areas stands have been destroyed by agricultural practices.

P. neriifolia forms a large upright shrub of 1,5 - 3,0 m in height and up to 2,0 m in crown diameter. Vegetative buds are initiated and start growing from July to October. Leaf growth is completed within 30 days from the start of development. The leaves are initially covered with downy hairs, but these are soon lost. The average leaf surface area is 1 800 mm^2, and leaves are oblong.
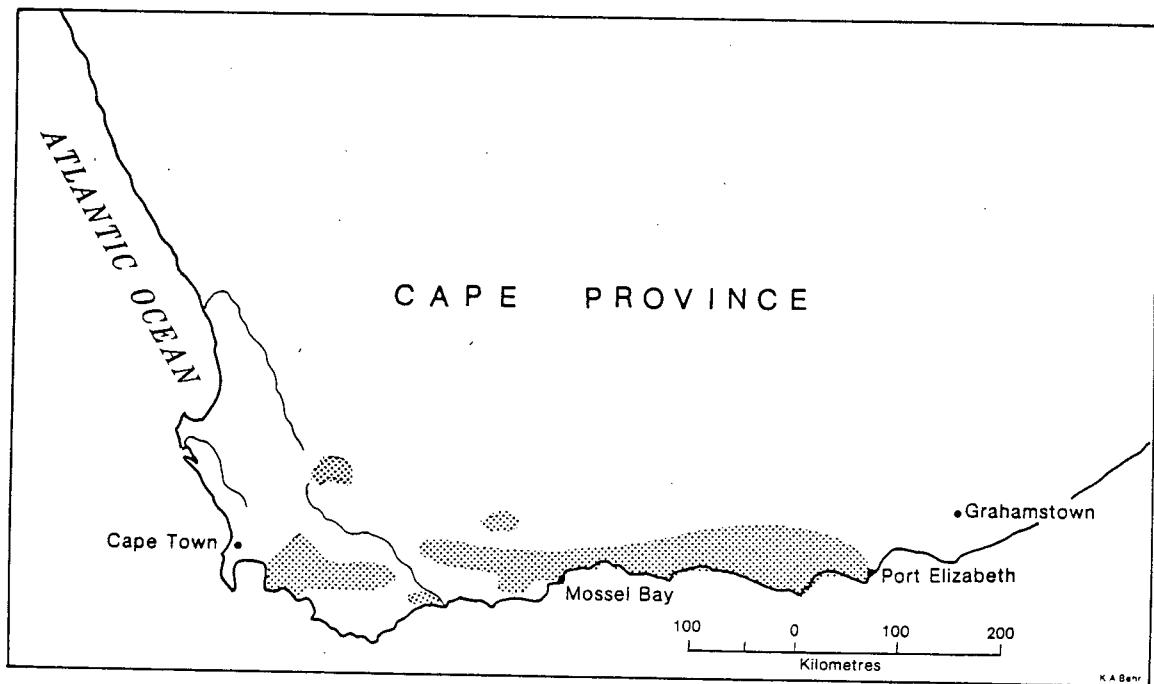
Fig. 3 Distribution of *Protea neriifolia* R. Br.(after Rourke 1980)

The reproductive buds start developing from November, immediately after shoot growth is complete, and are not subject to a period of inhibition, but proceed to develop inflorescences immediately. The flowering period is from February to November (Rourke 1980; Vogts 1982). As is the case in most other proteas, the varieties growing in the eastern Cape tend to flower in early to late summer, whereas the western populations flower in autumn and winter, from March to June.

The inflorescence is oval and the outer involucral bracts are irregular, hard and turn woody with age. The inner involucral bracts are oblong with a silky appearance, while the tips have a close woolly appearance with dense beards (Rourke 1980). The colour of the inner involucral bracts varies from creamy green to dull rose.

The inflorescence consists of many individual florets. After the inner involucral bracts have unfolded, anthesis takes place from the outside inward. In contrast to the inflorescences of some species, e.g. *P. repens* which close to form infructescences, the inflorescence of *P.neriifolia* remains open after fertilization has taken place. The seeds are only released after the involucral receptacle has been damaged by external factors such as fire or insects.
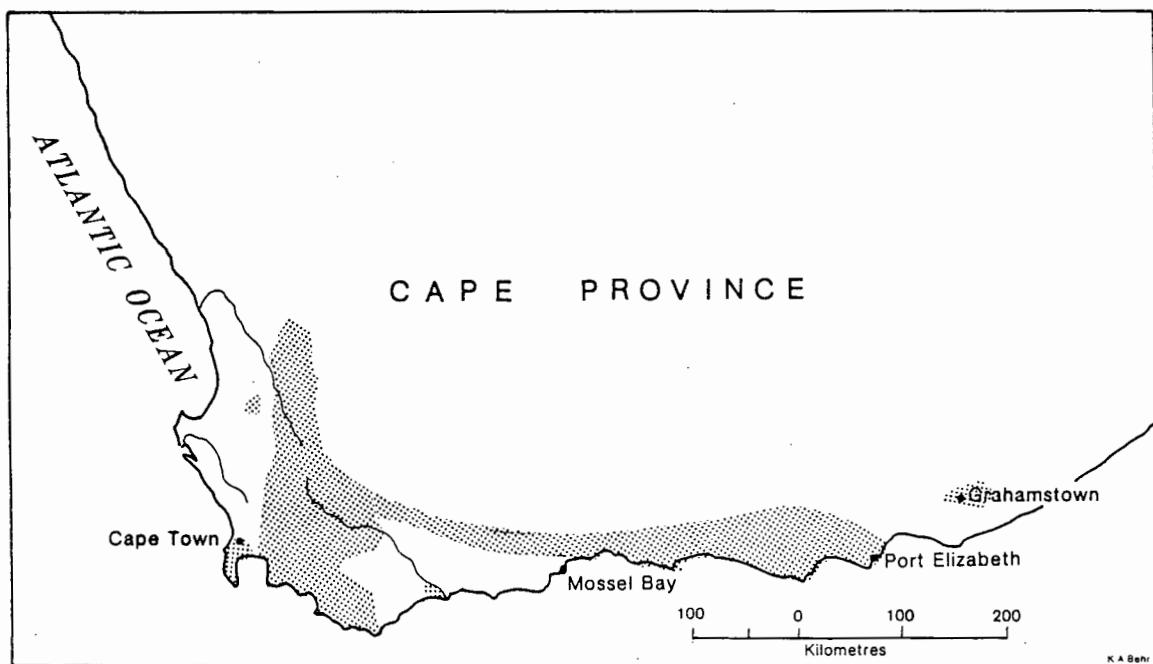
Fig. 4   *Distribution of Protea cynaroides* (L.) L. (after Rourke 1980)

Protea cynaroides (L.) L

Protea cynaroides is found in the south western, southern and eastern Cape Province on soils of Table Mountain sandstone origin or Witteberg quartzite. *P. cynaroides* grows in areas where the annual rainfall is 400 mm or more, and at altitudes of 200 to 1000 m (Rourke 1980). This species is one of the most widely distributed of the Cape proteas (Fig. 4) and characteristically does not form dense stands but under natural conditions occurs as individuals or in sparse colonies of 20 - 30 plants.

The height of a mature *P. cynaroides* varies from 0.3 to 2 m with an average height of 1 m and a crown diameter of 1.3 m (Vogts 1971). The height of the plant is not always an indication of its age, since the plants can regenerate from the underground lignotuber which, according to Vogts (1971), is part of the thickened root system.

P. cynaroides has two growth periods per year during the main growth cycle. According to Vogts (1971), the main cycle occurs at the same time as bud development, and shoot development ceases after the inflorescences open. New shoots can be formed from the axillary buds after 4-5 months. The distance between the bud scale rings could actually represent a year's growth, because not all shoots grow more than once a year. According to Vogts (1971), the growth season and the flowering periods of all the variants do not coincide.

The leaves of *P. cynaroides*, with their long stalks and smooth laminas are the most distinctive characteristic of the species. Three groups of *P. cynaroides* can be distinguished, viz. with (1) oval to round leaves, (2) broad elliptical leaves and (3) small elliptical leaves (Vogts 1971). The average surface area of oval and elliptical leaves is 3 500 mm^2. The flowering period is specific for each variety, and is a genetically stable characteristic. The flower bud development phase lasts for approximately six months (G. Jacobs personal communication). The inflorescences of *P. cynaroides* are the largest of the family Proteaceae, and each inflorescence consists of 150-650 florets (Vogts 1971). After the involucral bracts have unfolded, anthesis is initiated from the outside. This lasts for about three weeks until all the florets in the inflorescences have opened. The inflorescences are narrowly goblet-shaped to shallowly bowl-shaped. After fertilization, it takes approximately nine months for the seeds to ripen (Vogts 1971). The involucral bracts close during the ripening period, and seed is only released if the infructescence is damaged by wind or dried out by the sun (Vogts 1971).

Leucospermum cordifolium (Salisb. ex Knight) Fourcade

The genus *Leucospermum* consists of 48 taxa which are confined to southern Africa from Zimbabwe in the north to Namaqualand in the west (Vogts, 1982), although most of the species are found in a narrow belt in the southern Cape and coastal flats (Rourke 1972). *L. cordifolium* is one of the best-known species and is widely grown commercially. It has a round, shrub-like shape and grows to about 1.5 m high with a diameter of 2.0 m. It has a single main stem and horizontal branches. The population stretches from Kogelberg to Soetanysberg near Bredasdorp. The distribution area shown in Fig. 5 was compiled from data given by Rourke (1972). Plants grow only on acid soils originating from Table Mountain sandstone. The plants never form dominant stands.
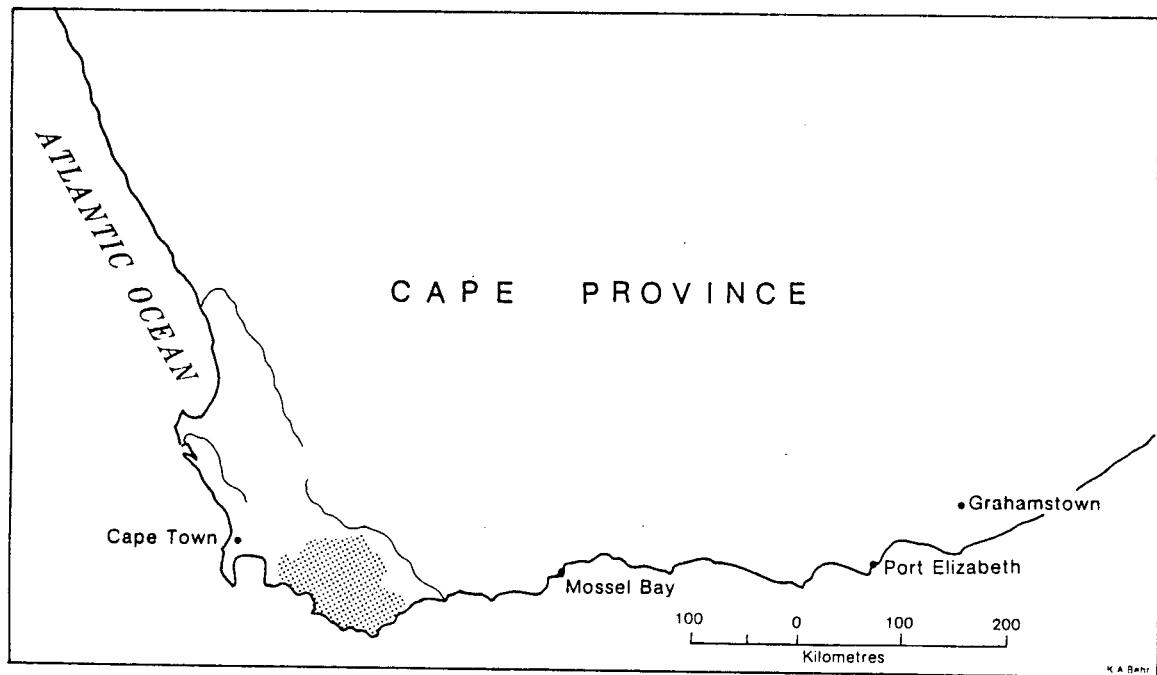
Fig. 5   Distribution of *Leucospermum cordifolium* (Salisb. ex Knight) Fourcade (from Rourke 1972)

Shoot growth commences in September, peaks in November and lasts until March. Reproductive development commences after shoot extension growth has terminated. The leaf size varies depending on its position on the shoot. Leaves become progressively smaller towards the apex of the shoot until directly below the inflorescences, and are almost scale-like (Rourke, 1972). The average size of the leaves is 1 355 mm^2. The leaves are densely pubescent at first but soon become glabrescent. Old leaves that do not drop turn dry, and these marcescent dead leaves remain on the shoots. The blade and most of the petiole die, but the tissues at the very base of the petiole, including the abscission zone, remain alive (G. Jacobs personal communication). Eventually the abscission zone will dry out, and abscission will occur after two years .

Inflorescences are formed on the youngest growth cycle and are initiated in March. Anthesis occurs from August to November. The inflorescences consist of small involucral bracts, conic involucral receptacles and florets. Each inflorescence is composed of the perianth, subsessile anthers, pollen presenter and style. After pollination, the nut-like seeds ripen and are released.
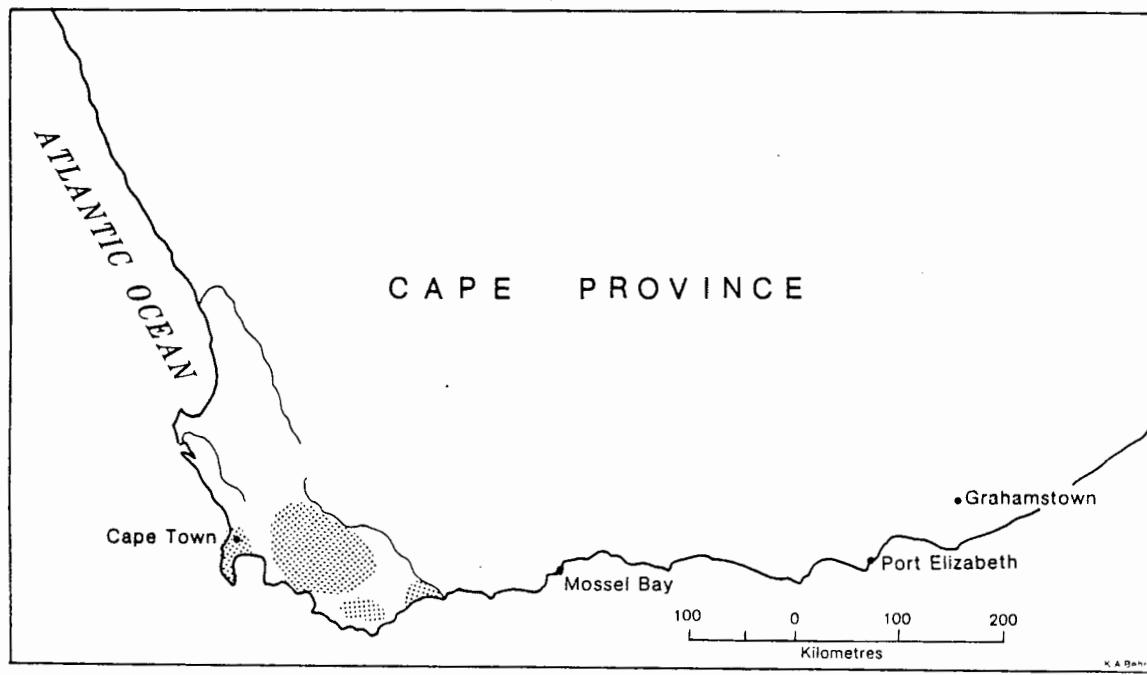
Fig. 6   Distribution of *Leucadendron laureolum* (Lamarck) Fourcade (from Williams 1972)

Leucadendron laureolum (Lamarck) Fourcade

Leucadendron and *Aulax* are the only dioecious genera of the family Proteaceae in southern Africa. According to Williams (1972), the genus *Leucadendron* consists of 91 species which, with the exception of a population in Pondoland and two subspecies in Natal, are restricted to the southern and south-western Cape Province (Vogts 1982). Williams (1972) divided the genus into two natural groups on the basis of fruit resemblance, namely section A, "*Leucadendron*", the nut-fruited species, and section B, "*Altosperma*", the flat-fruited species.

L. Laureolum is one of the species of the *Altosperma* section. Plants are found in fairly dense stands in association with other Fynbos plants from Cape Point eastward to Potberg, north-eastward to Jonaskop and northwards to Paarl Mountain (Fig. 6). This species is found growing on different soil types such as Cape granite, Table Mountain sandstone and limestone, with a pH ranging from acid to alkaline (Williams 1972). The male plant is approximately 2,0 m high and forms a symmetrical yellow bush, while the female plants are higher than 2m and asymmetrical with fewer branches but greener leaves.

Shoot growth is initiated in November, and the young pubescent shoots are slightly purple in colour. The young leaves are covered with a short velvety pubescence but become glabrescent later. The average area of the male and female leaves is 778 mm^2. A characteristic of L. laureolum is that the older branches are devoid of foliage. Leaf abscission occurs almost throughout the year, but a major drop of leaves takes place in summer, coinciding with the appearance of new leaves. The inflorescences of L. *laureolum* are concealed by long outer involucral leaves and yellow-greenish inner involucral leaves. The male inflorescences are up to 230 mm long and 211 mm in diameter, with florets arranged in 34 ascending spirals with about 22 flowers in each spiral (Williams 1972). The male inflorescences produce nectar, which releases an odour attractive to insects. At anthesis pollen is discharged, and the abortive stigma does not act as a pollen-presenter. The female inflorescences are 270 mm long and 140 mm in diameter with florets arranged in eight ascending spirals with about 10 flowers in each. Each floret has a woody floral bract. The spiral bracts continue growing to form the infructescence cone which retains the winged fruit (Williams 1972). This species flowers from June to July and the fruit is retained in the cone. The seeds are only released after a fire or mechanical damage to the infructescence.

MATERIAL AND METHODS

Insects have been collected on proteas in S.A. over a period of 30 years. This material is housed in the collection of the Fynbos Research Unit of Vegetable and Ornamental Plant Research Institute at Elsenburg. During 1982 and 1983 insects were collected over the distribution range of *P. repens* (Coetzee, 1984). From 1984 free-living insects of the five plant species described were collected by using "knock-down" and "beating" methods. A modification of the "knock-down" method, described by Southwood *et al.* (1982), was used. A sheet 1x1 m (1 m) or 0,5 x 0.5 (0,25 m^2), depending on the growth form of the plant, was placed under each of the plants. Each plant was then sprayed for four seconds with an aerosol formulation of dichlorvos. All insects falling onto the sheet after five minutes after spraying were collected. The "beating" method (Smithers 1981) entails the beating of the branches with a rod, causing the insects to be dislodged onto a beating sheet. Insects on flowers were collected by picking the inflorescences and placing the latter in plastic bags containing ethyl acetate as killing agent. After the insects were killed, they were removed from the inflorescences and, depending on size, were pinned or stored in 70% alcohol. Insects inhabiting the infructescences were collected from infructescences selected at random over their functional life-span. The infructescences were dissected and examined for insects. Specimens were classified into morphotype, and an accession number was given to each morphotype. Samples were sent to taxonomists for identification.

22

RESULTS

A. **Phytophagous insect fauna of *P. repens*.**

One hundred and thirteen insect morphotypes (hereafter referred to as species), representing 41 families were recorded from *P. repens*.

Flower visitors. Thirty eight insect species visited the inflorescences of *P. repens* to feed on the abundant nectar and pollen (Table 1a). Some of these insects are important pollen vectors (Coetzee & Giliomee 1985).

Thrips. Four species of three genera were present on *P. repens* (Table 1b) and were found not only in the inflorescences but also on the rest of the plant.

Endophagous insects. Ten borer species feed on *P. repens* (Table 1c). Seven species were seed predators that can destroy up to 80% of the seed reserves (Coetzee & Giliomee 1987 a, b). Two species of *Sphenoptera* (Buprestidae) are restricted to *P. repens* as host. Some species, e.g. Orophia sp. and the two *Sphenoptera* spp. can also bore into the receptacle, shoots or wood. Leaf damage found on *P. repens* indicated that two leaf miner species occured on the plant (Table 1c).

Ectophagous insects. Leaf feeders (in conjunction with leaf miners) can remove up to five percent of the leaf surface (Coetzee 1989e). Thirty-one ectophagous insect species were found on *P. repens* (Table 1d).

Sap-suckers. Table 1e lists 18 different mobile sap-suckers.
Scale insects and mealy-bugs were not very prevalent in the plant's natural habitat, but under cultivation, sedentary sap-suckers can reach epidemic proportions. Only one mealy-bug species and two scale insect species were found on *P. repens* (Table 1f).

Ants. Table 1g lists nine different ant species associated with *P. repens*, of which *Iridomyrmex humilis* is an alien species.

TABLE 1   PHYTOPHAGOUS INSECTS OF *P. repens*

TABLE 1a Flower visitors of *P. repens*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A815	Spermophagus		Bruchidae	Coleoptera
A172	Trichostetha	T.fascicularis (Linnaeus)	Scarabaeidae	Coleoptera
A61	Trichostetha	T.capensis	Scarabaeidae	Coleoptera
A708	Chirodica	C.elongata Baly	Chrysomelidae	Coleoptera
A706	Chirodica	C.chalcoptera Germar	Chrysomelidae	Coleoptera
A707	Chirodica	C.wollastoni Baly	Chrysomelidae	Coleoptera
A639	Chirodica		Chrysomelidae	Coleoptera
A640	Chirodica		Chrysomelidae	Coleoptera
A641	Chirodica		Chrysomelidae	Coleoptera
A722	Phyconomus	P.pallidus (Wollaston)	Rhizophagidae	Coleoptera
A721	Phyconomus	P.tricolor (Wollaston)	Rhizophagidae	Coleoptera
A653	Phyconomus		Rhizophagidae	Coleoptera
A759	Ceutorhynchus		Curculionidae	Coleoptera
A692	Derelomus		Curculionidae	Coleoptera
A1279	Isorhynchus		Curculionidae	Coleoptera
A667	Sibinia		Curculionidae	Coleoptera
A727	Platysoma	P.capense Wiedemann	Histeridae	Coleoptera
A730	Lytta	L.nitidula Fabricius	Meloidae	Coleoptera
A1031	Anisonyx	A.proletarius Péringuey	Melolonthidae	Coleoptera
A726	Diaplochelus	D.longipes (Fabricius)	Melolonthidae	Coleoptera
A658	Anaspis		Scraptiidae	Coleoptera
A714	Carpophilus	C.binotatus Murray	Nitidulidae	Coleoptera
A716	Carpophilus	C.dimidiatus(Fabricius)	Nitidulidae	Coleoptera
A718	Meligethes	M.rimulosus Reitter	Nitidulidae	Coleoptera
A719	Meligethes	M.viridulus Reitter	Nitidulidae	Coleoptera
A713	Pria	P.cinerascens Erichson	Nitidulidae	Coleoptera
A720	Soronia	S.marmorata (Erichson)	Nitidulidae	Coleoptera
A717	Olibrus	O.aeratus Champion	Phalacridae	Coleoptera
A118	Genuchus	G.hottentottus (Fabricius)	Scarabaeidae	Coleoptera
A865	Oxytelus	O.sculpturatus Gravenhorst	Staphylinidae	Coleoptera
A725	Phloeonomus		Staphylinidae	Coleoptera
A1850			Drosophilidae	Diptera
A1855			Drosophilidae	Diptera
A1866			Drosophilidae	Diptera
A781			Drosophilidae	Diptera
A926			Drosophilidae	Diptera
A874	Apis	A.mellifera Linnaeus	Apidae	Hymenoptera
A679	Hylaeus	H.immarginatus Alfken	Colletidae	Hymenoptera

TABLE 1b Thrips associated with *P. repens*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1890	Cylindrothrips	C.niger Moulton	Phlaeothripidae	Thysanoptera
A1894	Hoplandrothrips?	H.ellisi Bagnall	Phlaeothripidae	Thysanoptera
A1897	Synaptothrips	S.gezinae (Faure)	Thripidae	Thysanoptera
A1896	Synaptothrips	S.distinctus (Bagnall)	Thripidae	Thysanoptera

TABLE 1c Endophagous insects of *P. repens*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A997	Sphenoptera		Buprestidae	Coleoptera
A669	Sphenoptera		Buprestidae	Coleoptera
A118	Genuchus	G.hottentottus (Fabricius)	Scarabaeidae	Coleoptera
A458	Euderes	E.lineicollis (Wiedemann)	Curculionidae	Coleoptera
A358	Capys	C.alphaeus (Cramer)	Lycaenidae	Lepidoptera
A5	Orophia	O.ammopleura (Meyrick)	Oecophoridae	Lepidoptera
A22	Argyroploce		Torticidae	Lepidoptera
A9	Bostra	B.conspicualis Warren	Pyralidae	Lepidoptera
A277	Tinea		Tineidae	Lepidoptera
A504	Resseliella	R.proteae Gagné	Cecidomyiidae	Diptera
A698			Gracillariidae	Lepidoptera
A1168			Incurvariidae	Lepidoptera

24

TABLE 1d Ectophagous insects of *P. repens*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A626	Apion	A.angustithorax Wagner	Apionidae	Coleoptera
A997	Sphenoptera		Buprestidae	Coleoptera
A669	Sphenoptera		Buprestidae	Coleoptera
A1273	Cyphon		Helodidae	Coleoptera
A696	Monolepta	M.bioculata (Fabricius)	Chrysomelidae	Coleoptera
A587	Odontionopa	O.discolor (Lefeure)	Chrysomelidae	Coleoptera
A1027	Odontionopa	O.sericea (Gyllenhal)	Chrysomelidae	Coleoptera
A603	Xenoomorphus		Chrysomelidae	Coleoptera
A664	Afroleptops	A.coetzeei Oberprieler	Curculionidae	Coleoptera
A502	Eremnus	E.atratus(Sparrman)	Curculionidae	Coleoptera
A736	Eremnus	E.sp.near parcus Boheman	Curculionidae	Coleoptera
A458	Euderes	E.lineicollis (Wiedemann)	Curculionidae	Coleoptera
A1789	Synechops	S.nr.irregularis Marshall	Curculionidae	Coleoptera
A668	Tanyrhynchus	T.affaber Boheman	Curculionidae	Coleoptera
A793	Tanyrhynchus	T.tibialis Boheman	Curculionidae	Coleoptera
A690	Cardiophorus		Elateridae	Coleoptera
A1280	Cardiophorus		Elateridae	Coleoptera
A822	Heteroderes	H.pulchellus Candeze	Elateridae	Coleoptera
A695			Chrysomelidae	Coleoptera
A708	Pseudorupilia		Chrysomelidae	Coleoptera
A1028	Helodes		Helodidae	Coleoptera
A941	Helodes		Helodidae	Coleoptera
A1062	Adicocrita	A.koranata (Felder & Rogenhofer)	Geometridae	Lepidoptera
A1036	Semiothisa	S.semitecta (Walker)	Geometridae	Lepidoptera
A218	Catochria	C.catocaloides Herrich-Schäffer	Notodontidae	Lepidoptera
A705	Plutella	P.xylostella (Linnaeus)	Plutellidae	Lepidoptera
A1164	Crambus	C.sparsellus Walker	Pyralidae	Lepidoptera
A1037	Nomophila	N.noctuella (Denis & Schiffermüller	Pyralidae	Lepidoptera
A1696	Imbrasia	I.cytherea (Fabricius)	Saturniidae	Lepidoptera
A1069			Tettigoniidae	Orthoptera
A631	Oecanthus		Tettigoniidae	Orthoptera

TABLE 1e Ectophytic sap-suckers of *P. repens*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A850			Anthocoridae	Hemiptera
A866			Alydidae	Hemiptera
A1197	Gonocerus		Coreidae	Hemiptera
A1054			Fulgoroidea	Hemiptera
A936			Fulgoroidea	Hemiptera
A1664			Lygaeidae	Hemiptera
A682	Poeantius	nr. velox Bergroth	Lygaeidae	Hemiptera
A1254	Oxycarenus	O.maculatus Stål	Lygaeidae	Hemiptera
A262	Caprhiobia	C.similis Scudder	Lygaeidae	Hemiptera
A208	Macchiademus	M.diplopterus(Distant)	Lygaeidae	Hemiptera
A32	Nysius		Lygaeidae	Hemiptera
A749			Miridae	Hemiptera
A684			Miridae	Hemiptera
A879			Miridae	Hemiptera
A545	Antestiopsis	A.variegata Thunberg	Pentatomidae	Hemiptera
A680	Eurys	E.dilatatus(Thunberg)	Pentatomidae	Hemiptera
A772	Orthoschizops	O.lineaticeps Stål	Pentatomidae	Hemiptera
A554	Thelorus	T.costata (Thunberg)	Pentatomidae	Hemiptera

TABLE 1f   Sedentary sap-suckers of *P. repens*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1736	Ledaspis	L.distincta (Leonardi)	Diaspididae	Hemiptera
A426	Misericoccus		Pseudococcidae	Hemiptera
A1780	Psylla		Psyllidae	Hemiptera

TABLE 1g   Ants associated with *P. repens*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1812	Camponotus	C.niveosetotus Mayr	Formicidae	Hymenoptera
A1813	Camponotus	C.rufoglaucus (Jerdon)	Formicidae	Hymenoptera
A1814	Camponotus	C.werthi Forel	Formicidae	Hymenoptera
A1816	Crematogaster	C.liengmei Forel	Formicidae	Hymenoptera
A656	Iridomyrmex	I.humilis (Mayr)	Formicidae	Hymenoptera
A1818	Meranoplus	M.peringueyi Emery	Formicidae	Hymenoptera
A1820	Pheidole	P.sp.prop.capensis Mayr	Formicidae	Hymenoptera
A1821	Plagiolepis	P.jouberti Forel	Formicidae	Hymenoptera
A1822	Technomyrmex	T.albipes (Smith)	Formicidae	Hymenoptera

TABLE 2   PHYTOPHAGOUS INSECTS OF *P. neriifolia*

TABLE 2a   Flower visitors of *P. neriifolia*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A815	Spermophagus		Bruchidae	Coleoptera
A246	Trichostetha	T.capensis (Linnaeus)	Scarabaeidae	Coleoptera
A172	Trichostetha	T.fascicularis (Linnaeus)	Scarabaeidae	Coleoptera
A706	Chirodica	C.chalcoptera Germar	Chrysomelidae	Coleoptera
A707	Chirodica	C.wollastoni Baly	Chrysomelidae	Coleoptera
A1524			Cucujidae	Coleoptera
A1488	Phyconomus		Scraptiidae	Coleoptera
A759	Ceutorhynchus		Curculionidae	Coleoptera
A925	Ceutorhynchus		Curculionidae	Coleoptera
A692	Derelomus		Curculionidae	Coleoptera
A727	Platysoma	P.capense Wiedemann	Histeridae	Coleoptera
A1095	Dichelus		Melolonthidae	Coleoptera
A1096	Dichelus		Melolonthidae	Coleoptera
A713	Pria	P.cinerascens Erichson	Nitidulidae	Coleoptera
A717	Olibrus	O.aeratus Champion	Phalacridae	Coleoptera
A118	Genuchus	G.hottentottus (Fabricius)	Scarabaeidae	Coleoptera
A1649			Staphylinidae	Coleoptera
A919	Conosoma		Staphylinidae	Coleoptera
A865	Oxytelus	O.sculptus	Staphylinidae	Coleoptera
A725	Phloeonomus		Staphylinidae	Coleoptera
A1850			Drosophilidae	Diptera
A1866			Drosophilidae	Diptera
A781			Drosophilidae	Diptera
A926			Drosophilidae	Diptera
A874	Apis	A.mellifera L.	Apidae	Hymenoptera
A635	Hylaeus	H.immarginatus (Alfken)	Colletidae	Hymenoptera
A633	Nothylaeus		Colletidae	Hymenoptera
A632	Lasioglossum		Halictidae	Hymenoptera

B.   Phytophagous insect fauna of *P. neriifolia*

The phytophagous insects of *P. neriifolia* are represented by 48 families, including 114 species.

