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FACTORS INFLUENCING THE DIVERSITY OF GALL-FORMING INSECT SPECIES ON AUSTRALIAN PLANTS

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Thesis submitted for the degree of Doctor of Philosophy at the School of Biological Sciences, Macquarie University, North Ryde, Sydney, Australia.

May, 1995.

CERTIFICATE

The work described in this thesis is original and has not been submitted, in any form, for a higher degree at any other university or institution.

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TABLE OF CONTENTS

Frontispiece: A complex gall (probably Dipteran) on a eucalypt leaf.

Page

Abstract 5

Acknowledgments 8

Chapter 1 General introduction 10

1.1 Plant galls defined 10

1.2 Causes of plant galls 10

1.3 Morphology of insect induced galls 10

1.4 Host specificity 11

1.5 Possible advantages gained by an insect living in a gall 11

1.6 Galls and humans 12

1.7 Hypotheses about patterns in gall insect diversity 12

1.8 Main questions of the thesis 13

1.9 Organisation of the thesis 14

Chapter 2 Australian gall-forming insects 16

2.1 Australian gall-forming insect groups and their host plants 16

2.1.1 Introduction 16

2.1.2 Information sources 16

2.1.3 Summary of galling species and host plants 16

2.1.4 Comparison of the Australian gall fauna with other faunas 17

2.1.5 Host specificity 18

2.1.6 Host plants 18

2.1.7 Comparison of galled Australian plant groups with other galled floras 19

2.2 Galls on *Eucalyptus* 19

2.2.1 Variation in galling within the genus *Eucalyptus* 19

2.2.2 Influence of soil fertility on gall species richness 22

2.2.3 Influence of host plant species subgenus on gall species richness 23

2.2.4 Influence of host plant geographic range size on gall species richness 23

2.2.5 Influence of host plant geographic range rainfall zone on gall species richness 26

2.2.6 Factors affecting the number of *Apiomorpha* species on *Eucalyptus* species 26

2.3 Summary 30

Appendix 1 Australian gall-forming insects and their host plants 31

Appendix 2 Number of gall insect species compared with number of species in plant genus 35

Appendix 3 Eucalypt hosts of Psylloidea 36

Appendix 4 Eucalypt hosts of Coccoidea (excluding *Apiomorpha*) 38

Appendix 5 Eucalypt hosts of Diptera 39

Appendix 6 Eucalypt hosts of Hymenoptera 40

Appendix 7 Gall species on eucalypt species 41

Appendix 8 Number of gall species compared with eucalypt subgenus and geographic range 46

Appendix 9 Eucalypt hosts of *Apiomorpha* 57

Appendix 10 Eucalypt species names associated with codes in Appendix 9 62

Chapter 3 Comparison of gall-forming insect species diversity on vegetation at infertile and fertile soil sites 65

3.1 Introduction 65

3.2 Methods 66

3.3 Results 69

3.4 Discussion 76

Appendix 11 Plant species and their galls at each site 78

Appendix 12 Gall species and gall morphology at each site 88

Chapter 4 The effect of host plant taxon and geographic range size on gall-forming insect species richness on Australian eucalypts 93

4.1 Introduction 93

4.2 Methods 95

4.3 Results 97

4.3.1 Host plant taxon and geographic range size 97

4.3.2 Host plant geographic range rainfall zone 100

4.4 Discussion 102

4.4.1 Effect of host plant taxon 102

4.4.2 Effect of host plant geographic range size 102

4.4.3 Summary 103

Appendix 13 *Eucalyptus* species pairs and their geographic ranges 104

Appendix 14 Galls on eucalypt species at different sites 106

Chapter 5 The effect of host plant taxon, geographic range size and rainfall zone on gall-forming insect species richness on Australian acacias 114

5.1 Introduction 114

5.2 Methods 115

5.3 Results 119

5.4 Discussion 123

5.4.1 Host plant taxon 123

5.4.2 Host plant geographic range size 124

5.4.3 Host plant geographic range rainfall zone 125

5.4.4 Summary 126

Appendix 15 *Acacia* species and their geographic ranges 128

Appendix 16 Galls on acacia species at different sites 132

Chapter 6 General discussion 135

6.1 Australian gall insects 135

6.2 Factors tested in the thesis 135

6.2.1 Host plant taxon 136

6.2.2 Soil fertility 137

6.2.3 Host plant geographic range size 139

6.2.4 Host plant geographic range rainfall zone 140

6.3 Additional factors 141

6.3.1 Meristem availability 141

6.3.2 Plant architecture 142

6.3.3 Plant geographic range latitude 145

6.4 An Australian scenario 145

References 148

ABSTRACT

Factors with the potential to influence the species richness of insects which induce galls on plants include host plant taxon, plant adaptations to low soil fertility, and size and dryness of the host plant geographic range. These factors were investigated for gall-forming insects on Australian plants using a data base compiled from existing records and new information collected from field surveys.

The data base indicated that galling was concentrated in certain insect and plant lineages. Seven broad groups of insects were reported to cause galls. These were coccoid bugs, chalcidoid wasps, thrips, flies, psyllids, beetles and moths. The most gall-prone plant genus was *Eucalyptus*. Evidence from differences in galling on eucalypt species suggested that host plant species with many gall species belong to large subgenera. Gall species numbers seem to be limited on host plants with small geographic ranges. Soil fertility and environmental dryness did not appear to affect gall species richness.

The factors which might affect gall species richness were tested more rigorously by field surveys designed specifically for that purpose. To test whether the pattern of high gall species richness associated with plants adapted to low soil fertility, found for other biogeographical regions, applies in the Australian region, a field comparison of galling on vegetation at infertile and fertile sites was carried out. I recorded the number of gall-forming insect species (morphospecies), complex and simple gall species, host plant species, total plant species, and total soil phosphorus (a measure of soil fertility) at eight sites in the Sydney region of NSW, Australia.

Total soil phosphorus levels ranged from 65-961 mg P/kg. Gall-forming insect species richness was greater at less fertile sites than at more fertile sites, as was the proportion of gall-forming insect species with complex gall morphologies. At all sites where they occurred, myrtaceous tree species supported numerous gall insect species, while most other plant species were associated with only a few, or no gall insect species.

The greater gall-forming insect diversity and higher proportion of gall species with complex gall morphology at lower fertility soil sites could be accounted for largely by the greater number of myrtaceous tree species (mainly of the genus *Eucalyptus*) at these sites.

Gall-proneness was concentrated in only a few plant lineages and was not an intrinsic characteristic of plants adapted to infertile soils. Identification of the relevant characteristics of these gall susceptible plant groups is needed to help advance understanding of patterns in gall diversity and complexity.

Accordingly, the emphasis of the thesis shifted to consideration of factors which might influence gall species richness within gall-prone Australian plant genera. A field survey was designed to test whether host plant geographic range size, usually found to be positively correlated with insect species richness in other parts of the world, affected the number of gall species on Australian *Eucalyptus* species.

I assessed the local and regional species richness of gall-forming insects on five pairs of closely related eucalypt species. One pair belonged to the subgenus Corymbia, one to Monocalyptus, and three to different sections of Symphyomyrtus. Each eucalypt pair comprised a large and a small geographic range species. Species pairs were from coastal or inland regions of eastern Australia.

The total number of gall species on large geographic range eucalypt species was greater than on small range eucalypt species but only after the strong effect of eucalypt taxonomic grouping was taken into account. There was no relationship between eucalypt species geographic range size and the size of local gall species assemblages, but the variation in insect species composition between local sites was higher on large range eucalypt species than on small range eucalypt species. Thus the effect of host plant geographic range size on regional insect species richness was due to greater between-site differentiation among the more widespread local sites of host plant species with large ranges, rather than to greater numbers of gall species at each local site.

This study confirmed the role of host plant geographic range size in the determination of insect species richness and provided evidence of the importance of host plant taxon. Indications that dry environments favour galling, as suggested by gall surveys in North America and Brazil, were looked for but none were found.

To test whether patterns of galling found for Australian eucalypts generalized to a different radiation of gall insect species another field survey was undertaken, this time with *Acacia* as the host plant genus. This field survey was designed to determine the effect of acacia taxonomic group, geographic range size, and rainfall zone on gall-forming insect species numbers.

Local and regional gall insect species richness was estimated on eight pairs of closely related acacia species, from four *Acacia* sections, with ranges in low or high rainfall areas of NSW, Australia. Each acacia pair comprised a large and a small geographic range species.

Unlike eucalypts, where host plant geographic range size was positively related to regional gall species richness, there was no relationship between acacia range size and galling. It seems likely that the low absolute numbers of gall insect species on phyllodinous acacias may have masked the species-area effect. There was also no detectable effect of host plant range rainfall zone on gall species numbers on acacias. The lack of reliable gall sites on acacias in low rainfall areas, caused by the unreliability of rainfall, and the dominating effect of low soil fertility in wet as well as dry areas, may be stronger than the proposed positive effects of fewer enemies and diseases in drier areas. There was no relationship between acacia taxon size and gall species richness but galling on acacias in the bipinnate acacia taxon group (which has true leaves) was significantly higher than on most phyllodinous acacia taxa (which have modified petioles instead of leaves). Thus the effect of taxon in acacias is via structural differences between taxon groups, rather than differences in taxon size, as it was for eucalypts.

The results of the work undertaken for this thesis suggest that patterns of insect galling in Australia generally conform to global patterns in terms of the importance of host plant taxon and geographic range size. Sclerophylly, in response to widespread low soil fertility, seems to exert a strong effect but needs further investigation. Unlike other parts of the world, dry environments in Australia do not appear to be more favourable for gall insects than wet environments. The influence of meristem availability, host plant architecture and latitude on gall species richness, factors so far not fully explored, are promising areas for future research.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Plant galls defined

Plant galls are deformations resulting from a change in the normal pattern of growth and development of plant tissues or organs. There may be an abnormal increase in the number of plant cells (hyperplasy) and/or abnormal enlargement of the cells (hypertrophy) (Misra 1985). Galls can form on virtually all plant parts and generally originate in actively growing regions (undifferentiated meristematic tissue) (Ananthakrishnan 1984, Rohfritsch 1992). Few plant genera are free from galls but some plant groups are more susceptible to galling than others. According to Mani (1964) more than 93% of galls occur on members of the Dicotyledons and about 80% of all galls are on leaves.

1.2 Causes of plant galls

Gall formation on plants can be stimulated by mites, nematodes, protozoans, viruses, bacteria, fungi and insects (Brues 1946, Misra 1985). Insect induced galls, often the most structurally complex of these abnormal plant growths, are the subject of this study.
The mechanism by which insects initiate gall formation is unknown but may include mechanical injury of plant tissues and injection of chemical secretions during oviposition or feeding. Plant hormones (such as auxins), amino acids and amides, and digestive enzymes (Rohfritsch and Shorthouse 1982), as well as DNA particles in the form of viruses or plasmids (Cornell 1983), have been suggested as possible gall-inducing components of such insect secretions.

Many plant galls contain species other than the original gall-forming insect. These additional inhabitants may be inquilines which share the gall or parasitoids which eventually destroy the gall-forming species.

1.3 Morphology of insect induced plant galls

The external morphologies of insect induced galls are diverse. Each gall-former induces galls which are morphologically distinctive for that insect species (Metcalf and Flint

1939, Rohfritsch and Shorthouse 1982, Ananthakrishnan 1984). A few, for example coccoids (Gullan 1984a), produce sexually dimorphic galls. In gall-formers which have alternation of generations, such as some cynipid wasps (Ananthakrishnan 1984, Stone and Sunnucks 1993) and cecidomyiid flies (Mani 1964), the galls of the sexual and agamic generations are on different host plant species, or on different parts of the same host plant species, and are morphologically different.

Galls range from simple deformations like leaf rolls, masses, or pits, in which the insect is only partly surrounded by the gall, to completely enclosed, complex galls with spiny outgrowths. The internal structure of insect induced plant galls is variable, but usually includes an inner zone or several patches rich in nutrients, such as nitrogenous compounds and soluble sugars, surrounded by a stronger supporting layer (and often a cortical parenchyma layer with water filled vacuoles which contain tannins), enclosed by the epidermis (Mani 1964, Rohfritsch and Shorthouse 1982).

1.4 Host specificity

Each gall-forming insect species is generally restricted to one or a few closely related host plants within the same genus (Rohfritsch and Shorthouse 1982). Some insect generic complexes are associated with specific plant generic complexes (Ananthakrishnan 1984).

1.5 Possible advantages gained by an insect living in a gall

Price, Waring and Fernandes (1986) discuss hypotheses on the adaptive nature of insect induced plant galls. Galls are thought to provide insects with a rich food supply, a favourable microenvironment, and protection from natural enemies. Price *et al.* (1986) suggest that in the majority of cases galling only benefits the insect, not the host plant, so most gall-forming insects should be regarded as parasites. However, external chewing herbivores remove plant structures, as well as nutrients, whereas gall insects often leave plant parts relatively intact and functional. Therefore, even though nutrients are removed, there could be a nett benefit to a plant in being fed on by a gall insect, compared with a chewing herbivore, because the cost of replacing plant parts is avoided. (1)

1.6 Galls and humans

Insect induced plant galls have long been known and valued by humans. Galls have been used as remedies for disease, omens of future events, fuel for lamps, food, tanning agents for hides and skins, components of dye for fabric and fur, and ingredients in the manufacture of ink (Fagan 1918). More recently gall insect species have been employed in the biological control of weeds such as *Eupatorium adenophorum* Spreng. (crofton weed) by the tephritid stem gall fly *Procecidochares utilis* Stone (Bennett and Van Staden 1986); and *Acacia longifolia* Willd., in South Africa, by the galling wasp *Trichilogaster acaciae-longifoliae* (Froggatt) (Boucek 1988).

The role of gall-forming insects in studies of subjects such as plant-insect interaction, insect behaviour, insect herbivore community structure, and predator-prey interactions has become increasingly important over the last 15 years (Weis 1993). This is because galls are relatively easy to census, the developmental stage and cause of mortality of the gall insect can often be determined from the gall itself, and the host plant is unambiguous. In this study I have used Australian gall-forming insects as the tool to investigate questions about the factors which influence the species diversity of insects on plants.

1.7 Hypotheses about patterns in gall insect diversity

Fernandes and Price (1991) have suggested that low soil fertility and dry environments favour gall insects. They base their hypotheses on patterns of galling identified in North America and Brazil. Low soil fertility and low rainfall environments are both associated with sclerophyllous plants. The tough leaves of sclerophylls often persist for a long time and often contain high concentrations of secondary compounds (Turner 1994). Both features are potentially advantageous for gall insects (Cornell 1983, Taper and Case 1987). There also appear to be fewer gall insect enemies and diseases in dry environments (Fernandes and Price 1992). High concentrations of nutrients in the tissues of plants growing on fertile soils might be toxic for gall-forming insects (Fernandes and Price 1991).

Work by Cornell (1985a) on cynipid wasps on oaks in North America indicated that total gall species richness associated with a plant species is positively related to the size of the geographic range of the host plant species. In some cases the number of species in the host plant subgenus is also positively related to gall insect species numbers. The differences in habitat diversity, immigration rates and extinction rates, proposed by MacArthur and Wilson (1967) to explain differences in species richness on large and small islands, may also explain differences in gall species richness between hosts with different sized geographic ranges or from different sized subgenera.

My thesis was designed to look for evidence of patterns of gall species richness in the Australian context. Accumulation of such independent tests, from many parts of the world, is essential to the ultimate development of a theory on the global distribution of gall-forming insect species. The hypothesised mechanisms responsible for these patterns will be discussed in more detail in the relevant sections of this manuscript.

1.8 Main questions of the thesis

The main questions I wanted to answer about Australian gall-forming insects and their host plants were:

1) Which insect groups cause galls on Australian native plants?

2) Which Australian native plant genera have insect induced galls?

3) Does soil fertility influence gall diversity?

4) Does the generic subgroup, and size or rainfall zone of the geographic range, of a host plant species, influence gall-forming insect species richness?

In the first year, Question 3 was tackled by a field comparison of gall-forming insect species richness at sites of low and high soil fertility near Sydney. At the same time, a database was compiled of all available literature and museum records of Australian gall insects and their host plants, with a view to gaining answers to Questions 1, 2 and 4. The database was indeed used to consider all the questions, but during the field study for Question 3 it became apparent that actual gall-species richness on numerous plant species, observed in the field, was many times greater than indicated by the review of host records. Accordingly, field studies were undertaken to consider the various components of Question 4, rather than relying on the literature-derived database. Field surveys of gall species richness on pairs of plant species, from low and high rainfall areas, matched for generic subgroup and habitat location, but differing in geographic range size were carried out. In the first of these surveys the host plant species were from the genus *Eucalyptus*. In the second survey gall species richness was measured on species of *Acacia*.

1.9 Organisation of the thesis

Chapter 2 of the thesis examines literature and museum information available on Australian gall-forming insects and their host plants. The insect groups containing gall-inducing species and their main host plant groups are discussed. Evidence of positive relationships between gall species richness and host plant species subgenus size and geographic range size for the gall-prone genus *Eucalyptus* is presented.

Chapters 3 to 5 describe the results from the three field studies and constitute the core new findings of the thesis. These three chapters have been written as manuscripts for journals (at the time of writing Chapter 3 was in press in *Ecology* and Chapters 4 and 5 had been submitted to the *Australian Journal of Ecology*). Because each of these chapters has been written to stand alone, there is some commonality between their Introduction, Methods and Discussion sections, and detailed documentation of the galls found has been removed to Appendices.

Chapter 3 describes the field study, set up in the Sydney region, to discover whether low soil fertility favours galling. The survey tested the hypothesis that plant species growing on infertile soils would have more gall species, and more complex kinds of gall species, than plant species growing on fertile soils. The results supported the hypothesis but showed that the effect was concentrated in certain plant lineages, especially in the genus *Eucalyptus*.

The relationship between gall insect species richness and *Eucalyptus* species geographic range size was investigated in the broad scale, eastern Australian, field study described in Chapter 4. The number of gall species on pairs of *Eucalyptus* species, with members of each pair selected to be as alike as possible except for geographic range size, were compared to test the hypothesis that host species with large ranges have more gall species than those with small ranges. The hypothesis was supported when differences between *Eucalyptus* subgenera were taken into account. Evidence which might suggest that galling was favoured by dry environments was also looked for. Gall diversity on two

Symphyomyrtus eucalypt pairs, with geographic ranges predominantly in low rainfall inland areas was compared with gall diversity on a Symphyomyrtus eucalypt pair from the wetter coastal area. No trends were apparent.

The second broad scale field study, detailed in Chapter 5, was designed to test whether the patterns of galling found for *Eucalyptus* were unique to that genus or also applied to the genus *Acacia*. Gall species richness was compared on pairs of closely related *Acacia* species from four *Acacia* sections. One member of each pair had a large geographic range and the other a small geographic range. Half the pairs were from low rainfall areas and half from high rainfall areas. No species-area or rainfall zone effects were found for *Acacia*. The only significant result was the effect of *Acacia* section. The section comprising bipinnate acacia species had more gall species than those sections in which the acacia species were phyllodinous.

Chapter 6 provides a synthesis of the information contained in the rest of the thesis and relates it to patterns of gall species richness found by other workers. Directions for further research are suggested. A profile of a gall-susceptible Australian plant species, based on the information collected from the literature, museum, and field surveys, is proposed.

CHAPTER 2

AUSTRALIAN GALL-FORMING INSECTS

2.1 Australian gall-forming insects groups and their host plants

2.1.1 Introduction

The life histories and ecology of most Australian gall-forming insect species are poorly known and taxonomic studies are incomplete. No comprehensive overview of Australian galling species and their host plants was available prior to this study. Information on the subject was scattered throughout the literature.

2.1.2 Information sources

As a first step toward identifying patterns in species diversity of Australian gall-forming insects I compiled a data base of gall insect species and their host plant genera available from the relevant literature and from voucher specimens held at the Australian Museum, Sydney, and the Australian National Insect Collection, Canberra. The data and their literature sources are listed in Appendix 1. The main points are summarised below. The apparent size and importance of the galling groups and their host plant groups, suggested by this information, may reflect the unequal attention the groups have received rather than providing an indication of the real situation. The number of imprecise records suggests that the actual number of gall insect species and host plant genera could be much higher.

2.1.3 Summary of galling species and host plants

Some of the best studied and most conspicuous gall-forming insects come from the Coccoidea (Hemiptera: Sternorrhyncha). There are 106 known species of gall-forming coccoids, in 17 genera. Most occur on *Eucalyptus* and other Myrtaceae where they gall stems, leaves and flower buds.

Another group which apparently contains numerous galling species is the Chalcidoidea (Hymenoptera: Apocrita). The literature does not always clearly distinguish between primary galling species and inquiline or parasitoid wasp species but there appear to be at least 78 species of gall-forming chalcidoid wasps in 25 genera. Most form galls in the stems, leaves and flower buds of *Eucalyptus*, but many also gall the developing florets of *Ficus*, and the flower buds of *Acacia*.

Eleven genera of the family Phlaeothripidae (Thysanoptera: Tubulifera), are reported to contain gall-formers (at least 25 species). Thrips galls are mainly found on leaves or phyllodes (modified petioles which function as leaves). The plant genera known to be associated with the most species of thrips are *Acacia* and *Geijera*. There are no thrips galls recorded from *Eucalyptus*.

Dipteran gall-formers belong to the families Cecidomyiidae (Diptera: Nematocera), Tephritidae, Agromyzidae, and Fergusoninidae (Diptera: Brachycera). The taxonomy and biology of most species have received so little attention that no reliable estimate of the total number of galling species can be made. Nine genera are known to have species which cause galls. These are mainly on stems, leaves or flower buds. Host plant genera are numerous.

There are at least 20 gall-forming species (in 6 genera) in the family Psyllidae (Hemiptera: Sternorrhyncha). Most reported host plants are *Eucalyptus* species and most galls are on leaves.

Few Australian Coleoptera are gall-formers. Three species are known in the family Buprestidae. These beetle species each form galls on stems or roots of plant species from different genera (*Allocasuarina*, *Pultenaea* and *Dillwynia*). Species of the Sagrinae (Chrysomelidae) are thought to live in stem galls. The host plant species are not listed.

Gall-forming Lepidoptera are rarely mentioned in the literature. One species of *Coleophora* (Coleophoridae) is reported to form stem galls on Chenopodiaceae and some species of *Alucita* (Alucitidae) may gall the stems of *Canthium* species.

2.1.4 Comparison of the Australian gall fauna with other faunas

Galls formed by Coccoidea, Chalcidoidea, Thysanoptera, Diptera and Psylloidea are common throughout the world and the paucity of gall-forming Coleoptera and Lepidoptera is universal. The main difference between the Australian gall fauna and that of many other parts of the world is the absence of native gallers belonging to the Aphidoidea (Hemiptera: Sternorrhyncha) and the Tenthredinoidea (Hymenoptera: Symphyta) and the almost complete absence of Cynipoidea (Hymenoptera: Apocrita) gall species. These three groups contain many gall-inducing species in North America and Northern and Central Europe (Dreger-Jauffret and Shorthouse 1992).

2.1.5 Host specificity

Most gall-forming insect species are highly host specific. The host plant specificity of Australian galler insects is well illustrated by the genus *Synglycaspis* (Psyllidae) in which each of the 15 species is restricted to a single, different *Eucalyptus* species (Moore, 1970). Associations of insect generic complexes with plant generic complexes are found in genera such as *Apiomorpha* (Eriococcidae) which is confined to the single host genus *Eucalyptus* (Gullan 1984a), and *Kladothrips* (Phlaeothripidae) confined to *Acacia* (Mound 1971b).

2.1.6 Host plants

Hnatiuk (1990) lists 2268 native Australian vascular plant genera. Only 27 of these plant genera (~1%) are reported to support gall-forming insects. They are listed in Appendix 2. As Table 2.1 demonstrates, a disproportionate number of gall species occurs on a few plant genera.

Table 2.1 Distribution of gall insect species among Australian vascular plant genera.

Based on Appendix 2. Total native vascular plant species from Hnatiuk (1990).

Plant genus	Number of species in plant genus	Percentage of all vascular plant species	Number of known gall insect species	Percentage of gall fauna
Eucalyptus	>700	~4.5%	134	~54%
Acacia	~750	~4.9%	23	~9%
Ficus	76	~0.5%	22	~9%
Geijera	8	~0.05%	11	~4%
All other genera	~13,931	~90%	56	~23%
	Total = 15,465		Total = 246	

More than half of all known gall-inducing insect species are on *Eucalyptus*. The gall species on *Acacia, Ficus* and *Geijera* together make up another 22%. The remaining 23% of gall species are unevenly distributed among the other 23 galled plant genera. None of these genera are recorded as having more than 3% of the total gall fauna.

2.1.7 Comparison of galled Australian plant groups with other galled floras

Concentration of galling in only a few plant groups also occurs in other floras but the galled plant groups vary. According to Dreger-Jauffret and Shorthouse (1992) the most gall susceptible orders are the Fagales, Salicales, Asterales and Fabales. In South America, Africa and India, leguminous plants are most commonly attacked (Dreger-Jauffret and Shorthouse 1992), while half of the gall species in Europe and North America occur on Fagaceae (Mani 1964).

2.2 Galls on *Eucalyptus*

2.2.1 Variation in galling within the genus *Eucalyptus*

As most gall species recorded were on *Eucalyptus*, and information on taxonomy, and geographic range sizes and locations of eucalypt species was available, this genus was chosen for further study. Appendices 3, 4, 5, 6, 9 and 10 list the gall-forming insect species reported in the literature, or on voucher specimens, for individual *Eucalyptus* species. Appendix 7 combines these records to give the gall groups and total gall species for each eucalypt species. No Lepidoptera, Coleoptera or Thysanoptera are reported to cause galls on *Eucalyptus*.

It appears that eucalypt species are not equally gall prone. Fig. 2.1 summarises the variation of galling within the genus. Most eucalypt species have no gall species recorded for them and most of those reported to have galls apparently support only a few species. A small proportion of eucalypt species are reported to have many gall species.

Positive reports in the database will in most cases be reliable, but many occurrences of gall species on hosts will not have been reported. Therefore where a eucalypt species is recorded in the database as carrying many different galls, this is probably true, but where a eucalypt species is recorded as carrying zero or few galls, this may not be true.

Nevertheless, there is no obvious reason to expect that gall species would be more severely under-recorded on fertile soils compared to infertile, or in one eucalypt subgenus compared to another. Therefore it was thought worthwhile to investigate what tentative answers emerged from the database Questions 3) and 4) of the thesis regarding the effect of soil fertility, and host plant species subgenus, geographic range size and geographic range location, on gall species numbers.

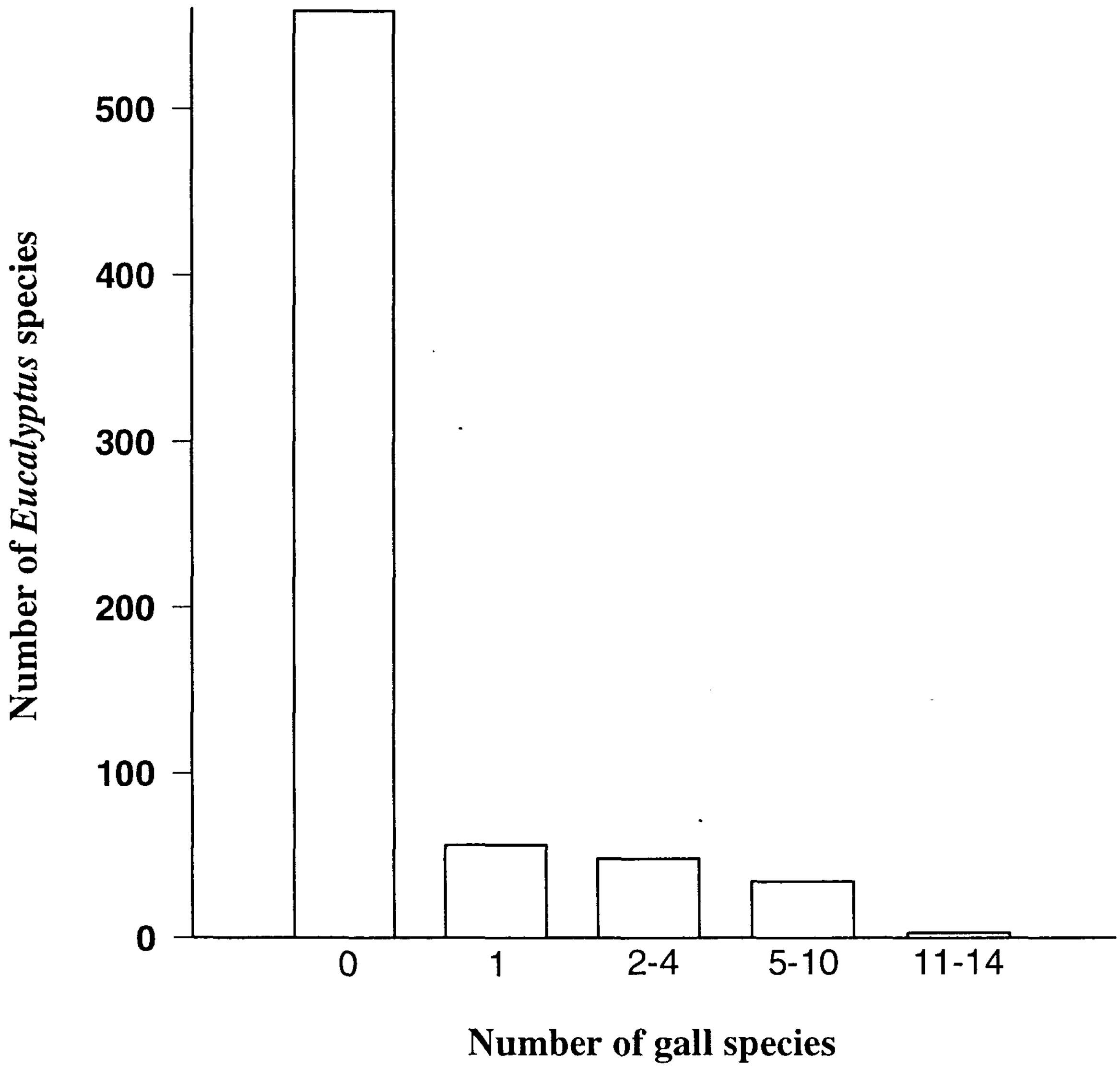


Figure 2.1 Variation in galling within the genus *Eucalyptus*.

Data sources: Appendix 7 and Gill, Belbin and Chippendale (1985).

2.2.2 Influence of soil fertility on gall species richness

Information on soil fertility requirements is not readily available for many eucalypt species so little can be deduced about the effect of this factor on gall species richness. Most of the eucalypt species reported to have 10 or more galls are recorded as growing on medium to relatively high fertility soils (Table 2.2). This is contrary to what would be expected if low soil fertility favours galling.

Table 2.2 Soil type and moisture availability in the environments occupied by *Eucalyptus* species reported to have 10 or more gall species (Appendix 7). Information on soil type and proximity to water is from Hill (1991). Eucalypt geographic ranges are from Chippendale and Wolf (1981). Environments of eucalypt species with geographic ranges mainly in regions where the median annual rainfall is $\geq$ 500 mm (Parkinson 1986), are listed as high rainfall; environments of eucalypt species with ranges mainly where the median annual rainfall is < 500 mm (Parkinson 1986), are listed as low rainfall. Environments of eucalypts with extensive ranges in both zones are described as mixed rainfall.

Eucalyptus species	Number of gall species	Soil type	Moisture
E. obliqua	14	deep and fertile	high r/f
E. crebra	12	shallow, medium fertility	mixed r/f
E. camaldulensis	11	deep, rich alluvium	low r/f but near watercourses
E. melliodora	10	moderately fertile	mixed r/f
E. polyanthemos	10	light, shallow soils	mixed r/f
E. tereticornis	10	medium to high fertility	high r/f
E. macrorhyncha	10	shallow, poor soils	mixed r/f

2.2.3 Influence of host plant species subgenus on gall species richness

Most gall-forming insect species that occur on more than one host species are restricted to closely related plant species. Sharing of gall insect species between host plant species from the same subgenus could help maintain gall species richness on a host species. The chance of sharing is likely to be greater within more speciose host genera and to result in host plant species from large subgenera having more gall species than host plant species from small subgenera (Lawton and Schröder 1977, Cornell 1985a, Zwölfer 1987).

The mean number of gall species per eucalypt species was not significantly different between subgenera (P >0.05) but there was a trend for the eucalypt species with high numbers of gall species to belong to the larger, more speciose, eucalypt subgenera (Fig. 2.2). This suggests that sharing of gall species between closely related host species could be one of the factors influencing gall species richness on individual eucalypt species.

2.2.4 Influence of host plant geographic range size on gall species richness

When the number of gall species reported for each eucalypt species was compared with the size of the geographic range of each eucalypt species a significant positive relationship was obtained (Fig. 2.3). Range size accounted for 17% of the variation in galling. The graph suggests that having a small geographic range may limit the number of gall species on a eucalypt species but having a large geographic range is not necessarily associated with having many gall species.

(6)

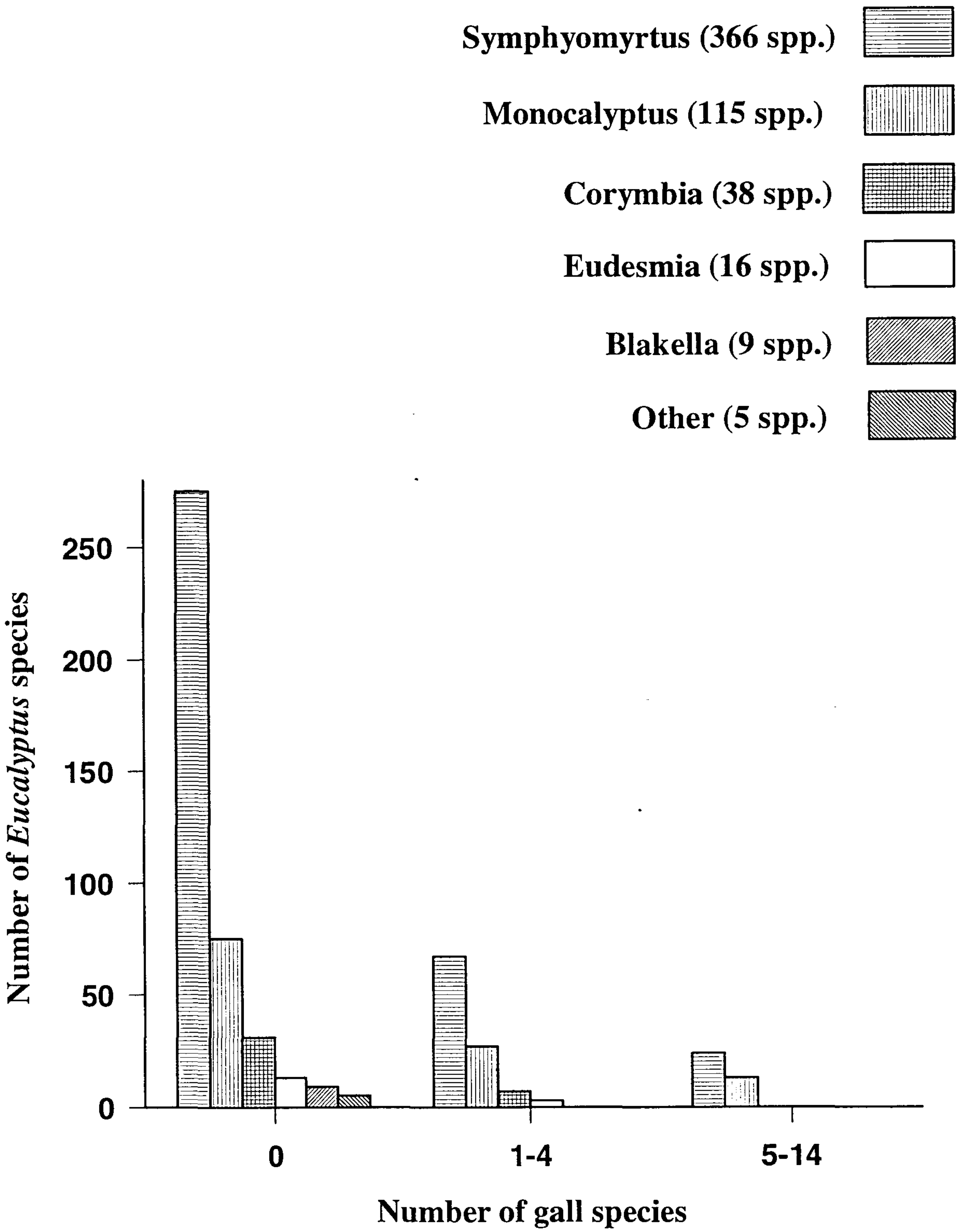


Figure 2.2 Number of described *Eucalyptus* species in each subgenus with zero, a few and many gall species.

Data sources: Appendix 8 and Gill, Belbin and Chippendale (1985).