Flower visitors. Twenty-eight insect species visited the inflorescences of *P. neriifolia* to feed on the nectar and pollen (Table 2a). These insects are important pollen vectors (Coetzee pers. obs.).

Thrips. Six species representing six genera were found on *P. neriifolia* (Table 2 b). The thrips that were found in the inflorescences complete their whole life cycle there and are one of the early colonizers of the young inflorescences.

Endophagous insects. Nine borer species fed on *P. neriifolia* (Table 2c). Seven of these species are seed predators and some, e.g. *O. ammopleura*, bore into young shoots. *Bostra conspicualis* larvae were found in the infructescences, but the larvae feed mainly on leaves. Two different leaf miners occured on the plant.

Sap-feeding insects. Table 2e lists 17 ectophytic sap-sucker species. The family Lygaeidae is mostly associated with achenes in the infructescences. The *Psylla* species on *P. neriifolia* do not form galls. One mealy bug (Pseudococcidae) and two scale insect species, of the Coccidae and Diaspididae respectively, are occasionally found on *P. neriifolia* (Table 2e)

Ants. Table 2g lists seven different ant species which are found on *P. neriifolia*

TABLE 2b   Thrips associated with *P. neriifolia*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1890	Cylindrothrips	C.niger Moulton	Phlaeothripidae	Thysanoptera
A1892	Haplothrips	H.nigricornis Bagnall	Phlaeothrididae	Thysanoptera
A1894	Hoplandrothrips	H.ellisi Bagnall	Phlaeothripidae	Thysanoptera
A1891	Frankliniella	F.schultzei (Trybom)	Thripidae	Thysanoptera
A1895	Limothrips	L.cerealium Haliday	Thripidae	Thysanoptera
A1896	Synaptothrips	S.distinctus (Bagnall)	Thripidae	Thysanoptera

TABLE 2c   Endophagous insects of *P. neriifolia*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A977	Sphenoptera		Buprestidae	Coleoptera
A458	Euderes	E.lineicollis (Wiedemann)	Curculionidae	Coleoptera
A118	Genuchus	G.hottentottus (Fabricius)	Scarabaeidae	Coleoptera
A504	Resseliella	R.proteae Gagnè	Cecidomyiidae	Diptera
A22	Argyroploce		Tortricidae	Lepidoptera
A638	Synanthedon	C.platyuriformis (Walker)	Sesiidae	Lepidoptera
A358	Capys	C.alphaeus (Cramer)	Lycaenidae	Lepidoptera
A5	Orophia	O.ammopleura (Meyrick)	Oecophoridae	Lepidoptera
A9	Bostra	B.conspicualis Warren	Pyralidae	Lepidoptera
A1688			Incurvariidae	Lepidoptera
A13	Phyllocnistis		Phyllocnistidae	Lepidoptera

TABLE 2d Ectophagous insects of *P. neriifolia*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A977	Sphenoptera		Buprestidae	Coleoptera
A1273	Cyphon		Helodidae	Coleoptera
A886	Oulema	O.erythrodera (Lacordaire)	Chrysomelidae	Coleoptera
A1027	Odontionopa	O.sericea (Gyllenhal)	Chrysomelidae	Coleoptera
A603	Xenoomorphus		Chrysomelidae	Coleoptera
A664	Afroleptops	A.coetzeei Oberprieler	Curculionidae	Coleoptera
A1281	Ceutorhynchinae		Curculionidae	Coleoptera
A458	Euderes	E.lineicollis (Wiedemann)	Curculionidae	Coleoptera
A1302	Phlyctinus	P.callosus Schoenherr	Curculionidae	Coleoptera
A1789	Synechops	S.nr.irregularis Marshall	Curculionidae	Coleoptera
A793	Tanyrhynchus		Curculionidae	Coleoptera
A903	Notiophygus	N.parvulus Gory	Discolomidae	Coleoptera
A690			Elateridae	Coleoptera
A1280	Cardiotarsus		Elateridae	Coleoptera
A1028			Helodidae	Coleoptera
A1094	Mauna	M.filia (Cramer)	Geometridae	Lepidoptera
A988	Prasinocyma		Geometridae	Lepidoptera
A1036	Semiothisa	S.semitecta (Walker)	Geometridae	Lepidoptera
A218	Catochria	C.catocaloides Herrich-Schäffer	Notodontidae	Lepidoptera
A1696	Imbrasia	I.cytherea (Fabricius)	Saturniidae	Lepidoptera
A770			Tettigoniidae	Orthoptera

TABLE 2e Ectophytic sap-suckers of *P. neriifolia*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1698	Elasmopoda	E.valga (L.)	Coreidae	Hemiptera
A749			Fulgoridae	Hemiptera
A1644			Fulgoridae	Hemiptera
A980			Fulgoridae	Hemiptera
A1054			Fulgoridae	Hemiptera
A262	Caprhiobia	C.similis Scudder	Lygaeidae	Hemiptera
A208	Macchiademus	M.diplopterus (Distant)	Lygaeidae	Hemiptera
A892	Oxycarenus	O.hyalinipennis (Costa)	Lygaeidae	Hemiptera
A624	Oxycarenus	O.maculatus Stål	Lygaeidae	Hemiptera
A32	Nysius		Lygaeidae	Hemiptera
A1634			Miridae	Hemiptera
A764			Miridae	Hemiptera
A684			Miridae	Hemiptera
A879			Miridae	Hemiptera
A554	Thelorus	T.costata (Thunberg)	Pentatomidae	Hemiptera
A545	Antestiopsis	A.variegata (Thunberg)	Pentatomidae	Hemiptera
A1088			Psyllidae	Hemiptera

TABLE 2f Sedentary sap-suckers of *P. neriifolia*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1013	Delottococcus	D.quaesitus Group	Pseudococcidae	Hemiptera
A73	Marsipococcus	M.proteae (Brain)	Coccidae	Hemiptera
A409	Aspidiotus	A.nerii Bouché	Diaspididae	Hemiptera

TABLE 2g Ants associated with *P. neriifolia*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1809	Acantholepis	A.capensis Mayr	Formicidae	Hymenoptera
A1810	Anoplolepis	A.custodiens (Smith)	Formicidae	Hymenoptera
A1812	Camponotus	C.niveosetosus Mayr	Formicidae	Hymenoptera
A1817	Crematogaster	C.peringueyi Emery	Formicidae	Hymenoptera
A1816	Crematogaster	C.liengmei (Forel)	Formicidae	Hymenoptera
A656	Iridomyrmex	I.humilis (Mayr)	Formicidae	Hymenoptera
A1821	Plagiolepis	P.jouberti Forel	Formicidae	Hymenoptera

C.   Phytophagous insect fauna of *P. cynaroides*

The phytophagous insects of *P. cynaroides* were represented by 39 families comprising 110 species or morphotypes.

Flower visitors. The large inflorescences were visited by 19 insect species (Table 3a). Chewers were also found in the inflorescences where they feed on the modified leaves, the inner involucral bracts.

Thrips. Three species were found on *P. cynaroides* (Table 3b).

Endophagous insects. Nine borer species were found to attack *P. cynaroides* (Table 3c). Seven of the species were seed predators and/or stem borers. Two species were leaf miners.

Ectophagous insects. Although only 19 chewing species have been found on the leaves of *P. cynaroides* (Table 3d), they (in conjunction with the leafminers), were capable of destroying more than 15% of the leaf surface (Coetzee 1989a)

Sap-suckers. Seventeen species were ectophytic sap-suckers (Table 3e) and two sedentary sap-suckers were also recorded on *P. cynaroides* (Table 3f).

Ants. Three species were associated with *P. cynaroides*.

TABLE 3a   Flower visitors of *P. cynaroides*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A706	Chirodica	C.chalcoptera Germ	Chrysomelidae	Coleoptera
A172	Trichostetha	T.fascicularis (Linnaeus)	Scarabaeidae	Coleoptera
A721	Phyconomus	P.tricolor (Wollaston)	Rhizophagidae	Coleoptera
A925	Ceutorhynchinae		Curculionidae	Coleoptera
A726	Diaplochelus	D.longipes (Fabricius)	Melolonthidae	Coleoptera
A1064	Knysna	K.humeralis (Burmeister)	Melolonthidae	Coleoptera
A714	Carpophilus	C.binotatus Murray	Nitidulidae	Coleoptera
A713	Pria	P.cinerascens Erichson	Nitidulidae	Coleoptera
A717			Phalacridae	Coleoptera
A118	Genuchus	G.hottentottus (Fabricius)	Scarabaeidae	Coleoptera
A975			Scraptiidae	Coleoptera
A865	Oxytelus	O.sculpturatus Gravenhorst	Staphylinidae	Coleoptera
A725	Phloeonomus		Staphylinidae	Coleoptera
A1866			Drosophilidae	Diptera
A781			Drosophilidae	Diptera
A874	Apis	A.mellifera	L.Apidae	Hymenoptera
A632			Apidae	Hymenoptera
A633			Apidae	Hymenotera
A635	Hylaeus		Colletidae	Hymenotera

TABLE 3b   Thrips associated with *P. cynaroides*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1892	Haplothrips	H.nigricornis Bagnall	Phlaeothripidae	Thysanoptera
A1898	Talitha	T.glandifera Faure	Phlaeothripidae	Thysanoptera
A1891	Frankliniella	F.schultzei (Trybom)	Thripidae	Thysanoptera

TABLE 3c Endophagous insects of *P. cynaroides*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1291	Sphenoptera		Buprestida	Coleoptera
A118	Genuchus	G.hottentottus (Fabricius)	Scarabaeidae	Coleoptera
A358	Capys	C.alphaeus (Cramer)	Lycaenidae	Lepidoptera
A5	Orophia	O.ammopleura Meyrick	Oecophoridae	Lepidoptera
A22	Argyroploce		Tortricidae	Lepidoptera
A9	Bostra	B.conspicualis Warren	Pyralidae	Lepidoptera
A277	Tinea		Tineidae	Lepidoptera
A53	Protaephagus	P.capensis ScobleIn	curvariidae	Lepidoptera
A13	Phyllocnistis		Phyllocnistidae	Lepidoptera

TABLE 3d Ectophagous insects of *P. cynaroides*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1291	Sphenoptera		Buprestidae	Coleoptera
A1273	Cyphon		Helodidae	Coleoptera
A886	Oulema	O.erythrodera (Lacordaire)	Chrysomelidae	Coleoptera
A1033	Eremnus	E.nr.atratus (Sparrman)	Curculionidae	Coleoptera
A962	Hexatmetus		Apionidae	Coleoptera
A827	Hypsomus		Curculionidae	Coleoptera
A968	Oosomus		Curculionidae	Coleoptera
A1789	Synechops	S.nr. Marshall	Curculionidae	Coleoptera
A793	Tanyrhynchus		Curculionidae	Coleoptera
A791	Tanyrhynchus		Curculionidae	Coleoptera
A1280	Cardiotarsus		Elateridae	Coleoptera
A17			Gelechiidae	Lepidoptera
A2671	llal	I.nefanda Warren	Geometridae	Lepidoptera
A3			Limacididae	Lepidoptera
A218	Catochria	C.catocaloides Herrich-Schäffer	Notodontidae	Lepidoptera
A705	Plutella	P.xylostella (Linnaeus)	Fulutellidae	Lepidoptera
A169	Imbrasia	I.cytherea (Fabricius)	Saturniidae	Lepidoptera
A1034			Acrididae	Orthoptera
A1069	Plangia	P.graminia	Tettigoniidae	Orthoptera

TABLE 3e Ectophytic sap-suckers of *P. cynaroides*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A837			Aphrophoridae	Hemiptera
A15			Cercopidae	Hemiptera
A1093			Coreidae	Hemiptera
A12	Elasmopoda	E.valga (L.)	Coreidae	Hemiptera
A1054			Fulgoroidae	Hemiptera
A749			Fulgoroidae	Hemiptera
A936			Fulgoroidae	Hemiptera
A980			Fulgoroidae	Hemiptera
A545	Antestiopsis	A.variegata (Thunberg)	Pentatomidae	Hemiptera
A680	Eurys	E.dilitatus (Thunberg)	Pentatomidae	Hemiptera
A451	Nezara		Pentatomidae	Hemiptera
A554	Thelorus	T.costata (Thunberg)	Pentatomidae	Hemiptera
A891	Cysteochila	C.incolana Drake	Tingidae	Hemiptera
A262	Caprhiobia		Lygaeidae	Hemiptera
A32	Nysius		Lygaeidae	Hemiptera
A892	Oxycarenus	O.hyalinipennis (Costa)	Lygaeidae	Hemiptera
A624	Oxycarenus	O.maculatus stål	Lygaeidae	Hemiptera

TABLE 3f Sedentary sap-suckers of *P. cynaroides*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A263	Delottococcus	D.nr.proteae (Hall)	Pseudococcidae	Hemiptera
A42	elottococcus		Pseudococcidae	Hemiptera

TABLE 3g Ants associated with *P. cynaroides*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1816	Crematogaster	C.liengmei (Forel)	Formicidae	Hymenoptera
A656	Iridomyrmex	I.humilis (Mayr)	Formicidae	Hymenoptera
A1822	Technomyrmex	T.albipes (Smith)	Formicidae	Hymenoptera

D.   Phytophagous insect fauna of *L. cordifolium*

The phytophagous insects of *L. cordifolium* were represented by 61 species belonging to 31 families.

Flower visitors. Sixteen insect species visited the inflores-cences of *L. cordifolium* for nectar and pollen (Table 4a). Although *L. cordifolium* is regarded as an ornitho-philous species, insects can act as pollen vectors in the absence of birds, but the proportion seed-set is lower (Coetzee, unpublished data).

Thrips. Three Thysanoptera species (Table 4b) were found on *L. cordifolium.*

Endophagous insects. Five borer species were found *L. cordifolium*, three of these belong to the family Buprestidae (Table 4c). No leafminers were present.

Ectophagous insects. Although the leaves of young *L. cordifolium* plants are highly pubescent, 17 insect species chewed on the leaves (Table 4b).

Sap-suckers. Seventeen free living sap-sucker species were associated with *L. cordifolium* (Table 4e) and two sedentary species (Table 4.f).

Ants. Eight species were associated with *L. cordifolium*.

TABLE 4a   Flower visitors of *L. cordifolium*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A815	Spermophagus		Bruchidae	Coleoptera
A61	Trichostetha	T.signata Fabricius	Scarabaeidae	Coleoptera
A991			Chrysomelidae	Coleoptera
A966			Chrysomelidae	Coleoptera
A1060	Isorhynchus		Curculionidae	Coleoptera
A1279	Isorhynchus		Curculionidae	Coleoptera
A1072	Dichelus		Melolonthidae	Coleoptera
A1064	Knysna	K.humeralis (Burmeister)	Melolonthidae	Coleoptera
A1077			Melyridae	Coleoptera
A1773			Mordellidae	Coleoptera
A713	Pria	P.cinerascens Erichson	Nitidulidae	Coleoptera
A717	Olibrus	O.aeratus Champion	Phalacridae	Coleoptera
A781			Drosophilidae	Diptera
A926			Drosophilidae	Diptera
A1855			Drosophilidae	Diptera
A874	Apis	A.mellifera	L.Apidae	Hymenoptera

TABLE 4b   Thrips associated with *L. cordifolium*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1889	Aeolothrips	A.?brevic Bagnall	Aeolothripidae	Thysanoptera
A1890	Cylindrothrips	C.niger Moulton	Phlaeothripidae	Thysanoptera
A1892	Haplothrips	H.?nigric Bagnall	Phlaeothripidae	Thysanoptera

TABLE 4c   Endophagous insects of *L. cordifolium*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1182			Cecidomyiidae	Diptera
A967	Psiloptera	P.albomarginata Herbst	Buprestidae	Coleoptera
A1298	Sphenoptera		Buprestidae	Coleoptera
A1299	Sphenoptera		Buprestidae	Coleoptera
A992			Oecophoridae	Lepidoptera

TABLE 4d Ectophagous insects of *L. cordifolium*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A967	Psiloptera	P.albomarginata Herbst	Buprestidae	Coleoptera
A1298		Sphenoptera	Buprestidae	Coleoptera
A1299	Sphenoptera		Buprestidae	Coleoptera
A1273	Cyphon		Helodidae	Coleoptera
A603	Xenoomorphus		Chrysomelidae	Coleoptera
A502	Eremnus	E.atratus (Sparrman)	Curculionidae	Coleoptera
A1302	Phlyctimus	P.callosus Schoenherr	Curculionidae	Coleoptera
A791	Tanyrhynchus		Curculionidae	Coleoptera
A822			Elateridae	Coleoptera
A1280	Cardiotarsus		Elateridae	Coleoptera
A1028			Helodidae	Coleoptera
A993	Mauna		Geometridae	Lepidoptera
A218	Catochria	C.catocaloides Herrich-Schäffer	Notodontidae	Lepidoptera
A889	Diocosma		Oecophoridae	Lepidoptera
A1696	Imbrasia	I.cytherea (Fabricius)	Saturniidae	Lepidoptera
A500	Epichoristodes	E.acerbella (Walker)	Tortricidae	Lepidoptera
A631	Oecanthus		Tettigoniidae	Orthoptera

TABLE 4e Ectophytic sap-suckers of *L. cordifolium*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A866			Alydidae	Hemiptera
A837			Aphrophoridae	Hemiptera
A1805			Coreidae	Hemiptera
A843			Coreidae	Hemiptera
A749			Fulgoridae	Hemiptera
A1054			Fulgoridae	Hemiptera
A982	Dismegistus	D.fimbriatus Thunberg	Pentatomidae	Hemiptera
A1802	Veterna	V.aberrans Germ	Pentatomidae	Hemiptera
A761			Lygaeidae	Hemiptera
A1664			Lygaeidae	Hemiptera
A262	Caprhiobia	C.similis Scudder	Lygaeidae	Hemiptera
A32	Nysius		Lygaeidae	Hemiptera
A624	Oxycarenus	O.maculatus Stål	Lygaeidae	Hemiptera

TABLE 4f Sedentary sap-suckers *L. cordifolium*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1009	Marsipococcus	M.proteae (Brain)	Coccidae	Hemiptera
A490	Saissetia	S.oleae (Olivier)	Coccidae	Hemiptera

TABLE 4g Ants associated with *L. cordifolium*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1809	Acantholepis	A.capensis Mayr	Formicidae	Hymenoptera
A1812	Camponotus	C.niveosetosus Mayr	Formicidae	Hymenoptera
A1813	Camponotus	C.rufoglaucus (Jerdon)	Formicidae	Hymenoptera
A1816	Crematogaster	C.liengmei (Forel)	Formicidae	Hymenoptera
A656	Iridomyrmex	I.humilis (Mayr)	Formicidae	Hymenoptera
A1822	Technomyrmex	T.albipes (Smith)	Formicidae	Hymenoptera
A1823	Tetramorium	T.erectum Emery	Formicidae	Hymenoptera
A1824	Tetraponera	T.clypeata (Emery)	Formicidae	Hymenoptera

E. Phytophagous insect fauna of *L. laureolum*

The phytophagous insect fauna of *L. laureolum* was represented by 79 species from 39 families.

Flower visitors. *L. laureolum* (a dioecious species) is insect pollinated, and 25 insect species are associated with the inflorescences (Table 5a). Not all the species were exclusively nectar or pollen feeders: some, e.g. the Curculionidae and Chrysomelidae, also fed on the involucral bracts, but because they carried pollen and also fed on pollen and/or nectar, these species were regarded as flower visitors.

Thrips. Only two Thysanoptera species were found on *L. laureolum* (Table 5 b).

Endophagous insects. Five insect species bored into in-florescences, infructescences and shoots of *L. laureolum*. Two leafminer species were also found on *L. laureolum* (Table 5c).

Ectophagous insects. Although 17 species of leaf feeders (Table 5d) were found on *L. laureolum*, they only removed two percent of the leaf surface (Coetzee 1989a).

Sap-suckers. Seventeen free living sap-sucker species (Table 5e) were associated with *L. laureolum*, but no sedentary sap-sucker.

Ants. Twelve species were associated with *L. laureolum* (Table 5f)

33

TABLE 5 PHYTOPHAGOUS INSECTS OF *L. laureolum*

TABLE 5a   Flower visitors of *L. laureolum*

ACCESSON NO.	GENUS	SPECIES	FAMILY	ORDER
A1784			Alleculidae	Coleoptera
A692	Derelomus		urculionidae	Coleoptera
A1284	Nanodes		Apionidae	Coleoptera
A1793			Chrysomelidae	Coleoptera
A247			Chrysomelidae	Coleoptera
A1786	Chirodica		Chrysomelidae	Coleoptera
A970	Chirodica	C.fulvipes Baly	Chrysomelidae	Coleoptera
A1756	Baridinae		Curculionidae	Coleoptera
A1282	Isorhynchus		Curculionidae	Coleoptera
A969	Isorhynchus		Curculionidae	Coleoptera
A1279	Isorhynchus		Curculionidae	Coleoptera
A968	Oosomus		Curculionidae	Coleoptera
A1776			Mordellidae	Coleoptera
A614			Mordellidae	Coleoptera
A1773	Anaspis		Scraptiidae	Coleoptera
A716	Carpophilus	C.dimidiatus (Fabricius)	Nitidulidae	Coleoptera
A713	Pria	P.cinerascens Erichson	Nitidulidae	Coleoptera
A1294			Phalacridae	Coleoptera
A717	Olibrus	O.aeratus Champion	Phalacridae	Coleoptera
A865	Oxytelus	O.sculpturatus Gravenhorst	Staphylinidae	Coleoptera
A1850			Drosophilidae	Diptera
A1855			Drosophilidae	Diptera
A1866			Drosophilidae	Diptera
A781			Drosophilidae	Diptera
A874	Apis	A.mellifera L.	Apidae	Hymenoptera

TABLE 5b   Thrips associated with *L. laureolum*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1890	Cylindrothrips	C.niger Moulton	Phlaeothripidae	Thysanoptera
A1893	Helenothrips	H.tinctus	Thripidae	Thysanoptera

TABLE 5c   Endophagous insects of *L. laureolum*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1296	Sphenoptera		Buprestidae	Coleoptera
A1300	Sphenoptera		Buprestidae	Coleoptera
A690			Elateridae	Coleoptera
A914			Elateridae	Coleoptera
A1280	Cardiotarsus		Elateridae	Coleoptera
A1041			Microlepidoptera	Lepidoptera
A698			Nepticulidae	Lepidoptera

TABLE 5d   Ectophages insects of *L. laureolum*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A875	Apiomorphus		Apionidae	Coleoptera
A1296	Sphenoptera		Buprestidae	Coleoptera
A1300	Sphenoptera		Buprestidae	Coleoptera
A1750			Chrysomelidae	Coleoptera
A1793			Chrysomelidae	Coleoptera
A1273	Cyphon		Holodidae	Coleoptera
A603	Xenoomorphus		Chrysomelidae	Coleoptera
A942	Perapion	P.antiquum (Gyllenhal)	Apionidae	Coleoptera
A1302	Phlyctinus	P.callosus Schoenherr	Curculionidae	Coleoptera
A791	Tanyrhynchus		Curculionidae	Coleoptera
A903	Notiophygus	N.parvulus Gory	Discolomidae	Coleoptera
A690			Elateridae	Coleoptera
A914			Elateridae	Coleoptera
A1280	Cardiotarsus		Elateridae	Coleoptera
A218	Catochria	C.catocaloides Herrich-Schäffer	Notodontidae	Lepidoptera
A1696	Imbrasia	I.cytherea (Fabricius)	Saturniidae	Lepidoptera
A631	Oecanthus		Tettigoniidae	Orthoptera

TABLE 5e   Ectophytic sap-suckers of *L. laureolum*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A837			Aphrophoridae	Hemiptera
A1805			Coreidae	Hemiptera
A749			Fulgoridae	Hemiptera
A1073			Fulgoridae	Hemiptera
A980			Fulgoridae	Hemiptera
A208			Lygaeidae	Hemiptera
A624	Oxycarenus	O.maculatus (Stål)	Lygaeidae	Hemiptera
A892	Oxycarenus	O.hyalinnipennis (Costa)	Lygaeidae	Hemiptera
A32	Nysius		Lygaeidae	Hemiptera
A879			Miridae	Hemiptera
A1796			Miridae	Hemiptera
A545	Antestiopsis	A.variegata (Thunberg)	Pentatomidae	Hemiptera
A982	Dismegistus	D.fimbriatus Thunberg	Pentatomidae	Hemiptera
A974	Solenostethium	S.liligerum (Thunberg)	Pentatomidae	Hemiptera
A1088			Psyllidae	Hemiptera
A1780			Psyllidae	Hemiptera
A978	Cenaeus	C.carnifex (Fabr)	Pyrrhocoridae	Hemiptera

TABLE 5f   Ants of *L. laureolum*

ACCESSION NO.	GENUS	SPECIES	FAMILY	ORDER
A1809	Acantholepis	A.capensis Mayr	Formicidae	Hymenoptera
A1810	Anoplolepis	A.custodiens (Smith)	Formicidae	Hymenoptera
A1812	Camponotus	C.niveosetosus Mayr	Formicidae	Hymenoptera
A1813	Camponotus	C.rufoglaucus (Jerdon)	Formicidae	Hymenoptera
A1816	Crematogaster	C.liengmei Forel	Formicidae	Hymenoptera
A656	Iridomyrmex	I.humilis (Mayr)	Formicidae	Hymenoptera
A1825	Monomorium	M.braunsi Mayr	Formicidae	Hymenoptera
A1819	Myrmicaria	M.nigra (Mayr)	Formicidae	Hymenoptera
A1820	Pheidole	P.sp.prop.capensis Mayr	Formicidae	Hymenoptera
A1821	Plagiolepis	P.jouberti Forel	Formicidae	Hymenoptera
A1822	Technomyrmex	T.albipes (Smith)	Formicidae	Hymenoptera
A1824	Tetraponera	T.clypeata (Emery)	Formicidae	Hymenoptera

35

DISCUSSION

As no other insect faunal lists of fynbos host plants have been compiled, it was difficult to determine whether insects are specific to Proteaceae from data gathered during this study.

The flower-visitor guild contributed the most species to the phytophagous fauna of the proteaceous species studied. This guild contained important pollen vectors. Most individuals that visited the inflorescences were Coleoptera. Other insects, (e.g. Apidae and Colletidae) that occured in small numbers were, however, also important as pollen vectors due to their relatively greater mobility which enabled them to visit a large number of plants and thus promote gene flow.

The Thysanoptera that were recorded on the Proteaceae were polyphagous; according to Jacot-Guillarmod (1937), these species are also found on other host plants.

The endophagous guild consisted of lepidopterous, coleopterous and dipterous borers and lepidopterous leaf miners. The endophagous insects were stenophagous (i.e. host restricted to the same genus [Goeden & Ricker 1987]). Some, e.g. *Sphenoptera* spp. were monophagous. No borers were found that were polyphagous in their larval stages. Since some uncertainty regarding the indexing of the lepidopterous miners exists, it was not possible to determine to what extent these were stenophagous or polyphagous.

The ectophagous sub-guild included three orders i.e. Coleoptera, Lepidoptera and Orthoptera, the former contributing most of the species.

Lepidoptera larvae were found in small numbers on protea species. Most ectophytic moth larvae were apparently not host specific, but polyphagous e.g. *Imbrasia cytherea* had a wide host plant range, including many alien plants.

Only four Orthoptera species were recorded and these were not abundant. The order Hemiptera formed the sap-sucker guild. The free-living families were mostly polyphagous, while some of the sedentary types were oligophagous e.g. *Marsipococcus proteae* and *Spilococcus proteae*. Aphididae and Ciccadelidae were found occasionally, but were regarded as tourists.

Many insects were only identified to family level in this study. More taxonomic work on the identification of insects on Proteaceae is necessary, and until this work is done, identification of insects on a morphospecies level will have to suffice.

36

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37

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CHAPTER 2

SPIDER COMMUNITIES OF FIVE PROTEACEOUS SPECIES IN THE FYNBOS BIOME, SOUTH-WESTERN CAPE PROVINCE OF SOUTH AFRICA

ABSTRACT

Between January 1985 and December 1985 monthly collections of spiders (Araneae) were made on five Proteaceae species in the south-western Cape. Thirty-five genera representing 15 spider families were recorded. Of the total number of spiders (837) collected 37,2% belonged to the Salticidae, 22,6% to the Clubionidae, 9,1% to the Theridiidae, 8,2% to the Araneidae and 7,0% to the Philodromidae. Sixty-one spiders were collected from the inflorescences. Similarity existed between the spider families present on the five plant species, but differences were found in the number of spiders which the plant species had in common.