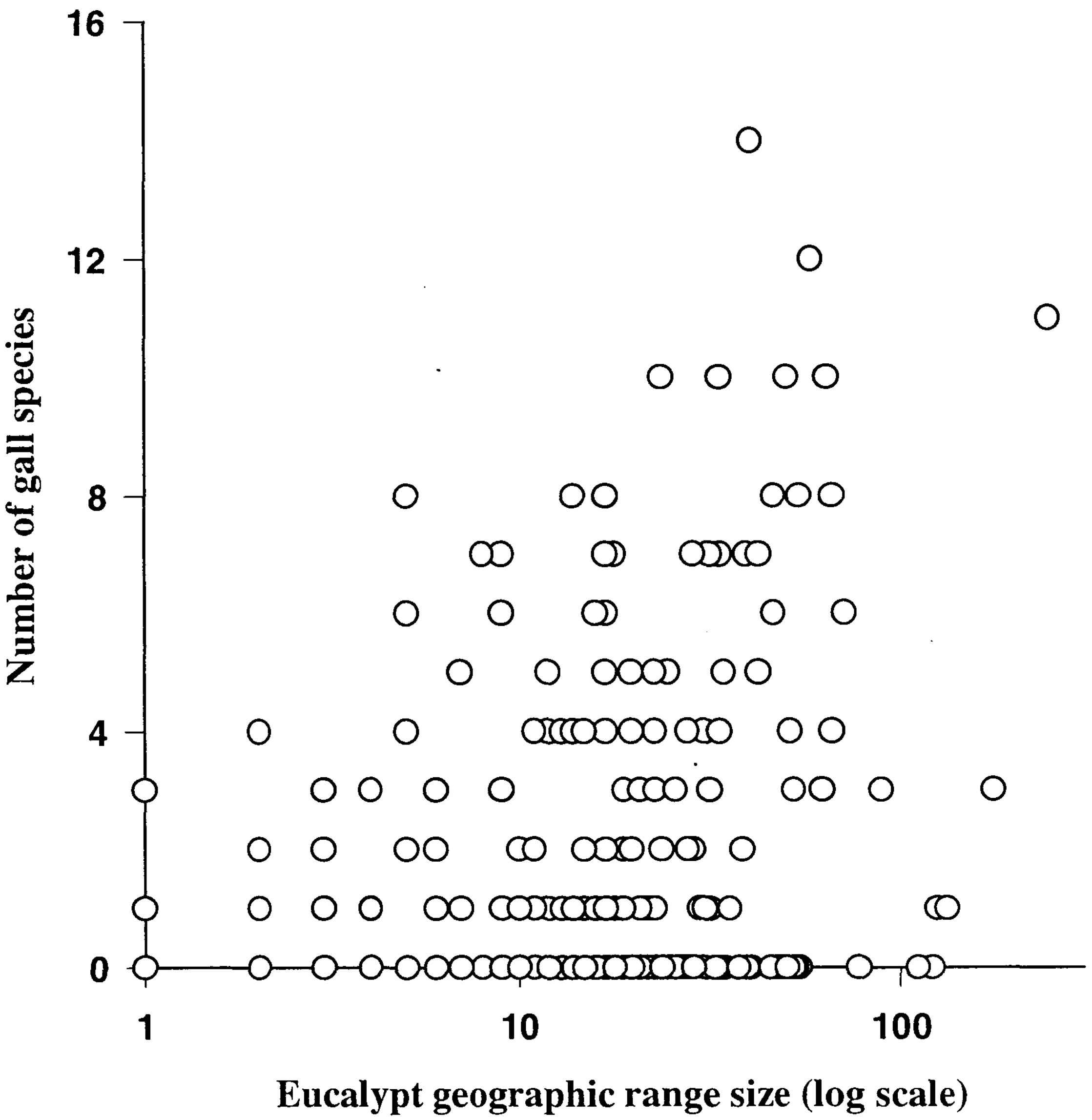


Figure 2.3 Relationship between gall species richness and eucalypt geographic range size (no. 1^ox1.5^o map grids occupied) (R^2 = 0.17, P = 0).

Data sources: Appendix 8 and Gill, Belbin and Chippendale (1985).

2.2.5 Influence of host plant geographic range rainfall zone on gall species richness

It was difficult to assess the importance of aridity from the data available. The geographic ranges of many eucalypt species extend over high and low rainfall zones. Some species which are restricted to low rainfall regions occur close to water so their environment is not truly dry. All the eucalypt species with 10 or more gall species have geographic ranges in high or mixed rainfall zones, or near water (Table 2.2). This suggests that aridity is not associated with increased gall species richness.

2.2.6 Factors affecting the number of *Apiomorpha* species on *Eucalyptus* species

The genus *Apiomorpha* is one of the best documented of the insect groups which cause galls on *Eucalyptus*. Species of *Apiomorpha* comprise a substantial proportion (30%) of the known gall species on *Eucalyptus* (Appendix 1). Most *Apiomorpha* species (69%) are restricted to eucalypt species of a single subgenus. The majority of these restricted *Apiomorpha* species are on species of Symphyomyrtus, a few on species of Monocalyptus and one on a species of Eudesmia (Gullan 1984a). Relationships between gall species richness and the factors under consideration might be expected to be more obvious if only galls caused by *Apiomorpha* species are considered. When this was done, similar results were obtained to those from the study of the complete gall fauna on *Eucalyptus*.

Sharing of gall species between closely related eucalypt species may contribute to the number of *Apiomorpha* species on a eucalypt species. The mean number of *Apiomorpha* gall species per eucalypt species was not significantly different between subgenera ($P > 0.05$) but there was a trend for the eucalypt species with high numbers of *Apiomorpha* species to belong to the larger eucalypt subgenera (Fig. 2.4).

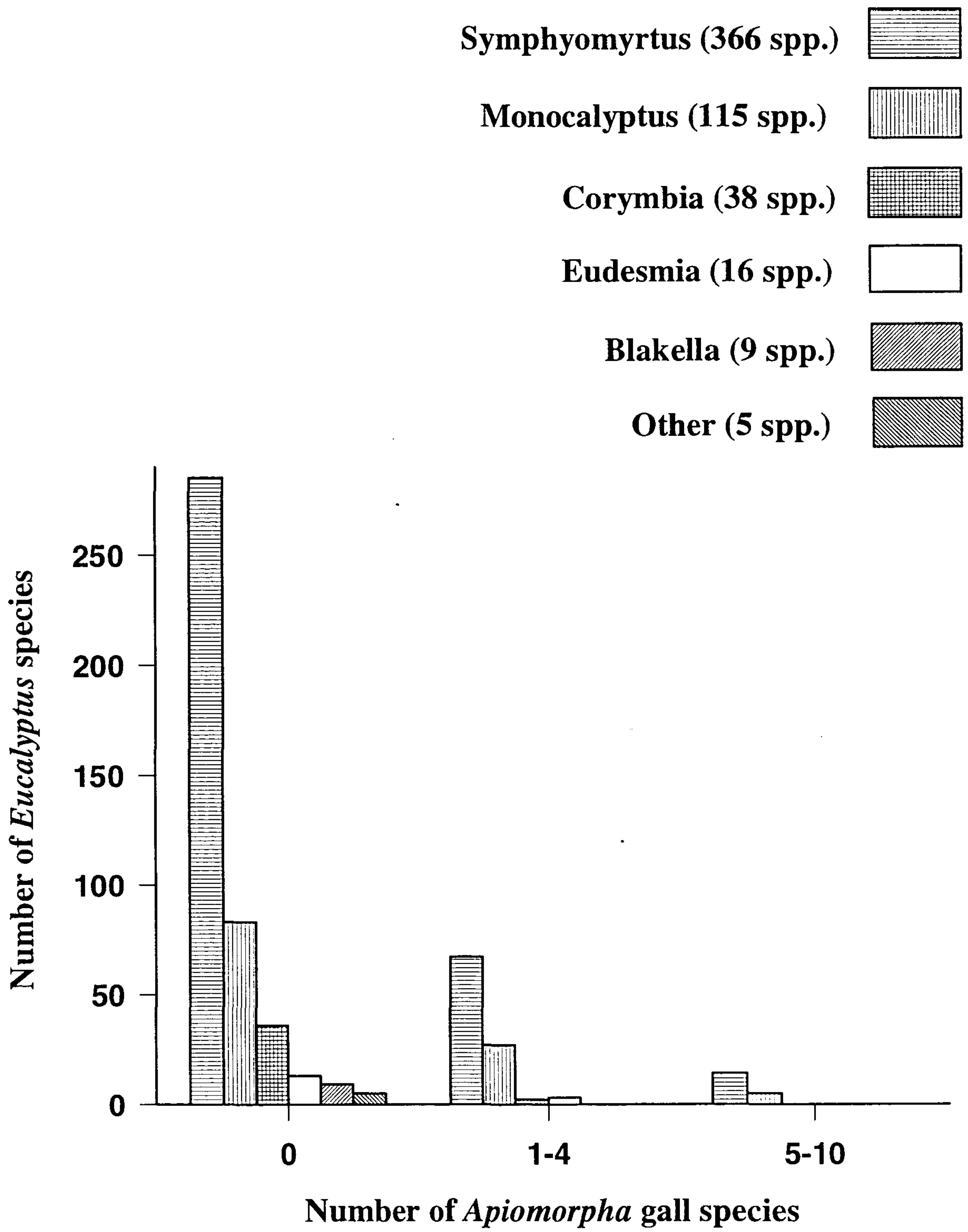


Figure 2.4 Number of described *Eucalyptus* species in each subgenus with zero, a few and many *Apiomorpha* gall species.

Data sources: Appendix 9 and Gill, Belbin and Chippendale (1985).

There were no clear patterns suggesting that low soil fertility or aridity were associated with high numbers of *Apiomorpha* species on a eucalypt species. For instance, eucalypt hosts with six or more *Apiomorpha* species comprised eucalypt species from both fertile and infertile soils and with geographic ranges in a variety of rainfall zones and microhabitats (Table 2.3).

Table 2.3 Soil type and moisture availability in the environments occupied by *Eucalyptus* species reported to have six or more *Apiomorpha* species (Appendix 9).

Data sources and definition of rainfall zones are the same as for Table 2.2.

Eucalyptus species	Number of *Apiomorpha* species	Soil type	Moisture
E. crebra	10	shallow, medium fertility	mixed r/f
E. pilligaensis	8	sand or light loam	high r/f
E. tereticornis	8	medium to high fertility	high r/f
E. siderophloia	7	medium fertility	high r/f
E. largiflorens	7	heavy black clay	low r/f but seasonally flooded
E. camaldulensis	7	deep, rich alluvium	low r/f but near watercourses
E. goniocalyx	6	dry, shallow, poor soils	mixed r/f
E. incrassata	6	sandy soils and dunes	low r/f
E. dumosa	6	red aeolian sands	low r/f

The limitation to galling imposed by the small geographic range of a host eucalypt species was also evident in the *Apiomorpha* data. The relationship between eucalypt species geographic range and number of *Apiomorpha* species was significant. Host species geographic range size accounted for 16% of the variation in *Apiomorpha* galling (Fig. 2.5).

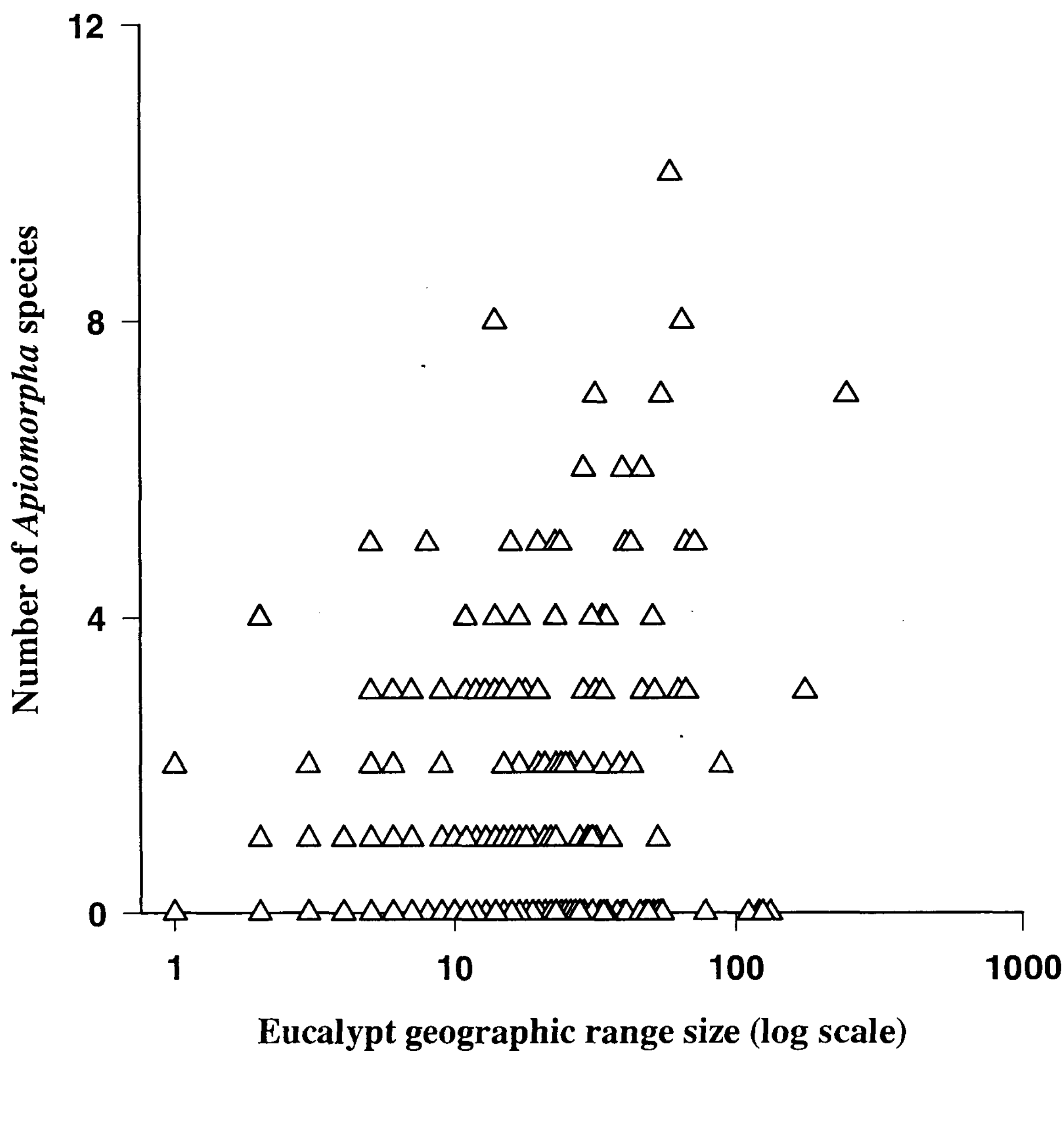


Figure 2.5 Relationship between *Apiomorpha* species richness and eucalypt geographic range size (no. 1°x1.5° map grids occupied) (R^2 = 0.16, P = 0).

Data sources: Appendix 9 and Gill, Belbin and Chippendale (1985).

2.3 Summary

Literature and museum records indicate that the Australian gall-forming insect fauna, like gall faunas of other regions, is concentrated in a small number of insect groups and concentrated on certain plant groups.

Evidence from the gall-prone genus *Eucalyptus* suggests that plant species with high numbers of gall species tend to belong to speciose plant subgenera. Host subgenus size may influence the number of gall species available for sharing between closely related hosts. There are no indications from existing eucalypt data that low soil fertility or dry environments favour galling but having a small geographic range seems to limit the number of gall species on a host eucalypt species.

These results must be viewed with caution because the data were not collected with the questions of this thesis in mind and so may suffer from sampling bias. The studies described in the following chapters were designed specifically to test hypotheses about the factors which affect the number of gall-forming insect species on Australian plant species.

Appendix 1 AUSTRALIAN GALL-FORMING INSECTS AND THEIR HOST PLANTS

INSECT GROUP	KNOWN INSECT GENERA AND SPECIES	TOTAL GALLING INSECT GENERA KNOWN	TOTAL GALLING INSECT SPECIES KNOWN	HOST PLANTS	TOTAL HOST GENERA KNOWN	MOST COMMON PLANT PART USED
HEMIPTERA		**17**	**106**		**9**	**STEMS, LEAVES**
Coccoidea:	(M) Araucariococcus (1 sp)			Araucaria	**(most on**	**FLOWER BUDS**
Margarodidae (M)	(E) Apiomorpha (ca 40 spp)			Eucalyptus	**Eucalyptus)**	
Eriococcidae (E)	(E) Ascelis (5 spp)			Eucalyptus		
Asterolecaniidae (A)	(E) Casuarinaloma (1 sp)			Allocasuarina		
Lecanodiaspididae (L)	(E) Cylindrococcus (4 spp)			Allocasuarina		
Diaspididae (D)	(E) Cystococcus (3 spp)			Eucalyptus		
	(E) Floracoccus (1 sp)			Eucalyptus		
	(E) Lachnodius (14 spp)			Eucalyptus		
	(E) Opisthoscelis (ca 15 spp)			Eucalyptus		
	(E) Sphaerococcopsis (4 spp)			Eucalyptus		
	(E) undescribed genus (2 spp)			Nothofagus		
	(A) Callococcus (1 sp)			Leptospermum		
	(A) Eremococcus (1 sp)			Leptospermum		
	(A) Frenchia (3 spp)			Casuarina/Banksia		
	(L) Gallinococcus (1 sp)			Leptospermum		
	(D) Maskellia (1 sp)			Eucalyptus		
	UNPLACED "Sphaerococcus":					
	cantentulatus Froggatt			Acacia		
	ferrugineus Froggatt			Melaleuca		
	froggatti Maskell			Melaleuca		
	morrisoni Fuller			Melaleuca		
	pustulans Green			Eucalyptus		
	rugosus Maskell			Leptospermum		
	socialis Maskell			Melaleuca		
	tepperi Fuller			Melaleuca		
	turbinata Froggatt			Melaleuca		

Appendix 1 (cont.)

INSECT GROUP	KNOWN INSECT GENERA AND SPECIES	TOTAL GALLING INSECT GENERA KNOWN	TOTAL GALLING INSECT SPECIES KNOWN	HOST PLANTS	TOTAL HOST GENERA KNOWN	MOST COMMON PLANT PART USED
HYMENOPTERA		**25**	**78 +**		**9**	**FLOWER BUDS,**
Cynipoidea:	(C) Cynipidae (? a few spp)			?	**(most on**	**LEAVES, STEMS,**
Cynipidae (C)	(Tor) Megastigmus (some spp)			Eucalyptus, Acacia	**Eucalyptus)**	
Chalcidoidea:	(Tor) Xenostigmus (3 spp)			Hakea, Eucalyptus		
Torymidae (Tor)	(A) Eufroggattisca (1 sp)			Ficus		
Agaonidae (A)	(A) Acophila (1 sp)			Ficus		
Pteromalidae (P)	(A) Epichrysomalla (1 spp)			Ficus		
Tanaostigmatidae (Ta)	(A) Herodotia (2 spp)			Ficus		
Eulophidae (Eul)	(A) Camarothorax (1 sp)			Ficus		
	(A) Otitesella (2 spp)			Ficus		
	(A) Walkerella (1 sp)			Ficus		
	(A) Micranisa (2 spp)			Ficus		
	(A) Grandiana (1 sp)			Ficus		
	(A) Pleistodontes (5 spp)			Ficus		
	(A) Ceratosolen (4 spp)			Ficus		
	(P) Trichilogaster (10 spp)			Acacia		
	(P) Encytrocephalus (10 spp)			Brachychiton, Acacia, Eucalyptus		
	(P) Coelocyba (5 spp)			Eucalyptus, Acacia		
	(P) Terobiella (3 spp)			Eucalyptus		
	(P) Nambouria (1 sp)			Eucalyptus		
	(P) Amerostenus (8 spp)			Eucalyptus		
	(P) Cybopella (3 spp)			Eucalyptus		
	(Ta) Tanaostigmodes (7 spp)			Leptospermum, Fabaceae		
	(Eul) Ophelimus (many spp)			Eucalyptus		
	(Eul) Quadrastichodella (6 spp)			Eucalyptus		
	(Eul) Pseudiglyphus (1 sp)			Eucalyptus		

Appendix 1 (cont.)