Key words: Araneae, fynbos, Proteaceae, spiders

39

INTRODUCTION

The fynbos covers an area of about 90 000 km^2 and is found in the south-western and southern parts of the Cape Province. This region, despite its small size has been recognized as one of the world's six floristic Kingdoms. It has a mediterranean climate with dry summers and wet winters. The vegetation can be described as sclerophyllous to microphyllous, consisting of shrubs of many families, notably Proteaceae, Ericaceae and Rutaceae. The ground cover consists largely of Restionaceae and Cyperaceae; true grasses are rare (Bond & Goldblatt 1984). Many plant taxa are endemic to the fynbos and gamma diversity appears to be higher than in any of the world's biogeographic zones except perhaps the tropical rain forest (Kruger & Taylor 1979).

The fynbos flora has been widely studied in recent years (Cowling et al. 1987 and cited references). Certain aspects of the vertebrate life in the fynbos received attention (Bigalke 1979 and cited references), but few ecological studies on the invertebrates have been made. However, the insects associated with the Proteaceae have received some attention (Gess 1968; Myburgh et al. 1973; Myburgh & Rust 1975a, 1975b & Coetzee & Giliomee 1985, 1987a, 1987b). The role of insects as pollen vectors (Coetzee & Giliomee 1985), dispersal agents (Bond & Slingsbly 1983), seed predators (Coetzee & Giliomee 1987a, 1987b), and herbivores (Coetzee 1989d) emphasizes the importance of interactions between insects and Proteaceous plants.

Spiders, as predators of the flower visitors, could have an effect on the interaction between insects and plants. Louda (1982) found that pollination and seed set of Haplopappus venetus (Asteraceae) was reduced on branches with spiders compared to those without, although the release of viable, undamaged seed was higher on inflorescence branches with spiders than from those without. Although several families of spiders are found on flowers and characteristically hunt on them (e.g. Morse 1979, 1981, 1983) only a few studies on the spider communities of flowers have been done (e.g. Shukla & andhu 1983; Stadelbacher & Lockley 1983 and Seiler et al. 1987). Certain aspects of the ecology of the spiders that inhabit flowers, such as the effect of predation on insects visiting the inflorescences and feeding behaviour have received attention (Louda 1982; Morse 1979, 1981, 1983, 1986). In southern Africa various spider species have been recorded from flowers in southern Africa (Dippenaar-Schoeman 1983), but nothing is known about their ecology.

This paper reports the results of a preliminary collection of spiders from five proteaceous species of the fynbos biome of the south-western Cape. The five plant species are all members of the family Proteaceae. This family is a major component of the fynbos and of considerable economic and aesthetic value. The collection was made over twelve months to determine the species composition and numbers of spiders present on the plant species and to compare these plant species with respect to the similarity and species composition of spider communities.

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METHODS

The survey was started in January 1985 and ended in December 1985.

Host Plants

Each of the plant species on which spiders were collected represented a distinct shrub like growth form which could be classified according to Duffey (1966) as "shrub type" vegetation. Three of the species belonged to the genus *Protea*, one to the genus *Leucospermum* and the fifth to the genus *Leucadendron*.

Protea cynaroides (L.) L. is a low shrub with an average height of 1 m and diameter of 1.3 m. The plants in this study flowered from September to January.

Protea neriifolia R. Br. grows as an erect bush ranging from 1,5 to 3,0 m in height, up to 2,0 m in diameter and flowered from March to August in the study area.

Protea repens (L.) L. is a bush which varies from 2,0 to 4,5 m in height and the crown diameter may reach 5,0 m. In the study area it flowered mainly in autumn and winter (May to August).

Leucadendron laureolum (Lamarck)Fourcade is dioecious and the plants reach heights of about 2,0 m. The male plants form a symmetrical bush with yellowish leaves, while the female plants differ from male plants by being asymmetrical, having fewer branches and bearing greener leaves; flowers appeared during June.

Leucospermum cordifolium (Salisb. ex Knight)Fourcade grows into a shrub, attaining a height of 1,5 m with a diameter of 2,0 m. Flowering occurred between August and November.

Study areas

Spiders were collected in six areas and each plant species was sampled monthly at two locations: Swartboskloof, Jonkershoek (33°58'41"E, 18°57'08"S) - *P. repens* and *P. neriifolia*; Jan Marais Park (33°55'52"E, 18°52'35"S) - *P. repens*; Protea Heights in Devon Valley area (33°54'16"E, 18°49'27"S) - *P. neriifolia* and *P. cynaroides*; Tierberg forming part of the Riviersonderend mountain range (34°08'08"E, 19°53'56"S) - *P. cynaroides*; the north-eastern side (34°12'31"E, 19°09'27"S) of the Houwhoek mountains - *L. cordifolium*; the south-eastern side (34°13'00"E, 19°11'17"S) of the Houwhoek mountains - *L. laureolum*; Helderfontein (33°54'58"E, 18°52'35"S) outside Stellenbosch - *L. laureolum* and *L. cordifolium*.

Collecting methods

Three collecting methods were used to collect spiders on the plants:

(i) Knock-down

Spiders on four plants of each of the five plant species were collected monthly, by a modification of the knock-down method described by Southwood et al. A sheet 1 x 1 m (1 m^2) or 0.5 x 0.5 (0.25 m^2), depending on the growth form of the plants, was placed on the ground under each of four plants selected at random. Each plant was then sprayed for four seconds with an aerosol formulation of dichlorvos (Insectigas^R). All invertebrates falling onto the sheet within five minutes after spraying were collected.

(ii)   Beating

The beating method entailed the beating of the branches with a rod, causing the invertebrates to be dislodged onto a 0.25 m^2 net placed under each branch. A unit consisting of 50 branches per plant species was sampled per month.

(iii)   Removal of inflorescences

Invertebrates inhabiting inflorescences were collected during the flowering period of 1985. Inflorescences were collected at random from plants, placed in plastic bags and fumigated with ethyl-acetate. Invertebrates killed were then removed from the flowers and stored in 70% alcohol. See table 3b for the number of inflorescences sampled from each plant species.

Treatment of collections

Collections were made monthly between 08:00 and 10:00, from January 1985 to December 1985. Specimens were transferred to 70% alcohol with a camel-hair brush. The family and species, sex and stage of development were recorded for each spider. It was not possible to identify all the spiders found during the collection to species level because of the large number of juveniles (> 80%) present, and the existing taxonomic problems within certain groups of spiders. Voucher specimens were deposited in the National Collection of Arachnida (NCA), Plant Protection Research Institute, Pretoria.

Data analyses

To determine whether the different habitats (plant species) were favoured by individuals of specific spider families, S∅rensens coefficient of similarity (Southwood 1978)

$$C_s \;=\; 2\,j/(a + b)$$

was used, where j is the number of families common to the two plants and a and b are the total number of morphospecies on each plant species respectively. As this index does not consider the number of individuals involved, the following modification of S∅rensens index (Southwood 1978) was used:

$$Cn = 2\,jN/(aN + bN)$$

where aN = the number of individuals on plant a and bN = the number of individuals on plant b and jN = the sum of the lesser values for the species common to both plants.

42

RESULTS AND DISCUSSION

Numbers present and species composition

(i)   <u>Knock-down and beating</u>

A total of 776 spiders (Table 1) representing 15 families were collected from the five Proteaceae species with the knock-down and beating methods. In terms of total numbers caught over the entire collecting period the Salticidae was the dominant family containing 37,2%, followed by the Clubionidae (22,6%), Theridiidae (9,1%), Araneidae (8,2%), Philodromidae (7,0%) and Linyphiidae (5,9%) (Fig. 1). Each of the remaining families had less than 6,0% of all spiders caught.

The highest number of spiders (340) of 13 families were caught on *L. laureolum*, followed by *P. neriifolia* with 156 spiders in 11 families. The lowest number of spiders were collected on *P. cynaroides*, 65 in eight families (Table 1). Of the 15 families recorded nine (60%) were wanderers, five families (33,3%) webbuilders and one, the Thomisidae (6,7%), ambushers.

(ii)   <u>Inflorescences</u>

A total of 61 spiders representing three families were collected from the inflorescences. The families found in the flowers were Salticidae, Linyphiidae and Clubionidae. No spiders were recorded from *P. repens* and the average numbers of spiders collected per inflorescence varied from 1,08 for *P. cynaroides* to 0,04 for *P. neriifolia*.
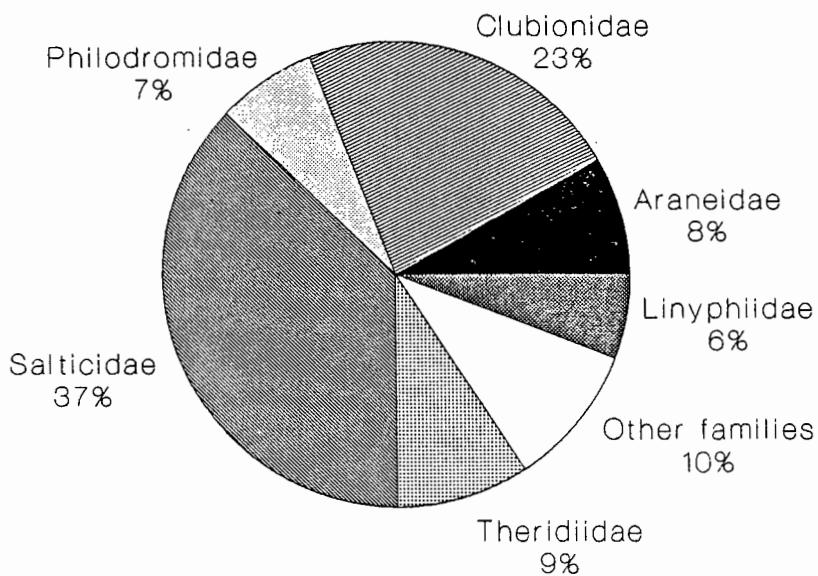
Fig. 1   The percentage composition of dominant spider families collected on Proteaceae between January 1985 and December 1985.

43

TABLE 1   Total number of spiders collected from five Proteaceae species in the south-western Cape between January 1985 and December 1985.

Family/Genus	Plant species					
	Protea repens	Protea neriifolia	Protea cynaroides	Leucospermum cordifolium	Leucodendron laureolum	Tot
ARANEIDAE						
Araneus				4	2	6
Cyclosa	2					2
Cyrtophora	1					1
Neoscona	2	1		5	2	10
Unidentified genus	2	8	9	14	12	45
CLUBIONIDAE						
Chiracanthium		1	1	3	5	
Clubiona	16	38	9	13	47	123
Unidentified genus		5	7	2	33	47
DICTYNIDAE						
Unidentified genus	1					1
GNAPHOSIDAE						
Platyoides	2	1			2	5
HETEROPODIDAE						
Olios			4		1	
Unidentified genus		6	1	6	1	14
LINYPHIIDAE						
Ceratinopsis	6	4	1	16	17	44
Pelecopsis janus					2	2
Unidentified genus		3			4	7
LYCOSIDAE						
Unidentified genus	1					1
OXYOPIDAE						
Oxyopes	1	3			3	7
PHILODROMIDAE						
Philodromus	8	10		3	16	37
Suemus					1	1
Tibellus				3		3
Unidentified genus	1		4	4	4	13
PISAURIDAE						
Voraptus					3	3
SALTICIDAE						
Myrmarachne						1
Unidentified genera(3)	41	46	19	28	154	288
THERIDIIDAE						
Dipoena					1	1
Euryopis				1		1
Theridion	6	10	2	4	3	25
Unidentified genus	3	14	4	13	10	44
THOMISIDAE						
Dieta	2		2		12	16
Misumena		1				1
Pherecydes					1	1
Sidymella				2		2
Synaema	1	3	1	2	1	8
Thomisus			1		1	2
ULOBORIDAE						
Miagrammopes				1	1	2
ZODARIIDAE						
Chariobas cylindraceus					2	2
TOTAL	94	156	65	121	340	776

44

Similarity index

Close similarity (Søsrensens index) existed between the spider community at family level collected from the five plant species, $C_s \geq 0.62$ (Table 2a), in spite of the differences in growth form between the plant species. This similarity was probably due to the presence of a large number (60%) of wandering spiders. These spiders wander around freely on the plants in search of food and do not require specialized hunting habitats.

If the total number of spiders collected was also taken into consideration (modified Søsrensens index), the similarity between spider commities on the plants became evident (Table 2b). The similarity index C_n for the spider community of *L. laureolum* deviates most from the other plant species ($C_n \leq 0.54$), whereas that for plant species with similar growth form such as *P.repens* and *P. neriifolia* exhibited strong similiarities (C_n P.repens x P.neriifolia = 0,67). *L.laureolum* and *P.cynaroides*, which differ in growth form were the least similar (C_n L.laureolum x P.cynaroides = 0,30) (Table 2b). The shape or architecture of the plant (Lawton, 1983) appeared to influence the abundance of spiders on plants.

TABLE 2a   Søsrensens coefficient of similarity ($Cs = 2j(a + b)$) between the spider families collected on five Proteaceae species in the south-western Cape between January 1985 and December 1985.

	P. repens	P. neriifolia	P. cynaroides	L. cordifolium
P. neriifolia	0,67			
P. cynaroides	0,62	0,62		
L. cordifolium	0,63	0,69	0,71	
L. laureolum	0,62	0,62	0,63	0,64

TABLE 2b The modified Søsrensens coefficient of similarity ($Cn = 2jN$) ($aN + bN$) between the total number of spiders and spider families collected on five Proteaceae species in the south-western Cape between January 1985 and December 1985.

	P. repens	P. neriifolia	P. cynaroides	L. cordifolium
P. neriifolia	0,67			
P. cynaroides	0,50	0,46		
L. cordifolium	0,59	0,61	0,57	
L. laureolum	0,41	0,54	0,30	0,42

45

Seasonal change

The total number of spiders collected per month during the year is shown in Fig. 2. The seasonal abundance of the spiders fluctuated from a maximum of > 90 spiders per month in January and August to minimum numbers of < 40 per month in April and July. Smaller numbers were recorded during the colder months (April to September), with an average of 57,9 spiders per month compared to the 74,5 spiders per month during the warmer period (October to March). This seasonal fluctuation corresponded with the findings of Dippenaar-Schoeman et al.(1989).
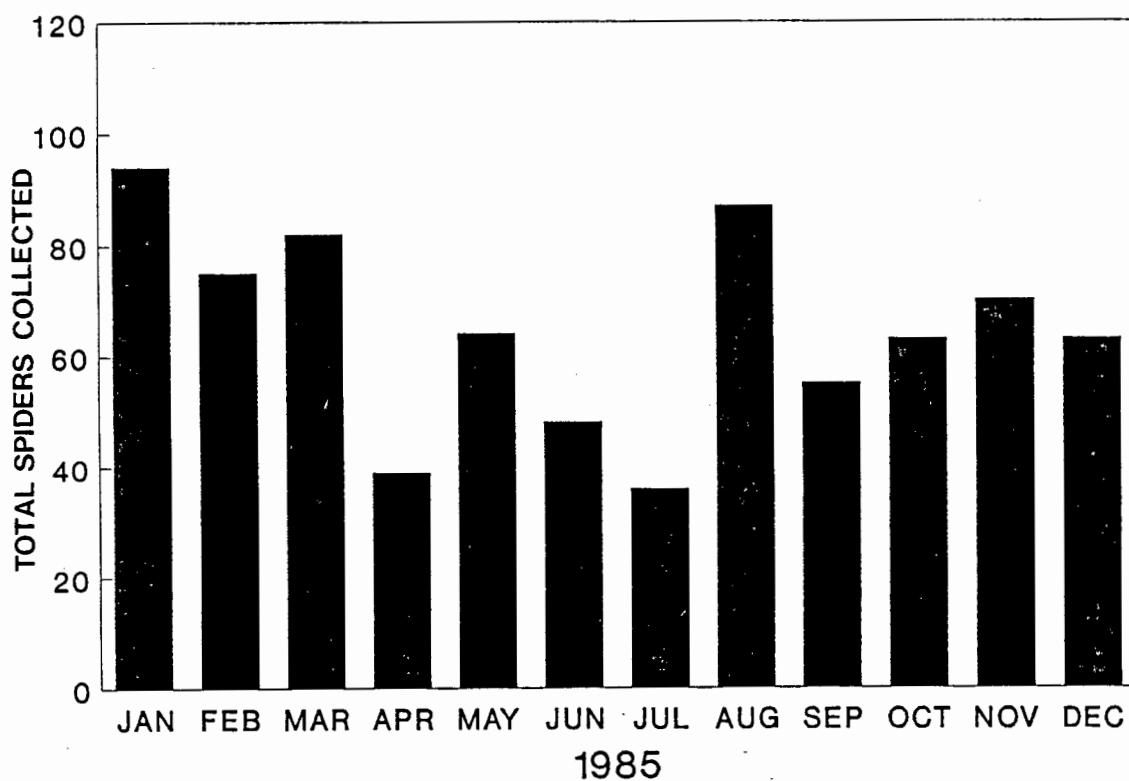
Fig. 2   Histogram of seasonal changes of spiders on the five Proteaceae plants.

TABLE 3a   Total number of spiders collected on five Proteaceae species relative to the number of insects collected by knock-down and beating from January 1985 to December 1985 in the south-western Cape.

	P. repens	P. neriifolia	P. cynaroides	L. cordifolium	L. laureolum	Total
Spiders	94	156	65	121	340	776
Insects[a]	2515	4113	884	1289	4562	13 371
Ratio	1 : 27	1 : 26	1 : 14	1 : 11	1 : 13	1 : 17

[a] Includes all other arthropods

46

TABLE 3b   Total number of spiders collected on the inflorescences of five Proteaceae species relative to the total number of insects collected between January 1985 to December 1985 in the south-western Cape.

	P. repens	P. neriifolia	P. cynaroides	L. cordifolium	L. laureolum	Total
N^a	220	240	12	50	100	
Spiders	0	10	13	27	11	61
Insects[b]	6783	8107	712	424	683	16 709
Ratio		1 : 810	1 : 55	1 : 16	1 : 62	1 : 275

[a] Number of inflorescences
[b] Includes all other arthropods

Interaction with insects

In Table 3a the number of spiders collected on the five plant species in relation to the total number of insects collected during the survey is given. On L. cordifolium a ratio of 1:11 was recorded and on L.laureolum, with the largest number of spiders, a ratio of 1:13. On average a ratio of 1:17 for all plant species was recorded during the survey. Abundance of insects visiting the flowers, however, did not lead to large numbers of spiders as the figures for P. neriifolia and P. repens showed.

This tendency was also noted in the inflorescences, where small numbers of spiders in relation to those of insects were found (Table 3b). On L. cordifolium the ratio was 1:16 compared to P. neriifolia with a ratio of 1:810. No spiders were found in the inflorescences of P. repens. On average the ratio of spiders to insects found in the inflorescences was 1:275 for the collection period. Spiders comprised only 0,36% of the flower community in contrast to the 5,49% found on the plants (Table 3a). Except for P. cynaroides, the plant species studied flowered in the winter, a period when fever spiders were recorded with a larger proportion of juveniles present. The data in Table 3b show that although large numbers of invertebrates occur in the inflorescences, they are not fully exploited by spiders. It is possible that the insects present (mainly Coleoptera) were not suitable prey. It is also possible that the excretion of resin and nectar by the protea inflorescences discouraged spiders from visiting them.

The influence of the spiders on the herbivores and other arthropods found on Proteaceae is unknown, as no data are available on their food preferences and the numbers of prey they consume. Perhaps their diet consists mostly of casual visitors to the plants, such as small insects perching on the plants. Since the herbivorous and flower visitors are mostly beetles that appear to be well protected against most spiders and because of the relatively small number of spiders, their influence on interaction between insects and the five plant species is probably not significant.

47

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CHAPTER 3

GUILD COMPOSITION, SPECIES PACKING AND SEASONAL DISTRIBUTION OF THE ARTHROPOD COMMUNITIES ON FIVE PROTEACEOUS SPECIES

ABSTRACT:

A total of 14 382 free-living arthropod individuals representing 541 morphospecies were collected from five species of Proteaceae over a period of one year. The arborescent plant species, *Protea repens, P. neriifolia* and *Leucadendron laureolum* harbored greater numbers of morphospecies and individuals than the architecturally less complex species, *P.cynaroides* and *Leucospermum cordifolium*. The proportion of species based on the number in the arthropod guilds was similar on the various plant species. Similar species of ants, flower visitors and sap-sucking species were found on the plant species, whereas there were fewer leaf chewing species common to all plant species, which suggested that some species were monophagous. Arthropod abundance increased during the wet winter months when the plants were in flower.

Keywords: Guild composition, species packing, similarity indices, seasonal distribution, Proteaceae, fynbos.

50

INTRODUCTION

The fynbos has been studied intensively, especially during the last decade, with the emphasis on community studies of the diverse flora (Cowling et al. 1987 and cited references) and aspects of vertebrate life (Bigalke 1979 and cited references). Studies on invertebrates in fynbos have concentrated on pests, seed dispersal, seed predation and pollination (e.g. Gess 1968, Myburgh & Rust 1975a,b, Bond & Slingsby 1983, Coetzee & Giliomee 1985, 1987a,b), or on specific taxonomic groups such as ants, leafhoppers and grasshoppers (Donnelly & Giliomee 1985a, b; Schlettwein & Giliomee, 1987).

Free-living arthropod faunas of plants are generally used to gather ecological information on insect-plant relations (Southwood 1961, Janzen 1973, Southwood, Moran & Kennedy 1982 a,b, Moran & Southwood 1982, Fowler 1985, Stork 1987b). Zwölfer (1987) emphasized the importance of plant-insect interaction studies in understanding the structure and function of terrestrial ecosystems. It is, however, not feasible to undertake detailed studies of thousands of species in a complex terrestrial ecosystem. Zwölfer (1987) therefore suggests that subsystems be studied in order to gain insight into complex terrestrial ecosystems. The Proteaceae are an important component of the fynbos (Taylor 1978) and in this study the free-living arthropods associated with the five proteaceous species were investigated in an attempt to contribute to the understanding of the interaction of insects with the fynbos.

Free-living arthropods associated with the different plant species were collected regularly to determine the extent of the total arthropod community on the host plant, to compare arthropod communities among plants and to determine the seasonal distribution of this fauna.

51

MATERIALS AND METHODS

As in Southwood, Moran & Kennedy (1982a), the free-living arthropods of the plant species were grouped into guilds according to the niches filled by various taxonomic groups collectively rather than considering taxonomic groups separately. The following guilds were distinguished: phytophagous (including the flower visitor, chewer and sap-sucker sub-guilds), non-detrimental feeders (arthropods feeding on detritus as well as fungivores), predators and parasitoids, ants (considered a separate group due to their feeding habits) and tourists. The tourist guild included all rthropods using the plant for perching or shelter only. This group is important as it forms an integral part of the food chain. The allocation of species to these guilds was based on personal observations and unpublished data.

The proteaceous species studied were: *Protea repens*(L.)L. that has an arboreal growth form ranging from 1,5 to 3,0 m in height, up to 2,0 m in diameter and flowers from March to August in the study area. With a distribution area of ca.77 000 km². *P. neriifolia* R.Br. has a arboreal erect shape ranging from 1,5 to 3,0 m in height, up to 2,0m in diameter and flowers from March to August in the study area. With a distribution area of ca. 20 570 km². *P. cynaroides*(L.)L is a low shrub with an average height of 1 m and a diameter of 1,3 m and flowers from March to August in the study area. With a distribution area of ca. 378 00 km². *Leucospermum cordifolium* (Salisb. ex Knight) Fourcade grows into a shrub, attaining a height of 1,5 m with a diameter of 2,0 m. Flowers occur between August and November. With a distribution area of ca. 6860 km². *Leucadendron laureolum* (Lamarck) Fourcade is dioecious and male plants reach heights of about 2,0 m forming a symmetrical bush with yellowish leaves. Female plants differ from male plants by being asymmetrical, having less branches and bearing greener leaves; flowers appear during June. The distribution area is ca. 8040 km².

Collections of arthropods on their hosts were made every month from January to December 1985. Collections were made at two locations for each of the five plant species. Arthropods were collected from *P. repens* and *P. neriifolia* in Swartboskloof, Jonkershoek (33°58'41"E, 18°57'08"S). The other location for *P. repens* was the Jan Marais Nature Reserve, Stellenbosch (33°55'52"E, 18°52'35"S), and for *P. neriifolia*, Protea Heights (33°54'16"E, 18°49'27"S) in the Devon Valley area. On *Protea cynaroides* arthropods were collected at Tierberg (34°08'08"E, 19°53'56"S), part of the Riviersonderend mountain range, and at Protea Heights(33°54'16"E, 18°49'27"S). Arthropods on *Leucospermum cordifolium* and *Leucadendron laureolum* were collected from the north eastern side of Houwhoek mountain (34°12'31"E, 19°09'27"S) and on the south eastern side (34°13'00"E, 19°11'17"S) respectively, as well as at Helderfontein (33°56'52"E, 18°52'35"S) near Stellenbosch.

52

Invertebrates were collected on four plants from each of the five species monthly at each site by means of a modified knock-down method described by Southwood et.al. (1982a). A sheet 1 x 1 m (1 m^2) or 0.5 x 0.5 (0.25 m^2), depending on the growth form of the plants was placed on the ground under each of four randomly selected plants. Each plant was then sprayed for four seconds with dichlorvos (Insectigas^R), an aerosol formulation. All invertebrates falling onto the sheets within five minutes of spraying were collected. Arthropods were also collected monthly on a beating sheet from 50 branches of 10 plants of each species. Interplant variation of arthropods was not estimated, collections from individual plants being too small to allow such analysis, and collections from individual plants were pooled. Collected specimens were killed with ethyl acetate and later pinned or preserved in 70% alcohol. They were separated into the six guilds as described and then sorted into morphospecies and classified. Unidentified but apparently similar morphospecies on the various host plants were linked by cross references to facilitate comparison of communities between plants. Voucher specimens were housed in the collection of the Fynbos Research Unit of the Vegetable and Ornamental Plant Research Institute at Elsenburg, Stellenbosch.

The degree of similarity between the arthropods on the different plant species was determined by using Sørensens coefficient of similarity

$$C_s = 2 \, j/(a + b)$$

where j is the number of morphospecies common to the two plants and a and b are the total number of morphospecies on each plant species respectively (Southwood, 1978). As this index does not consider the number of individuals concerned, the following modification of Sørensens index was also used:

$$C_n = 2 \, jN/(aN + bN)$$

where aN = the number of individuals on plant a and bN = the number of individuals on plant b and jN = the sum of the lesser values for the species common to both plants. (Southwood 1978).

53

RESULTS AND DISCUSSION

A total of 14 382 individual arthropods representing 532 morphospecies were collected. They represented 16 insect orders and four other invertebrate groups. It was not possible to identify all individuals to species level as taxonomic information of some insect groups in the fynbos is limited. (See Coetzee, 1989a for lists of the morphospecies and the guilds to which they were allocated). A number of borer species of which the adult stage feeds on leaves were included in the chewer guild. Some phytophagous insects were included in the tourist guild, as only occasional individuals not known to feed on the host plant (e.g. Cicadellidae) were collected. Most morphospecies of the free-living arthropods belonged to the Order Coleoptera (Coetzee 1989a).

The guild composition according to both the number of species (species richness) and number of individuals indicated that the large, arborescent plant species, *Protea repens, P. neriifolia* and *Leucadendron laureolum*, harbored the most morphospecies (Fig. 1a) and individuals (Fig. 1b), while the shrub like plants (*P. cynaroides* & *L. cordifolium*) hosted fewer species. These results support Lawton's (1983) "plant architecture hypothesis" as well as the "larger plant hypothesis" of Lawton & Price (1979) and Moran (1980).

The species-area relationship theory as discussed by i.a. Strong, Lawton & Southwood (1984) appeared to be applicable with regard to the species richness on *P. repens*, this plant having the widest distribution and harboring almost the highest number of morphospecies. In contrast, *P. cynaroides* (also widely distributed), harbored fewer species than *P. neriifolia* and *L. laureolum*, each with restricted distribution areas. From these results it seems that "plant architecture" has a stronger influence in determining species richness than the range of the host plant. Other factors which may have influenced species richness were the high plant diversity and endemic character of the fynbos (Bond & Goldblatt 1984), habitat heterogeneity (Zwölfer 1987), taxonomic closeness with other proteaceous species and destruction of natural habitats (e.g. by agriculture or alien plant invasions). The proportions of the number of morphospecies (gamma-diversity) that occupied the different guilds on the five species appeared to be very similar (Fig. 1a). The ant guild had the lowest species numbers (< 5,2%) on all plant species monitored (Fig. 1a).

54
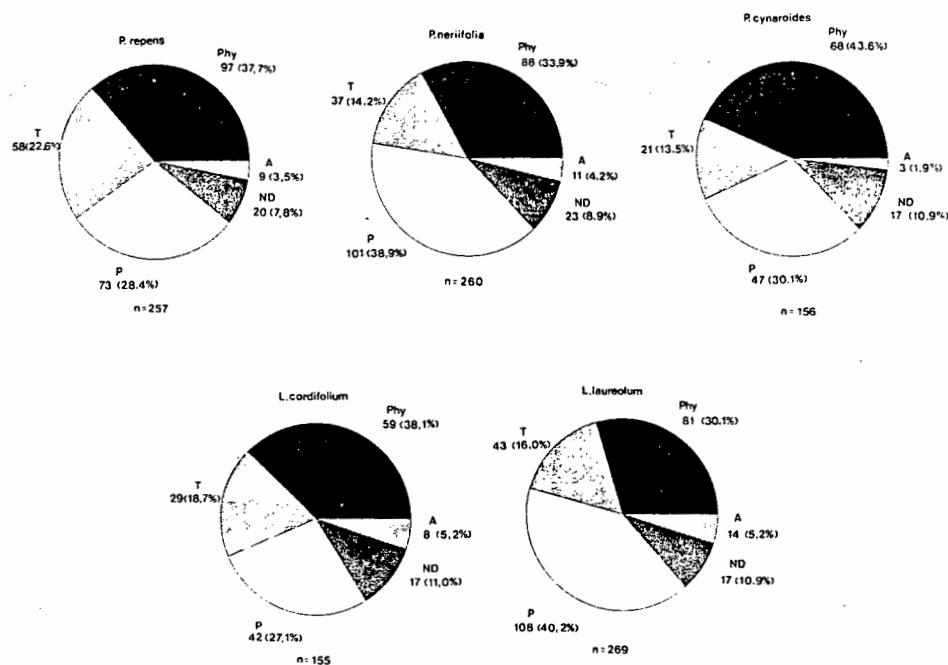
Fig. 1a Guild structure of the arthropod fauna from five proteaceous species according to number of morphospecies. Phy: phytophagous, P: predators and parasitoids, ND: non detrimental feeders, A: ants, T: tourists and n : number of morphospecies.