INSECT GROUP	KNOWN INSECT GENERA AND SPECIES	TOTAL GALLING INSECT GENERA KNOWN	TOTAL GALLING INSECT SPECIES KNOWN	HOST PLANTS	TOTAL HOST GENERA KNOWN	MOST COMMON PLANT PART USED
THYSANOPTERA		**11**	**25**		**9**	**LEAVES**
Phlaeothripidae	Teucothrips (2 + spp)			Melaleuca, Callistemon		**or PHYLLODES**
	Oncothrips (2 spp)			Acacia		
	Onychothrips (3 spp)			Acacia, Hakea (?)		
	Eugynothrips (1 sp)			Smilax	**(most on**	
	Thaumatothrips (1 sp)			Casuarina	**Geijera;**	
	Kladothrips (4 spp)			Acacia	**none on**	
	Moultonides (1 spp)			Geijera	**Eucalyptus)**	
	Chleothrips (2 spp)			Geijera		
	Sacothrips (7 spp)			Geijera		
	Neocecidothrips (1 sp)			Bursaria		
	Gynaikothrips (1 sp)			Ficus		
DIPTERA		**9**	**? many**		**10**	**(C) LEAVES**
Cecidomyiidae (C)	(C) Cecidomyia (? spp)			(C) Acacia, Melaleuca,		**(T) STEMS**
Tephritoidea:	(C) Lestremyia (? spp)			Callistemon, Eucalyptus,		**(A) LEAVES**
Tephritidae (T)	(C) Epidosis (? spp)			Leptospermum and etc.		**(F) FLOWERBUD**
Opomyzoidea:	(C) Diplosis (? spp)					
Agromyzidae (A)	(C) Miastor (? spp)					
Fergusoninidae (F)	(C) Campylomyza (? spp)					
	(T) Chrysotrypanea & 3 n. gen. (6 spp)			Asteraceae (3 genera), Goodenia		
	(A) Phytobia (2 spp)			Pittosporum		
	(F) Fergusonina (many spp)			Eucalyptus and other Myrtaceae		
HEMIPTERA		**6**	**at least 20**		**3**	**LEAVES**
Psylloidea:	(P) Glycaspis (? some spp)			Eucalyptus	**(most on**	
Psyllidae (P)	(P) Synglycaspis (15 spp)			Eucalyptus	**Eucalyptus)**	
Calophyidae (C)	(P) Austropsylla (3 spp)			Eucalyptus		
Triozidae (T)	(C) Cecidopsylla (2 spp)			Geijera and Banksia		
	(T) Trioza (a few spp)			many (incl. Eucalyptus)		
	(T) Schedotrioza (a few spp)			Eucalyptus		

Appendix 1 (cont.)

INSECT GROUP	KNOWN INSECT GENERA AND SPECIES	TOTAL GALLING INSECT GENERA KNOWN	TOTAL GALLING INSECT SPECIES KNOWN	HOST PLANTS	TOTAL HOST GENERA	MOST COMMON PLANT PART
COLEOPTERA		**3**	**at least 4**		**3**	**STEMS**
Buprestoidea:	(B) Paracephala (1 sp)			Allocasuarina		**(some on roots)**
Buprestidae (B)	(B) Ethon (2 spp)			Pultenaea/Dillwynia		
Chrysomeloidea:	(C) ? Sagrinae genera (? spp)			?	**(none on**	
Chrysomelidae (C)					**Eucalyptus)**	
LEPIDOPTERA		**2**	**a few**		**? a few**	**STEMS**
Gelechioidea:	(C) Coleophora (1 sp)			Chenopodiaceae	**(none on**	
Coleophoridae(C)	(A) Alucita (? some spp)			Canthium	**Eucalyptus)**	
Alucitoidea						
Alucitidae (A)						

References:

Coccoidea: Fuller 1897, Froggatt 1923, 1933, Brimblecombe 1960, Mani 1964, Lambdin & Kosztarab 1973, Beardsley 1974a, 1974b, Gullan 1978, Lambdin & Kosztarab 1981, Gullan 1983, 1984b, Gullan & Jones 1989, Beardsley 1984.

Hymenoptera: Noble 1939a, 1939b, 1939c, 1940, 1941, Mani 1964, Boucek 1988, Naumann 1991.

Thysanoptera: Moulton 1927, Bagnall 1929, Mani 1964, Mound 1971a, 1971b, Ananthakrishnan 1978, New 1984, Ananthakrishnan & Raman 1989.

Diptera: Skuse 1888-1890, Froggatt 1923, Tillyard 1926, Currie 1937, Tonnoir 1937, Hering 1962, Bush 1966, New 1988.

Psylloidea: Froggatt 1900, 1901, 1903, Moore 1961, 1970, Hodkinson 1974, Taylor 1976, Moore 1983, Madden & Stone 1984, Morgan 1984, Taylor 1984, Taylor 1985,Taylor 1987, Moore 1988, Taylor 1990.

Coleoptera: Saunders 1847, Froggatt 1893, 1923, Lawrence and Britten 1991.

Lepidoptera: Nielsen and Common 1991.

Data also obtained from specimen vouchers at the Australian Museum, Sydney , NSW, and ANIC, Canberra, ACT.

Appendix 2 NUMBER OF GALL INSECT SPECIES COMPARED WITH NUMBER OF SPECIES IN PLANT GENUS

PLANT GENUS	SPECIES IN PLANT GENUS	GALL INSECT SPECIES KNOWN
Eucalyptus (Myrtaceae)*	700	134
Acacia (Mimosaceae)*	750	23
Ficus (Moraceae)	76	22
Geijera (Rutaceae)	8	11
Melaleuca (Myrtaceae)*	215	7
Bossiaea, Eutaxia, Daviesia, (Fabaceae)*	179	7
Hakea (Proteaceae)*	140	6
Allocasuarina (Casuarinaceae)	41	6
Leptospermum (Myrtaceae)*	77	5
Casuarina (Casuarinaceae)	14	3
Brachychiton (Sterculiaceae)	12	3
Helichrysum (Asteraceae)	110	2
Olearia (Asteraceae)	108	2
Banksia (Proteaceae)	72	2
Pittosporum (Pittosporaceae)	19	2
Nothofagus (Fagaceae)	3	2
Goodenia (Goodeniaceae)	140	1
Pultenia (Fabaceae)*	120	1
Callistemon (Myrtaceae)	35	1
Dillwynia (Fabaceae)*	24	1
Bursaria (Pittosporaceae)	19	1
Cassinia (Asteraceae)	17	1
Canthium (Rubiaceae)	10	1
Smilax (Smilacaceae)	8	1
Araucaria (Araucariaceae)	5	1

Gall insect species numbers from Appendix 1

Plant species numbers from Hnatiuk (1990) except those from Harden (1991) marked *

Appendix 3 EUCALYPT HOSTS OF PSYLLOIDEA

EUCALYPTUS SPECIES	CODE	PSYLLOIDEA
acmenoides Schau.	MAG:C	Synglycaspis amplificata Moore
agglomerata Maiden	MAHCG	Synglycaspis encystis Moore
amygdalina Labill.	MATEH	Synglycaspis cellula Moore, Unknown sp., Schedotrioza
		tasmaniensis (Froggatt), Trioza dobsoni
annulata Benth	SIDAK	Schedotrioza occidentalis sp.nov.
baxteri (Benth.) Maiden & Blakely ex J. Bl	MAHCA	Schedotrioza multitudinae (Maskell), S. serrata sp. nov.,
		S. orbiculata (Froggatt), ? Synglycaspis sp.
caleyi Maiden	SUV:K	Schedotrioza distorta sp. nov.
camaldulensis Dehnh.	SNEEP	Australopsylla marmorata (Froggatt)
capitellata Smith	MAHCF	Unknown sp., Synglycaspis bullata,
		Schedotrioza orbiculata (Froggatt)
cladocalyx F.Muell.	SIS:A	Australopsylla revoluta (Froggatt)
coccifera J.D. Hook	MATES	Synglycaspis brunosa Moore
conglomerata Maiden & Blakely	MAHEJ	Synglycaspis surculina
cosmophylla F. Muell.	SECGB	Schedotrioza apicobystra sp. nov.
crebra F. Muell.	SUP:S	Schedotrioza distorta sp. nov.
cylindriflora Maid. & Blakely	SIF:A	Schedotrioza occidentalis sp. nov.
decipiens Endl.	SIP:G	Schedotrioza occidentalis sp. nov.
dichromophloia F. Muell.	CAFEG	Synglycaspis belua Moore ?
diversifolia Bonpl.	MABAC	Synglycaspis morgani Moore, Austropsylla marmorata (Froggatt)
dives Schauer	MATEP	Synglycaspis bullata, (? Synglycaspis ecphymata)
fasciculosa F. Muell.	SUT:F	Australopsylla marmorata (Froggatt)
gomphocephala DC.	SICAA	Schedotrioza distorta sp. nov.
gracilis F. Muell.	SIX:A	Australopsylla revoluta (Froggatt)
haemastoma Smith	MATKA	Synglycaspis perthecata Moore
leptocalyx Blakely	SLI:F	Schedotrioza occidentalis sp. nov.
leucoxylon F. Muell.	SUX:C	Schedotrioza (distorta), S. near orbiculata, ? Synglycaspis sp.
macarthuri Dean & Maiden	SPIKC	Schedotrioza (apicobystra), Austropsylla revoluta (Froggatt)
macrorhyncha F. Muell. ex Benth.	MAHAC	Synglycaspis inclusa Moore
melliodora Cunn. ex Schauer	SUX:A	Australopsylla revoluta (Froggatt)

Appendix 3 (cont.)

EUCALYPT SPECIES	CODE	PSYLLOIDEA
microcarpa (Maiden) Maiden	SUL:DB	Schedotrioza apicobystra sp. nov., S. distorta sp.nov.
muelleriana Howitt	MAHAA	Schedotrioza multitudinae (Maskell)
nesophila Blakely	CAFUL	Unknown sp.
nitida J.D. Hook.	MATEJ	Synglycaspis munita Moore, S. occulta Moore
obliqua L'Her.	MAKAA	? sp., Schedotrioza marginata Taylor, S. orbiculata (Froggatt),
		S. eucalypti (Froggatt), S. multitudinae (Maskell),
		? Synglycaspis sp.
odorata Behr in D.F.L. von Schlechtendal	SUNEB	Schedotrioza orbiculata (Froggatt)
oleosa F. Muell. ex Miq.	SIT:C	Schedotrioza cornuta sp.nov.
pauciflora Sieber ex Sprengel	MAKHA	Synglycaspis belua Moore, Australopsylla carinata (Froggatt),
		+?
pilularis Smith	MAIAAA	Synglycaspis cyta Moore
piperita Smith	MATHA	Synglycaspis cyrtoma Moore, Schedotrioza serrata sp. nov.
platypus Hook.	SIDCB	Schedotrioza occidentalis sp. nov.
pulchella Desf.	MATEG	Synglycaspis longaeva Moore, Unknown sp.
rossii R. Baker & H.G. Smith	MATKF	Synglycaspis immaceria Moore
sideroxylon Cunn. ex Woolls	SUX:I	Schedotrioza distorta sp. nov.
sieberi L. Johnson	MAKED	(? euc) Synglycaspis obvelata Moore,
		Schedotrioza eucalypti (Froggatt)
socialis F. Muell. ex Miq.	SIT:L	Schedotrioza cornuta sp. nov.
sphaerocarpa L. Johnson & Blaxell	MAIBC	Unknown sp.
stellulata Sieber ex DC.	MAKMA	Schedotrioza marginata Taylor
stricta Sieber ex Sprengel	MAKIG	Synglycaspis constricta
torquata Leuhm.	SLI:M	Schedotrioza distorta sp. nov.
umbra R. Baker	MAG:A	Synglycaspis inclusa Moore
wandoo Blakely	SIGQQ	Unknown spp.

Eucalyptus species codes (classification codes) from Gill, Belbin and Chippendale (1985)
Psylloidea data sources: Froggatt (1900), Madden and Stone (1984), Morgan (1984), Moore (1988),
Taylor (1990) (Schedotrioza)

Appendix 4 EUCALYPT HOSTS OF COCCOIDEA (excluding Apiomorpha)

EUCALYPTUS SPECIES	CODE	COCCOIDEA (except Apiomorpha spp.)
aromaphloia Pryor & J.H. Willis	SPECA	Opisthoscelis sp.
behriana F. Muell.	SUDGA	Maskellia globosa Fuller, Opisthoscelis fibularis
bleeseri Blakely	CAFEC	Cystococcus sp. nov.
camaldulensis Dehnh.	SNEEP	Sphaerococcopsis simplicior (Maskell), ?sp., Lachnodius eucalypti Froggatt
camaldulensis var. obtusa Blakely	SNEEPE	Opisthoscelis subrotunda Schrader
cephalocarpa Blakely	SPINUC	Sphaerococcopsis sp., Opisthoscelis sp.
dichromophloia F. Muell.	CAFEG	Cystococcus pomiformis Froggatt
dumosa Cunn. ex Oxley	SLE:G	Floracoccus elevans Maskell
fasciculosa F. Muell.	SUT:F	Maskellia globosa, Lachnodius sp., Opisthoscelis convexa
foecunda Schau.	SIZ:B	Maskellia globosa
froggattii Blakely	SUNEF	Maskellia globosa
gomphocephala DC.	SICAA	Maskellia globosa
goniocalyx F. Muell. ex Miq.	SPIFB	Opisthoscelis mammularis Froggatt
gracilis F. Muell.	SIX:A	Sphaerococcopsis umbilicus, Maskellia globosa
gummifera (Sol. ex Gaertn.) Hochr.	CAFUF	Ascelis sp.
incrassata Labill.	SLOAB	Maskellia globosa, Opisthoscelis conica Fuller
largiflorens F. Muell.	SUDEC	Maskellia globosa
leucoxylon F. Muell.	SUX:C	Maskellia globosa
macrocarpa Hook.	SIVEE	Opisthoscelis fibularis
melliodora Cunn. ex Schauer	SUX:A	Sphaerococcopsis platynotum, Maskellia globosa, Opisthoscelis maskelli Froggatt
microcarpa (Maiden) Maiden	SUL:DB	Sphaerococcopsis umbilicus, Opisthoscelis convexa
miniata A. Cunn. ex Schau.	EFC:A	Cystococcus sp. nov.
odorata Behr DFL von Schlechtendal	SUNEB	Opisthoscelis sp.
ovata Labill.	SPEAB	Opisthoscelis sp.
polyanthemos Schauer	SUT:D	Maskellia globosa, Opisthoscelis maskelli, O. globosa, O. fibularis
porosa F. Muell. ex Miq.	SUNCC	Opisthoscelis sp.
resinifera Smith	SECCC	Opisthoscelis subrotunda
sideroxylon Cunn. ex Woolls	SUX:I	Maskellia globosa, Opisthoscelis maskelli
terminalis F. Muell.	CAFEP	Cystococcus pomiformis
viminalis Labill.	SPIKK	Sphaerococcopsis inflatipes (Maskell), S. simplicior, Opisthoscelis mammularis
wandoo Blakely	SIGQQ	Maskellia globosa, Opisthoscelis conica

Eucalyptus species codes (classification codes) from Gill, Belbin and Chippendale (1985)

Coccoidea data sources: Beardsley 1974a, 1974b, voucher specimens ANIC, Canberra

Appendix 5 EUCALYPT HOSTS OF DIPTERA

EUCALYPTUS SPECIES	CODE	DIPTERA
amygdalina Labill.	MATEH	Fergusonina carteri Tonnoir
blakelyi Maiden	SNEEF	Fergusonina tillyardii Tonnoir
bridgesiana R.T. Baker	SPIDC	Fergusonina carteri Tonnoir + sp7
camaldulensis Dehnh.	SNEEP	Fergusonina tillyardii Tonnoir
crebra F. Muell.	SUP:S	Fergusonina brimblecombei Tonnoir
gomphocephala DC.	SICAA	Fergusonina newmani Tonnoir
gummifera (Sol. ex Gaertn.) Hochr.	CAFUF	Diplosis parilis sp.nov.
haemastoma Smith	MATKA	Diplosis eucalypti sp. nov.
macrorhyncha F. Muell. ex Benth.	MAHAC	Fergusonina curreie Tonnoir, F. nicholsoni Tonnoir, F. 2spp
maculata Hook.	CCC:B	Fergusonina eucalypti Malloch, F. 3spp
mannifera subsp. maculosa (R. Baker) L. Johnson	SPECHD	Fergusonina 2spp
melanophloia F. Muell.	SUP:V	Fergusonina brimblecombei Tonnoir
melliodora Cunn. ex Schauer	SUX:A	Fergusonina evansi Tonnoir, F. sp.
moluccana Roxb.	SUL:B	Fergusonina brimblecombei Tonnoir
odorata Behr in D.F.L. von Schlechtendal	SUNEB	Fergusonina brimblecombei Tonnoir
pauciflora Sieber ex Sprengel	MAKHA	Fergusonina 2spp
polyanthemos Schauer	SUT:D	Fergusonina greavesii Currie
rudis Endl.	SNEER	Fergusonina lockharti Tonnoir
sideroxylon Cunn. ex Woolls	SUX:I	Fergusonina 1sp
tereticornis Smith	SNEEB	Fergusonina tillyardii Tonnoir

Eucalyptus species codes (classification codes) from Gill, Belbin and Chippendale (1985)
Diptera data sources: Skuse 1888-1890 (Diplosis), Currie (1937) Tonnoir (1937) (Fergusoninae)

Appendix 6 EUCALYPT HOSTS OF HYMENOPTERA

EUCALYPTUS SPECIES	CODE	HYMENOPTERA
bridgesiana R.T. Baker	SPIDC	Terobiella flavifrons Ashmead
camaldulensis Dehnh.	SNEEP	Nambouria ramulorum sp. n.
globulus Labill.	SPIFL	Ophelimus eucalypti (Gahan) comb.n.
leucoxylon F. Muell.	SUX:C	Terobiella nigriceps (Ashmead)
macrorhyncha F. Muell. ex Benth.	MAHAC	Megastigmus quinquesetae (Girault)
miniata A. Cunn. ex Schau.	EFC:A	Megastigmus hilli Dodd
obliqua L'Her.	MAKAA	Megastigmus ater (Girault) comb. n., Amerostenus varidentatus Girault,
		Terobiella flavifrons Ashmead
robusta Smith	SECAF	Terobiella sp
stellulata Sieber ex DC.	MAKMA	Cybopella eucalypti sp. n., Pseudiglyphus grotiusi Girault
tereticornis Smith	SNEEB	Quadrastichodella nova Girault

Eucalyptus species codes (classification codes) from Gill, Belbin and Chippendale (1985)

Hymenoptera data source Boucek (1988)

Appendix 7 GALL SPECIES ON EUCALYPT SPECIES

CODE = Eucalypt classification from Gill, Belbin and Chippendale (1985)
1st code letter = subgenus
C = Corymbia, E = Eudesmia, M = Monocalyptus, S = Symphyomyrtus
Data for gall groups from Appendices 3, 4, 5, 6 and 9

EUCALYPT SPECIES	CODE	PSYLLOIDEA	COCCOIDEA	DIPTERA	HYMENOPTERA	TOTAL GALL SPECIES
bleeseri Blakely	CAFEC		1			1
terminalis F. Muell.	CAFEP		1			1
intermedia R. Baker	CAFID		1			1
nesophila Blakely	CAFUL	1				1
eudesmioides F. Muell. sensu lato	EAAAE		1			1
gittinsii Brooker & Blaxell	EAAAE		1			1
patens Benth.	MABBA		1			1
todtiana F. Muell.	MABBB		1			1
muelleriana Howitt	MAHAA	1				1
agglomerata	MAHCG	1				1
nigra R. Baker	MAHEB		1			1
planchoniana F. Muell.	MAIBB		1			1
sphaerocarpa L. Johnson & Blaxell	MAIBC	1				1
delegatensis R. Baker	MAKBE		1			1
luehmanniana F. Muell.	MAKDB		1			1
consideniana Maiden	MAKEA		1			1
stricta Sieber ex Sprengel	MAKIG	1				1
elata Dehnh.	MATEN		1			1
coccifera J.D. Hook	MATES	1				1
andrewsii Maiden	MATHD		1			1
rossii R. Baker & H.G. Smith	MATKF	1				1
diversicolor F. Muell.	SEB:A		1			1
deanei Maiden	SECAA		1			1
grandis W. Hill ex Maiden	SECAB		1			1

Appendix 7 (cont.)

EUCALYPT SPECIES	CODE	PSYLLOIDEA	COCCOIDEA	DIPTERA	HYMENOPTERA	TOTAL GALL SPECIES
propinqua Deane et Maiden	SECEA		1			1
occidentalis Endl.	SIDAA		1			1
annulata Benth	SIDAK	1				1
platypus Hook.	SIDCB	1				1
spathulata Hook.	SIDCD		1			1
cylindriflora Maid. & Blakely	SIF:A	1				1
redunca Schauer	SIGAC		1			1
loxophleba Benth.	SIN:A		1			1
falcata Turcz. var. ecostata Maiden	SIP:E		1			1
cneorifolia DC.	SIP:K		1			1
cladocalyx F.Muell.	SIS:A	1				1
transcontinentalis Maiden	SIT:K		1			1
flocktoniae (Maiden) Maiden	SIT:T		1			1
salmonophloia F. Muell.	SIV:A		1			1
burracoppinensis Maiden & Blakely	SIVEJ		1			1
uncinata Turcz.	SIZ:E		1			1
anceps (Maiden) Blakely	SLE:IB		1			1
clelandii (Maiden) Maiden	SLE:M		1			1
torquata Leuhm.	SLI:M	1				1
angulosa Schau.	SLOAB		1			1
seeana Maiden	SNECA		1			1
amplifolia Naudin	SNEEA		1			1
rudis Endl.	SNEER			1		1
mannifera Mudie	SPECH		1			1
kitsoniana Maiden	SPIAC		1			1
cypellocarpa L. Johnson	SPIFE		1			1
gunnii J.D. Hook.	SPINI		1			1
cinerea F. Muell. ex Benth.	SPINU		1			1
froggattii	SUNEF		1			1

Appendix 7 (cont.)						TOTAL GALL
EUCALYPT SPECIES	CODE	PSYLLOIDEA	COCCOIDEA	DIPTERA	HYMENOPTERA	SPECIES
caleyi Maiden	SUV:K	1				1
leucoxylon subsp. pruinosa (F. Muell. ex Miq.) Boland	SUX:CC		1			1
diversifolia Bonpl.	MABAC	2				2
eugenioides Sieber ex Sprengel	MAHEA		2			2
oblonga DC.	MAHEL		2			2
campaspe S.Moore	SIK:C		2			2
longicornis (F. Muell.) F. Muell. ex Maiden	SIT:A		2			2
kochii Maiden & Blakely	SIT:E		2			2
leptopoda Benth.	SIVAA		2			2
macrocarpa Hook.	SIVEE		2			2
calycogona Turcz.	SIX:D		2			2
nicholii Maiden & Blakely	SPECE		2			2
mannifera subsp. maculosa (R. Baker) L. Johnson	SPECHD			2		2
macarthuri Dean & Maiden	SPIKC	2				2
porosa F. Muell. ex Miq.	SUNCC		2			2
polybractea R. Baker	SUNED		2			2
microcorys F. Muell.	SWA:A		2			2
gummifera (Sol. ex Gaertn.) Hochr.	CAFUF		2	1		3
miniata A. Cunn. ex Schau.	EFC:A		2		1	3
umbra R. Baker	MAG:A	1	2			3
conglomerata Maiden & Blakely	MAHEJ	1	2			3
stellulata Sieber ex DC.	MAKMA	1			2	3
pulchella Desf.	MATEG	2	1			3
racemosa Cav.	MATKE		3			3
resinifera Smith	SECCC		3			3
punctata DC.	SECED		3			3
cosmophylla F. Muell.	SECGB	1	2			3
socialis F. Muell. ex Miq.	SIT:L	1	2			3
blakelyi Maiden	SNEEF		2	1		3

Appendix 7 (cont.)

EUCALYPT SPECIES	CODE	PSYLLOIDEA	COCCOIDEA	DIPTERA	HYMENOPTERA	TOTAL GALL SPECIES
rubida Deane & Maiden	SPINF		3			3
microtheca F. Muell.	SUADF		3			3
populnea F. Muell.	SUDEA		3			3
maculata Hook.	CCC:B			4		4
camfieldii Maiden	MAHCE		4			4
regnans F. Muell.	MAKCA		4			4
nitida J.D. Hook.	MATEJ	2	2			4
dives Schauer	MATEP	1	3			4
saligna Smith	SECAC		4			4
robusta Smith	SECAF		3		1	4
gomphocephala DC.	SICAA	1	2	1		4
decipiens Endl.	SIP:G	1	3			4
foecunda Schau.	SIZ:B		4			4
leptocalyx Blakely	SLI:F	1	3			4
dealbata Cunn. ex Schauer	SNEEJ		4			4
ovata Labill.	SPEAB		4			4
aromaphloia Pryor & J.H. Willis	SPECA		4			4
globulus Labill.	SPIFL		3		1	4
odorata Behr in D.F.L. von Schlechtendal	SUNEB	1	2	1		4
melanophloia F. Muell.	SUP:V		3	1		4
paniculata Smith	SUV:D		4			4
acmenoides Schau.	MAG:C	1	4			5
globoidea Blakely	MAHEF		5			5
pilularis Smith	MAIAAA	1	4			5
sieberi L. Johnson	MAKED	2	3			5
radiata Sieb. ex DC.	MATEL		5			5
bridgesiana R.T. Baker	SPIDC		2	2	1	5
cephalocarpa Blakely	SPINUC		5			5
drepanophylla F. Muell. ex Benth.	SUP:F		5			5

Appendix 7 (cont.)						TOTAL GALL
EUCALYPT SPECIES	CODE	PSYLLOIDEA	COCCOIDEA	DIPTERA	HYMENOPTERA	SPECIES
capitellata Smith	MAHCF	3	3			6
amygdalina Labill.	MATEH	3	2	1		6
oleosa F. Muell. ex Miq.	SIT:C	1	5			6
viminalis Labill.	SPIKK		6			6
behriana F. Muell.	SUDGA		6			6
moluccana Roxb.	SUL:B		5	1		6
baxteri (Benth.) Maiden & Blakely ex J. Black	MAHCA	4	3			7
pauciflora Sieber ex Sprengel	MAKHA	3	2	2		7
piperita Smith	MATHA	2	5			7
wandoo Blakely	SIGQQ	1	6			7
dumosa Cunn. ex Oxley	SLE:G		7			7
goniocalyx F. Muell. ex Miq.	SPIFB		7			7
microcarpa (Maiden) Maiden	SUL:DB	2	5			7
siderophloia Benth.	SUP:I		7			7
fasciculosa F. Muell.	SUT:F	2	5			7
sideroxylon Cunn. ex Woolls	SUX:I	1	5	1		7
haemastoma Smith	MATKA	1	5	2		8
gracilis F. Muell.	SIX:A	1	7			8
incrassata Labill.	SLOAB		8			8
largiflorens F. Muell.	SUDEC		8			8
pilligaensis Maiden	SUL:F		8			8
leucoxylon F. Muell.	SUX:C	3	4		1	8
macrorhyncha F. Muell. ex Benth.	MAHAC	1	4	4	1	10
tereticornis Smith	SNEEB		8	1	1	10
polyanthemos Schauer	SUT:D		9	1		10
melliodora Cunn. ex Schauer	SUX:A	1	7	2		10
camaldulensis Dehnh.	SNEEP		10		1	11
crebra F. Muell.	SUP:S	1	10	1		12
obliqua L'Her.	MAKAA	6	5		3	14

Appendix 8 NUMBER OF GALL SPECIES COMPARED WITH EUCALYPT SUBGENUS AND GEOGRAPHIC RANGE

*Symphyomyrtus = 1
Monocalyptus = 2
Corymbia = 3
Eudesmia = 4
Blakella = 5
all others = 6

**No. of 1 x 1.5 degree map grids occupied

EUCALYPT SUBGENUS*	EUCALYPT RANGE SIZE**	TOTAL GALLS RECORDED
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	1	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	1
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
1	2	0
1	2	2
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	2	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	3
1	3	0
1	3	0
1	3	0
1	3	0
1	3	1
1	3	0
1	3	0
1	3	0
1	3	2
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	0
1	3	1
1	3	0
1	3	0
1	3	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	4	0
1	5	0
1	5	2
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	4
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	0
1	5	2
1	5	0
1	5	0
1	5	0
1	5	0
1	6	0
1	6	0
1	6	0

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
1	6	0
1	6	0
1	6	0
1	6	1
1	6	0
1	6	0
1	6	0
1	6	1
1	6	1
1	6	0
1	6	2
1	6	0
1	6	0
1	6	0
1	6	0
1	6	0
1	6	0
1	7	0
1	7	1
1	7	0
1	7	0
1	7	5
1	7	1
1	7	0
1	7	1
1	7	0
1	7	0
1	7	0
1	7	0
1	7	1
1	7	0
1	7	0
1	7	0
1	7	0
1	7	0
1	7	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	8	0
1	9	1

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
1	9	0
1	9	0
1	9	0
1	9	0
1	9	0
1	9	0
1	9	7
1	9	0
1	9	0
1	9	0
1	9	0
1	9	3
1	9	0
1	9	0
1	9	1
1	9	0
1	9	0
1	10	0
1	10	1
1	10	1
1	10	0
1	10	0
1	10	2
1	10	0
1	10	0
1	10	0
1	10	1
1	10	1
1	10	0
1	11	0
1	11	0
1	11	1
1	11	0
1	11	0
1	11	4
1	11	1
1	11	0
1	11	0
1	11	0
1	11	0
1	11	0
1	12	4
1	12	0
1	12	0
1	12	0
1	12	0
1	12	0
1	12	0
1	12	0
1	13	1
1	13	0

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
1	13	4
1	13	0
1	13	0
1	13	0
1	13	1
1	13	0
1	14	0
1	14	4
1	14	4
1	14	0
1	14	4
1	14	0
1	14	8
1	14	0
1	14	0
1	14	1
1	14	0
1	15	1
1	15	0
1	15	0
1	15	0
1	15	2
1	15	0
1	15	4
1	16	0
1	16	0
1	16	1
1	16	6
1	16	1
1	16	0
1	17	6
1	17	0
1	17	1
1	17	0
1	17	0
1	17	8
1	17	2
1	17	0
1	17	0
1	17	0
1	17	1
1	17	7
1	18	0
1	18	1
1	18	1
1	18	0
1	19	0
1	19	0
1	19	0
1	20	0
1	20	2

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
1	20	0
1	21	0
1	21	1
1	21	0
1	21	0
1	21	3
1	21	0
1	22	1
1	22	0
1	22	0
1	22	0
1	23	0
1	23	3
1	23	0
1	23	1
1	23	0
1	23	4
1	24	2
1	24	10
1	24	0
1	25	5
1	25	0
1	26	0
1	28	0
1	28	0
1	28	2
1	29	7
1	29	7
1	29	0
1	29	0
1	30	1
1	31	4
1	31	1
1	32	3
1	32	7
1	33	0
1	34	0
1	34	4
1	36	1
1	38	0
1	39	2
1	40	7
1	40	0
1	41	0
1	43	5
1	43	7
1	47	8
1	47	6
1	48	0
1	49	0
1	51	10

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
1	52	4
1	53	0
1	54	0
1	55	8
1	59	12
1	63	3
1	65	10
1	67	4
1	67	8
1	72	6
1	89	3
1	176	3
1	245	11
2	1	0
2	1	0
2	1	0
2	1	0
2	1	0
2	1	3
2	1	0
2	1	0
2	1	0
2	1	0
2	1	0
2	1	0
2	1	0
2	1	0
2	1	0
2	1	0
2	1	0
2	1	1
2	1	0
2	1	0
2	2	0
2	2	0
2	2	0
2	2	0
2	2	4
2	2	0
2	2	0
2	2	0
2	2	0
2	2	0
2	2	0
2	2	0
2	2	0
2	3	0
2	3	0
2	3	0
2	3	0
2	3	0

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
2	3	1
2	3	0
2	3	0
2	3	1
2	3	0
2	3	0
2	4	0
2	4	0
2	4	0
2	4	0
2	4	0
2	4	0
2	4	0
2	4	0
2	4	0
2	4	0
2	4	0
2	4	3
2	4	0
2	4	0
2	5	6
2	5	8
2	5	0
2	5	0
2	5	0
2	6	0
2	6	0
2	6	1
2	6	0
2	6	3
2	6	1
2	6	0
2	7	0
2	7	0
2	7	1
2	7	1
2	7	0
2	7	1
2	8	0
2	8	0
2	8	0
2	8	0
2	8	0
2	8	7
2	9	6
2	11	1
2	11	1
2	11	1
2	11	2
2	11	4
2	12	1

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
2	12	1
2	12	0
2	12	0
2	12	5
2	12	0
2	12	0
2	13	1
2	13	0
2	14	0
2	16	1
2	17	4
2	17	5
2	18	7
2	18	0
2	19	2
2	20	4
2	20	5
2	23	5
2	23	3
2	25	0
2	26	3
2	29	2
2	34	10
2	34	7
2	35	5
2	41	14
3	3	0
3	4	0
3	4	0
3	4	0
3	4	0
3	4	0
3	4	0
3	4	0
3	5	0
3	6	0
3	7	0
3	7	0
3	8	0
3	9	0
3	10	0
3	10	0
3	11	0
3	13	0
3	15	0
3	15	0
3	16	1
3	16	0
3	19	3
3	19	1
3	20	0

Appendix 8 (cont.)

EUCALYPT SUBGENUS	EUCALYPT RANGE SIZE	TOTAL GALLS RECORDED
3	22	0
3	25	0
3	26	0
3	27	0
3	28	4
3	28	0
3	32	1
3	35	0
3	38	0
3	78	0
3	111	0
3	125	1
3	133	1
4	3	0
4	4	0
4	4	1
4	4	0
4	6	0
4	8	0
4	12	0
4	12	1
4	12	0
4	13	0
4	19	0
4	22	0
4	23	0
4	46	0
4	51	0
4	53	3
5	4	0
5	8	0
5	13	0
5	19	0
5	31	0
5	34	0
5	53	0
5	55	0
5	121	0
6	2	0
6	3	0
6	6	0
6	7	0
6	7	0
6	14	0
6	20	0

Eucalypt subgenus and range size from Gill, Belbin and Chippendale (1985) (no information available for approximately 149 eucalypt species)
Total galls from Appendix 7

Appendix 9 EUCALYPT HOSTS OF APIOMORPHA

Apiomorpha species names pg 61, Appendix 10 Eucalyptus species names. Y = yes eucalypt spp.has Apiomorpha spp.

EUCALYPT																	APIOMORPHA SPECIES																								
CODE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	TOTAL
CAFID																			Y																						1
CAFUF																									Y?																1
EAAAEA		Y																																							1
EAAAEB		Y																																							1
EFC:A																Y																									1
MABBA																	Y																								1
MABBB																	Y																								1
MAHEB				Y																																					1
MAIBB																			Y																						1
MAKBE																								Y																	1
MAKDB			Y																																						1
MAKEA			Y																																						1
MATEG			Y																																						1
MATEN																								Y																	1
MATHD																				Y																					1
SEB:A																																									1
SECAA																																			Y						1
SECAB					Y																																				1
SECEA																																							Y		1
SICAA															Y																										1
SIDAA				Y																																					1
SIDCD																															Y										1
SIGAC																																Y?									1
SIN:A															Y																										1
SIP:E	Y																																								1
SIP:K																																									1
SIT:K																		Y																							1
SIT:T	Y																																								1
SIU:A																																								Y	1
SIVEE																															Y										1

Appendix 9 (cont.)

EUCALYPT CODE	APIOMORPHA SPECIES 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	TOTAL
SIVEJ												Y																													1
SIZ:E																																									1
SLE:IB															Y																										1
SLE:M															Y																										1
SLOAB															Y																										1
SNECA					Y																																				1
SNEEA																																							Y		1
SPECH						Y																																			1
SPIAC						Y																																			1
SPIFE																							Y																		1
SPINI																																			Y						1
SPINU						Y																																			1
SUNCC														Y																											1
SUNEB																														Y											1
SUX:CC														Y																											1
MAG:A			Y																Y																						2
MAHEA				Y																Y																					2
MAHEJ				Y																	Y																				2
MAHEL																				Y	Y																				2
MAKHA																								Y	Y?																2
MATEH			Y																						Y																2
MATEJ																																			Y	Y					2
SECCC					Y																																		Y		2
SECGB							Y?																	Y																	2
SIK:C															Y																	Y									2
SIT:A															Y															Y											2
SIT:E																							Y							Y											2
SIT:L	Y																																							Y	2
SIVAA	Y											Y																													2
SIX:D								Y																							Y										2
SNEEF							Y																																Y		2

Appendix 9 (cont.)

EUCALYPT																			APIOMORPHA SPECIES																						
CODE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	TOTAL
SPECE			Y																																Y						2
SPIDC						Y																													Y						2
SUL:DB							Y		Y				Y																												2
SUNED							Y							Y?																											2
SUT:F														Y																	Y										2
SWA:A					Y									Y																											2
MAHCA																				Y				Y	Y																3
MAHCF																				Y					Y	Y															3
MAKED			Y																Y						Y?																3
MATEP																				Y				Y											Y						3
MATKE			Y	Y															Y																						3
SECAF			Y		Y																														Y						3
SECED																		Y																	Y				Y		3
SIP:G																		Y																						Y	3
SIZ:B					Y																																			Y	3
SLI:F	Y														Y															Y											3
SNEEPE											Y			Y																							Y				3
SPEAB						Y																	Y												Y						3
SPECA						Y																													Y	Y					3
SPIFL						Y																	Y												Y						3
SPIKK						Y																													Y				Y		3
SPINF						Y																			Y?										Y						3
SPINUC						Y																		Y											Y						3
SUADF									Y?					Y	Y																										3
SUDEA					Y				Y					Y?																											3
SUP:V				Y	Y									Y																											3
SUX:C							Y																								Y										3
SUX:I						Y?								Y																	Y										3
MAG:C			Y																Y			Y				Y															4
MAHAC																				Y				Y	Y											Y?					4
MAHCE			Y	Y															Y	Y																					4

Appendix 9 (cont.)