Phytophagous insects constituted most of the species on *P. repens*, *P. cynaroides* and *L. cordifolium* (> 36%) while predators and parasitoids were the most diversified group associated with *P. neriifolia* and *L. laureolum*. In contrast to the nearly constant proportion in the number of species, the guild composition based on individual level (Fig. 1b) differed greatly from plant to plant, even between architecturally similar species (e.g. *P. neriifolia* and *P. repens*). Ants contributed the most individuals on three of the plant species, viz. *P. repens. P. cynaroides* and *L. cordifolium*. On *P. neriifolia* non-detrimental feeders were most abundant, while numbers of phytophagous insects were the highest on *L. laureolum*. Abundant phytophagous insects on *L. laureolum* was attributed to the high number of insects associated with the inflorescences (n = 1 144).
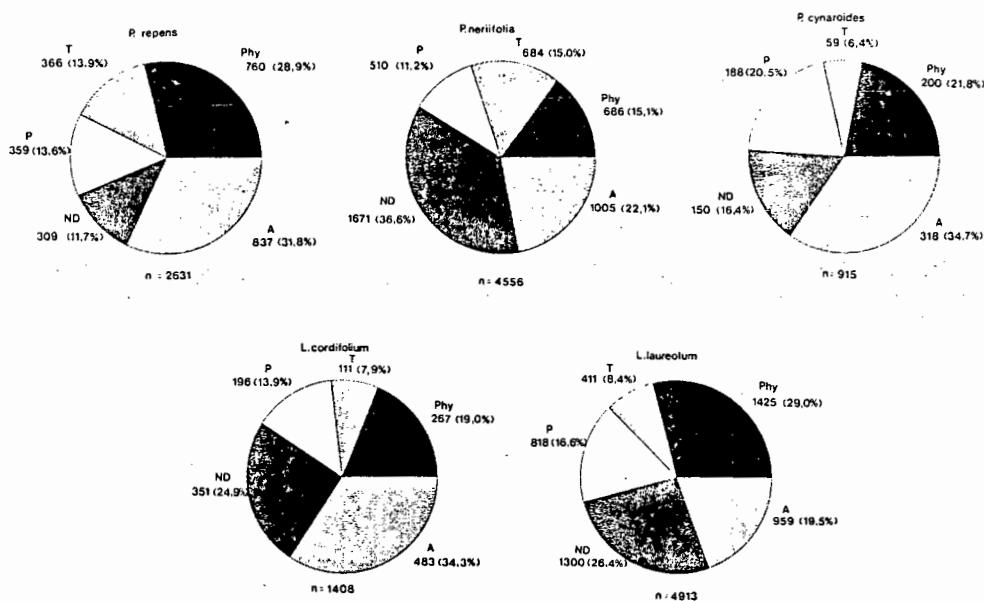
Fig. 1b Guild structure of the arthropod fauna from five proteaceous species according to number of individuals. Phy: phytophagous, P: predators and parasitoids, ND: non detrimental feeders, A: ants T: tourists and n : number of individuals.

The use of guilds is criticised by Stork (1987a) as errors may arise owing to the incorrect assignment of species to guilds. In determining coefficient of similarity C_s and C_n, attention was focused on the ants and phytophages, as the taxonomy and feeding habits of these groups are known. The ants represent a well defined guild, and in this study they were the only guild where all individuals could be identified to species level. Insects belonging to the phytophagous guild for Proteaceae have been collected for 25 years, and many specimens have not yet been identified to species level, but only to morphospecies, which allowed similarity analyses to be undertaken. The assignment of species to the three subguilds of the phytophagous guild, i.e. flower visitors, chewers and sap-suckers was based on personal observations.

For the ant guild some, plants with similar architecture like P. repens and as between other similar species (P. repens and P. neriifolia) it was low (C_s = 0.40) (Fig. 2a). The low number of ant species exploiting the five proteaceous species may be the reason for these differences in Cs values between plant species of similar architecture. However when the numbers of individuals per species were taken into account plants with similar architectural structure showed close similarity (C_n > 0.70) (Fig. 2b).

Indices of similarity (C_s) for flower visitors on P. repens and P. neriifolia had values as high as 0.65 (Fig. 2c). The structure of inflorescences and flowering time of these two species are fairly similar, and could probably explain the high C_s value for these two plants. The low C_s values for the other plant species combinations indicated that, although most flower visitors are polyphagous, some species are restricted to certain plant species studied. The low C_n values (Fig. 2d) indicated differences between the number of flower visitor individuals on the different plant species.

56
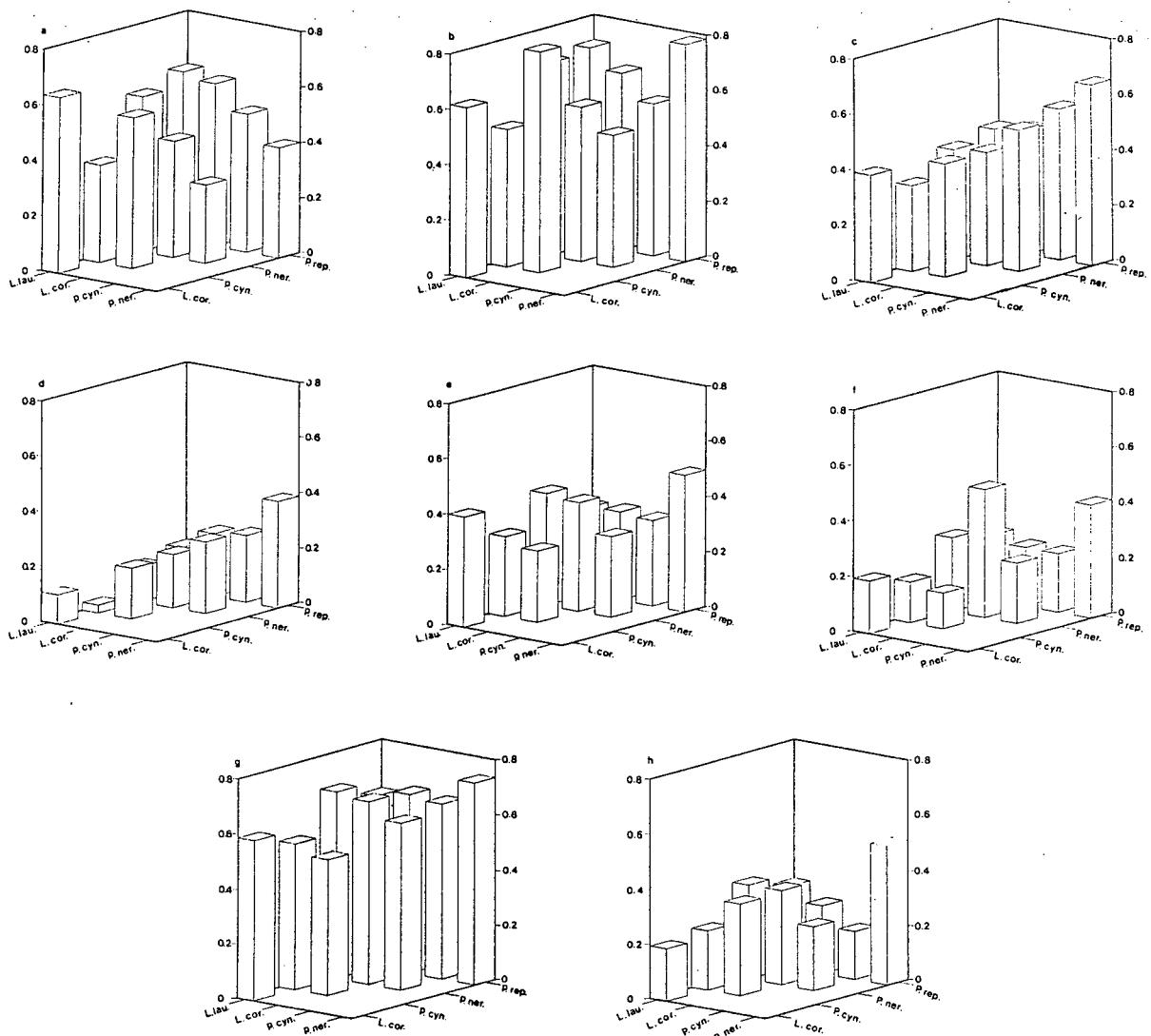
Fig. 2 Sørensen's coefficients of similarity for different guilds on five proteaceous species: (a) C_s ants, (b) C_n ants, (c) C_s flower visitors, (d) C_n flower visitors, (e) C_s chewers, (f) C_n chewers, (g) C_s sap-suckers, (h) C_n sap-suckers. C_s is the coefficient of similarity for the number of species common to pairs of plants and C_n the coefficient of similarity for the number of species and individuals within a species common to pairs of plants. P. rep. = *Protea repens*, P. ner. = *Protea neriifolia*, P. cyn. = *Protea cynaroides*, L. cor. = *Leucosperum cordifolium*, L. lau. = *Leucadendron Laureolum*,

57

The low similarity indices values (Fig. 2e,f) for the chewer subguild can be attributed to the fact that some of the insect species were apparently monophagous since they were only found on one of the plant species. In contrast, the high C_s values (Fig. 2g) for the sap-sucker subguild showed that the Hemiptera did not show preference for any of the plant species. Low C_n values (Fig. 2h) for this group indicated that there were marked differences in the number of individuals attacking different plants.

Total numbers of arthropods collected on a monthly basis (Fig. 3) showed that they were slightly more abundant during the wet winter months (May - September) than in summer. This trend is largely due to the presence of flowers during winter and their concomitant visitors which form part of the phytophagous guild.
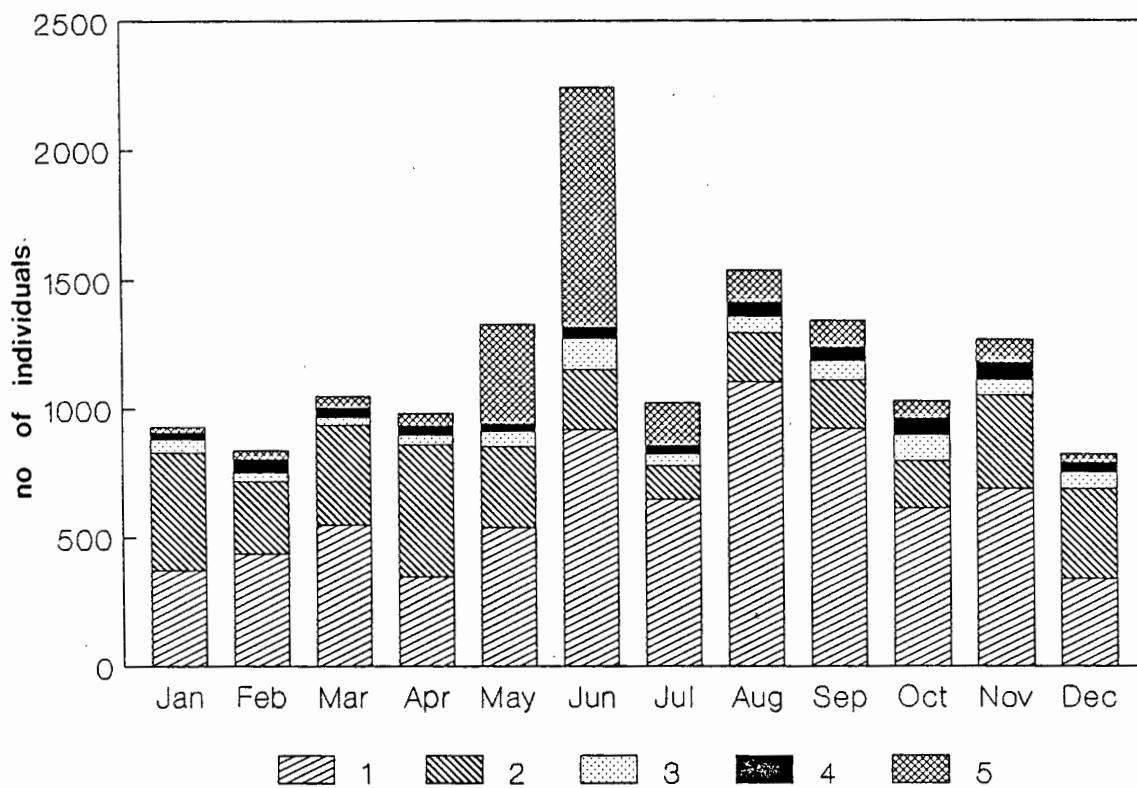
Fig. 3 The seasonal distribution of guilds of five proteaceous species: 1. non-detrimental feeders, predators, parasitoids and tourists, 2. ants, 3. sap-suckers, 4. chewers and 5. flower visitors.

Although the flower visitors peaked in numbers during the flowering period, they were recorded in small numbers throughout the year. This may have been due to oligophagous or polyphagous flower visitors which used the observed plants as a shelter while feeding on other plants. On *L. laureolum* some flower visitors such as Centorhynchinae were present in small numbers throughout the year, as they fed on the involucral bracts of the inflorescences, which are present throughout the year.

58

Chewers and sap-suckers showed no seasonal change in numbers. Neither the phenology of the plants nor climate seemed to affect these groups. Newly initiated and developing leaves of the plants studied exhibited little or no herbivore damage, indicating that they were effectively protected by defence mechanisms. These defence mechanisms might have inhibited an increase in insect numbers when the plants were actively growing.

The ant guild increased during summer and decreased in late winter and spring. An increase in activity around mid to late summer by epigaeic Formicidae in fynbos was recorded by Donnelly & Giliomee (1988). On the Proteaceae, ant activity was not only influenced by climatic conditions, but also by the presence of flowers on plants. The number of *Iridomyrex humilis* therefore declined after the flowering season had ended in late winter when nectar was no longer available. It is interesting to note, however, that ants scavenged on the plants throughout the year.

In general, the seasonal distribution of insects at guild level on proteas therefore indicated that the phenology of the host plants and the temperate climate of the fynbos did not have a marked effect on the total number of phytophagous, non-detrimental feeders, tourists and parasitoids and predators. Slightly lower numbers of spiders were recorded on the Proteaceae during the colder months of April to September (Coetzee 1989b). At species level, however, a definite succession was recorded by Coetzee & Giliomee (1987b).

Although the results reported here represent a small subsystem of the fynbos, they do provide a starting point for further insect-plant community studies. The plant species diversity in fynbos is of the highest for all floral kingdoms (Kruger & Taylor 1979) and little information pertaining to diversity of arthropods in the fynbos is available. In this study the insect similarity data provided some indication that a number of species appeared to be monophagous. To establish whether this is a common phenomenon in fynbos and whether plant species richness is matched by a high species diversity in arthropods, more insect-plant studies are needed. Extensive taxonomic work is also required to facilitate this work - numerous morphospecies presently considered to be single species may prove to be groups of sibling species, possibly with specific host plant requirements. Such studies will assist in determining whether fynbos species have acted as evolutionary islands (i.e. centers of speciation) to the insects utilizing them.

59

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62

CHAPTER 4

THE INSECT HERBIVORE GUILD AND ITS EFFECT ON THE FOLIAGE OF FIVE PROTEACEOUS SPECIES OF THE CAPE FYNBOS

ABSTRACT

A total of 5 883 arboreal arthropoda were collected on five Proteaceae species. The herbivore guild contributed 32,3% of the total number of individuals and consisted of 170 species. Of the total number of herbivorous individuals collected, flower visitors represented 69,5%, leaf feeders 14,5% and sap-suckers 16,1%. The chewers constituted 60,1% of the total herbivore biomass. Leaf damage increased with age : young leaves were almost free of herbivore damage while older leaves were acceptable as food. The level of insect damage differed amongst the plant species ranging from less than 2 % on *Leucadendron laureolum* to 15 % on *Protea cynaroides*.

Key words: Fynbos, Proteaceae, insect herbivory, leaf damage.

63

INTRODUCTION

The Proteaceae are an important component of the Cape Flora (Bond & Goldblatt 1984) or fynbos and because of the beauty of their flowers and foliage, many species are utilized commercially. Information on insect herbivory in this family is therefore of both ecological and economic significance.

Lawton (1978, 1983) stressed the importance of plant architecture in explaining insect diversity on plants; the term "architecture" referring to plant attributes such as size, growth form, seasonal development and variety of above-ground parts. In this respect most Proteaceae (including the five species studied) are structurally complex plants, providing a diversity of niches for insects to exploit. One would thus expect to find many different insect species on these plants, and this is confirmed by the long list of insects shown to be associated with the Proteaceae by Gess (1968); Myburgh *et. al.*; Coetzee & Latsky (1986); Coetzee & Giliomee (1987b).

Herbivores affect the distribution and abundance of plants directly when they kill seeds, seedlings or the adult plants, or indirectly when the competitive capacity and resistance of plants to adverse factors are changed (Fuentes *et. al.* 1981). Sap suckers, leaf eaters and stem borers lower the fitness of individual plants by reducing their ability to produce progeny (Huffaker *et al.* 1984). Huffaker *et al.* (1984) point out that we cannot know what effect a given species component of the herbivore load is having on a plant population unless we remove the species and see what happens. This will not be easy to demonstrate experimentally, but some indications from the spectacular success with which the alien proteoid *Hakea* spp. have invaded the fynbos in the absence of their natural enemies.

Various aspects of insect-plant interactions concerning the Proteaceae have been studied. Insect seed predators were shown to destroy up to 84% of *Protea repens* seed reserves (Coetzee & Giliomee 1987a,b), probably reducing the competitive ability of these plants. Ants are involved in a mutualistic relationship with certain Proteaceae whereby they transport the seeds and store them in protected, nutrient rich environments before the elaiosomes are removed (Slingsby & Bond 1981; Bond & Slingsby 1983). Insects were also shown to be important pollen vectors in *Protea repens* influencing the amount of seed set (Coetzee & Giliomee 1985).

64

An aspect on which information is lacking, is the effect of folivorous insects on the leaves of the plant and ultimately on the fitness of the plant itself. The leaves, in addition to the inflorescences, infructescences and stems form one of the four ecologically discrete regions of the above-ground plant structure in the Proteaceae, each harbouring its own guild of insects. For mediterranean ecosystems generally, very little information is available on the amount of plant material removed by insects and published figures vary considerably for the different areas. In Australia insects remove 9-22% of the leaf area from the dominant mallee *Eucalyptus trees* (Fox & Morrow 1981) and for a complex of mattoral species in Chile it is about 10% (Fuentes et al. 1981). For South African and Californian mediterranean type ecosystems it is considered to be lower (Morrow *et. al.* 1983) and less than 2% on nutrient poor soil (Morrow 1983). Since most Proteaceae grow on nutrient poor soil (Rourke 1980) it can be expected that levels of leaf damage would be low.

In this study insect feeding on the leaves of five species of proteaceae, via. *Protea repens, P. neriifolia, P. cynaroides, Leucospermum cordifolium* and *Leucadendron laureolum* in their natural habitat was investigated. The aims were to characterize the insect fauna on the leaves and flowers, particularly the herbivore guild, and to measure and compare leaf consumption over time for the five host plants. We also wanted to test the hypothesis that leaf damage does not increase with time, indicating that old leaves are unacceptable as food for insects.

65

MATERIALS AND METHODS

The study sites were situated in the mountain fynbos vegetation of the South-Western Cape. Insects and leaves were collected from *P. repens* and *P. neriifolia* in Swartboskloof, Jonkershoek (33°58'41"E, 18°57'08"S), from *P. cynaroides* on Tierberg (34°08'08"E, 19°53'56"S) near Riviersonderend, from *L. cordifolium* on the north-eastern side of Houwhoek Mountain (34°12'31"E, 19°09'27"S) and from *L. laureolum* on the south-eastern slopes of the Houwhoek mountains (34°13'00"E, 19°11'17"S).

To determine the extent of leaf damage, leaves were collected from the beginning of the main growth cycle until the cohort of leaves were 21 months old and had become senescent. The main growth cycle in these areas started in August for *P. cynaroides* and *P. neriifolia*, in September for *P. repens*, in November for *L. cordifolium* and in December for *L. laureolum*.

Collecting was started during 1985 with the initiation of the main growth cycles. The line transect method (Sampford 1962), was used to select ten individual plants at each collection site; no distinction was made between male and female plants in *L. laureolum*. From each plant one branch was cut off at a point just below the oldest leaves. In the laboratory the leaves were stripped off and divided into age classes, determined by the position of the hypsophyls on the stem. Leaves from the ten plants in each class were then thoroughly mixed, and 100 leaves selected at random from each class. All leaves which showed herbivore damage were counted and of these 10 were randomly selected (if less than 10 then all the damaged leaves were used); the rest were discarded. These damaged leaves were photocopied (on a one to one scale) and an estimate of the original outline of the undamaged leaf was drawn on the photocopy. Total leaf area and leaf area lost were measured by means of a digital tablet (Summergraphics[R] MM1200 series) connected to a computer (Olivetti M24[R]).

The expected proportion of leaf area lost for all the plants of a population, E(p), was calculated by the Fuentes *et al.* (1981) expression:

$$E(p) = P(L)\ L$$

where E (p) is the expected proportion of the leaf area lost, P (L) is the probability that a leaf will be attacked and L is the average proportion of leaf area removed by insects.

In order to determine which insects were responsible for leaf damage, the free-living insects were collected monthly from plants at each site for 12 months. Two collecting methods were used: 1) a modification of the "knock-down" method described by Southwood, Moran & Kennedy (1982) whereby a sheet 1x1 m (1 m^2) or 0.5x0.5 m (0.25 m^2), depending on the growth form of the plant, was placed under the branches of each of four plants. Each plant was then sprayed for four seconds with an aerosol formulation of dichlorvos (Insectigas[R]). All invertebrates which dropped onto the sheet within five minutes after the plants had been

66

sprayed, were collected. 2) The beating method which entailed dislodging insects from 50 branches of 10 plants by beating the branches with a rod until all the insects had dropped off. Dislodged insects which fell onto a 0,25 m^2 sheet placed under the branch were collected. Collections from individual plants were not kept separate and interplant variation of the invertebrate community was not estimated as samples from individual trees were too small to allow for such an analysis. The insects were killed with ethyl acetate, transferred to the laboratory, pinned or preserved in 70% alcohol and labelled with date, plant species and site location. Samples were sorted into guilds according to feeding habits, similar to those recognised by Moran & Southwood (1982). Insects of the herbivore guild were classified into morphospecies and then submitted to local experts for identification.

The allocation of insects into the herbivore guild was based on known feeding habits described in the literature and personal records. This guild was then divided into four sub-guilds according to specific feeding habits, i.e. flower visitors, leaf chewers (including leaf miners), leaf sap-suckers and seed sap-suckers. The flower visitors fed on pollen, nectar and parts of the inflorescences. All Thysanoptera were allocated to the flower visitors sub-guild, although zur Strassen (personal communication) associated some species with other parts of the plant.

Biomass of the herbivores was calculated using the expression of Rogers, Hinds and Buschbom (1976),

$$W = N \ (0.0305L)^{2.62}$$

where W is the dry weight in mg, N is the number of individuals, and L is the body length in mm.

The hypotheses that the extent of insect damage does not differ between the five host plants, and that leaf damage does not increase with time were tested by using dummy variable regression (Gujarati 1970 a, b) of leaf damage on time. In the full model dummy variables were used to assign separate intercepts and slopes to the regression of damage on time for each plant species. Inspection of the value and significance levels of the regression coefficients indicated which slopes and/or intercepts could be combined in a reduced model. The appropriate reduced model was then fitted and the justification for reducing the model was tested in the usual way by comparing the extra mean square with the residual mean square of the full model using an F-test (Draper & Smith 1981).

67

RESULTS AND DISCUSSION

A total of 5883 arboreal Arthropoda were collected on the five species of Proteaceae over the 12 month period (Table 1). As the architecture of the plant species differed considerably, no attempt was made to compare the populations on them statistically. It appeared, however, that the structure of the plants influenced the abundance of individual insects on them, this is in accordance with Lawton (1983). *Protea cynaroides*, which is small and shrub-like, accommodated fewer individuals than *L. laureolum* (Table 1) which is shaped more like a small tree.

Table 1   Number of insect specimens of the free-living arthropod guilds collected on five species of Proteaceae over a 12 month period, LC = *Leucospermum cordifolium* (Salisb. ex Knight) Fourc., LL = *Leucadendron laureolum* (Lam.) Fourc., PC = *Protea cynaroides* (L.) L, PN = *Protea neriifolia* R. Br. and PR = *Protea repens* (L.) L.

No. of individual insects on	LC	LL	PC	PN	PR	Total	%
Flower visitors°	60	1096	47	68	48	1319	22.4
Leaf chewers°	98	53	9	53	61	274	4.7
Leaf sap-suckers°	32	40	3	65	66	206	3.5
Seed sap-suckers°	3	49	6	13	28	99	1.7
Ants	203	385	128	319	470	1505	25.6
Predators and parasitoids	110	343	87	220	124	884	15.0
Other	195	677	75	532	117	1596	27.1
Total	701	2607	355	1270	914	5883	

° Herbivore guild

68
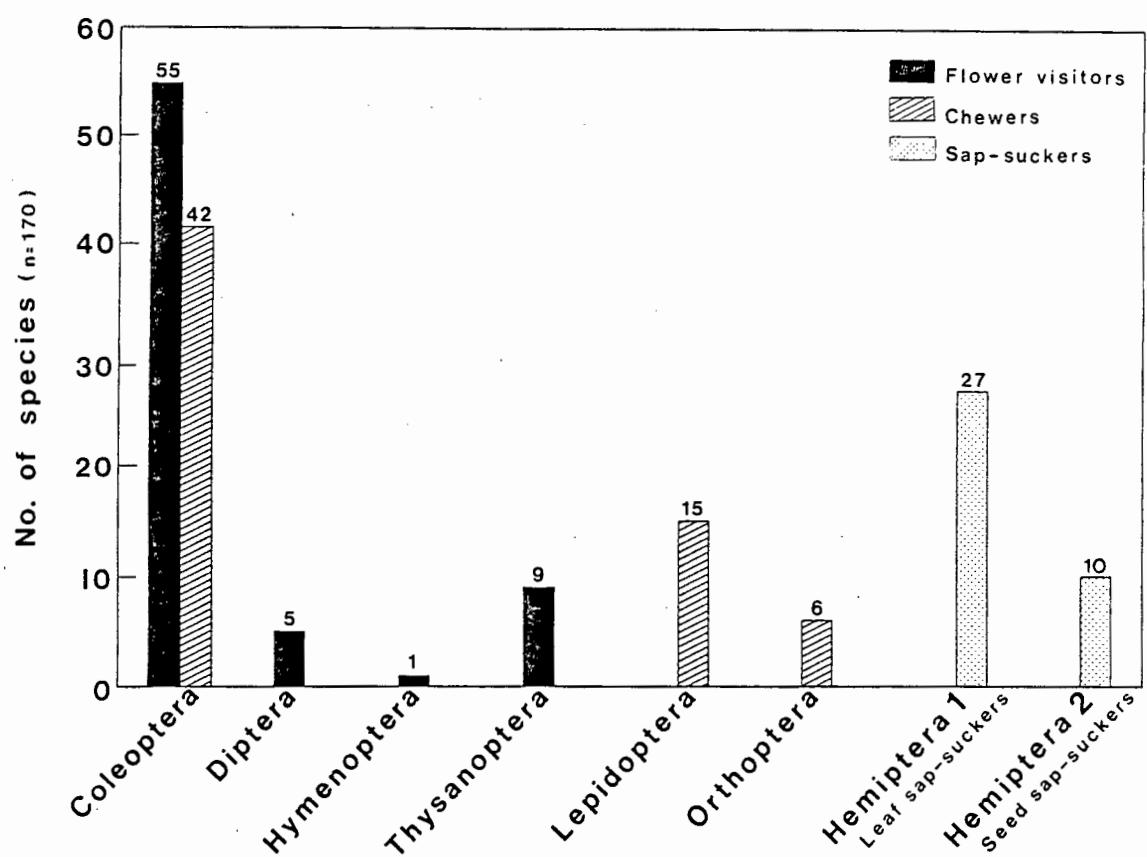
Fig. 1 The number of herbivorous insect species of different orders found on five species of Proteaceae in their natural environment

The herbivore guild, as defined by Moran & Southwood (1982), contributed 32,3% of the total number of individuals collected (Table 1) and consisted of 170 different species (Fig. 1). The Coleoptera was the dominant group numerically and 75,7% of all herbivorous species collected belonged to this order (Fig. 2a). Flower visitors represented 22,4% of the total number of individuals collected: the leaf-chewers 4,7% and sap-suckers 5,2% (Table 1). Expressed as a percentage of the herbivores, the figures are 69,5, 14,5 and 16,1% respectively (Fig. 2a). Although the chewers were numerically a relatively small sub-guild, they constituted 60,1% of the total herbivore biomass (Fig. 2b), in contrast with the 13,2% and 26,8% of the flower visitors and sap-suckers respectively.