EUCALYPT	APIOMORPHA SPECIES																																								
CODE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	TOTAL
MAIAAA				Y															Y	Y					Y																4
MAKCA			Y																				Y	Y											Y						4
SECAC				Y	Y														Y																				Y		4
SIGQQ						Y									Y								Y									Y									4
SNEEJ							Y?				Y												Y											Y							4
SUDGA							Y							Y				Y															Y								4
SUV:D					Y				Y					Y?				Y																							4
SUX:A							Y							Y				Y													Y										4
MAHEF			Y	Y																Y	Y				Y																5
MAKAA				Y		Y														Y				Y											Y						5
MATEL			Y			Y														Y				Y											Y						5
MATHA			Y	Y	Y														Y						Y																5
MATKA			Y	Y			Y?												Y	Y																					5
SIT:C	Y				Y													Y												Y										Y	5
SIX:A					Y								Y	Y?																Y	Y										5
SUL:B							Y			Y			Y	Y?				Y																							5
SUP:F				Y					Y					Y?				Y										Y													5
SUT:D							Y							Y				Y		Y											Y										5
SLE:G	Y							Y							Y															Y	Y		Y								6
SLOAB								Y							Y			Y												Y			Y							Y	6
SPIFB						Y														Y			Y								Y				Y		Y				6
SNEEP											Y			Y									Y											Y	Y		Y		Y		7
SUDEC							Y						Y	Y?									Y								Y		Y		Y						7
SUP:I							Y		Y	Y				Y				Y					Y																Y		7
SNEEB			Y		Y						Y			Y?									Y											Y	Y?				Y		8
SUL:F			Y		Y					Y			Y	Y?													Y				Y							Y			8
SUP:S				Y	Y				Y	Y			Y	Y				Y								Y			Y										Y		10

Data sources for Apiomorpha species and host eucalypt species: Gullan (1984a), Gullan and Jones (1989)

Eucalypt codes from Gill, Belbin and Chippendale (1985)

Appendix 9 (cont.)

KEY:

	APIOMORPHA SPECIES		APIOMORPHA SPECIES
1	Apiomorpha malleeacola Gullan	30	A. calycina (Tepper)
2	A. pomaphora Gullan and Jones	31	A. urnalis (Tepper)
3	A. pileata (Schrader)	32	A. helmsii Fuller
4	A. duplex (Schrader)	33	A. densispinosa Gullan
5	A. munita (Schrader)	34	A. frenchii Froggatt
6	A. munita munita (Schrader)	35	A. conica (Froggatt)
7	A. munita tereticornuta Gullan	36	A. intermedia Gullan
8	A. munita malleensis Gullan	37	A. attenuata (Froggatt)
9	A. exculpa (Fuller)	38	A. amarooensis Brimblecombe
10	A. dipsaciformis (Froggatt)	39	A. pedunculata (Fuller)
11	A. baeuerleni (Froggatt)	40	A. regularis (Tepper)
12	A. tepperi Gullan		
13	A. withersi Froggatt		
14	A. ovicola (Schrader)		
15	A. ovicoloides (Tepper)		
16	A. hilli Froggatt		
17	A. maliformis Fuller		
18	A. strombylosa (Tepper)		
19	A. variabilis (Froggatt)		
20	A. minor Froggatt		
21	A. sessilis (Froggatt)		
22	A. annulata Froggatt		
23	A. karschi Rubsaamen		
24	A. spinifer Froggatt		
25	A. pharetrata (Schrader)		
26	A. rosaeformis (Froggatt)		
27	A. macqueeni Froggatt		
28	A. sloanei (Froggatt)		
29	A. longiloba Brimblecombe		

Appendix 10 EUCALYPT SPECIES NAMES ASSOCIATED WITH CODES IN APPENDIX 9

EUCALYPT SPECIES	CODE
intermedia R. Baker	CAFID
gummifera (Sol. ex Gaertn.) Hochr.	CAFUF
eudesmioides F. Muell. sensu lato	EAAAEA
gittinsii Brooker & Blaxell	EAAAEB
miniata A. Cunn. ex Schau.	EFC:A
patens Benth.	MABBA
todtiana F. Muell.	MABBB
nigra R. Baker	MAHEB
planchoniana F. Muell.	MAIBB
delegatensis R. Baker	MAKBE
luehmanniana F. Muell.	MAKDB
consideniana Maiden	MAKEA
pulchella Desf.	MATEG
elata Dehnh.	MATEN
andrewsii Maiden	MATHD
diversicolor F. Muell.	SEB:A
deanei Maiden	SECAA
grandis W. Hill ex Maiden	SECAB
propinqua Deane et Maiden	SECEA
gomphocephala DC.	SICAA
occidentalis Endl.	SIDAA
spathulata Hook.	SIDCD
redunca Schauer	SIGAC
loxophleba Benth.	SIN:A
falcata Turcz. var. ecostata Maiden	SIP:E
cneorifolia DC.	SIP:K
transcontinentalis Maiden	SIT:K
flocktoniae (Maiden) Maiden	SIT:T
salmonophloia F. Muell.	SIU:A
macrocarpa Hook.	SIVEE
burracoppinensis Maiden & Blakely	SIVEJ
uncinata Turcz.	SIZ:E
anceps (Maiden) Blakely	SLE:IB
clelandii (Maiden) Maiden	SLE:M
angulosa Schau.	SLOAB
seeana Maiden	SNECA
amplifolia Naudin	SNEEA
mannifera Mudie	SPECH
kitsoniana Maiden	SPIAC
cypellocarpa L. Johnson	SPIFE
gunnii J.D. Hook.	SPINI
cinerea F. Muell. ex Benth.	SPINU
porosa F. Muell. ex Miq.	SUNCC
odorata Behr in D.F.L. von Schlechtendal	SUNEB
leucoxylon subsp. pruinosa (F. Muell. ex Miq.) Boland	SUX:CC
umbra R. Baker	MAG:A
eugenioides Sieber ex Sprengel	MAHEA
conglomerata Maiden & Blakely	MAHEJ
oblonga DC.	MAHEL
pauciflora Sieber ex Sprengel	MAKHA
amygdalina Labill.	MATEH

Appendix 10 (cont.)

EUCALYPT SPECIES	CODE
nitida J.D. Hook.	MATEJ
resinifera Smith	SECCC
cosmophylla F. Muell.	SECGB
campaspe S. Moore	SIK:C
longicornis (F. Muell.) F. Muell. ex Maiden	SIT:A
kochii Maiden & Blakely	SIT:E
socialis F. Muell. ex Miq.	SIT:L
leptopoda Benth.	SIVAA
calycogona Turcz.	SIX:D
blakelyi Maiden	SNEEF
nicholii Maiden & Blakely	SPECE
bridgesiana R.T. Baker	SPIDC
microcarpa (Maiden) Maiden	SUL:DB
polybractea R. Baker	SUNED
fasciculosa F. Muell.	SUT:F
microcorys F. Muell.	SWA:A
baxteri (Benth.) Maiden & Blakely ex J. Black	MAHCA
capitellata Smith	MAHCF
sieberi L. Johnson	MAKED
dives Schauer	MATEP
racemosa Cav.	MATKE
robusta Smith	SECAF
punctata DC.	SECED
decipiens Endl.	SIP:G
foecunda Schau.	SIZ:B
leptocalyx Blakely	SLI:F
camaldulensis var. obtusa Blakely	SNEEPE
ovata Labill.	SPEAB
aromaphloia Pryor & J.H. Willis	SPECA
globulus Labill.	SPIFL
viminalis Labill.	SPIKK
rubida Deane & Maiden	SPINF
cephalocarpa Blakely	SPINUC
microtheca F. Muell.	SUADF
populnea F. Muell.	SUDEA
melanophloia F. Muell.	SUP:V
leucoxylon F. Muell.	SUX:C
sideroxylon Cunn. ex Woolls	SUX:I
acmenoides Schau.	MAG:C
macrorhyncha F. Muell. ex Benth.	MAHAC
camfieldii Maiden	MAHCE
pilularis Smith	MAIAAA
regnans F. Muell.	MAKCA
saligna Smith	SECAC
wandoo Blakely	SIGQQ
dealbata Cunn. ex Schauer	SNEEJ
behriana F. Muell.	SUDGA
paniculata Smith	SUV:D
melliodora Cunn. ex Schauer	SUX:A
globoidea Blakely	MAHEF
obliqua L'Her.	MAKAA
radiata Sieb. ex DC.	MATEL
piperita Smith	MATHA

Appendix 10 (cont.)

EUCALYPT SPECIES	CODE
haemastoma Smith	MATKA
oleosa F. Muell. ex Miq.	SIT:C
gracilis F. Muell.	SIX:A
moluccana Roxb.	SUL:B
drepanophylla F. Muell. ex Benth.	SUP:F
polyanthemos Schauer	SUT:D
dumosa Cunn. ex Oxley	SLE:G
incrassata Labill.	SLOAB
goniocalyx F. Muell. ex Miq.	SPIFB
camaldulensis Dehnh.	SNEEP
largiflorens F. Muell.	SUDEC
siderophloia Benth.	SUP:I
tereticornis Smith	SNEEB
pilligaensis Maiden	SUL:F
crebra F. Muell.	SUP:S

Eucalypt species names from Chippendale (1988)

CHAPTER 3

COMPARISON OF GALL-FORMING INSECT SPECIES DIVERSITY ON VEGETATION AT INFERTILE AND FERTILE SOIL SITES

3.1 Introduction

Studies by Fernandes and Price (1988, 1991) at sites in Arizona, USA, and Brazil, suggested that plants growing on infertile soils have higher numbers of gall-forming insect species than those growing on fertile soils. For example, the gall species richness in vegetation on depauperate sands along the Rio Negro, in northern Amazonia, Brazil, was three to four times higher than in adjacent rain forest.

Plants growing on infertile soils tend to retain their parts longer (Coley, Bryant and Chapin 1985, Escudero, del Arco, Sanz, and Ayala 1992), and perhaps abscise damaged parts less readily, than plants growing on fertile soils do. Most gall-forming insects are unable to move successfully to new plant sites once gall initiation has commenced. It seems likely that plants with long-lived parts (ie. plants on infertile soils) would be more favourable hosts for such insects and would acquire and retain, over evolutionary time scales, a greater number of gall insect species.

Similarly, the presence of secondary compounds may also be an advantage for gall-forming insects. Cornell (1983) and Taper and Case (1987) suggest that tannins (phenolic compounds), concentrated away from the gall insect in the outer wall of galls during gall formation, protect gall insects from attack by chewing herbivores, fungi and other micro organisms. Secondary compounds such as oils and phenols are often high in the tissues of plants growing on infertile soils (Janzen 1974, McKey, Waterman, Mbi, Gartlan and Struhsaker 1978).

As described in section 1.3, insect induced galls vary in complexity from simple, open deformations to complex, highly organized, enclosed structures. Complex galls may require more time to reach maturity than simple galls or may be occupied by the gall insect for longer periods than simple galls. Some support for this suggestion comes from life history studies of Australian psyllids (Morgan 1984). Psyllids with complex galls, such as the 'bubble' galls formed on leaves by *Glycaspis morgani* Moore, have annual generations.

Those with simple galls, like the leaf pit galls induced by *Trioza eugeniae* (Froggatt), are trivoltine to pentavoltine. Additional evidence comes from observations of Australian coccoid galls. Some complex gall-forming coccoids are known to inhabit their galls for at least two years (Gullan, 1984b).

The need for long lived plant parts and protection from herbivores and disease would be particularly important for gall-forming insect species with long lived, enclosed, complex galls. If these needs are met by the adaptations of plants to low soil fertility then it would be expected that the proportion of gall-forming insect species with complex gall morphologies would be higher on infertile than on fertile soil plants.

Longevity of plant parts and production of secondary plant chemicals are just two potential reasons why gall induction, especially of complex galls, might be more prevalent in vegetation growing on low nutrient soils than in vegetation on higher nutrient soils. Other factors might also be involved. Several factors might operate together. This study did not pretend to be able to identify the reasons behind patterns of gall diversity but simply aimed to test whether the species richness of gall-forming insects, and induction of the complex kind of gall, was higher in vegetation on infertile soils than on fertile soils.

3.2 Methods

Eight locations in National Parks or State Forests close to Sydney, ~34° S, 151° E, were chosen for this study (Fig. 3.1). At each location a 50 x 20m site was marked out. The total soil phosphorus at six sites was known from previous studies (Westoby, Rice and Howell 1990, French and Westoby 1992). At the remaining two sites total soil phosphorus was measured, as before, by taking five (20cm x 20cm) random samples of the top 20cm of soil, bulking the samples, and analysing them by standard methods (Lambert 1983). Total soil phosphorus was used as the best single indicator of soil fertility (Bowen 1981, Williams and Raupach 1983) as it is a limiting macronutrient, is not very soluble, and atmospheric inputs are small.

The eight sites were visited three times between May 1991 and April 1992. During each visit 200 plants < 50cm high and 100 plants > 50cm high were chosen randomly and searched for insect-induced galls. All plant growth forms present were included. Samples of

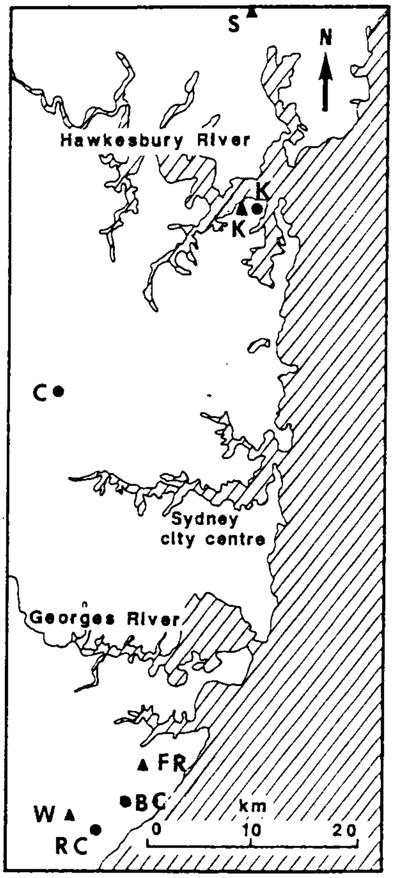


Figure 3.1 Map of the study area near Sydney, Australia.

Relatively fertile sites are marked with circles and relatively infertile sites with triangles. Sites RC = Red Cedar Creek (34^0 9' S, 151^0 2' E), BC = Bola Creek (34^0 7' S, 151^0 3' E), W = Waterfall (34^0 7' S, 151^0 0' E) and FR = Flat Rock Crossing (34^0 5' S, 151^0 5' E) were in Royal National Park. Other sites were in C = Cumberland State Forest (33^0 44' S, 151^0 1' E), K = Kuring gai Chase National Park (two sites, 33^0 34' S, 151^0 17' E and 33^0 36' S, 151^0 13' E) and S = Strickland State Forest (33^0 22' S, 151^0 18' E).

all insect stages obtained, their galls, and their host plant species were preserved in wet or dry reference collections, as appropriate. Lists of all the plant species at the sites were compiled.

Gall insects were keyed to species level when possible but the taxonomy for many groups is poorly known, some galls never contained the galling insect and some galls only ever contained very immature insects which could not be reared through to adults. Often the original gall-forming insect species could not be distinguished from inquiline or parasitoid species. For these reasons morphospecies (based on the external and internal morphology of the gall and the insects in it) was used in conjunction with gall species to estimate gall insect diversity. When the term 'gall species' is used in subsequent parts of this chapter 'gall morphospecies' is implied. Number of gall morphospecies is a relatively reliable estimate of species number because gall morphology is usually distinctive for each insect species (Cornell 1985, Taper and Case 1987, Birch, Brewer, and Rohfritsch 1992).

Gall species were grouped into two categories according to whether they had a complex or simple form. Galls in the complex category were enclosed, often woody, and without an exit hole or with a hole that was very small or blocked. Those classified as simple galls were deformations like leaf masses, rolls, or pits, in which the insect was only partly surrounded by gall tissue.

At the end of the collection period gall-forming insect species richness, numbers of complex and simple kinds of gall species, total number of plant species and number of galled plant species at each site were calculated from the accumulated species in the reference collections and species lists.

3.3 Results

Details of the plant species and gall species at each site are in Appendices 11 and 12 and are summarised in Table 3.1. The initial design was in terms of two groups of sites, infertile and fertile, but it became apparent that there was much variation between sites within each soil fertility group, both with regard to total soil phosphorus concentrations and with regard to galling. Thus results are reported as eight sites graphed against gradients of soil phosphorus concentration (log mg P/kg) as a measure of soil fertility.

Table 3.1 Site characteristics.

The number of myrtaceous tree species is included because this was the most gall prone plant group. All myrtaceous trees were *Eucalyptus spp.* except at the Strickland and Kuringai (fert.) sites where *Syncarpia glomulifera* was present.

Site	Total soil P (mg/kg)	Total gall species	Complex gall species	Total plant species	Galled plant species	Myrtaceous tree species
Strickland	65	29	21	42	15	3
Waterfall	100	23	20	87	12	3
Kuringai (infert.)	103	23	17	83	6	3
Flat Rock	110	17	14	89	10	4
Cumberland	216	7	4	70	3	0
Bola Creek	650	8	3	41	6	0
Kuringai (fert.)	786	10	6	86	1	1
Red Cedar	961	5	2	26	4	0

There were more total gall species on less fertile sites (Fig. 3.2). This pattern in total gall species came about, to a large extent, because there were far more gall species per plant

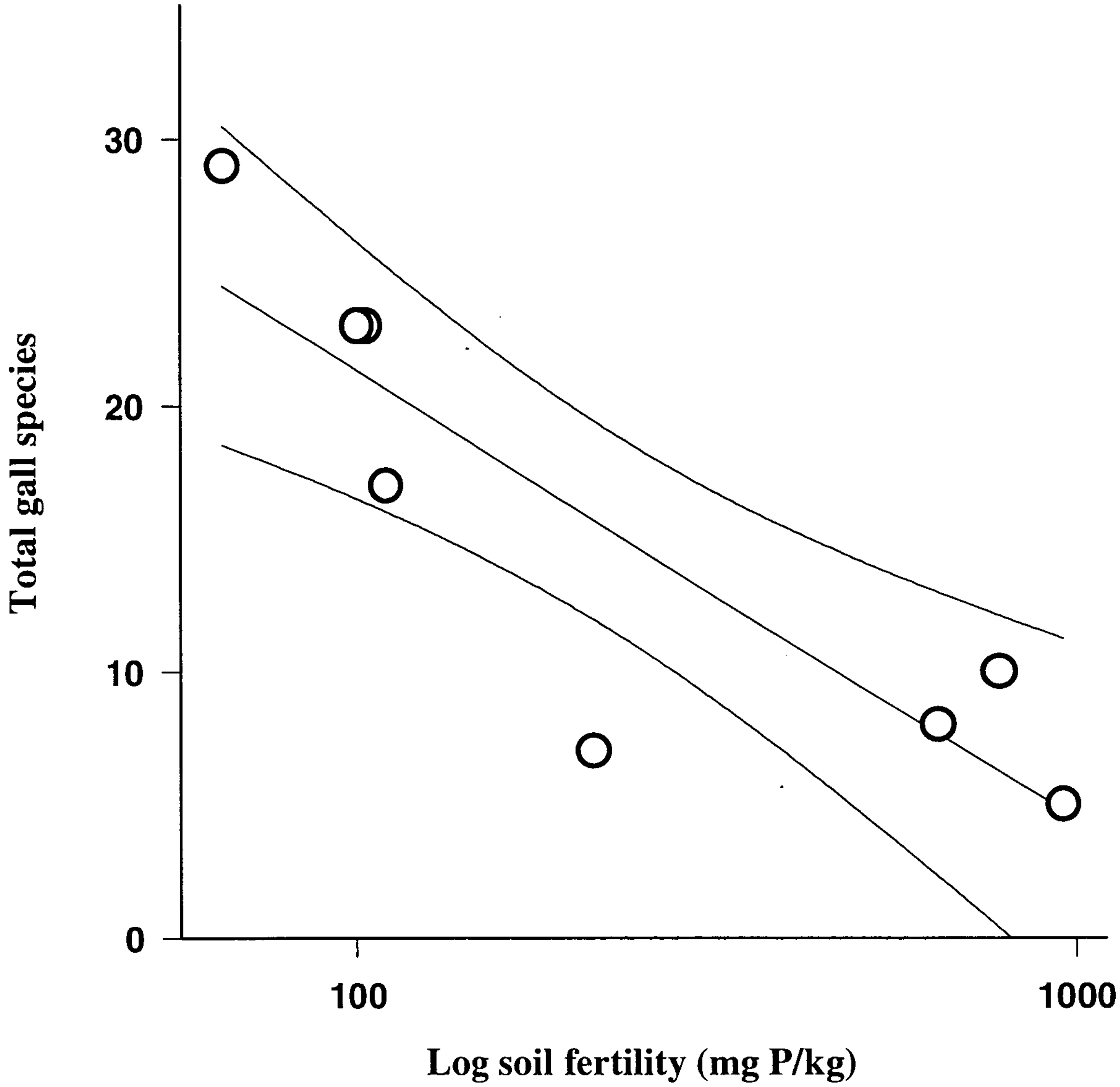


Figure 3.2 Relationship between total gall species richness and log soil fertility (± 95% confidence limits) (R^2 = 0.76, P = 0.004).

species on myrtaceous tree species (species of the genus *Eucalyptus* and the closely related genus *Syncarpia*) than on other plant species (Fig. 3.3). Although there appeared to be more gall species per myrtaceous tree species on more fertile sites, this relationship was due to a single plant species (*Syncarpia glomulifera*) at a single fertile site, carrying a large number of gall species. The apparent trend was not significant. Within the category of plant species other than myrtaceous tree species there was obviously no relationship between the number of gall species per plant species and soil fertility.

The pattern of more total gall species at less fertile sites appears to be the product of two factors. First, myrtaceous tree species were present at all four of the less fertile sites but at only one of the four more fertile sites (Table 3.1). Second, there was a tendency for there to be more total plant species at the less fertile sites (Table 3.1). Thus the total number of galled plant species was greater at less fertile sites (Fig. 3.4a), even though the proportion of galled plant species to total plant species did not vary significantly across sites (Fig. 3.4b).

There were more complex than simple gall species on less fertile sites (Table 3.1). This pattern holds when the number of complex gall species at each site is expressed as a proportion of the total number of gall species (Fig. 3.5). There were clearly higher proportions of complex gall species associated with myrtaceous tree species than with other plant species (Fig. 3.6). (There are seven instead of eight points on the plot for the 'all other plant species' category in Fig. 3.6 because, at one fertile site, all gall species were on a single myrtaceous tree species). The apparent trend of lower proportions of complex gall species on myrtaceous tree species with increasing site fertility was not significant; only one fertile site had any myrtaceous tree species. Further, the apparent trend of lower proportions of complex gall species on other plant species with increasing site fertility was also not significant; in fact, at one low fertility site, plant species other than myrtaceous tree species only had simple galls.

In summary, the tendency for there to be more total gall species and greater proportions of complex gall species at infertile sites does not appear to be a strong and consistent result in itself. The strong result emerging from this study is the much greater number and structural complexity of gall insect species on a particular category of plant irrespective of soil fertility.

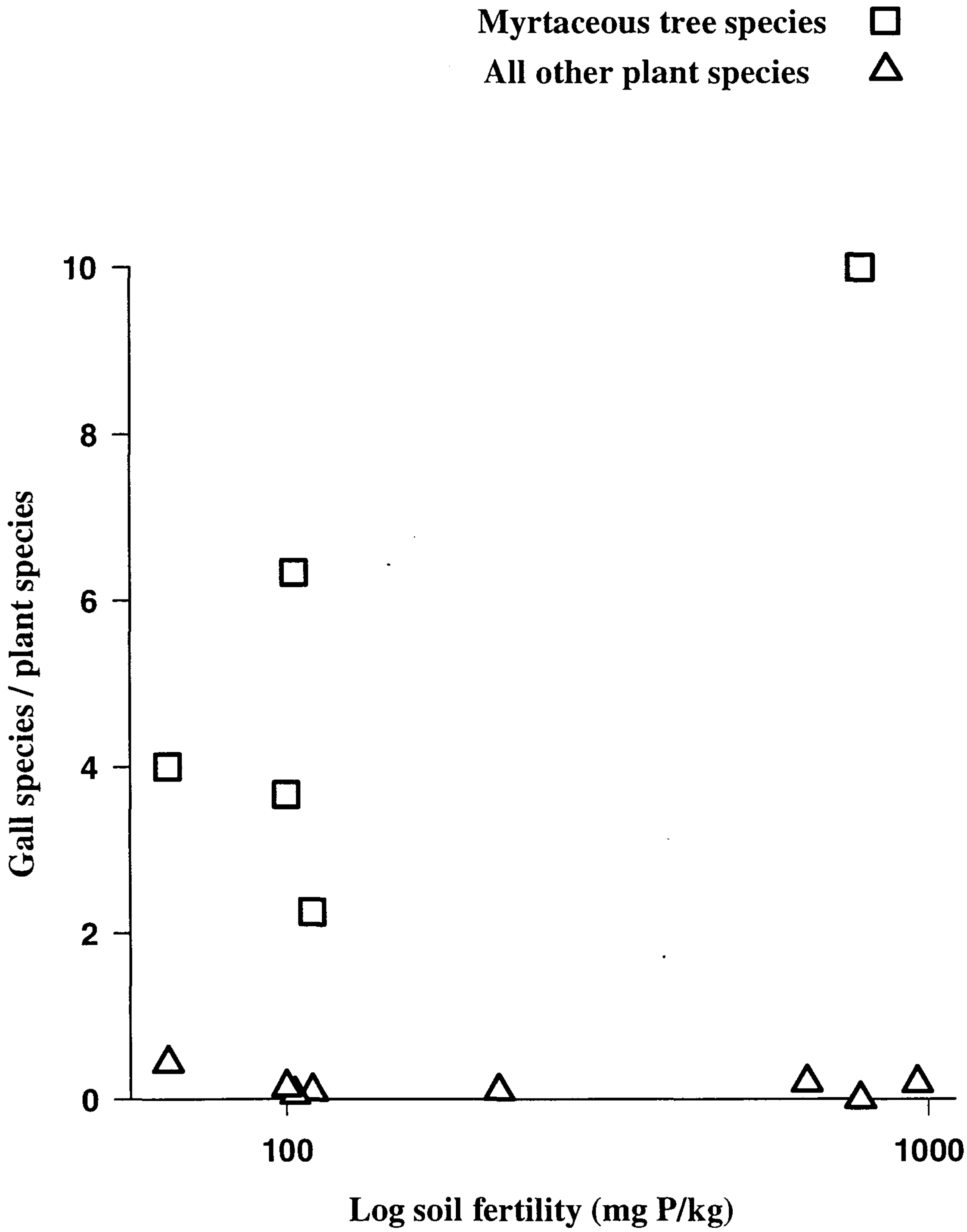


Figure 3.3 Linear regression of gall species per myrtaceous tree species onto log soil fertility (R^2 = 0.72, P = 0.07) and gall species per other plant species (except myrtaceous tree species) onto log soil fertility (R^2 = 0.09, P = 0.46). The regression for myrtaceous tree species was derived from only five sites as this category of plant was missing from the other three sites.

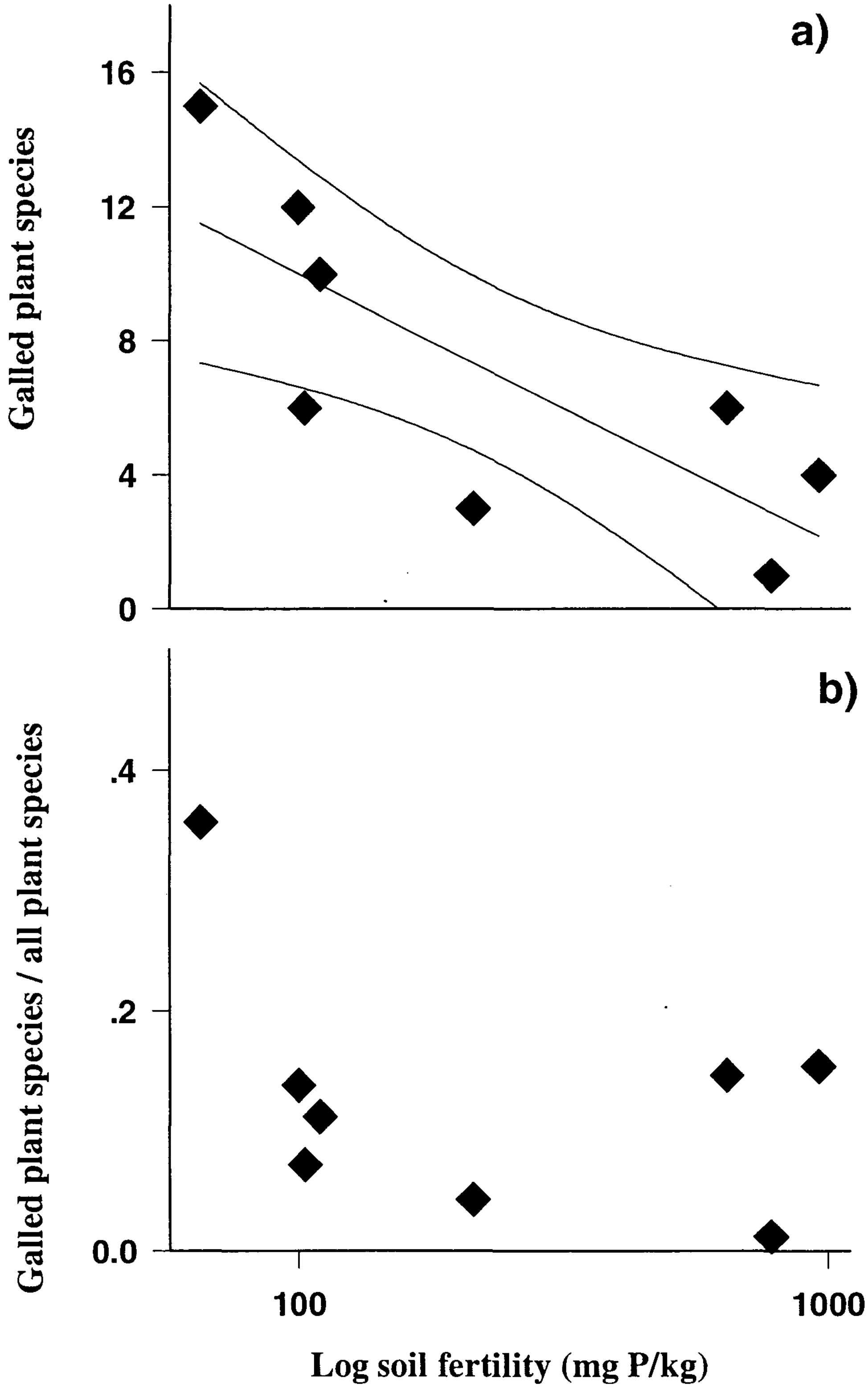


Figure 3.4 Linear regression (± 95% confidence limits) of:

a) number of galled plant species onto log soil fertility (R^2 = 0.61, P = 0.02).

b) proportion of plant species galled onto log soil fertility (R^2 = 0.16, P = 0.32).

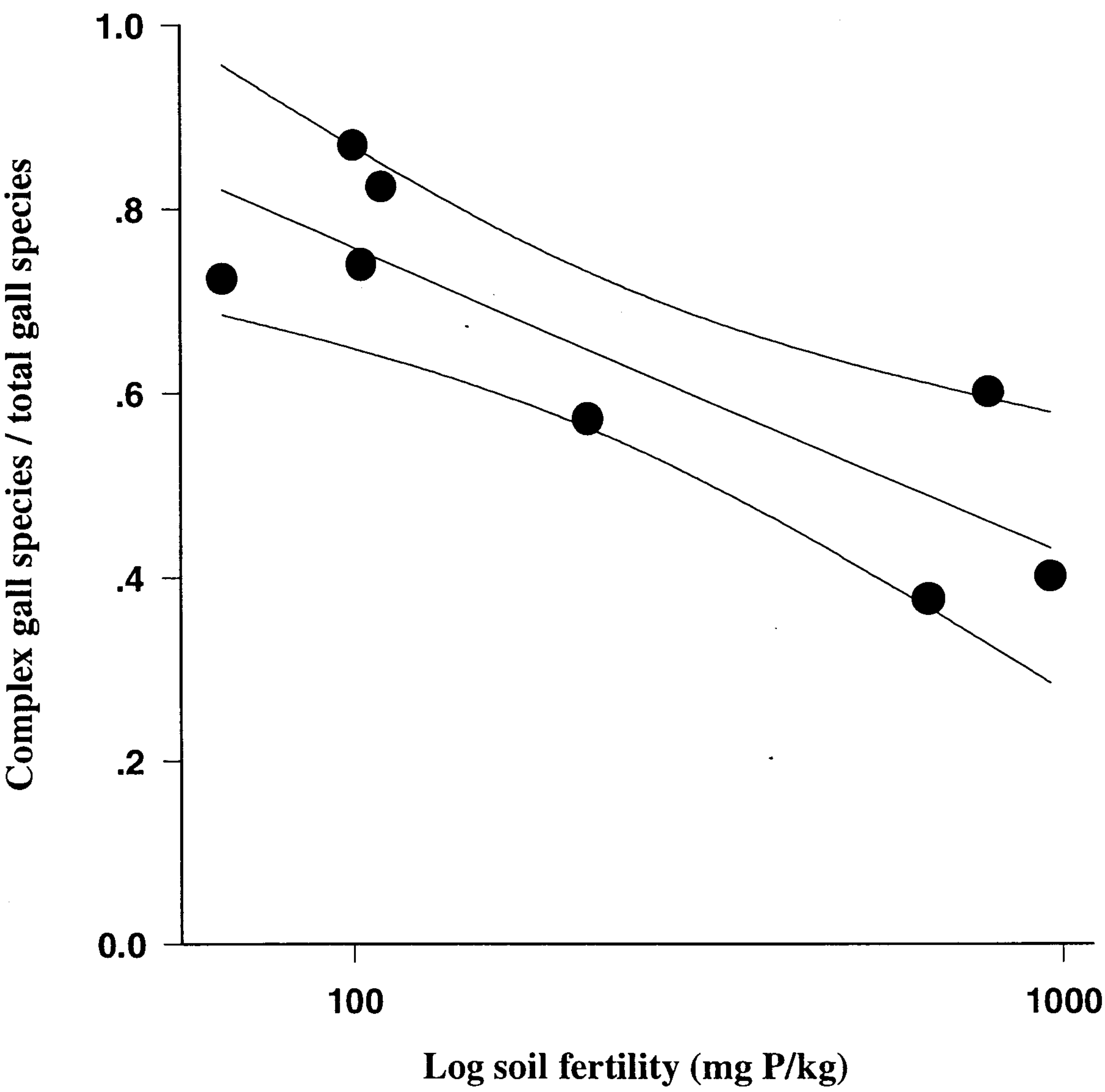


Figure 3.5 Relationship between the proportion of complex gall species and log soil fertility (± 95% confidence limits). (R^2 = 0.72, P = 0.008).

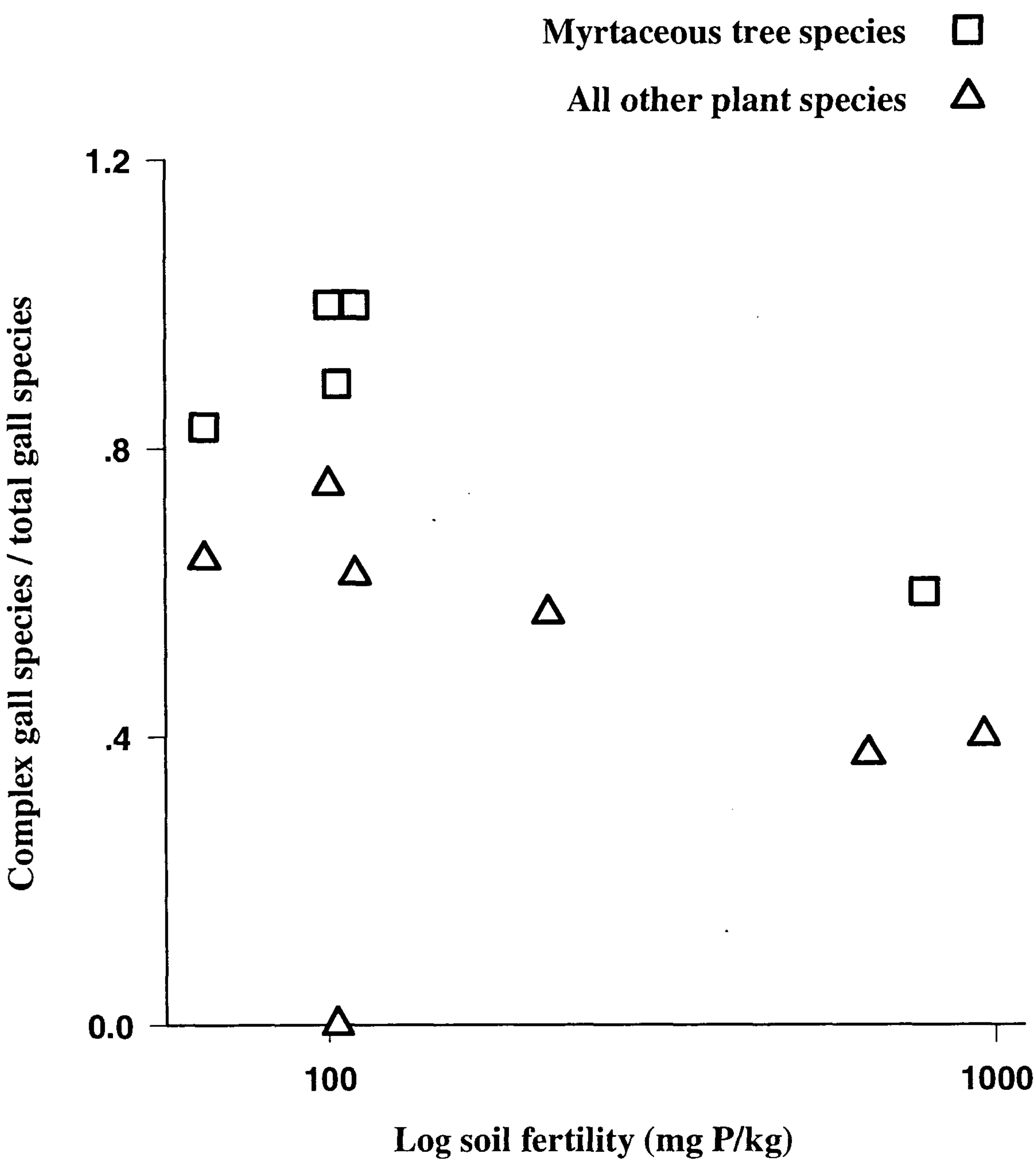


Figure 3.6 Analysis of covariance indicated that the mean regression of proportion of complex gall species onto log soil fertility on myrtaceous tree species was significantly greater than on other plant species ($P = 0.02$). These regressions were not significant with soil fertility (myrtaceous trees: $R^2 = 0.64$, $P = 0.1$; all other plant species: $R^2 = 0.06$, $P = 0.59$). Covariance analysis also indicated that there was no significant interaction between the regression lines ($P = 0.62$).