69

N=1898
(S)-Sap-suckers
(F)-Flower visitors
(C)-Chewers
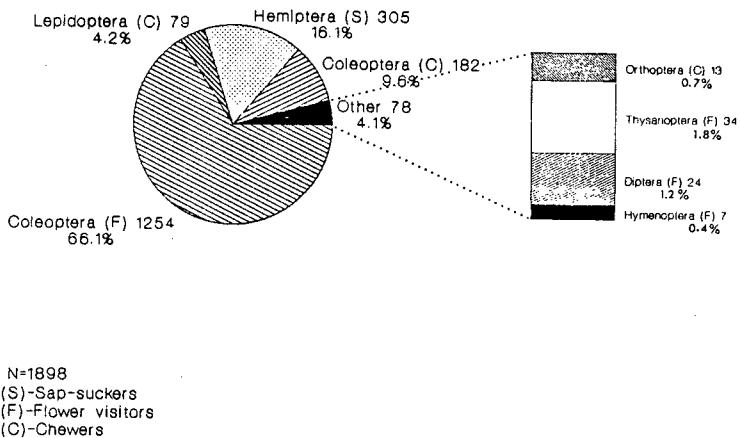
Fig. 2 a Number and percentage of herbivorous individuals of various taxonomic groups collected on five species of Proteaceae

N=11.86
(S)-Sap-suckers
(F)-Flower visitors
(C)-Chewers
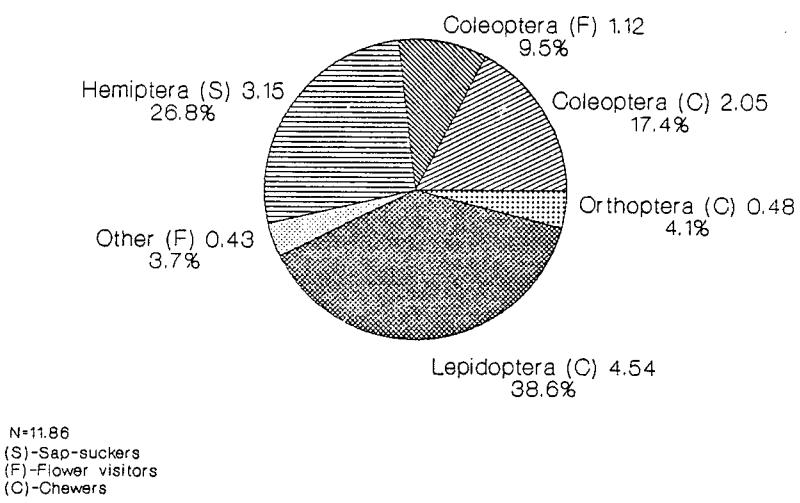
Fig. 2 b Biomass (in mg and percentage) of herbivorous individuals of various taxonomic groups collected on five species of Proteaceae

The number of flower visitors collected appeared to be influenced by the structure of the inflorescence. The *Protea* species have cone-shaped inflorescences with florets surrounded by involucral bracts. These inflorescences were visited by a large number of insects (Gess 1968; Coetzee & Giliomee 1985). In contrast, the bird pollinated genus *Leucospermum* has an open inflorescence, with florets exposed, whereas the dioecious *Leucadendron* bears naked cones. Fewer insect species visited the flowers of the genus *Leucospermum* than those of the genus *Protea* (pers. obs.). The number of flower visitors collected on the three *Protea* species (Table 1) was surprisingly low, probably because the cone-shaped inflorescences of these species protected flower visitors against the insecticides used and prevented insects from being dislodged from flowers during beating. The collection techniques were more suitable for collecting flower visitors on *Leucadendron* and *Leucospermum*. Although both *Leucadendron laureolum* and *Leucospermum cordifolium* have exposed florets, more flower visitors were collected on *L. laureolum* than on *L. cordifolium* (Table 1). This is probably a reflection of the relative importance of insects in the pollination of the two species.

In determining the effect of the herbivores on the plants both sap-suckers and chewers should be considered. The effect of sap-suckers is usually difficult to determine (Price, 1984), but due to their low numbers (Fig 2a) they were not regarded as being of great importance in primary consumption on the plant species investigated. The sap-suckers did not appear to damage or kill young shoots. According to Von Broembsen (personal communication), sap-suckers can transmit fungal diseases in Proteaceae, but little is known of their importance as disease vectors.

The expected monthly leaf damage E(p) caused by the chewers to a cohort of leaves up until they are 21 months old, is shown for each of the five species in Fig. 3. The full dummy variable regression model of percentage leaf damage on time with separate slopes and intercepts for each of the five plant species could be reduced ($F_{7.95}$ = 1.64; P = 0.14) to one with a common intercept (a = 0.34) for all five species and a common slope for *P. repens, P. neriifolia, L. cordifolium* and *L. laureolum* (b = 0.14) and a separate and steeper slope for *P. cynaroides (b = 0.65)*. This indicated that insect damage does differ between *P. cynaroides* and the other four plant species. The hypothesis that insect damage did not differ between plant species was partially rejected. The steeper slope of the regression for *P. cynaroides* indicated that damage increased faster on this species than on the other four, suggesting that older leaves of *P. cynaroides* were more attractive to folivorous insects than those of the other four species. Measured leaf damage to *P. cynaroides* exceeded three percent after the first four months, and increased to as high as 16 % on leaves older than 12 months. *Leucadendron laureolum* leaves sustained the least damage, on average less than 1 % of leaves younger than 12 months, and less than 2 % of older leaves was removed by insects.

71
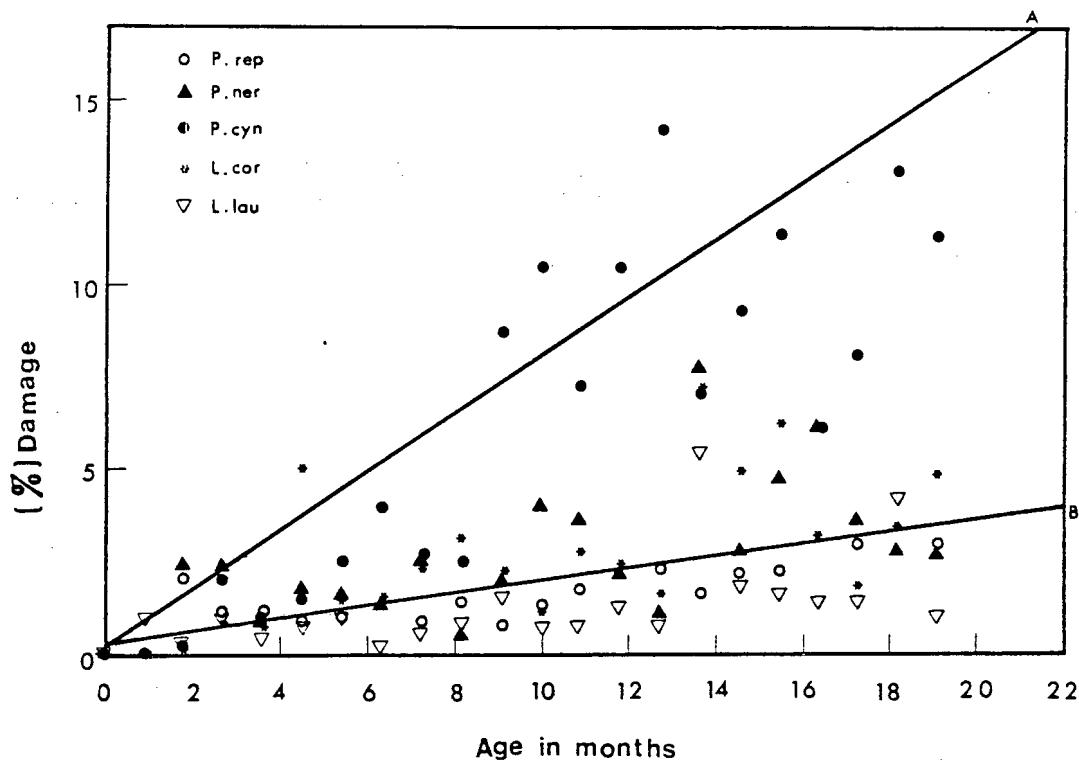
Fig. 3 The expected leaf damage on five species of Proteaceae as a percentage of total leaf surface plotted against age of the leaves in months. A = *Protea cynaroides* = 0.34 + 0.65 x, and B = *Protea neriifolia, Protea repens, Leucadendron laureolum* and *Leucospermum cordifolium* = 0.34 + 0.14 x, r^2 = 0.75

The common intercept for all five species indicated that the initial amount of damage over the first three months was the same for all five species. It was also clear (Fig. 3) that young developing leaves accrued little or no damage. This indicated that their leaves were well protected against insect herbivores or were unattractive. In addition, the slope values for both P. cynaroides and the other four species were highly significant (t_{102} = 15.16, P < 0.001 for P. cynaroides; t_{102} = 4.94, PL 0.001 for the other four species), indicating that in all cases damage increased with time. Older proteaceous leaves were therefore acceptable as food for herbivorous insects especially in the case of P. cynaroides as indicated by the steeper slope. The hypothesis that old leaves are not acceptable as food for insects is rejected.

72

The extent of leaf damage on plants is *inter alia* influenced by the insect community (number of species and individuals) feeding on the leaves and by the third trophic level, i.e. predators and parasitoids. Leaf damage is also influenced by the availability and accessibility of the food source, i.e. the ability of the herbivores to find their food source and how well these food sources are protected by chemical and physical defence mechanisms.

More leaf chewing individuals (Table 1) and species (personal observations) were found on *L. laureolum* than on *P. cynaroides*. This did not correspond with the difference in leaf damage measured. The reason for the high number of individuals and species on *L. laureolum* is possibly a result of the complex architecture of the plant compared to *P. cynaroides*. The herbivore to natural enemy ratio (Table 1) does not give any indication as to why the leaf damage differs between these species either.

The relatively low insect damage on leaves of proteaceous species can possibly be attributed in part to the heterogeneous nature of the fynbos biome. Huffaker *et al*. (1984) point out that total defoliation very rarely occurs in areas that are rich in plant species, because of the difficulty with which monophagous herbivores locate their specific host plants. This may partly account for low levels of damage in the fynbos in general, but it does not explain the different levels of insect damage on the different species of Proteaceae studied. With the exception of *P. cynaroides*, which usually has a scattered distribution, all the species studied can form dense stands. Yet contrary to the generally accepted hypothesis that dense stands are more susceptible to insect damage, *P. cynaroides* had the highest damage levels.

The accessibility of the leaves of a plant to insect herbivores is determined by the stage reached in the co-evolutionary process between the defence mechanisms of the plant and these herbivores (Price 1984). However no information is available on the nature of the defence mechanisms that the plants of this study may have developed to protect their leaves against insect attacks. The differences in the efficacy of the chemical defences of these plants may well have been responsible for some of the variation observed in plant damage, and were the subject of a separate investigation.

73

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74

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75

CHAPTER 5

ANTIHERBIVORE MECHANISMS OF THE FOLIAGE OF FIVE PROTEACEOUS SPECIES IN THE CAPE FYNBOS

ABSTRACT

The leaves of five plant species of the family Proteaceae were investigated to determine which leaf characteristics were possibly involved with defence against insect attack. Although the young leaves showed little or no herbivore damage, the older leaves were foraged by herbivores. This indicated the possible presence of an effective defence mechanism of chemical and/or physical nature in younger foliage. The presence of phenolic compounds such as tannins in the leaves of all five plant species and the ability of tannins to precipitate proteins varied between the plant species. This indicated that the tannin content in various proteaceaous species may have differed in its effect in deterring certain insects . The young leaves of *L. laureolum* were able to form HCN, while those of *L. cordifolium* and *P. neriifolia* were covered by a thick layer of trichomes. The glabrous young leaves of *P. repens* and *P. cynaroides* were apparently protected by phenolic compounds. The increasingly sclerophyllous character of ageing proteaceous leaves afforded these leaves some protection against certain insects.

Keywords: Proteaceae, defence mechanisms, herbivores, fynbos.

76

INTRODUCTION

The study of plant-insect interactions is still a relatively new field, (Schowalter *et. al.* 1986) but it is already clear that it is difficult to generalise on the defensive actions of plants against herbivores. Leaf characteristics influencing herbivory have recently received a great deal of attention (Rosenthal & Janzen 1979; Coley 1983; Strong *et al.* 1984 and Coley *et al.* 1985). In addition these different defence actions should not be viewed as single factors (Beck 1965; Chew & Rodman 1979). Plant species growing in soil with low nutrient levels cannot afford to lose large quantities of plant material to herbivores (Janzen 1974 and Coley *et al.* 1985). The soils in the southern and western Cape, where most African Proteaceae species occur, are leached and poor in nutrients (Groves *et al.* 1983). Effective antiherbivore defence mechanisms would under these circumstances greatly enhance their survival. Severe herbivore pressure also lowers the competitive ability of plants (Coley 1983 and references cited). In order to compete successfully in the fynbos vegetation, known for its great vegetational diversity (Bond & Goldblatt 1984), plants require well developed antiherbivore mechanisms. The extent to which herbivore pressure affects competition is demonstrated by the success gained by introduced plants in the fynbos in the absence of their natural enemies.

The leaves of proteaceaous plants persist on the plant for a number of years. Perennial plants must protect their evergreen leaves against herbivores throughout the functional life of the leaves (Rhoades & Cates 1976). Habitat, competition and leaf longevity are therefore possible factors contributing to the development of an antiherbivore syndrome in the Proteaceae. Damage due to herbivory of certain proteaceous species varied between 2% and 15% (Coetzee 1989d). This variation range suggested that defense mechanisms differ among species.

To determine the functional role of leaf characteristics as defence mechanisms, including seasonal or age related differences regarding their antiherbivore effects, leaves were regularly sampled and examined for the duration of their functional life on the plant. Special attention was given to the defence mechanisms of young leaves as they exhibit little or no feeding damage (Coetzee 1989d) by insects. To detect the presence of defence mechanisms (if any) in the leaves of certain proteaceous plants, some leaf characteristics were investigated for five species. These included leaf chemical characteristics such as total phenolic content, protein precipitating ability, cyanogenesis and nitrogen content as well as physical characteristics such as leaf toughness, woodiness, and fibre content. The five species investigated were *Protea repens, P. neriifolia, P. cynaroides, Leucospermum cordifolium* and *Leucadendron laureolum*.

MATERIALS AND METHODS

Leaves of four species, namely *P. repens, P. neriifolia, L. cordifolium* and *L. laureolum*, were collected at Helderfontein, while *P. cynaroides* leaves were collected at Protea Heights, both sites are in the Stellenbosch area. To minimize intraspecific variation, plant material was collected from the same group of plants each month, but not necessarily from the same plant. Ten plants of each species were selected each month. One shoot, bearing leaves of the most recent season (new leaves) as well as from the previous years main growth cycle (old leaves), was picked from each plant. All the assays (except protein precipitation) were performed on a monthly basis. Collection of leaf material for all assays except hydrogen cyanide analysis and protein precipitation, commenced in September 1986 and ended in September 1987. The leaves used in the hydrogen cyanide analysis were collected from October 1986 to January 1988, and those for the protein precipitation assays in September 1988. Shoots were collected before 10:00 on sunny days, placed in cold storage within 60 min and processed within four hours of collection. New and old leaves were analysed separately.

Determination of total phenolic content: For each plant species 50 old and 50 young leaves were dried at 50°C for 72 h, ground and sieved (212 μm diameter mesh). The material was stored in glass flasks with screw-on lids in the dark at room temperature. For extractions *ca.* 0,3 g dry material (the exact mass of the material was recorded) was mixed with 10 cm^3 of an 90% (v/v) methanol solution, and the mixture was brought to boiling point in a thermal bath. The supernatant was decanted and filtered through glass wool. This process was repeated three times, and then three more times with a 50% (v/v) methanol solution. The supernatant was then concentrated under vacuum in a rotary evaporator after which it was made up to 50 cm^3 with distilled water and stored in plastic containers at -30°C. The Folin-Ciocalteu method was used to determine total polyphenol levels (Singleton & Rossi 1965; Slinkard & Singleton 1977). Values were standardised against gallic acid (Riedel - De Haën A G), and the results expressed in terms of gallic acid equivalent (mass basis). A standard series of gallic acid was prepared in duplicate, one at the start of the test and one at the end, to compensate for a possible difference in reaction time. Using 2 cm^3 of each standard dilution or extract, the test was started with the addition of 10 cm$_3$ Folin-Ciocalteu reagent (10%) to each reaction flask. Within 8 min after this addition, 8 cm^3 Na_2CO_3 (75 g/l) was added. The solution was mixed thoroughly and left at room temperature for 2 h, after which the absorption was read at 765 nm.

78

Protein precipitation: Leaves were freeze-dried within 60 min of collection, ground and sieved (212 μm). The extraction method was adapted from Martin & Martin (1982). Leaf powder (0,5 g for the genus *Protea* and 0,06 g for *L. cordifoloium* and *L. laureolum*) was extracted twice for 8 min with 4 cm of boiling 50% (v/v) methanol in a centrifuge tube (capped with a marble) placed in a thermal bath at 92° - 95°C. After centrifugation (12,000 x g, 15 min, 5°C), the pellet was resuspended in a small volume of 50% methanol and centrifuged as before. The volume of the combined supernatants was adjusted to 10 cm^3, and dilutions kept for approximately 2 h at 4 - 10°C in plastic containers. To perform the astringency test, the method of Hagerman & Butler (1978) was used to determine the ability of the tannins to precipitate proteins. A colour test, using ferric chloride (0,01 mol/dm^3 ferric chloride in 0,01 mol/dm^3 hydrochloric acid) as the reagent, was performed to determine to what extent proteins had precipitated. To each sample 0,5 colour reagent was added and 15-30 min later the absorbance was read at 510 nm. The absorption values were then used to compare the precipitation ability of the tannins.

Determination of the ability of leaves to produce hydrogen cyanide: A method to estimate cyanide was adapted from Aldridge (1944). Plant material was collected and leaves chopped finely within 60 min after collection. To one gram of each sample, 10 cm^3 HgCl$_2$ (10 g HgCl$_2$ in 1 000 cm^3 distilled water) and 1 cm^3 ß-galactosidase (0, 08 g ß-galactosidase in 50 cm^3 distilled water) were added; the tubes were sealed and stored at room temperature for 30 days. The ß-galactosidase solution was added to ensure the hydrolysis of the cyanogenic glycosides. After 30 days, each sample was flushed (with distilled water) into a glass tube of an extraction apparatus. Separately calibrated test tubes, containing 5 cm^3 NaOH (0,2 mol/dm^3), were used to obtain absorption of the hydrogen cyanide gas. Absorption of HCN was facilitated by adding three drops of n-butanol to the NaOH solution. Immediately prior to commencing HCN extraction, 5 cm SnCl$_2$ solution (0,5 mol/dm^3 in 1 mol/dm^3 HCl) was simultaneously added to each sample. Air was then bubbled through the samples. After 2 h, the extraction was stopped and the tubes containing the NaOH and dissolved HCN gas were removed. A standard was prepared using KCN to make a dilution series ranging from 0,1 μg/cm^3 to 3,0 μg/cm^3. One cm^3 of the solutions and standard was measured into separate tubes. One cm^3 concentrated HCl was added while the tubes were cooled in crushed ice to prevent the volatile cyanide gas from escaping. After 5 min, 1 cm^3 saturated bromine water was added and the solution shaken thoroughly. To remove surplus bromine, 1 cm^3 ascorbic acid (5 g/100 cm^3) was added 5 min later. After another 5 min, 8 cm^3 pyridine colour reagent was added, while shaking the solution thoroughly and 10 min later the absorbance was read at 520 nm. The cyanide content was calculated using the standard curve and taking the dilution factors into account. The colour reagent was prepared by first dissolving 1,77 g anthranilic acid in 25 cm^3 of a 24% (v/v) HCl solution. The solution was heated slightly on a magnetic stirrer. A solution of 10 cm^3 concentrated HCl and 70 cm^3 pyridine was added to 20 cm^3 of the anthranilic acid solution and diluted to 250 cm^3 with distilled water.

79

The **sclerophyllous** nature of leaves was influenced by the degree of toughness, woodiness, nitrogen and fibre. To elucidate the role of sclerophylly the following factors were determined:

Leaf toughness: Ten leaves from each monthly sample were used to determine the leaf toughness by using a penetrometer (Feeny 1970). The penetrometer measures the force required to drive a 5 mm diameter rod through the leaf surface. Leaves were placed in such a way that the main veins were not touched by the rod. Force on the rod was applied by pouring water slowly into a container that was secured to a platform on top of the rod. As soon as the leaf was penetrated, the addition of water was stopped and the mass of the water in the container determined. Leaf toughness was expressed as the mass of water required to force the rod through the leaf.

Woodiness: Woodiness was determined monthly by selecting 10 leaves from each sample. The leaves were submerged in distilled water and kept in a dark cold store for 24 h at 10°C to obtain maximum hydration. The wet mass was determined and the leaves were then dried for 24 h at 105°C, after which the dry mass was determined. Sclerophylly was then expressed as a percentage of dried mass over hydrated mass.

Nitrogen: Leaves were analysed monthly to determine nitrogen content. The plant material was freeze-dried and then ground. Nitrogen content, determined by using the automated analyser technique (Starr & Smith 1978), was expressed as percentage nitrogen of total dry mass of leaves.

Fibre: The fibre content was determined by using the "Tecator Fibertec System" (A.O.A.C. 1984).

Data analysis: Plots of the data were inspected and according to the observed trends quadratic, asymptotic or linear regression were fitted. If the significance level for the regression model which fitted best was greater than 0,05; it was assumed that there was no trend and no model was fitted.

80

RESULTS

Total phenolic content: The leaves of *P. repens* contained the highest percentage of total phenolic compounds (Fig. 1A) with a mean of 17,77 % (range: 12,53 - 30,03 %), but no age-related change was observed. The phenolic compounds in both *P. neriifolia* and *L. laureolum* leaves also showed no trend as the leaves aged (Fig. 1B and 1E). This contrasted with the phenolic compounds of the leaves of *P. cynaroides* which showed an asymptotically decreasing change (y = 11.47 + 20.83e$^{-0.635x}$, R^2 = 0.76) (Fig. 1C) while the phenolic compounds in the leaves of *L. cordifolium* (Fig. 1d) exhibited an increase as the leaves aged.
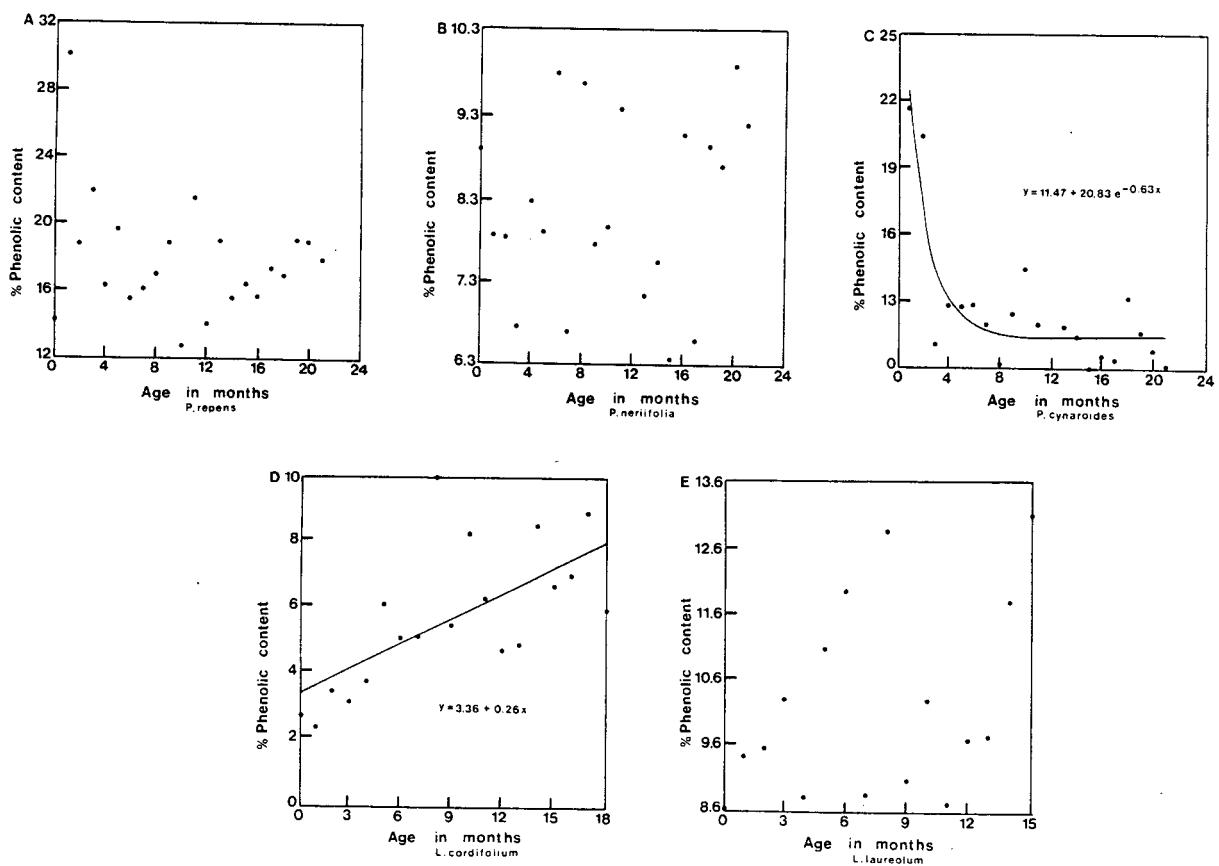
Fig. 1   The percentage total phenolic content in the leaves of five Proteaceae species

Protein precipitation: The ability of phenols to precipitate proteins differed between the genera. In the *Protea* spp. it was less than in the genera *Leucadendron* and *Leucospermum* (Table 1). The phenols from old *L. cordifolium* leaves exhibited the highest protein precipitation ability (Table 1). The phenols from young *L. laureolum* leaves precipitated proteins more effectively than the young leaves of *L. cordifolium*. Of the three *Protea* spp. the phenols of *P. neriifolia* were the most effective (Table 1). In all the species the precipitation ability of phenols of the old folia was higher than in the young leaves (Table 1).

TABLE 1 :   Absorption (510 nm) values of the protein precipitation ability of phenols of five species of the family Proteaceae. The precipitation ability of the plant species varies and different masses of plant material were used to extract the phenols. For the genus *Protea*, 0,5 g was used and for the other 0,06 g.

Species	Age of leaf	
	New	Old
Protea repens *	0,193	0,240
Protea neriifolia *	0,316	0,574
Protea cynaroides *	0,122	0,412
Leucospermum cordifolium °	0,248	0,481
Leucadendron laureolum °	0,291	0,435

*   0.5g   plant material
°   0.06g   plant material

82

Hydrogen cyanide: The ability to form hydrogen cyanide was observed in all five species. The leaves of *L. cordifolium, P. repens, P. neriifolia* and *P. cynaroides* showed low cyanogenic levels, with the amount of cyanide measured never more than 4 μg/g leaf mass (Fig. 2). In contrast, young leaves of *L. laureolum* measured almost 110 μg/g leaf mass. Production of HCN in *L. laureolum* (Fig. 2E) showed an age-related asymptotic distribution ($y = 124{,}31e^{-0{,}4318x}$, $R^2 = 0{,}88$). The ability to form HCN decreased rapidly with leaf age, and after five months the leaves had lost this ability almost completely. The results indicate that leaves of approximately 12 months old retain a slight ability to produce HCN.
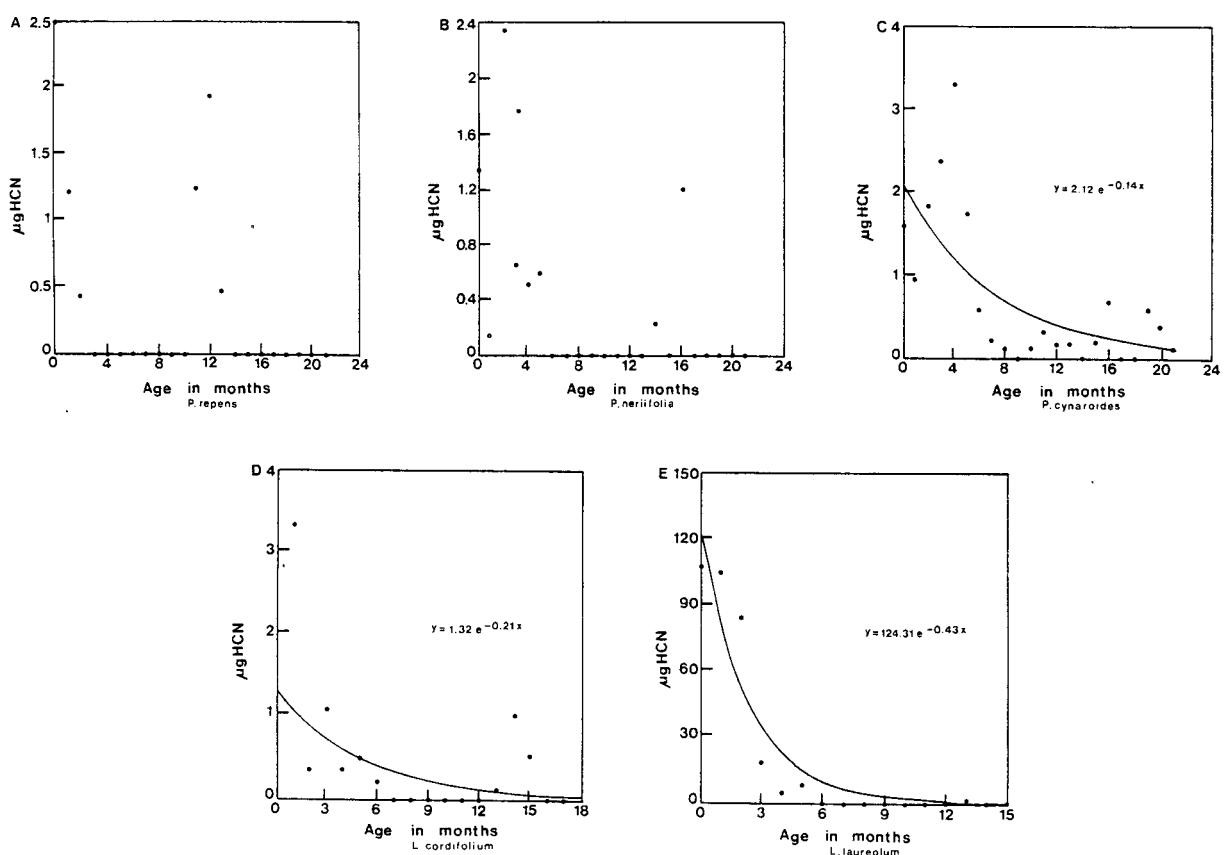
Fig. 2   Cyanogenic potential in μg/g leaf mass of the leaves of five Proteaceae species (note differences in scale).

Toughness: Leaf toughness (Fig. 3) showed an asymptotic increase with leaf age, reaching an upper limit after four to eight months. The leaf toughness of *P. repens* (Fig. 3A) and *P. cynaroides* (Fig. 3C) decreased after 12 months.
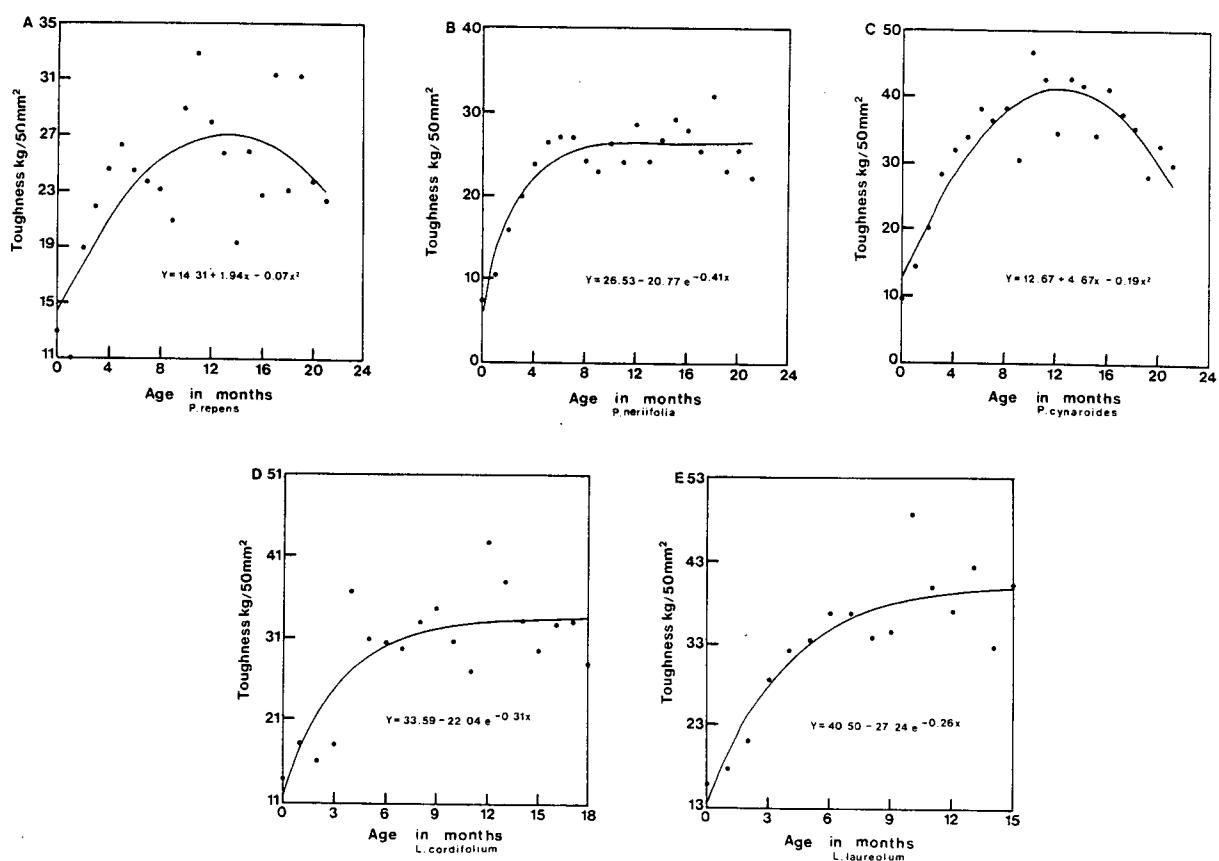
Fig. 3   Leaf toughness of five Proteaceae species

84

Woodiness: As the leaves aged, woodiness (Fig. 4) increased asymptotically. The woodiness in leaves of the three *Protea* species reached an upper limit after four to twelve months but in *L. cordifolium* after six to nine months. In *L. laureolum* this was already reached after three months.
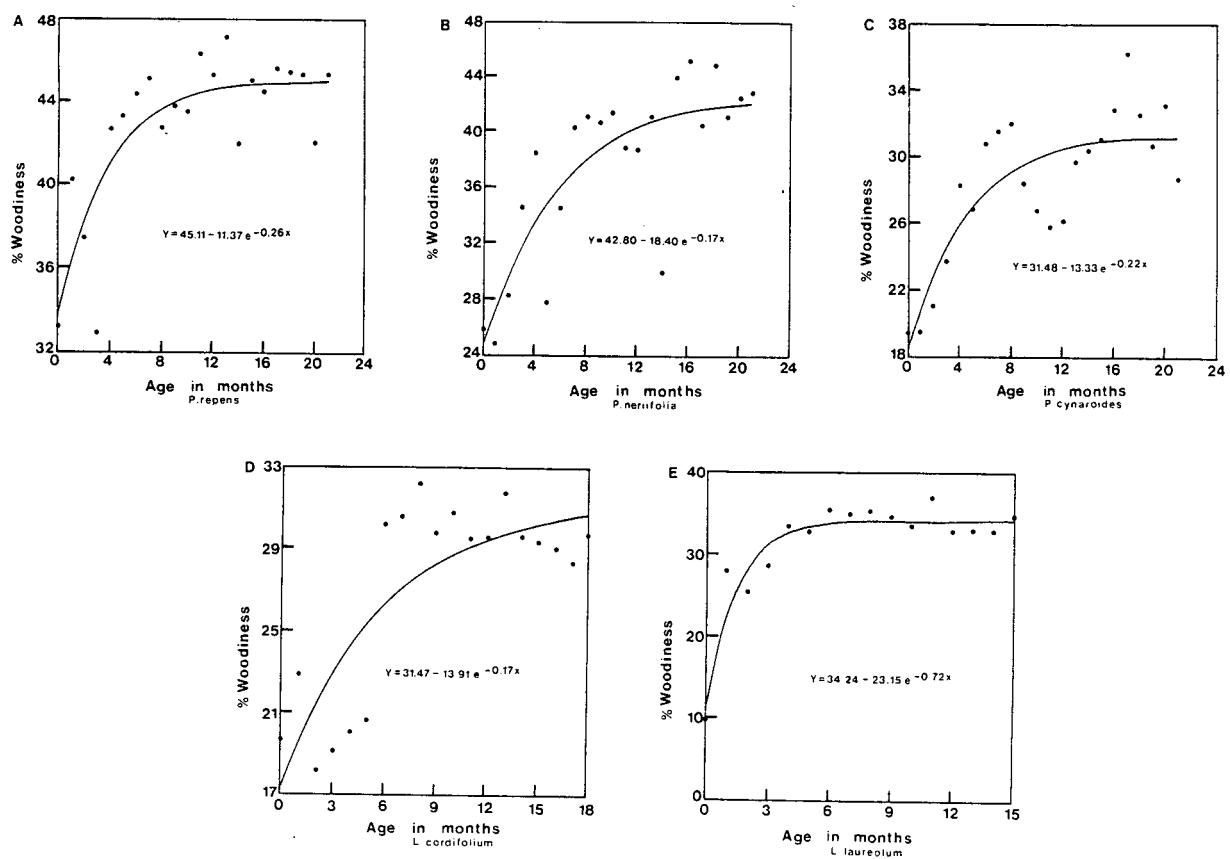
Fig. 4   The percentage woodiness of the leaves in five Proteaceae species (note differences in scale)

85

Fibre: The fibre content of *P. neriifolia* and *L. cordifolium* revealed an asymptotically decrease associated with age (Fig. 5C,D). In the case of *P. repens*, *P. cynaroides* and *L. laureolum* there was no trend in the fibre content of the leaves (Fig. 5A,B,E).
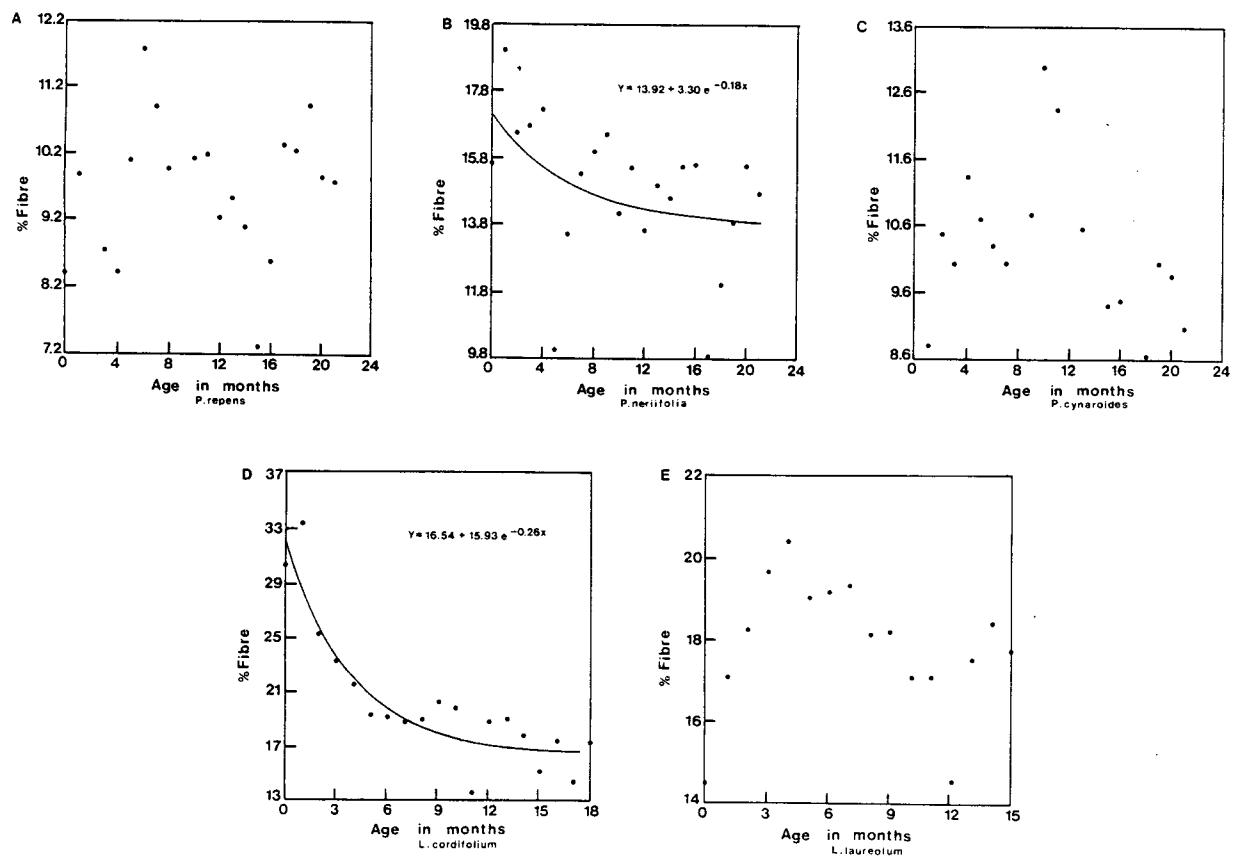
Fig. 5   The percentage fibre content in the leaves of five Proteaceae species (note differences in scale).

Nitrogen: The nitrogen content of the leaves of the five proteaceous species investigated varied between 0,40 % and 1,55 %. (Fig. 6). Nitrogen content of *P. cynaroides* leaves was the highest (Fig. 6b) with an average of 0,85%, whereas that of *L. laureolum* was the lowest (average 0,54%). The amount of nitrogen tended to decrease asymptotically as the leaves aged. The poorly correlated decreasing asymptotic trend possibly shows that the nitrogen content of leaves is influenced by external factors.
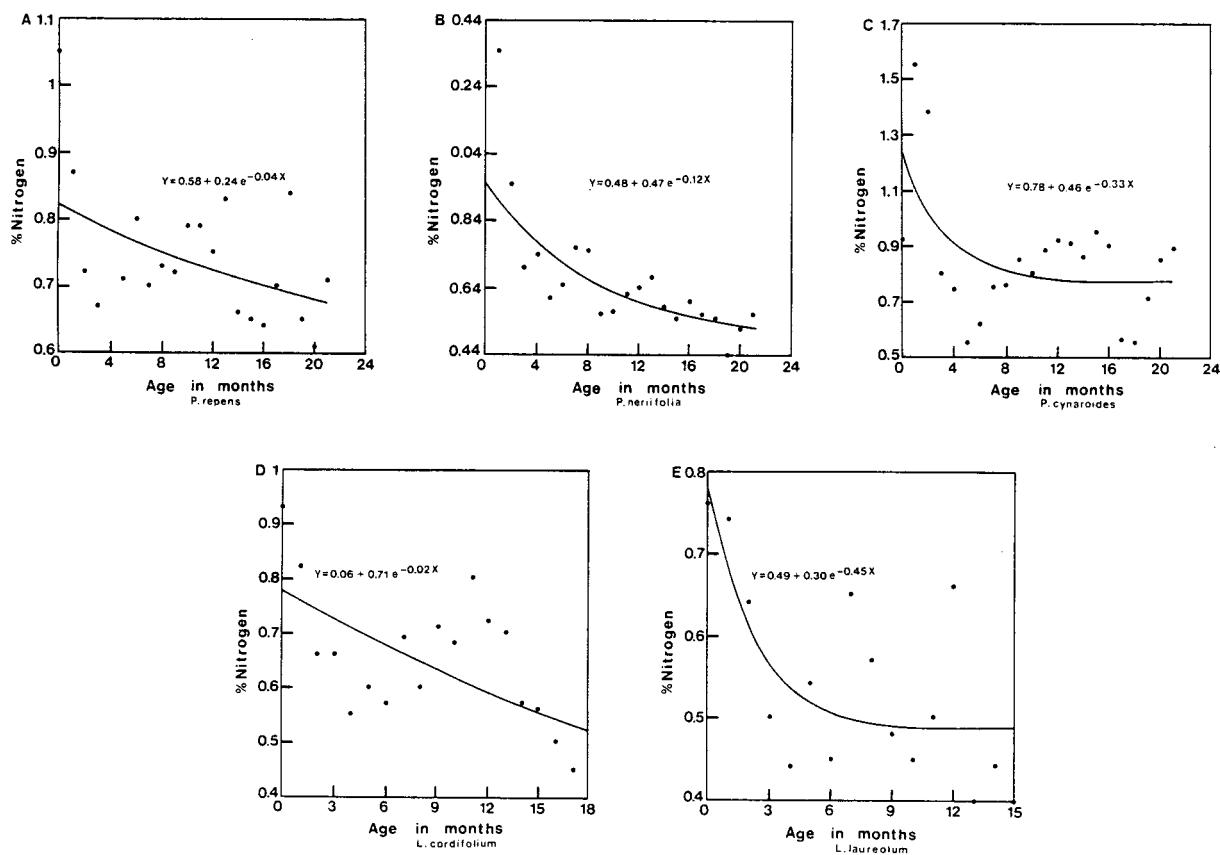
Fig. 6   The percentage (dry mass) of nitrogen in the leaves of five Proteaceae species (note differences in scale).

DISCUSSION

Various phenolic compounds have been identified in Proteaceae (Bate-Smith & Metcalfe 1957; Perold & Pachler 1964; Hegnauer 1969; Elsworth & Martin 1971; Kruger & Perold 1970; Perold 1984, 1986; Perold et al. 1972). Although it was found that phenolic compounds have no effect on insects (Bernays 1978), there is sufficient indication that some of these phenolic compounds may act in plant defence (Feeny 1970; Fox & Macauley 1977; Bernays 1981; Zucker 1983). The effectiveness of tannins as antifeedants lies in the fact that proteins are precipitated and enzymes become immobilised (Bate-Smith 1973; Becker & Martin 1982). This leads to poor digestion and a decrease in nutrient value of plant material (Bernays 1978). According to Zucker (1983), hydrolysable tannins protect the plant against herbivores and condensed tannins are reserved primarily for defence against microbes and pathogens.

The total phenolic content of the leaves of the five proteaceous species studied varied a great deal. It also appears that the chemical nature of the phenols differ, although this was not studied specifically. Protea spp. contain aryl-O-glycoside esters as typical leaf constituents (Perold et al. 1979). These esters are theoretically hydrolysable tannins (G. Perold personal communication). Each of the three Protea spp. studied have different aryl-O-glycoside esters. The hydrolysable tannins of the three Protea spp. probably act in the defence of the plants against herbivores. The total phenolic content of leaves of P. repens is high and could act as an effective defence mechanism. In the case of P. cynaroides, the initial phenolic content of the young leaves is high (Fig. 1b). This high concentration of phenols which, according to G. Perold (personal communication), could consist mainly of aryl-O-glycoside esters, probably defended the young leaves effectively, but as the leaves became older and the metabolite levels decreased, the leaves might have lost this defence mechanism. This may, in part, explain the high insect damage on old leaves of P. cynaroides (Coetzee 1989d).

The ability of the aryl-O-glycoside esters in the genus Protea to precipitate proteins was weak in comparison with the phenols of L. laureolum and L. cordifolium (Table 1). Aryl-O-glycoside esters are relatively small molecules (molecular weights of 400), and interaction with tertiary protein structures seems unlikely (G. Perold personal communication). In spite of their inability to precipitate proteins, the phenolic compounds may still have defended leaves. L. laureolum contained leucodrin and leudrin (phenolic lactones) as major leaf metabolites (Perold, 1984). Further work by Perold (personal communication) showed that these metabolites were not comparable with hydrolysable tannins. In L. cordifolium the nature of the phenolic metabolites is unknown (Perold, 1984). Their colour reactions with Pauly's reagent indicate that they could be low molecular weight condensed tannins (Perold personal communication) The phenolic compounds extracted from L. laureolum and L. cordifolium, could have contained condensed tannins. Their strong ability to precipitate proteins, thus influencing protein absorption and/or digestion in some insects, suggests an antiherbivore potential. Zucker's (1983) hypothesis that condensed tannins could not protect leaves against insect herbivory was not supported by these results.

According to Hegnauer (1969), a number of Proteaceae exuded hydrogen cyanide after being damaged. This characteristic was particularly present in the Australian Proteaceae. Hegnauer however, observed poor cyanogenenesis in *P. cynaroides*. Glennie & Davidson (1978) found *P. cynaroides* and other species in the genus *Protea* not capable of forming HCN, but found other species in the genera *Leucadendron* and *Leucospermum* positive for cyanogenesis. In this study relatively strong cyanogenesis was observed in *L. laureolum*, whereas leaves of the other four plant species exhibited low cyanogenic activity (Fig. 2e). There was a distinct age-related ability to form hydrogen cyanide in some species, and as a result of this, negative results could be obtained from leaf samples collected at certain times of the year. Cyanogenic glucosides could be re-utilized (Blumental *et al* . 1968) and the possible recirculation of cyanogenic glucosides may explain the variations shown in Fig. 2. Cyanogenic glucosides and the hydrolytic enzyme glucosidase are effective anti-herbivore chemicals (Dement & Mooney 1974; Jones 1979). Glucosidase enzymes are compartmented in undamaged plant tissue; if cell walls are damaged, an organic aldehyde plus the highly toxic gas hydrogen cyanide is formed (Dement & Mooney 1974). The formation of relatively large amounts of HCN and the low leaf damage observed in *L. laureolum* (Coetzee 1989d) show that cyanogenesis was one of the factors possibly responsible for more effective protection by decreased acceptability to herbivores.

Leaves of plants of the mediterranean climatic areas are generally sclerophyllous, a characteristic recognised as one of the adaptations making leaves less acceptable to chewing herbivores (Mooney & Dunne 1969). Sclerophyllous leaves are characterised by a high degree of woodiness, accompanied by low water content, toughness and low nitrogen content, all of which influence the suitability of the leaves as food for herbivores. The five proteaceous species investigated all possessed the characteristics of typical sclerophyllous leaves. There was, however, no evidence that these characteristics can explain the differences between species with regard to damage by herbivores. The low nitrogen content observed (usually lower than 1%) probably also contributed to limiting herbivory. According to Soo Hoo & Fraenkel (1966 a, b), leaves with a nitrogen content lower than 3% are not optimal as food for herbivores. Proteaceous leaves are therefore a relatively unsuitable type of herbivore food. Soo Hoo & Fraenkel (*loc cit*) intimated that a low nitrogen content compels herbivores to ingest more food. In the case of sclerophyllous leaves, however, there are characteristics, such as high wood content, low water content, toughness and toxic substances which make it impossible for the insects to ingest larger quantities of plant material in order to compensate for a decrease in nutritional value.

The trichomes, which formed a dense mat on young leaves, disappeared as the leaves aged. The decrease in fibre content of *L. cordifolium, L. laureolum* and *P. neriifolia* was the direct result of the loss of trichomes which were high in fibre content. The high fibre content probably contributed to making young leaves unacceptable to herbivores.

It appeared that a combination of defence mechanisms was involved in the protection of proteaceous leaves against herbivores. These defence mechanisms differed at the intergeneric as well as at the inter-specific levels. Variations may even have occured within the same species. The age-related changes in these mechanisms indicated that old and young leaves were not protected by the same antiherbivore mechanisms. The low damaged level of young leaves (personal observation) and the accumulated increase in damage with ageing of the leaves (Fig. 3, Coetzee 1989d) indicated that old leaves were more susceptable to insect damage than young leaves. This tendancy is not clearly illustrated in Fig.3, (Coetzee 1989d) due to the scatter of the data points. Although the effect of physical defence mechanisms such as high wood content, low water contented and toughness increased with ageing, herbivores still consumed old leaves to some extent. It was probably of greater importance for the plant to protect its young leaves, as the photosynthetic rate of such leaves was higher (Salisbury and Ross 1978), and therefore a more intricate defence strategy utilizing chemical defence was justified in protecting young leaves. The different antiherbivore mechanisms were not equally effective against the various herbivores and it was not possible to predict the most effective defence strategy. This can only be established when the leaf damage of the different species is compared. Since the leaves of *L. laureolum* showed the least damage of the five species investigated (Coetzee 1989d), it would appear that this plant's defence strategy against herbivores was the best developed.

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91

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92

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93

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94

CHAPTER 6

COEXISTENCE AND RESOURCE UTILIZATION OF LARVAL COLEOPTERA AND LEPIDOPTERA IN THE INFRUCTESCENCES OF *Protea repens* (PROTEACEAE)

ABSTRACT :

The serotinous infructescences of *Protea repens* are exploited by the larvae of four Coleoptera species namely *Genuchus hottentottus* F. (Scarabeidae), *Sphenoptera* sp. A (Buprestidae), *Sphenoptera* sp. B (Buprestidae), and *Euderes lineicollis* Weid. Curculionidae and four Lepidoptera species namely *Orophia ammopleura* Meyrick (Oecophoridae), *Bostra conspicualis* Warren (Pyralidae), *Argyroploce* sp. (Olethreutidae) and *Tinea* sp. (Tineidae). The food resource is eventually over-utilized, leading to a shortage of food. The community structure of these phytophagous insects is largely determined by negative interactions. Various strategies are followed (e.g. niche segregation in time and space) to lessen interspecific competition. Niche overlap, however, does occur in some cases and in these cases the species exhibit competitive abilities, such as confrontation, copious egg-laying, mobility of larvae and the exploitation of a wide host series to ameliorate interspecific competition.

Keywords: Interaction, competition, community structure, niche overlap, resource utilization, species packing, Proteaceae.

95

INTRODUCTION

The infructescence of *Protea repens* (L.)L. (Proteaceae) provides a suitable habitat for the larvae of eight insect species (Coetzee & Giliomee 1987a). Four Coleoptera species namely *Genuchus hottentottus F.* (Scarabeidae), *Sphenoptera* sp. A (Buprestidae), *Sphenoptera* sp. B (Buprestidae), and *Euderes lineicollis* Weid. Curculionidae and four Lepidoptera species namely *Orophia ammopleura* Meyrick (Oecophoridae), *Bostra conspicualis* Warren (Pyralidae), *Argyroploce* sp. (Olethreutidae) and *Tinea* sp. (Tineidae) bore into the achenes, the involucral receptacle, the florets and may also feed on the involucral bracts. Up to 80% of *P. repens* achene reserves may be destroyed by borers within two years of seed set (Coetzee & Giliomee 1987b). Such an infructescence can be considered as a mini-ecosystem (see Zwölfer 1979,1984) and, because of its small size, discrete boundaries, accessibility and long functional life, as a very suitable unit for ecological studies.

Infructescences are formed after the individual florets of the inflorescence have opened and pollination has taken place. At the end of the flowering period a closed cone is formed by the folding of the inner involucral bracts. The infructescences are serotinous, and only after they have been damaged by fire, insects, disease or mechanically will achenes be released. The functional life of an infructescence may be as long as two years in the absence of fire. After two years factors such as insect damage usually destroy the infructescences. General observations indicated that limited food resources rather than natural enemies are important in regulating the community inside the infructescences. This investigation was therefore undertaken to establish how the various species in the infructescences share the available food resources in space and time.

96

MATERIALS AND METHODS

Infructescences of *P. repens* from a succession of flowering seasons were collected at three-weekly intervals from three areas in the western Cape Province, South Africa, namely Swartboskloof (33°58'41"E, 18°57'08"S), Jan Marais Nature Reserve (33°55'52"E, 18°52'35"S) and Stellenbosch Mountain (33°58'21"E, 18°52'48"S). Collection was started in November 1981 and completed in April 1986, except at Stellenbosch Mountain where a fire destroyed the study site in 1984. A total of 2419 infructescences were collected from the three areas. Mid-May was regarded as the peak of the flowering season and infructescences collected at that time were considered to be zero weeks of age. Collection of infructescences from a specific flowering season was terminated 102-108 weeks after flowering. After this infructescence age and too few infructescences were available (due to high achene predation) to obtain samples.

Sampford's (1962) line transect method was used to choose plants at each collection in each of the three areas. One infructescence from each of the two most recent flowering seasons was collected from each of ten plants, using Lombaard's (1971) approach to distinguish between infructescences from different flowering seasons on the same plant. Infructescences were dissected and the number of damaged and undamaged achenes, as well as the number of larvae present in each of the infructescences was documented. Three discrete zones of the infructescences were distinguished viz. the base, middle and upper zones. The base comprised the involucral receptacles and outer involucral bracts, the middle the achenes and the upper inner involucral bracts, perianth segments and styles of the florets (Fig.1). The following parameters were estimated :

(a) **Niche overlap (O_{ij}) :**

$$O_{ij} = 1,0 - 0,5 \sum_{h=1}^{n} | p_{ih} - p_{jh} |$$

where O_{ij} is the percentage overlap and p_{ih} and p_{jh} are the proportion of species i and j associated with the resource category h. The index was standardized and varied from zero (no overlap) to one (complete overlap). This index has been used by Schoener (1970), Rathcke (1976) and Kephart (1983).

(b) **Expected presence of individuals ($f*_{ij}$):**

$$f*_{ij} = n_{ih} n_{jh} / n_h$$

where n_{ih} and n_{jh} represent the number of species i and j present during the time interval h; n_h represents the number of "sources" (infructescences) investigated during time interval h (weeks after flowering) (see Rathcke, 1976).

(c) **Co-occurrence coefficient (c_{ij} and c_{jj}):**

$$c_{ij} = (\Sigma f*_{ij}) / n_i$$

where $\Sigma f*_{ij}$ is the sum of the expected presence of species i and j, and n_i is the number of species i. According to Rathcke (1976), c_{ij}, the average interspecific co-occurrence coefficient provides an index of species packing and on the diagonal of the matrix lie the intraspecific co-occurrences (c_{jj}).

(d)   Degree of overlapping γ and $\gamma_{(ind.)}$, and spatial correlation index $\omega_{(+)}$ or $\omega_{(-)}$:

$$\gamma = \frac{\sum X_{xj} X_{yj}}{\sqrt{\sum X^2_{xj} \sum X^2_{yj}}}$$

where X_{xj} and X_{yj} are the numbers of individuals of species x and species y in the jth quadrant (Iwao 1979).

$$\gamma_{(ind.)} = 1 / \sqrt{\frac{(\overset{*}{x}_x + 1)}{\bar{x}_x} \frac{(\overset{*}{x}_y + 1)}{\bar{x}_y}}$$

where $\bar{x}$ = mean density, and $\overset{*}{x}$, mean crowding = $\bar{x} + (\sigma^2/x - 1)$ and is defined as the mean number per individual in the same quadrant (Lloyd, 1967).

$$\omega_{(+)} = \frac{\gamma - \gamma_{(ind.)}}{1 - \gamma_{(ind.)}} \quad , \qquad \gamma \geq \gamma_{(ind.)}$$

$$\omega_{(-)} = \frac{\gamma - \gamma_{(ind.)}}{\gamma_{(ind.)}} \quad , \qquad \gamma \leq \gamma_{(ind.)}$$

The value of changes from a maximum of +1.0 for complete overlapping, through 0 for independent occurrence, to a minimum of -1.0 for complete exclusion (Iwao 1979).

(e)   **Demand and supply in the infructescence :**

If infructescences were collected in which only one individual had completed its life cycle, the damaged achenes were counted. These data were used to determine the number of achenes required by this species to complete its life cycle and is referred to as demand or S. The demand of specie i, S_i, relative to the species with the highest demand, S_H, was used to determine relative insect demand,

$$ID_i = S_i / S_H$$

where S_i = the number of achenes required by species i to complete its life cycle and S_H =   the number of achenes required by the insect with the highest demand to complete its life cycle.

Demand in each time interval, h, was calculated by using:

$$\text{Demand}_h = K \sum_{i=1}^{n} n_i \left(ID_i \right)$$

where N = Total number of species, n_i = number of individuals in species i, and k = the number of achenes required by species, S_H with ID = 1. The supply was calculated by counting all undamaged achenes in the infructescensces.

RESULTS

A. Niche overlap in space and time

The infructescences were exploited by the larvae of four Coleoptera and four Lepidoptera (Tabel 1). The spatial arrangement of the eight species in the infructescences indicated that more than one species occupied the same niche space (Table 2a,b). A schematic representation (Fig. 1) showed that most species occurred in the middle or basal zones. Although six species could exploit the basal zone (Fig. 1), more individuals occurred in the middle zone (Table 2a), the region where the achenes are situated. There was however, a slight degree of niche segregation in space, because some species were restricted to certain zones. *Bostra conspicualis* were confined to the upper zone, *Sphenoptera* sp.A to the middle zone whereas *Orophia ammopleura* and *Sphenoptera* sp. B were found in the basal zone.

TABEL 1:   Borers in the infructescences of *Protea repens* (L) L.

Coleoptera

Genuchus hottentottus F.	Scarabaeidae
Sphenoptera sp. A	Buprestidae
Sphenoptera sp. B	Buprestidae
Euderes lineicollis Weid.	Curculionidae

Lepidoptera

Orophia ammopleura Meyrick	Oecophoridae
Bostra conspicualis Warren	Pyralidae
Argyroploce sp.	Olethreutidae
Tinea sp.	Tineidae

99

The borers appeared to follow a successional pattern in the   colonization of the infructescences. Two species (*Euderes lineicollis* and *O. ammopleura*) colonized the inflorescence before the infructescence had been formed and their life cycles were usually completed before the infructescence reaches the age of one year.   Another borer (*Argyroploce* sp.) utilized the infructescences immediately after they were formed and the larvae occurred sporadically in the infructescences older than 30 weeks.   Larvae of *Tinea* sp. occurred sporadically in young infructescences, but were most abundant in infructescences between ca 30-50 and ca 78-108 weeks old. The two *Sphenoptera* spp. and *G. hottentottus* were present from ca 30 weeks until the end of the functional life of the infructescences. There were therefore   indications of a succession in infructescence colonization   by the various species, but no total avoidance in time. Table 3 b showed that the temporal niche overlap could be as high as 63 %.

TABLE 2a: Number of borer larvae (n = 268) found at each zone in the infructescences of *Protea repens*

Borer species[d]

	1	2	3	4	5	6	7	8	Total
Zone									
Upper[a]	2				3	7			12
Middle[b]	73	51			70		16	5	215
Base[c]	14		6	9	9		2	1	41
Total	89	51	6	9	82	7	18	6	268

[a] =innerer involucral bracts, perianth segments and styles of the florets [b] =achenes [c] =involucral receptacles and outer involucral bracts

[d] =   1. *Genuchus hottentottus*, 2. *Sphenoptera* sp A, 3. *Sphenoptera* sp B, 4. *Orophia ammopleura*, 5. *Euderes lineicollis* 6. *Bostra conspicualis*, 7. *Argyroploce* sp 8. *Tinea* sp.

TABLE 2b: Niche overlaps between species of borers based on exploitation of zones within the infructescences (n = 268).

	1[a]	2	3	4	5	6	7	8
1								
2	0.82							
3	0.16	0						
4	0.16	0	1					
5	0.95	0.85	0.11	0.11				
6	0.02	0	0	0	0.04			
7	0.61	0.89	0.11	0.11	0.96	0		
8	0.98	0.83	0.17	0.19	0.94	0.50	0.94	

[a] =   see Table 2a for codes of borer species
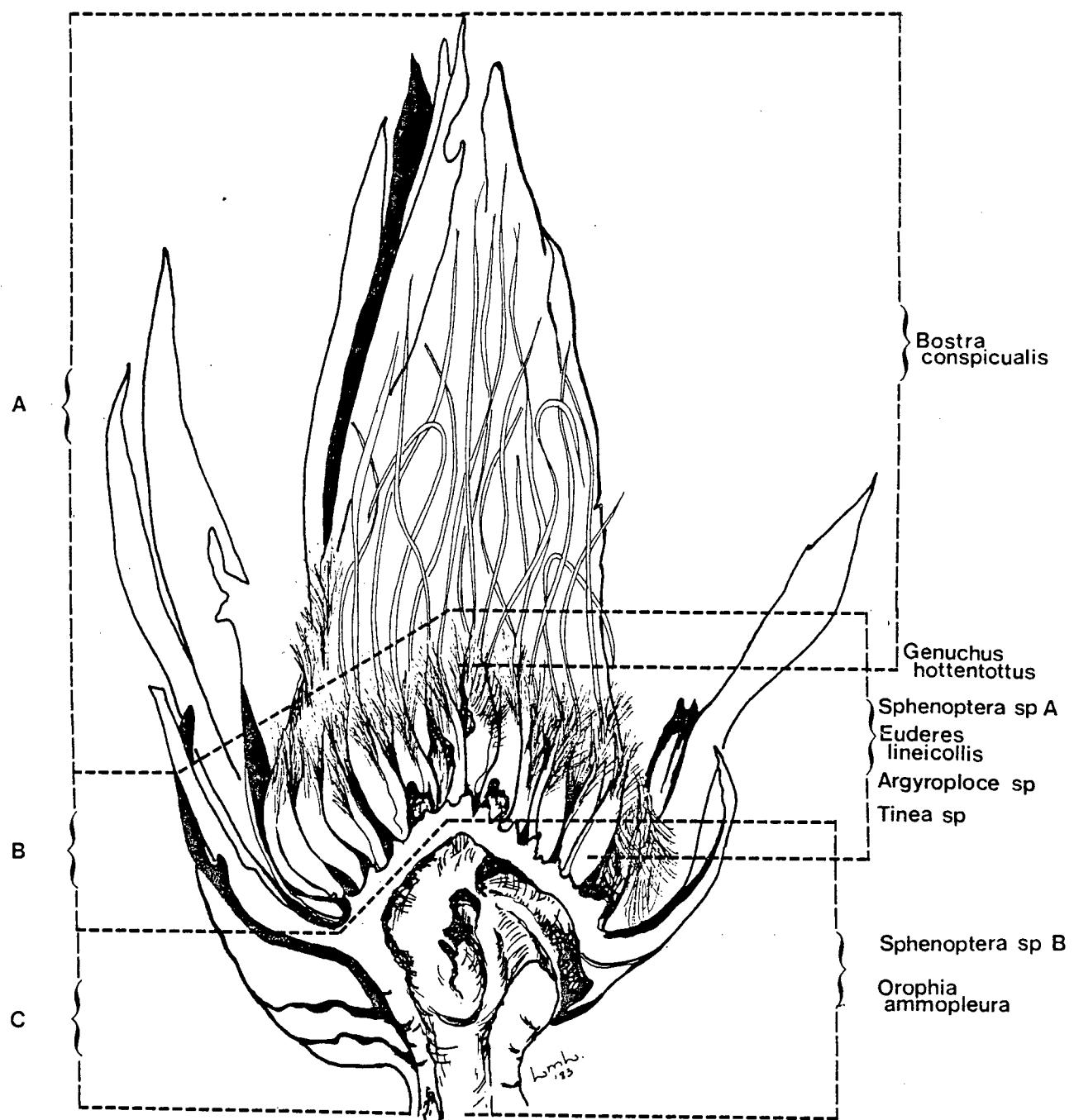
Fig. 1 A schematic representation of the infructescence of *Protea repens* showing the preferred niches of various species according to feeding zone (A = upper, B = middle and C = basal zone).

101

B. Species packing

A total of 1861 larvae were found in the 2419 infructescences dissected ; their relative abundance is shown in Fig. 2. *G. hottentottus* was the most abundant species, comprising 33% of the larvae. The average number of larvae per infructescence was 0,77 (range: 0-13).

The interspecific co-occurrence coefficient (c_{ij}) matrix (Table 4) showed that the probability of two species occuring together, is low. The co-occurrence coefficient was usually lower than 30%, with the exception of *Sphenoptera* sp.A with *Sphenoptera* sp.B, *O.ammopleura* with *E.lineicollis* and *E.lineicollis* with *Argyroploce* sp. The *Sphenoptera* spp did not compete directly because the larvae utilized different zones in the infructescences (Fig. 1), whereas *O.ammopleura* and *E.lineicollis* individuals showed low niche overlap in space (Table 2b). *E.lineicollis* and *Argyroploce* sp. apparently do compete for the same niche in space and time (Table 2b and 3b).

The intraspecific co-occurrence coefficients (c_{ii}) on the diagonal of the matrix showed that individuals of *E.lineicollis* were likely to co-occur, while other conspecific co-occurrences were low (Tabel 4).
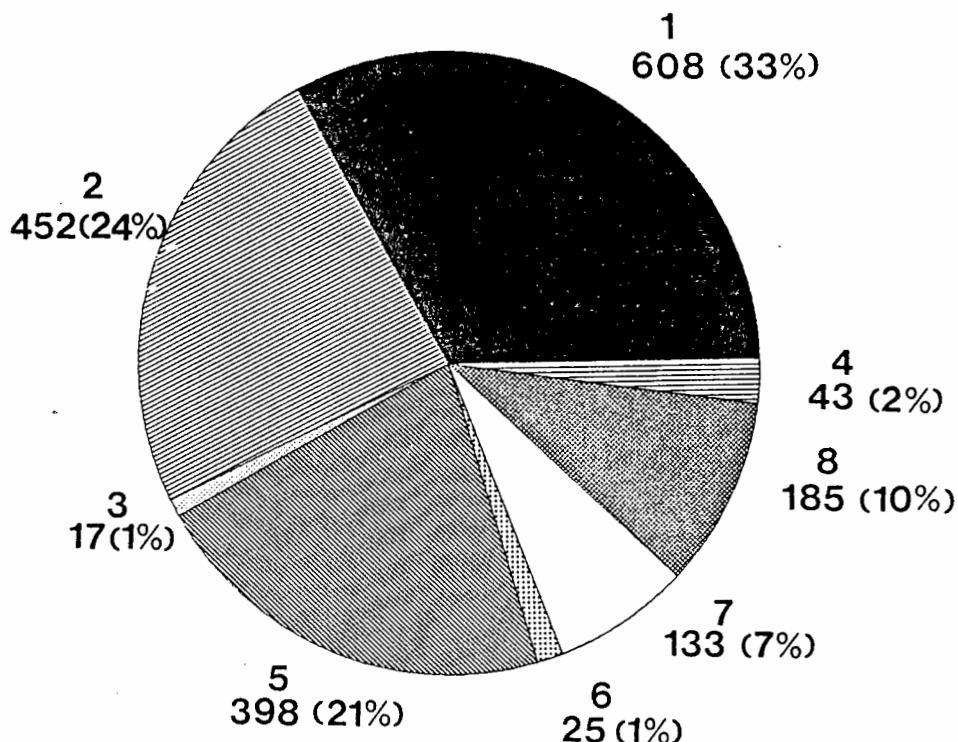
Fig. 2 Numbers and percentages of larvae from eight species in 2369 infructescences of *Protea repens,* (see table 2a for codes of borer species).

TABLE 3a: The number of borer larvae found in the infructescences of *P. repens* at successive intervals after flowering.

weeks[c]	n[b]	Borer species[a]								Total
		1	2	3	4	5	6	7	8	
0	50	0	0	0	3	19	3	4	2	31
3	59	2	0	0	2	92	0	6	3	105
6	70	0	0	0	6	56	0	19	1	82
9	30	0	1	0	4	33	1	8	0	47
12	40	2	0	0	2	52	0	9	0	65
15	30	0	0	0	1	25	1	4	0	31
18	50	3	0	0	0	47	1	25	0	76
21	50	2	0	0	0	19	1	9	0	31
24	50	2	1	0	0	9	0	8	0	20
27	70	4	0	0	2	8	0	5	13	32
30	100	20	28	0	1	1	0	8	10	68
33	90	17	32	1	0	3	0	4	12	69
36	50	8	22	0	2	0	0	1	1	34
39	100	25	42	5	0	1	0	1	8	82
42	80	13	16	1	2	0	2	0	3	37
45	70	17	27	0	1	0	0	1	4	50
48	70	16	30	2	10	0	3	2	3	66
51	80	24	14	1	2	0	1	0	9	51
54	90	20	22	1	2	0	0	3	2	50
57	80	24	26	1	0	0	0	0	2	53
60	40	8	11	0	1	0	2	0	0	22
63	40	12	9	0	0	0	1	1	5	28
66	40	28	9	2	0	0	0	1	0	40
69	40	9	9	0	0	0	2	0	0	20
72	50	31	5	0	0	0	1	3	0	40
75	50	17	0	0	0	0	0	0	0	17
78	70	28	0	0	0	1	0	3	1	33
81	100	49	4	0	1	1	0	0	10	65
84	90	57	22	0	0	10	2	2	12	105
87	80	21	37	1	1	16	1	2	11	90
90	80	35	14	0	0	1	0	0	17	67
93	80	25	30	1	0	1	0	1	25	83
96	70	34	16	0	0	1	0	2	0	53
99	70	18	10	0	0	0	0	0	10	38
102	70	15	4	0	0	0	2	0	8	29
105	70	16	11	1	0	2	1	1	10	42
108	70	6	0	0	0	0	0	0	3	9
Total	2419	608	452	17	43	398	25	133	185	1861

[a] = see Table 2a for codes of borer species

[b] = number of infructescences

[c] = time interval in weeks after flowering time

TABLE 3b: Temporal niche overlap between species of borers (n = 1861) based on exploitation of infructescences in time intervals

	Borer species[a]							
	1a	2	3	4	5	6	7	8
1								
2	0.63							
3	0.38	0.55						
4	0.25	0.33	0.28					
5	0.12	.10	0.06	0.43				
6	0.35	0.33	0.30	0.39	0.28			
7	0.27	0.24	0.11	0.47	0.64	0.27		
8	0.60	0.57	0.38	0.27	0.15	0.30	0.26	

[a] = see Table 2a for codes of borer species

C.   Spatial correlation:

The spatial correlation indices $\omega_{(+)}$ or $\omega_{(-)}$ (Table 5) show that no species occurred completely independently in the infructescences, but neither was there complete overlapping. The high number of negative values showed that species could have had an effect on one another. Although this is not a measurement of competition it gives an indication that one borer species could have an exclusion effect on other species.

TABLE 4:   The expected co-occurrence coefficient (C_{ij}) matrix for the larvae of the infructescences of *Protea repens*.

	Borer species[a]							
	1	2	3	4	5	6	7	8
1	0.37	0.29	0.30	0.13	0.06	0.21	0.11	0.28
2	0.21	0.31	0.34	0.19	0.04	0.18	0.08	0.23
3	0.01	0.01	0.00	0.01	0.00	0.01	0.00	0.01
4	0.01	0.02	0.02	0.07	0.04	0.04	0.03	0.01
5	0.04	0.03	0.02	0.40	0.95	0.19	0.61	0.07
6	0.01	0.01	0.01	0.02	0.01	0.03	0.01	0.01
7	0.02	0.02	0.02	0.10	0.20	0.06	0.22	0.02
8	0.09	0.09	0.08	0.04	0.03	0.05	0.03	0.15

[a] = see Table 2a for codes of borer species

D.   Limiting value of food resource:

Five of the borers namely *G. hottentottus, Sphenoptera* sp A, *E. lineicollis, Argyroploce* sp and *Tinea* sp (Fig.1) utilized the achenes as a food source. The average number of undamaged achenes in each time interval (Fig. 3) and the number of achenes required for each achene predator to complete its life cycle were determined (Table 6). In Fig. 3 the total demand, based on the number of achenes the larvae would need at any particular time to complete their development, was plotted against the supply index, representing the number of achenes available at that time. Eighteen weeks after flowering the supply was almost equal to demand, but as the number of larvae diminished, the supply again exceeded the demand. In infructescences older than 60 weeks demand usually exceeded supply. This indicated that the infructescences were under insect pressure at all times, irrespective of the number of achenes available.
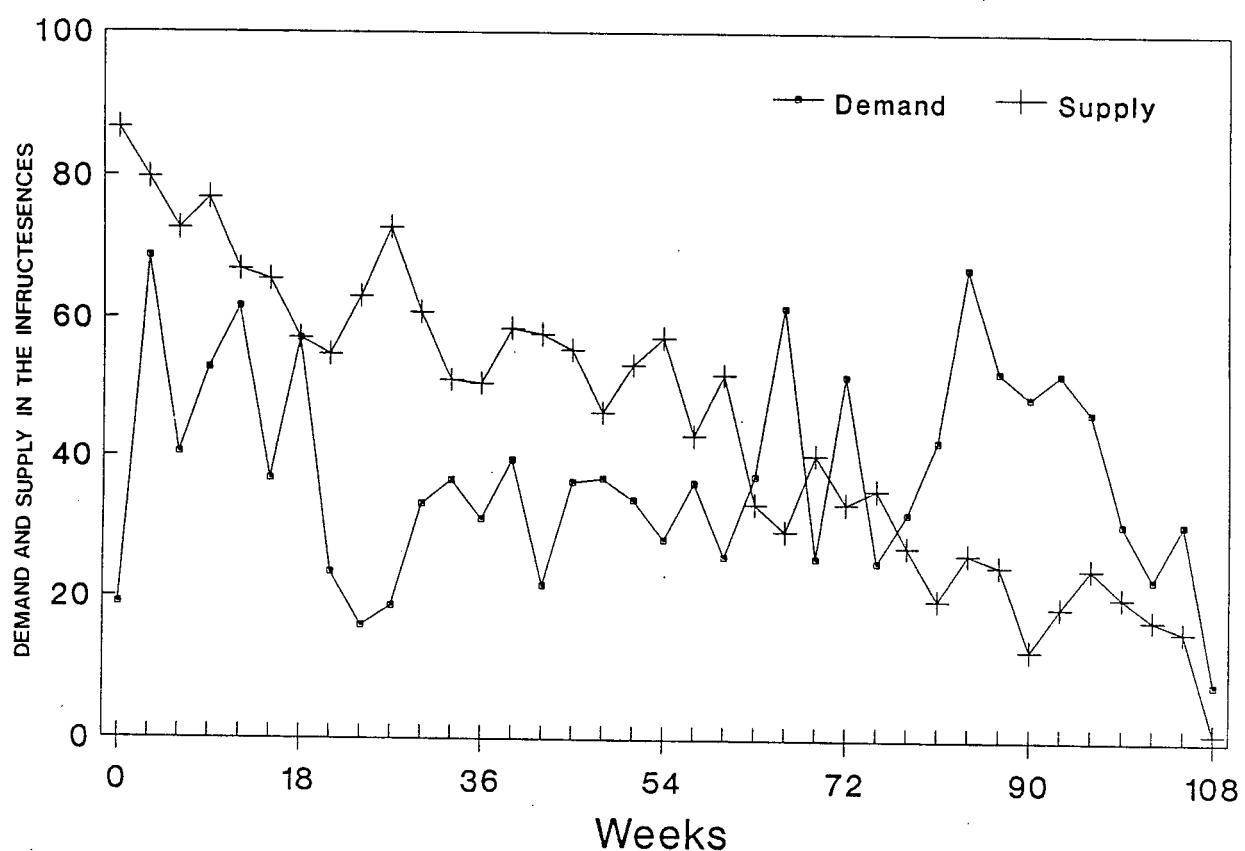
Fig. 3 Demand and supply of achenes; demand shows total number of achenes needed for the larvae to complete their life cycle and supply total number of undamaged achenes per infructesences in each time interval.

E.   Entomophagous predators:

The infructescence is a closed cone which protects the borers against predators such as birds, although rodents may chew off entire infructescences. However, insects could prey on the borers. The insect predators and parasitoids encounterd in this study are listed in Table 7. The ants (Formicidae) were included as predators because the mean density of larvae was low (0,06 as opposed to an average of 0,77) when infructescences were infested by ants. Ants were found in 2,66% of the infructescences. Mortality due to parasitism and fungal infection was low (< 1%) and could not have had a major influence on the borer population.

TABLE 5:   Degree of spatial correlation in time $\omega_{(+)}$ or $\omega_{(-)}$ between borer species in the infructescences of P.repens.

Borer species[a]

	1	2	3	4	5	6	7	8
1								
2	-0.089							
3	0.273	0.344						
4	-0.544	-0.294	0.038					
5	-0.802	-0.893	-0.230	0.440				
6	-0.202	-0.311	-0.286	0.387	0.067			
7	-0.600	0.726	0.726	0.323	0.733	0.072		
8	0.189	0.025	0.196	-0.454	-0.633	0.340	-0.620	

[a] = see Table 2a for codes of borer species

TABLE 6:   The number of achenes in the infructescences of *Protea repens* needed for borer species to reach the adult stage and the insect demand (ID).

Species	Achene needed x	ID SD	
Genuchus hottentottus	73,9	12,8	1,000
Sphenoptera sp. A	40,5	14,5	0,548
Euderes lineicollis	39,0	14,4	0,528
Tinea sp.	41,8	9,6	0,566
Argyroploce sp.	31,9	5,9	0,432

TABLE 7:   Predators and parasitoids of the borers in the infructescences of *P. repens*.

HYMENOPTERA

Crematogaster liegmei	Formicidae
Crematogaster peringueyi	Formicidae
Meranoplus peringueyi	Formicidae
Camponotus werthi var. *skaifei*	Formicidae
Iridomyrmex humilis	Formicidae
Himertosoma sp.	Ichneumonidae
Unidentified	Braconidae

COLEOPTERA

Xenitemus singularis	Carabidae
Xenitemus tessellatus	Carabidae
Gyponyx indicus	Cleridae
Gyponyx pallidus	Cleridae

DIPTERA

Unidentified	Tachinidae

DISCUSSION

The question arises whether there is intra- and interspecific interaction between the larvae in the infructescences of *P. repens* that could lead to competition. Despite evidence of partial niche segregation most of the larvae shared feeding zones in space and time with other individuals of the same or other species. The potential for interaction existed but if there is no indication of food limitation, competition for this resource would not occur.

The demand and supply graph for the achene predator guild (Fig. 3) showed that at *ca* 60 weeks after flowering, demand exceeded the supply. When all the achenes were destroyed the borers were forced to move down into the receptacle. This was last resort as receptacle destruction lead to the death of the entire infructescence. Shortage of food may therefore have been directly (when two or more larvae occured together) or indirectly (when they succeeded each other) resulted in competition between borer larvae. The above only applied to the five species of achene predators, representing 95,5% of all individuals collected. A shortcoming in the demand and supply model was that when the demand of the guild was determined, some had already been satisfied. The demand was therefore over-estimated.

The borers could destroy the infructescence, and should this happen all larvae would perish as they were restricted to this space. It also appeared that the adults could not distinguish whether or not an infructescence had already been infested, since the demand graph (Fig. 3) showed no decrease in number of larvae with the decrease in achene supply over time. The low numbers of predators and parasitoids (Table 2) encountered indicated a relatively "enemy free habitat" and that the major populating mechanism was inter - and intraspecific competition. In view of all these interactions one would have expected the larvae to develop competition avoidance strategies. Evidence of how the limited resource was shared could be obtained by considering the strategy of each insect species separately.

Genuchus hottentottus: Larvae of this beetle were found over a long period (Table 3), and it was the dominant species of time(Fig. 2). The larvae exhibited inter- and intra specific aggressive behavior. More than one early instar larva were often found in the same infructescences, but only single pupae were found, indicating eradication of competitors. This suggested that *G. hottentottus* was a superior competitor, making use of confrontation as a survival strategy. The feeding zone of the larvae was also not restricted (Table 2), but included both achenes and the receptacle. In addition, *G. hottentottus* could feed on other species within the genus *Protea* (Coetzee & Giliomee, 1987a) which probably contributed to its high survival ability.

Sphenoptera sp. A: The degree of niche overlap (Tables 2b, 3b) showed that this species shared the infructescences in time and space with *G. hottentottus* and other species. These larvae occurred in close contact with others, and could not be considered aggressive competitors. There was potential for intraspecific competition as a cluster of eggs was laid on a single infructescence. However this was avoided as the first hatchlings eat their sibling's eggs, giving those that remain a better chance of surviving. This species was also restricted to *P. repens* (Coetzee 1989a).

Sphenoptera sp. B: This species was restricted to the involucral receptacle (Fig.1) and low numbers were encountered (Fig.3). The larva exhibited complete spatial niche overlap with *O. ammopleura* (Table 2b), but only a 29% temporal overlap (Table 3b). It could avoid competition by boring into the stems of infructescences. This species was restricted to *P. repens* (Coetzee, 1989a).

Orophia ammopleura: These moth larvae were restricted to the involucral receptacle (Fig. 1). They could destroy the entire receptacle, leading to the death of infructescence. Larvae attacked young buds to avoid competition (Coetzee & Giliomee, 1987a). They could feed on various *Protea* spp. and there were also indications that these larvae could move between infructescences. Pupation occured outside the infructescences, and this was possibly a strategy to avoid destruction by other borers.

Euderes lineicollis: This curculionid larva fed in the achene zone and in the involucral receptacle (Fig. 1), but avoided competition temporarily by infesting the developing inflorescences. The first instar larvae showed gregarious tendencies, but later intraspecific pressures appeared to be relieved in a cannibalistic fashion. Although up to 13 larvae were found per infructescence, more than one pupa were seldom encountered. This species could feed on other species within in the genus *Protea* (Coetzee & Giliomee, 1987a).

Bostra conspicualis: The larvae of this moth were not achene predators, but fed mostly on leaves, and could also supplement their diet with perianth segments and styles. They appeared to use the infructescences mainly to escape enemies diurnally. These larvae are the sole inhabitants of the upper part of the infructescence, and were able to exit the infructescence regularly.

Argyroploce sp.: These lepidopterous larvae shared the achenes and the receptacle zone with four other species and to avoid niche overlap to some extent the infructescences were attacked early when they were still young (Table 3a). No cannibalistic tendencies were apparent, as more than one moth has been seen to emerge from an inflorescence. Owing to taxonomic difficulties with this species it was not possible to establish its complete host range.

Tinea sp.: *Tinea* larvae appeared to exhibit a confrontation strategy, as they were found together with G. *hottentottus* in space and time. The low numbers (Fig. 3) suggested that this species may not have been a very effective competitor. No data is available regarding its host range.

From the above it appeared that the larvae showed several strategies to ameliorate interspecific competition : segregation in time and space, confrontation (superior competitors), profusion of eggs laid by adult, position of pupation, the ability to leave the feeding space and polyphagy within the genus Protea. The distinct structure and functioning of the guild of larvae in the infructescences could be the result of coevolution of the phytophagous taxa in space and time ,superimposed on sequential evolution with the host as suggested by Zwölfer (1988) for the flower head guild of *Carduea*.

Protea repens is one of the most common species of the Proteaceae in the fynbos. Other *Protea* spp. are utilized by other insect species (often con-generic with those above). Valuable information pertaining to the structuring of insect species within the Proteacae and related families can be obtained by extending this study to other plant species in the fynbos.

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109

CONCLUSIONS

The total arthropod communities found on the Proteaceae plants studied indicated that these plants provided a diversity of habitats which could be exploited by numerous insect (and other Arthropoda) taxa. The number of species as well as number of individuals per species occurring on plants appeared to be influenced by plant architecture. Architecture appeared to be more important than geographic distribution in this regard.

The chemical and physical characteristics of the leaves indicated that the Proteaceae have developed different antiherbivore mechanisms, even at species level. No overall strategy seemed apparent across the range of three genera examined. Cognisance should be given to this factor when the breeding of commercial cultivars of the Proteaceae is undertaken.

Food limits the number of insects attacking infructescences and determines the structure of the guild composition of these insects. Various strategies such as spatial and temporal niche segregation have been developed to limit competition in the infructescences. Natural enemies may determine guild structure on the rest of the above-ground parts of the plants. Defence mechanisms of plants may also play a role.

The Arthropoda on the Proteaceae are often closely associated with the plants, and may have a profound effect on the ecological functioning of this plant group. Beneficial associations (viz. myrmecochory, entomophily) as well as negative associations (viz. herbivory, seed predation) contribute to this scenario. A considerable volume of information regarding arthropod plant interactions in fynbos has been gathered here by treating five Proteaceae as subsystems (senu Zwölfer 1987). This study should be regarded as a pioneer project, and may be used as a basis for further studies. Collection techniques and approaches to analysis should be standardized to allow for comparison of results. Data arising from comparative studies with other fynbos plants as well as with Proteaceae from other climatic regions and continents will not only be of academic value, but will be applicable to post fire studies (e.g. effect of fire on arthropods) and conservation. Also plant breeding programmes and pest management regarding the Proteaceae will benefit.

A problem experienced during this study was the dearth of taxonomic information relating to insects of the fynbos region. This problem was partially overcome by using the "morphospecies" approach. Specimens will continue to be supplied to taxonomists in an attempt to solve this problem. Much more work on the Arthropoda is required before we shall fully understand the influence of insects and other arthropods on Proteacea. It is suggested that studies on proteaceous insects be limited to the phytophagous guild in future. Insects associated with inflorescences and infructescences of Proteaceae merit further study, and this also applies to other families of plants in fynbos.

110

PPENDIX 1 The arthropod species recorded from five proteaceous species in the Cape fynbos. Guild A: ants, F: flower visitors, C: chewers, S: sap-suckers, ND: non detrimental feeders, P: predators and parasitoids.

ACHRP	GENUS	SPECIES	FAMILY	ORDER	GUILD	P. rep.	P. ner.	P. cyn.	L. cor.	L.lau.
A1809	Acantholepis	A.capensis	Formicidae	Hymenoptera	A	*		*	*	
A1810	Anoplolepis	A.custodiens	Formicidae	Hymenoptera	A	*			*	
A1812	Camponotus	C.niveosetosus	Formicidae	Hymenoptera	A	*	*		*	*
A1813	Camponotus	C.rufoglaucus	Formicidae	Hymenoptera	A	*		*	*	*
A1814	Camponotus	C.werthi	Formicidae	Hymenoptera	A	*				
A1816	Crematogter	C.liengmei	Formicidae	Hymenoptera	A	*	*	*	*	*
A1817	Cremataster	C.peringueyi	Formicidae	Hymenoptera	A		*			
A656	Iridyrmex	I.humilis	Formicidae	Hymenoptera	A	*	*	*	*	*
A1818	Menoplus	M.peringueyi	Formicidae	Hymenoptera	A	*				*
A1825	nomoruim	M.braunsi	Formicidae	Hymenoptera	A				*	
A1819	Myrmicaria	M.nigra	Formicidae	Hymenoptera	A	*		*	*	
A1820	Pheidole	P.sp.prop.capensis	Formicidae	Hymenoptera	A	*			*	
A182	Plagiolepis	P.jouberti	Formicidae	Hymenoptera	A	*	*		*	
A1826	Plagiolepis	P.pygmaea	Formicidae	Hymenoptera	A	*	*			
A1822	Technomyrmex	T.albipes	Formicidae	Hymenoptera	A	*		*	*	*
A1823	Tetramorium	T.erectum	Formicidae	Hymenoptera	A					*
A1824	Tetraponera	T.clypeata	Formicidae	Hymenoptera	A				*	*
A1784			Alleculidae	Coleoptera	F					*
A962	Hexatmetus		Apionidae	Coleoptera	F			*		
A1284	Nanodes		Apionidae	Coleoptera	F					*
A815	Spermophagus		Bruchidae	Coleoptera	F	*	*		*	
A1292			Chrysomelidae	Coleoptera	F		*			
A1793			Chrysomelidae	Coleoptera	F					*
A247			Chrysomelidae	Coleoptera	F					*
A966			Chrysomelidae	Coleoptera	F				*	
A991			Chrysomelidae	Coleoptera	F				*	
A1786	Chirodica		Chrysomelidae	Coleoptera	F					*
A706	Chirodica	C.chalcoptera	Chrysomelidae	Coleoptera	F	*	*	*		
A970	Chirodica	C.fulvipes	Chrysomelidae	Coleoptera	F					*
A707	Chirodica	C.wollastoni	Chrysomelidae	Coleoptera	F	*	*			
A641	Chirodica		Chrysomelidae	Coleoptera	F	*				
A1273	Cyphon		Chrysomelidae	Coleoptera	F				*	
A721	Phyconomus	P.tricolor	Cucujidae	Coleoptera	F				*	
A956	Aporimus		Curculionidae	Coleoptera	F	*				
A1756	Baridinae		Curculionidae	Coleoptera	F					*
A1281	Ceutorhynchus		Curculionidae	Coleoptera	F		*			
A759	Ceutorhynchus		Curculionidae	Coleoptera	F	*	*			
A925	Ceutorhynchus		Curculionidae	Coleoptera	F		*	*		
A692	Derelomus		Curculionidae	Coleoptera	F	*	*			*
A1282	Isorhynchus		Curculionidae	Coleoptera	F					*
A1060	Isorhynchus		Curculionidae	Coleoptera	F				*	
A969	Isorhynchus		Curculionidae	Coleoptera	F					*
A1279	Isorhynchus		Curculionidae	Coleoptera	F				*	*
A968	Oosomus		Curculionidae	Coleoptera	F					*
A727	Platysoma	P.capense	Histeridae	Coleoptera	F		*			
A1031	Anisonyx	A.proletarius	Melolonthidae	Coleoptera	F	*				
A726	Diaplochelus	D.longipes	Melolonthidae	Coleoptera	F			*		
A1072	Dichelus		Melolonthidae	Coleoptera	F				*	
A1095	Dichelus		Melolonthidae	Coleoptera	F		*			
A1096	Dichelus		Melolonthidae	Coleoptera	F		*			
A1064	Knysna	K.humeralis	Melolonthidae	Coleoptera	F			*	*	
A1776			Mordellidae	Coleoptera	F					*
A614			Mordellidae	Coleoptera	F			*		*
A658	Anaspis		Mordellidae	Coleoptera	F	*			*	*
A1204	Carpophilus		Nitidulidae	Coleoptera	F	*				
A714	Carpophilus	C.binotatus	Nitidulidae	Coleoptera	F	*		*		
A716	Carpophilus	C.dimidiatus	Nitidulidae	Coleoptera	F	*				*
A713	Pria	P.cinerascens	Nitidulidae	Coleoptera	F	*	*	*	*	*
A1294			Phalacridae	Coleoptera	F					*
A717	Olibrus	O.aeratus	Phalacridae	Coleoptera	F	*	*	*	*	*
A118	Genuchus	G.hottentottus	Scarabaeidae	Coleoptera	F	*		*		
A975			Scraptiidae	Coleoptera	F			*		
A1649			Staphylinidae	Coleoptera	F		*			
A919	Conosma	C.gilli	Staphylinidae	Coleoptera	F		*			
A865	Oxytelus	O.sculpturatus	Staphylinidae	Coleoptera	F	*	*	*		*
A725	Phloeonomus		Staphylinidae	Coleoptera	F	*	*	*		

111

Code	Genus	Species	Family	Order		1	2	3	4	5
A926			Drosophilidae	Diptera	F	*	*	*	*	
A874	Apis	A.mellifera	Apidae	Hymenoptera	F	*	*	*	*	*
A1734				Thysanoptera	F	*				
A1770				Thysanoptera	F					*
A757				Thysanoptera	F	*	*	*	*	*
A742			Blattidae	Blattodea	ND		*		*	
A751			Blattidae	Blattodea	ND	*	*	*	*	*
A880			Blattidae	Blattodea	ND					*
A1886				Chilopoda	ND		*	*		*
A1030			Anthicidae	Coleoptera	ND		*	*		
A739	Anthicus		Anthicidae	Coleoptera	ND	*	*		*	*
A788	Anthicus		Anthicidae	Coleoptera	ND	*	*	*		*
A971	Endomia	E.obscura	Anthicidae	Coleoptera	ND					*
A776	Formicomus	F.coeruleus	Anthicidae	Coleoptera	ND	*	*	*		*
A777	Formicomus	F.rubricollis	Anthicidae	Coleoptera	ND	*	*			
A1632				Collembola	ND	*	*	*	*	*
A839				Collembola	ND	*	*			*
A1667				Dermaptera	ND		*	*		
A1764				Dermaptera	ND					*
A946				Dermaptera	ND					
A964	Brachylabis		Labiduridae	Dermaptera	ND				*	
A1738				Diplopoda	ND	*	*	*	*	*
A952				Psocoptera	ND	*	*	*	*	
A760	Micrambe	M.tenuicornis	Cryptophagidae	Coleoptera	ND	*	*	*	*	*
A1610			Lathridiidae	Coleoptera	ND	*	*	*	*	*
A1690			Lathridiidae	Coleoptera	ND		*			
A899			Lathridiidae	Coleoptera	ND	*	*		*	*
A1061				Psocoptera	ND	*	*		*	*
A1692				Psocoptera	ND					*
A1735				Psocoptera	ND	*	*	*	*	*
A1887				Psocoptera	ND	*	*	*	*	
A758				Psocoptera	ND	*	*	*	*	*
A801				Psocoptera	ND		*			
A818				Psocoptera	ND	*	*	*	*	*
A830				Psocoptera	ND			*		*
A935				Psocoptera	ND	*	*	*	*	*
A1075				Trichoptera	ND	*				*
A1890			Araneidae	Araneae	P	*	*	*		*
A1086			Anobiidae	Coleoptera	C					*
A626	Apion	A.angustithorax	Apionidae	Coleoptera	C	*				
A628			Apionidae	Coleoptera	C	*				
A876			Apionidae	Coleoptera	C					*
A875	Apiomorphus		Apionidae	Coleoptera	C					*
A1286	Apion		Apionidae	Coleoptera	C			*		
A1721	Perapion		Apionidae	Coleoptera	C			*		
A942	Perapion	P.antiquum	Apionidae	Coleoptera	C	*	*	*		*
A967	Psiloptera	P.albomarginata	Buprestidae	Coleoptera	C				*	
A1298	Sphenoptera		Buprestidae	Coleoptera	C				*	
A1299	Sphenoptera		Buprestidae	Coleoptera	C				*	
A977	Sphenoptera		Buprestidae	Coleoptera	C		*			
A997	Sphenoptera		Buprestidae	Coleoptera	C	*				
A1296	Sphenoptera		Buprestidae	Coleoptera	C					*
A1300	Sphenoptera		Buprestidae	Coleoptera	C					*
A1790	Sphenoptera		Buprestidae	Coleoptera	C			*		
A669	Sphenoptera		Buprestidae	Coleoptera	C	*				
A1750			Chrysomelidae	Coleoptera	C	*		*		*
A1026	Aphthoma		Chrysomelidae	Coleoptera	C	*				
A886	Hapsidolema	H.erythrodera	Chrysomelidae	Coleoptera	C	*	*	*		
A696	Monolepta	M.bioculata	Chrysomelidae	Coleoptera	C	*				
A521	Odontionopa		Chrysomelidae	Coleoptera	C		*			
A587	Odontionopa	O.discolor	Chrysomelidae	Coleoptera	C	*				
A1027	Odontionopa	O.sericea	Chrysomelidae	Coleoptera	C	*	*			
A603	Xenoomorphus		Chrysomelidae	Coleoptera	C	*	*		*	*
A664	Afroleptops	A.coetzeei	Curculionidae	Coleoptera	C	*	*			
A1033	Eremnus	E.nr.atratus	Curculionidae	Coleoptera	C			*		
A458	Euderes	E.lineicollis	Curculionidae	Coleoptera	C	*				
A827	Hypsomus		Curculionidae	Coleoptera	C			*		
A1302	Phlyctinus	P.callosus	Curculionidae	Coleoptera	C		*		*	*
A965	Proleptomimus		Curculionidae	Coleoptera	C				*	
A1789	Synechops	S.nr.irregularis	Curculionidae	Coleoptera	C	*	*			
A793	Tanyrhynchus	T.tibiolis	Curculionidae	Coleoptera	C	*	*	*	*	

112

Code	Genus	Species	Family	Order		1	2	3	4	5
A914			Elateridae	Coleoptera	C				*	*
A1280	Cardiophorus		Elateridae	Coleoptera	C	*	*	*	*	*
A822	Heteroderes	H.pulchellus	Elateridae	Coleoptera	C	*			*	
A695			Galerucidae	Coleoptera	C	*				
A708			Galerucidae	Coleoptera	C	*				
A1028	Helodes		Helodidae	Coleoptera	C	*	*		*	
A941	Helodes		Helodidae	Coleoptera	C	*				
A1091			Lagriidae	Coleoptera	C	*				
A1085			Tenebrionidae	Coleoptera	C				*	*
A743			Cecidomyiidae	Diptera	C	*	*	*	*	*
A1035				Lepidoptera	C					*
A1340				Lepidoptera	C		*			
A1783				Lepidoptera	C		*		*	*
A1787				Lepidoptera	C		*			*
A1788				Lepidoptera	C		*			
A1798				Lepidoptera	C			*		
A1800				Lepidoptera	C			*		
A2002				Lepidoptera	C	*	*		*	*
A622				Lepidoptera	C			*		
A662				Lepidoptera	C					*
A785				Lepidoptera	C					*
A871				Lepidoptera	C					*
A885				Lepidoptera	C			*		
A920				Lepidoptera	C				*	*
A959	Ceromitia		Adelidae	Lepidoptera	C		*			
A883			Gelechiidae	Lepidoptera	C		*		*	
A689			Geometridae	Lepidoptera	C	*	*	*	*	*
A1062	Adicocrita	A.koranata	Geometridae	Lepidoptera	C					*
A666	Haplolabida	H.inaequata	Geometridae	Lepidoptera	C					*
A1094	Mauna	M.filia	Geometridae	Lepidoptera	C		*			
A993	Mauna		Geometridae	Lepidoptera	C				*	
A988	Prasinocyma		Geometridae	Lepidoptera	C		*			
A1036	Semiothisa	S.semitecta	Geometridae	Lepidoptera	C	*	*			
A703	Opogona	O.omoscopa	Hieroxestidae	Lepidoptera	C	*				
A697			Nepticulidae	Lepidoptera	C					*
A345	Catochria	C.catocaloides	Notodontidae	Lepidoptera	C	*	*	*	*	*
A889	Diocosma		Oecophoridae	Lepidoptera	C					*
A1792			Plutellidae	Lepidoptera	C			*		
A705	Plutella	P.xylostella	Plutellidae	Lepidoptera	C	*		*	*	*
A2001			Pyralidae	Lepidoptera	C					*
A1797	Crambus		Pyralidae	Lepidoptera	C			*		
A1164	Crambus	C.sparsellus	Pyralidae	Lepidoptera	C	*				
A1037	Nomophila	N.noctuella	Pyralidae	Lepidoptera	C	*				
A1696	Imbrasia	I.cytherea	Saturniidae	Lepidoptera	C				*	*
A1782			Sphingidae	Lepidoptera	C		*			*
A443	Tortrix		Tortricidae	Lepidoptera	C		*			
A1034			Acrididae	Orthoptera	C				*	*
A1155			Acrididae	Orthoptera	C		*			
A1069	Plangia	P.graminia	Tettigoniidae	Orthoptera	C	*	*	*		
A770			Tettigoniidae	Orthoptera	C	*	*	*		
A869			Tettigoniidae	Orthoptera	C		*		*	
A627			Tettigoniidae	Orthoptera	C	*				
A631	Oecanthus		Tettigoniidae	Orthoptera	C	*	*		*	*
A1891	Araneus		Araneidae	Araneae	P					*
A1892	Cyclosa		Araneidae	Araneae	P	*				
A1893	Cyrtophora		Araneidae	Araneae	P		*			
A1894	Neoscona		Araneidae	Araneae	P	*	*			*
A1895			Clubionidae	Araneae	P	*	*	*		*
A1896	Chiracorthium		Clubionidae	Araneae	P			*		
A1897	Clubiona		Clubionidae	Araneae	P	*	*	*		*
A1898			Dictynidae	Araneae	P		*			
A1930			Erigonidae	Araneae	P					
A1900	Platyoides		Gnaphosidae	Araneae	P	*	*	*		*
A1901			Heteropodidae	Araneae	P		*	*		*
A1902			Linyphiidae	Araneae	P	*	*	*		*
A1903	Pelecopsis		Linyphiidae	Araneae	P		*			*
A1904			Lycosidae	Araneae	P	*				
A1907	Oxyopes		Oxyopidae	Araneae	P		*			*
A1908	Philodromus		Philodromidae	Araneae	P	*		*		*
A1909	Philodromus		Philodromidae	Araneae	P	*	*			*
A1910	Suemus		Philodromidae	Araneae	P					*

113

Code	Genus	Species	Family	Order	P	1	2	3	4	5
A1917			Theridiidae	Araneae	P	*	*	*		*
A1918	Dipoena		Theridiidae	Araneae	P					*
A1919	Euryopis		Theridiidae	Araneae	P					
A1920	Thoridion		Theridiidae	Araneae	P	*	*	*		*
A1924			Thomisidae	Araneae	P		*			
A1926			Thomisidae	Araneae	P		*			
A1921	Dieta		Thomisidae	Araneae	P	*		*		*
A1922	Misumena		Thomisidae	Araneae	P					
A1923	Pherecydes		Thomisidae	Araneae	P					*
A1925	Synaema		Thomisidae	Araneae	P	*			*	*
A1927	Miagrammopes		Uloboridae	Araneae	P					*
A1928	Chariobas		Zodariidae	Araneae	P					*
A951			Carabidae	Coleoptera	P		*			
A1882			Carabidae	Coleoptera	P			*		*
A625	Xinetemus	X.tessellatus	Carabidae	Coleoptera	P	*	*			*
A1104			Cleridae	Coleoptera	P			*		*
A1747			Cleridae	Coleoptera	P					*
A744			Cleridae	Coleoptera	P	*	*			
A1052	Dolichopsis	D.cocrulea	Cleridae	Coleoptera	P			*		
A258	Gyponyx		Cleridae	Coleoptera	P	*			*	*
A910	Necrobia	N.atra	Cleridae	Coleoptera	P	*	*			
A613	Adonia	A.variegata	Coccinellidae	Coleoptera	P		*	*	*	*
A617	Scymnus	S.morelleti	Coccinellidae	Coleoptera	P		*	*	*	*
A1272			Coccinellidae	Coleoptera	P	*	*			
A1290			Coccinellidae	Coleoptera	P	*	*			
A1647			Coccinellidae	Coleoptera	P		*			
A1728			Coccinellidae	Coleoptera	P	*				*
A1748			Coccinellidae	Coleoptera	P					*
A1757			Coccinellidae	Coleoptera	P				*	*
A1883			Coccinellidae	Coleoptera	P		*		*	*
A704	Cheilomenes		Coccinellidae	Coleoptera	P	*	*	*	*	*
A792	Cheilomenes	C.lunata	Coccinellidae	Coleoptera	P	*	*	*	*	*
A881	Cheilomenes	C.propinqua	Coccinellidae	Coleoptera	P	*	*	*	*	
A922	Exochomus		Coccinellidae	Coleoptera	P		*		*	*
A753	Pharoscymnus	P.sexguttatus	Coccinellidae	Coleoptera	P		*	*	*	*
A766	Rhyzobius	R.javeti	Coccinellidae	Coleoptera	P	*	*		*	*
A1293	Scymnus		Coccinellidae	Coleoptera	P		*			*
A863	Telsimia	T.tetrasticta	Coccinellidae	Coleoptera	P		*		*	*
A1029	Thea	T.variegata	Coccinellidae	Coleoptera	P		*			
A1077			Melyridae	Coleoptera	P			*	*	
A1159			Melyridae	Coleoptera	P	*	*		*	
A1665			Melyridae	Coleoptera	P		*			
A720			Melyridae	Coleoptera	P		*			
A930			Melyridae	Coleoptera	P		*			*
A978			Melyridae	Coleoptera	P	*				*
A825	Cybocephalus		Nitidulidae	Coleoptera	P	*				*
A780			Dolichopodidae	Diptera	P	*				*
A786			Dolichopodidae	Diptera	P	*	*		*	*
A896			Empididae	Diptera	P	*	*		*	*
A1871			Rhagionidae	Diptera	P		*			
A1872			Tachididae	Diptera	P		*			
A1040			Tachinidae	Diptera	P		*			
A1858			Tachinidae	Diptera	P	*			*	*
A924			Tachinidae	Diptera	P		*			
A938			Tachinidae	Diptera	P	*				
A1666			Anthocoridae	Hemiptera	P		*			*
A850			Anthocoridae	Hemiptera	P	*			*	*
A943			Anthocoridae	Hemiptera	P		*			
A1106			Reduviidae	Hemiptera	P					*
A1717			Reduviidae	Hemiptera	P		*			*
A1645			Reduviidae	Hemiptera	P		*			
A1737				Hymenoptera	P	*	*		*	*
A1874				Hymenoptera	P		*			*
A1324	Aphidiur		Aphodiidae	Hymenoptera	P					
A824			Bethylidae	Hymenoptera	P		*			*
A878			Bethylidae	Hymenoptera	P		*			*
A1307			Braconidae	Hymenoptera	P	*	*			
A1320			Braconidae	Hymenoptera	P		*		*	
A1326			Braconidae	Hymenoptera	P					*
A1328			Braconidae	Hymenoptera	P					*
A1332			Braconidae	Hymenoptera	P					*

ID	Genus	Family	Order	P					
A923		Braconidae	Hymenoptera	P		*			
A947		Braconidae	Hymenoptera	P		*			
A948		Braconidae	Hymenoptera	P		*			
A983		Braconidae	Hymenoptera	P	*	*			*
A985		Braconidae	Hymenoptera	P					*
A817	Apanteles	Braconidae	Hymenoptera	P	*				
A1327	Chelonus	Braconidae	Hymenoptera	P					*
A763		Braconidae	Hymenoptera	P		*			
A909	Glytopanteles	Braconidae	Hymenoptera	P	*				
A1316	Phaenocarpa	Braconidae	Hymenoptera	P		*			
A1318	Phaenocarpa	Braconidae	Hymenoptera	P			*		
A691	Phanerotoma	Braconidae	Hymenoptera	P		*			
A857	Phanerotoma	Braconidae	Hymenoptera	P			*		
A907	Physaraia	Braconidae	Hymenoptera	P	*				*
A931	Rogadinae	Braconidae	Hymenoptera	P		*	*		*
A1310	Rogas	Braconidae	Hymenoptera	P	*				
A1334		Ceraphronidae	Hymenoptera	P			*		*
A1344		Ceraphronidae	Hymenoptera	P					
A960		Chalcididae	Hymenoptera	P		*			
A1314	Brachymeria	Chalcididae	Hymenoptera	P				*	
A972	Dirhinus	Chalcididae	Hymenoptera	P					*
A981	Hockeria	Chalcididae	Hymenoptera	P		*			*
A635	Hylaeus	Colletidae	Hymenoptera	P		*	*		
A633	Nothylaeus	Colletidae	Hymenoptera	P	*	*	*		
A1353		Elasmidae	Hymenoptera	P	*				
A819		Elasmidae	Hymenoptera	P	*				
A897		Encyrtidae	Hymenoptera	P		*		*	
A1349	Pediobius	Eulophidae	Hymenoptera	P	*	*			*
A832	Tetrastichus	Eulophidae	Hymenoptera	P		*			*
A1345		Eupelmidae	Hymenoptera	P		*			
A1347		Eupelmidae	Hymenoptera	P		*			
A740		Eupelmidae	Hymenoptera	P		*	*		
A767		Eupelmidae	Hymenoptera	P		*			
A768		Eurytomidae	Hymenoptera	P		*			
A1084		Evaniidae	Hymenoptera	P	*				*
A826		Evaniidae	Hymenoptera	P			*		
A632	Lasioglossum	Halictidae	Hymenoptera	P	*	*	*		
A1308		Ichneumonidae	Hymenoptera	P					
A1058		Ichneumonidae	Hymenoptera	P		*			
A1304		Ichneumonidae	Hymenoptera	P	*				
A1306		Ichneumonidae	Hymenoptera	P	*	*			*
A1311		Ichneumonidae	Hymenoptera	P	*				
A1319		Ichneumonidae	Hymenoptera	P		*			
A1329		Ichneumonidae	Hymenoptera	P					*
A620		Ichneumonidae	Hymenoptera	P					*
A693		Ichneumonidae	Hymenoptera	P			*		
A779		Ichneumonidae	Hymenoptera	P	*				
A870		Ichneumonidae	Hymenoptera	P					*
A872		Ichneumonidae	Hymenoptera	P					*
A976		Ichneumonidae	Hymenoptera	P					*
A1323	Aptesis	Ichneumonidae	Hymenoptera	P					*
A748	Diplazon	Ichneumonidae	Hymenoptera	P					*
A1100	Enicospilus	Ichneumonidae	Hymenoptera	P					*
A1305	Mesochorus	Ichneumonidae	Hymenoptera	P	*				
A1330	Phaisura	Ichneumonidae	Hymenoptera	P					*
A1322	Pristomerus	Ichneumonidae	Hymenoptera	P			*		*
A1309	Spilopimpla	Ichneumonidae	Hymenoptera	P	*				
A1331	Xestapelta	Ichneumonidae	Hymenoptera	P					*
A1321		Microgasteridae	Hymenoptera	P	*				
A820		Ormyridae	Hymenoptera	P	*	*			
A1350		Platygasteridae	Hymenoptera	P	*	*			
A1352		Platygasteridae	Hymenoptera	P	*	*			
A868		Platygasteridae	Hymenoptera	P		*		*	
A1325		Pteromalidae	Hymenoptera	P					*
A1333		Pteromalidae	Hymenoptera	P		*			*
A1348		Pteromalidae	Hymenoptera	P		*			
A861		Pteromalidae	Hymenoptera	P			*		
A915		Pteromalidae	Hymenoptera	P	*			*	
A1335		Scelionidae	Hymenoptera	P		*			*
A851		Scelionidae	Hymenoptera	P	*	*			
A902		Scelionidae	Hymenoptera	P					*

ID	Genus	Species	Family	Order							
A958			Torymidae	Hymenoptera	P		*				
A1342	Podagrion		Torymidae	Hymenoptera	P						*
A834	Podagrion		Torymidae	Hymenoptera	P						*
A900	Podagrion		Torymidae	Hymenoptera	P						*
A901	Podagrion		Torymidae	Hymenoptera	P	*					*
A953	Polister	P.marginalis	Vespidae	Hymenoptera	P		*		*		*
A623				Mantodea	P				*		*
A663				Mantodea	P						
A906				Mantodea	P						
A1752				Neuroptera	P						*
A754				Neuroptera	P	*				*	
A1881				Neuroptera	P		*			*	*
A1152			Chrysopidae	Neuroptera	P						*
A1196			Chrysopidae	Neuroptera	P		*		*		
A1653			Chrysopidae	Neuroptera	P		*				
A1654			Chrysopidae	Neuroptera	P		*				
A755			Chrysopidae	Neuroptera	P	*	*		*	*	*
A1063	Pseudoclimaciella		Mantispidae	Neuroptera	P						*
A1915			Solifugae	Neuroptera	P						
A1799				Hemiptera	S	*	*		*	*	*
A866			Alydidae	Hemiptera	S	*				*	
A837			Aphrophoridae	Hemiptera	S	*	*		*	*	*
A1804			Coccidae	Hemiptera	S		*				
A1805			Coreidae	Hemiptera	S					*	*
A1093	Pendulinus	P.hastricornis	Coreidae	Hemiptera	S				*		
A1736	Lepaspis	L.distincta	Diaspididae	Hemiptera	S	*					
A1054			Fulgoridae	Hemiptera	S	*	*		*	*	*
A749			Fulgoridae	Hemiptera	S	*	*		*	*	*
A936			Fulgoridae	Hemiptera	S	*	*		*	*	
A980			Fulgoridae	Hemiptera	S	*	*		*		*
A1795			Fulgoridae	Hemiptera	S	*	*		*	*	*
A652			Fulgoridae	Hemiptera	S	*	*			*	*
A843			Fulgoridae	Hemiptera	S	*				*	
A1664			Lygaeidae	Hemiptera	S	*	*		*	*	*
A756			Lygaeidae	Hemiptera	S		*			*	*
A761			Lygaeidae	Hemiptera	S	*	*		*	*	*
A849			Lygaeidae	Hemiptera	S	*	*		*		
A949			Lygaeidae	Hemiptera	S				*		
A961			Lygaeidae	Hemiptera	S				*		
A262	Caprhobia	C.similis	Lygaeidae	Hemiptera	S	*	*		*	*	
A208	Macchiademus	M.diplopterus	Lygaeidae	Hemiptera	S	*	*				*
A32	Nysius		Lygaeidae	Hemiptera	S	*	*		*	*	*
A892	Oxycarenus	O.hyalinnipennis	Lygaeidae	Hemiptera	S		*		*		*
A624	Oxycarenus	O.maculatus	Lygaeidae	Hemiptera	S	*	*		*	*	*
A724	Oxycarenus	O.maculatus	Lygaeidae	Hemiptera	S						*
A1796			Miridae	Hemiptera	S	*					*
A684			Miridae	Hemiptera	S	*	*				
A764			Miridae	Hemiptera	S	*	*				
A879			Miridae	Hemiptera	S	*	*				*
A545	Antestiopsis	A.variegata	Pentatomidae	Hemiptera	S		*		*		*
A982	Dismegistus	D.fimbriatus	Pentatomidae	Hemiptera	S					*	*
A680	Eurys	E.dilatatus	Pentatomidae	Hemiptera	S	*			*		
A451	Nezara		Pentatomidae	Hemiptera	S				*		
A722	Orthoschizops	O.lineaticeps	Pentatomidae	Hemiptera	S		*		*		
A772	Orthoschizops	O.lineaticeps	Pentatomidae	Hemiptera	S	*	*		*	*	*
A554	Thelorus	T.costata	Pentatomidae	Hemiptera	S	*	*		*		
A1157			Psyllidae	Hemiptera	S	*					*
A1780			Psyllidae	Hemiptera	S	*	*			*	*
A891	Cysteochila	C.incolana	Tingidae	Hemiptera	S		*		*		
A1056				Coleoptera	T						
A1885				Coleoptera	T						
A2003				Coleoptera	T						
A1156			Anobiidae	Coleoptera	T	*					
A1160			Cantharidae	Coleoptera	T	*					
A994	Afronucha	A.tetra	Cantharidae	Coleoptera	T						*
A1112	Afronycha		Cantharidae	Coleoptera	T		*				
A1089	Afronycha	A.picta	Cantharidae	Coleoptera	T	*					*
A944	Afronycha	A.tetra	Cantharidae	Coleoptera	T						*
A955			Colydiidae	Coleoptera	T		*				*
A1295			Corylophidae	Coleoptera	T						*
A890	Sitophilus	S.oryzae (prob)	Curculionidae	Coleoptera	T	*					

116

Code	Family	Order	T						
A145	Temnochilidae	Coleoptera	T			*			
A1743		Diptera	T						*
A1833	Agromyzidae	Diptera	T	*					
A979	Anthomyiidae	Diptera	T	*					
A831	Bibionidae	Diptera	T					*	
A940	Bibionidae	Diptera	T	*	*	*	*	*	
A847	Calliphoridae	Diptera	T	*	*			*	*
A1083	Calliphoridae	Diptera	T	*				*	
A1848	Calliphoridae	Diptera	T	*					
A1864	Chironomidae	Diptera	T	*	*				*
A835	Chironomidae	Diptera	T	*	*		*	*	*
A1839	Chloropidae	Diptera	T		*		*		
A1854	Chloropidae	Diptera	T	*				*	*
A1862	Chloropidae	Diptera	T	*	*				
A1869	Chloropidae	Diptera	T	*	*				
A1873	Clusiidae	Diptera	T				*		
A1867	Culicidae	Diptera	T	*	*			*	*
A783	Culicidae	Diptera	T	*	*			*	*
A1835	Ephydridae	Diptera	T						*
A1162	Heleomyzidae	Diptera	T	*					
A858	Heleomyzidae	Diptera	T					*	
A1851	Lauxaniidae	Diptera	T			*	*		*
A795	Lauxaniidae	Diptera	T	*		*	*		*
A884	Lonchaeidae	Diptera	T				*		
A1841	Muscidae	Diptera	T	*					
A1852	Muscidae	Diptera	T						*
A1860	Muscidae	Diptera	T	*					
A787	Muscidae	Diptera	T	*			*	*	*
A803	Muscidae	Diptera	T	*	*				*
A846	Muscidae	Diptera	T	*					*
A957	Otididae	Diptera	T		*				
A741	Phoridae	Diptera	T	*	*			*	*
A778	Phoridae	Diptera	T	*				*	*
A859	Phyllomyzidae	Diptera	T						
A1074	Platystomatidae	Diptera	T					*	
A816	Psychodidae	Diptera	T						
A916	Psychodidae	Diptera	T				*	*	
A1843	Rhinophoridae	Diptera	T	*					
A1853	Rhinophoridae	Diptera	T	*					
A1857	Rhinophoridae	Diptera	T	*					
A828	Sarcophagidae	Diptera	T	*					
A1081	Scatophagidae	Diptera	T						*
A1836	Sciaridae	Diptera	T				*		
A1837	Sciaridae	Diptera	T	*	*			*	*
A700	Sciaridae	Diptera	T	*	*				*
A1863	Sciomyzidae	Diptera	T	*					
A1840	Sepsidae	Diptera	T				*		
A701	Sepsidae	Diptera	T						*
A893	Sepsidae	Diptera	T	*	*		*	*	*
A1846	Simuliidae	Diptera	T	*					
A808	Sphaeroceridae	Diptera	T				*		
A860	Sphaeroceridae	Diptera	T				*		
A1090	Syrphidae	Diptera	T	*					*
A1108	Syrphidae	Diptera	T	*	*				
A750	Syrphidae	Diptera	T	*			*		
A986	Syrphidae	Diptera	T		*				
A1154	Tephritidae	Diptera	T	*					
A800	Tephritidae	Diptera	T					*	
A852	Tephritidae	Diptera	T					*	
A854	Tephritidae	Diptera	T	*					
A913	Tephritidae	Diptera	T	*	*				
A782	Tipulidae	Diptera	T	*					
A1739		Ephemeroptera	T	*					
A784		Ephemeroptera	T	*	*				*
A853		Ephemeroptera	T	*	*				
A1055	Aphididae	Hemiptera	T	*			*		
A844	Aphididae	Hemiptera	T		*		*	*	*
A1087	Cicadellidae	Hemiptera	T						*
A1101	Cicadellidae	Hemiptera	T						*
A1151	Cicadellidae	Hemiptera	T						*
A1723	Cicadellidae	Hemiptera	T				*		

ID	Genus	Species	Family	Order		C1	C2	C3	C4
A771	Acia	A.lineatifrons	Cicadellidae	Hemiptera	T	*	*	*	*
A1774	Molopopoterus		Cicadellidae	Hemiptera	T				
A1806			Fulgoridae	Hemiptera	T				
A1646			Membracidae	Hemiptera	T	*	*	*	
A1642			Piesmatidae	Hemiptera	T				
A974	Solenostethium	S.lilligerum	Scutelleridae	Hemiptera	T				*
A621			Phasmatidae	Phasmatodea	T				
A789				Trichoptera	T	*			
A954				Trichoptera	T	*			