3.4 Discussion

I suggested at the beginning of this chapter that longer-lived plant parts or higher concentrations of secondary compounds in plant tissues could be responsible for increasing gall species richness and complexity with decreasing soil fertility. If correct, this would lead to the expectation that galling would be widely distributed among Australian plant taxa having those attributes on low fertility soils. This was not the case. As galling was concentrated in myrtaceous tree species (especially the genus *Eucalyptus*), the explanation of the results must lie in the reasons why there are more myrtaceous tree species at low fertility sites, and why Myrtaceae such as eucalypts have so many associated gall species.

Eucalypts are known to have several features which plausibly might favour gall species richness. They are dominant canopy trees in Australia. Thus they tend to account for more total foliage and photosynthesis per species in a given area, and so represent larger 'islands' for colonization, than many understorey plant groups. Large islands have more species than small islands because species immigration rates are higher and species extinction rates are lower than on small islands (MacArthur and Wilson 1967).

Eucalypts are also unusual in producing new cohorts of leaves several times during the year. Macauley and Fox (1980) found leaf initiation occurred up to five times during the period (mid-December - mid-August) over which they monitored seven eucalypt species. Repeated leaf production may increase the number of temporal niches available to gall insects.

Some eucalypts are known to continue assimilation under drought conditions which cause many other plant groups to shut down (Grieve 1956). It is thought that eucalypts maintain assimilation during drought either by tapping into ground water supplies via deep roots or by being capable of tolerating high levels of desiccation. The resulting provision of a continuous food supply is likely to be advantageous to sedentary insects like gall-formers, particularly those which induce long-lived, complex galls.

Many gall-forming insects require actively growing plant tissue for gall initiation (Rohfritsch 1992). Eucalypts are noted for their ability to resprout readily in response to defoliation by fire, severe drought, or intense herbivore impact. New shoots can be produced from axillary, accessory, and epicormic buds, and from lignotubers (Ohmart and

Edwards 1991). Some other plant genera, such as *Salix* and *Quercus*, which are known to carry large gall radiations in other parts of the world (Price 1992), also have well-developed sprouting capacity (Plumb 1980, Price, Cobb, Craig, Fernandes, Itami, Mopper and Preszier 1990). Washburn and Cornell (1981) suggested that *Xanthoteras politum* (Bassett), a cynipid wasp which galls the leaves of *Quercus stellata*, requires the continued production of post-fire sucker shoots for maintenance of local gall populations.

In many plant groups the concentration of secondary compounds in leaves increases as they age but in eucalypts the levels of tannins and other phenols are high in young as well as old leaves (Macauley and Fox 1980). Consequently, the protection from secondary herbivores and micro-organisms, thought to be afforded by the concentration of secondary compounds in the gall wall, may be available early in gall-formation. This could make eucalypts better hosts for gall-forming insects than plant groups whose secondary compounds are less readily available. The protective effect of a layer of defensive chemicals is likely to be more important for complex galls, in which the insect is completely enclosed, rather than for simple, open galls. This may explain why eucalypts are able to support many gall species which induce complex galls.

Thus various possibilities can be put forward as to why eucalypts might have features that favour gall species, some connected to the adaptation of eucalypts to infertile soils, others to adaptations to water shortage or to fire-prone environments. The results presented here cannot prove which of these possibilities are important in favouring galls, but do show that the high gall species richness and complexity in Australian infertile soil vegetation needs to be explained by reference to particular attributes of eucalypts, rather than by reference to adaptations to infertility in general.

Appendix 11 PLANT SPECIES AND THEIR GALL SPECIES AT EACH SITE

Key: 1 in P (plants) columns indicates the presence of the plant species at a site. The numbers in G (galls) columns indicate the number of gall species on a plant species at a site. Sites: S = Strickland, W = Waterfall, K INF. = Kuring gai Chase (infertile), FR = Flat Rock, C = Cumberland, BC = Bola Creek, K FERT. = Kuring gai Chase (fertile), RC = Red Cedar

		SITE															
PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Acacia brownei	Mimosaceae	1	1														
Acacia elata	Mimosaceae	1															
Acacia floribunda	Mimosaceae									1				1			
Acacia cf irrorata	Mimosaceae									1							
Acacia linifolia	Mimosaceae			1													
Acacia sauveolens	Mimosaceae			1		1		1	1								
Acacia terminalis	Mimosaceae			1	1												
Acacia ulicifolia	Mimosaceae			1				1									
Acianthus sp.	Orchidaceae																
Aciathus exsertus	Orchidaceae									1				1			
Actinotus minor	Apiaceae			1		1		1									
Adiantum diaphanum	Adiantaceae									1		1				1	
Alectryon subcinereus	Sapindaceae											1					
Allocasuarina distyla	Casuarinaceae							1	2								
Allocasuarina littoralis	Casuarinaceae									1				1			
Allocasuarina torulosa	Casuarinaceae	1	2							1				1			
Alphitonia petriei	Rhamnaceae	1															
Aneilema acuminatum	Commelinaceae											1					
Anisopogon avenaceus	Poaceae					1		1									
Anisopogon sp.	Poaceae			1													
Aotus ericoides	Fabaceae			1						1				1			
Asplenium australasicum	Aspleniaceae											1					
Astrotricha flocculosa	Araliaceae													1			
Baekea diosmifolia	Myrtaceae					1											
Banksia ericifolia	Proteaceae			1				1									
Banksia marginata	Proteaceae	1	1	1				1									

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K	FERT	RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Banksia oblongilfolia	Proteaceae					1		1									
Banksia serrata	Proteaceae	1	1	1	1	1	1	1	1								
Banksia spinulosa	Proteaceae	1	1	1	2	1											
Bauera rubioides	Proteaceae			1				1									
Billardiera scandens	Pittosporaceae					1		1		1							
Blandfordia nobilis	Liliaceae																
Blechnum cartilagineum	Blechnaceae									1		1				1	
Blechnum sp. 1	Blechnaceae															1	
Boronia ledifolia	Rutaceae			1													
Boronia pinnata	Rutaceae					1											
Boronia serrulata	Rutaceae							1									
Bossiaea heterophylla	Fabaceae			1		1		1									
Brachychiton sp.	Sterculiaceae									1							
Brachyloma daphnoides	Epacridaceae			1													
Breynia oblongifolia	Euphorbiaceae									1		1		1			
Burchardia umbellata	Liliaceae					1											
Bursaria spinosa	Pittosporaceae	1								1							
Caesia vittata	Liliaceae													1			
Caladenia aurantiaca	Orchidaceae									1				1			
Callicoma serratifolia	Cunoniaceae															1	
Calochilus campestris	Orchidaceae							1									
Carex appressa	Cyperaceae											1					
Carex breviculmis	Cyperaceae									1				1			
Cassine australis	Celastraceae									1		1	1			1	
Cassinia sp.	Asteraceae	1															
Cassytha glabella	Cassythaceae							1									
Cassytha pubescens	Cassythaceae			1				1									
Caustis flexuosa	Cyperaceae			1				1									
Caustis pentandra	Cyperaceae							1									
Cayratia clematidea	Vitaceae															1	
Ceratopetalum apetalum	Cunoniaceae											1	1			1	1
Ceratopetalum gummiferum	Cunoniaceae			1	1			1									

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Cissus hypoglauca	Vitaceae													1		1	
Citriobatus pauciflorus	Pittosporaceae											1	1				
Claoxylon australe	Euphorbiaceae											1					
Clematis aristata	Ranunculaceae	1								1				1			
Clematis glycinoides	Ranunculaceae									1				1			
Clerodendrum tomentosum	Verbenaceae									1		1		1		1	
Comesperma sphaerocarpum	Polygalaceae					1											
Comesperma volubile	Polygalaceae													1			
Conospermum longifolium	Proteaceae					1											
Cordyline stricta	Agavaceae									1							
Correa reflexa	Rutaceae													1			
Corybas pruinosus	Orchidaceae									1				1			
Cryptocaria glaucescens	Lauraceae											1					
Cryptocaria microneura	Lauraceae															1	1
Culcita dubia	Dicksoniaceae									1				1			
Cyathochaeta diandra	Cyperaceae					1											
Cyperus tetraphyllus	Cyperaceae									1							
Dampiera stricta	Goodeniaceae					1		1									
Davalia pyxidata	Davalliaceae													1			
Decussate leafed herb	?			1										1			
Dianella cerulea	Liliaceae			1				1		1				1			
Dianella revoluta	Liliaceae	1															
Dillwynia juniperina	Fabaceae	1	1														
Dillwynia retorta	Fabaceae					1		1									
Diospyros australis	Ebenaceae											1	1			1	1
Dipodium cf punctatum	Orchidaceae									1							
Dodonaea triquetra	Sapindaceae			1	2												
Doodia aspera	Blechnaceae											1		1		1	
Doryanthes excelsa	Agavaceae			1				1									
Doryphora sassafras	Monimiaceae											1	3			1	2
Drosera peltata	Droseraceae					1		1						1			
Echinopogon caespitosus	Poaceae													1			

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Elaeocarpus reticulatus	Elaeocarpaceae	1	1														
Empodisma minus	Restionaceae			1				1									
Entolasia stricta	Poaceae			1		1		1		1				1			
Epacris longiflora	Epacridaceae			1				1									
Epacris microphylla	Epacridaceae							1									
Epacris pulchella	Epacridaceae			1		1											
Eucalyptus globoidea	Myrtaceae					1	13										
Eucalyptus gummifera	Myrtaceae	1	1	1	3	1	1	1	4								
Eucalyptus haemastoma	Myrtaceae					1	5	1	1								
Eucalyptus piperita	Myrtaceae			1	1			1									
Eucalyptus sieberi	Myrtaceae			1	7			1	4								
Eucalyptus sp.	Myrtaceae	1	6														
Eustrephus latifolius	Philesiaceae									1		1		1			
Fern	?															1	
Ficus sp.	Moraceae									1	1						
Gahnia aspera	Cyperaceae											1					
Gahnia erythrocarpa	Cyperaceae	1						1						1			
Gahnia melanocarpa	Cyperaceae													1			
Gahnia sp.	Cyperaceae	1		1													
Galium binifolium	Rubiaceae									1							
Galium propinquum	Rubiaceae													1			
Geitonoplesium cymosum	Philesiaceae									1		1		1		1	
Geranium homeanum	Geraniaceae											1					
Gleichenia dicarpa	Gleicheniaceae			1													
Gleichenia rupestris	Gleicheniaceae							1									
Glochidion ferdinandi	Euphorbiaceae									1				1			
Glossodia minor	Orchidaceae					1											
Glycine clandestina	Fabaceae									1				1			
Gompholobium glabratum	Fabaceae					1		1									
Gompholobium grandiflorum	Fabaceae			1		1											
Gonocarpus teucrioides	Haloragaceae			1		1		1									
Goodenia bellidifolia	Goodeniaceae					1											

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Grass	Poaceae	4												1			
Grevillea sericea	Proteaceae			1													
Grevillia buxifolia	Proteaceae					1		1									
Grevillia oleoides	Proteaceae							1									
Grevillia speciosa	Proteaceae			1		1											
Guoia semiglauca	Sapindaceae											1					
Gymnostachys anceps	Araceae											1		1		1	
Haemodorum corymbosum	Haemodoraceae					1											
Hakea dactyloides	Proteaceae					1		1									
Hakea gibbosa	Proteaceae					1		1									
Hakea sericea	Proteaceae			1										1			
Hakea teretifolia	Proteaceae					1		1									
Hardenbergia violacea	Fabaceae			1													
Helichrysum diosmifolium	Asteraceae									1							
Hemigenia purpurea	Lamiaceae			1		1		1									
Hibbertia aspera	Dilleniaceae			1						1							
Hibbertia bracteata	Dilleniaceae			1		1											
Hibbertia dentata	Dilleniaceae													1			
Hibbertia empetrifolia	Dilleniaceae			1		1								1			
Hibbertia linearis	Dilleniaceae							1									
Hibbertia riparia	Dilleniaceae					1											
Hibbertia scandens	Dilleniaceae									1							
Hovea linearis	Fabaceae					1											
Hybanthus monopetalus	Violaceae													1			
Hybanthus vernonii	Violaceae							1									
Hydrocoltyle acutiloba	Apiaceae									1		1		1			
Imperata cylindrica	Poaceae									1				1			
Isopogon anemonifolius	Proteaceae			1	1	1		1	1								
Isopogon anethifolius	Proteaceae					1											
Kunzea capitata	Myrtaceae							1									
Lagenifera stipitata	Asteraceae													1			
Lambertia formosa	Proteaceae			1		1		1									

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Lasiopetalum ferrugineum	Sterculiaceae							1						1			
Lastreopsis decomposita	Aspidiaceae											1				1	
Lastreopsis microsora	Aspidiaceae											1					
Lepidosperma laterale	Cyperaceae			1		1				1				1			
Lepidosperma sp. A	Cyperaceae							1									
Lepidosperma urophorum	Cyperaceae			1				1						1			
Leptocarpus tenax	Restionaceae			1				1									
Leptomeria acida	Santalaceae			1													
Leptospermum attenuatum	Myrtaceae			1		1		1									
Leptospermum juniperinum	Myrtaceae	1	1	1		1		1	1								
Leptospermum laevigatum	Myrtaceae					1	2										
Leptospermum polygalifolium	Myrtaceae	1	5	1	2			1						1			
Lepyrodia scariosa	Restionaceae			1		1		1									
Leucopogon amplexicaulis	Epacridaceae			1				1									
Leucopogon esquamatus	Epacridaceae					1											
Leucopogon juniperinus	Epacridaceae									1							
Leucopogon lanceolatus	Epacridaceae									1							
Leucopogon microphyllus	Epacridaceae					1		1									
Leucopogon sp.	Epacridaceae	1															
Ligustrum lucidum	Oleaceae									1							
Ligustrum sinense	Oleaceae									1							
Lindsaea linearis	Lindsaeaceae			1		1		1									
Livistona australis	Arecaceae	1										1		1		1	
Logania pusilla	Loganiaceae					1											
Lomandra confertifolia	Xanthorrhoeaceae													1			
Lomandra cylindrica	Xanthorrhoeaceae					1											
Lomandra filiformis	Xanthorrhoeaceae			1						1				1			
Lomandra glauca	Xanthorrhoeaceae					1		1									
Lomandra gracilis	Xanthorrhoeaceae	1		1										1			
Lomandra longifolia	Xanthorrhoeaceae	1		1						1				1			
Lomandra multiflora	Xanthorrhoeaceae							1						1			
Lomandra obliqua	Xanthorrhoeaceae			1		1											

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Lomatia silaifolia	Proteaceae			1		1		1						1			
Macrozamia communis	Zamiaceae													1			
Marsdenia flavescens	Asclepiadaceae											1					
Maytenus silvestris	Celastraceae									1				1			
Micrantheum ericoides	Euphorbiaceae			1				1									
Microlaena stipoides	Poaceae									1				1			
Mirbelia rubiifolia	Fabaceae							1									
Mitrasacme polymorpha	Loganiaceae					1		1									
Monotoca scoparia	Epacridaceae			1		1		1									
Morinda jasminoides	Rubiaceae									1	3	1	1			1	
Notelaea venosa	Oleaceae									1				1			
Ochna serrulata	Ochnaceae									1							
Olea africana	Oleaceae									1							
Opercularia aspera	Rubiaceae									1							
Oplismenus aemulus	Poaceae									1		1		1			
Orchidaceae sp.	Orchidaceae	1		1		1											
Oxalis chnoodes	Oxalidaceae											1					
Oxalis exilis	Oxalidaceae									1				1			
Palmeria scandens	Monimiaceae											1					
Pandorea pandorana	Bignoniaceae									1		1		1			
Parsonsia straminea	Apocynaceae									1		1					
Paspalidium sp.	Poaceae									1							
Passiflora edulis	Passifloraceae									1							
Patersonia glabrata	Iridaceae					1		1						1			
Patersonia sericea	Iridaceae			1		1											
Patersonia sp.	Iridaceae	1															
Pellaea falcata	Adiantaceae											1					
Persoonia lanceolata	Proteaceae					1	1	1	1								
Persoonia laurina	Proteaceae							1									
Persoonia levis	Proteaceae	1		1		1		1									
Persoonia linearis	Proteaceae	1								1				1			
Persoonia molis	Proteaceae	1															

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Persoonia pinifolia	Proteaceae			1		1		1									
Petrophile pulchella	Proteaceae			1		1											
Phyllanthus thymoides	Euphorbiaceae					1											
Phyllota grandiflora	Fabaceae			1													
Phyllota phylicoides	Fabaceae					1											
Pimelia latifolia	Thymelaeaceae													1			
Pimelia linifolia	Thymelaeaceae			1		1		1									
Pittosporum revolutum	Pittosporaceae									1							
Pittosporum undulatum	Pittosporaceae									1	3						
Platylobium formosum	Fabaceae			1						1							
Platysace lanceolata	Apiaceae	1															
Platysace linearifolia	Apiaceae	1		1		1		1	1								
Poa compressa	Poaceae									1				1			
Poa sp.	Poaceae			1													
Polyosma cunninghamii	Escalloniaceae											1					
Polyscias sambucifolia	Araliaceae									1						1	
Pomaderris sp.	Rhamnaceae													1			
Pomax umbellata	Rubiaceae	1	1	1										1			
Poranthera ericifolia	Euphorbiaceae					1											
Poranthera microphylla	Euphorbiaceae													1			
Pratia purpurescens	Lobeliaceae									1				1			
Pseuderanthemum variabile	Acanthaceum									1		1		1		1	
Psychotria loniceroides	Rubiaceae											1					
Pteridium esculentum	Pteridaceae	1		1						1		1		1			
Pterostylus cf nutans	Orchidaceae													1			
Pterostylus pedunculata	Orchidaceae									1							
Pterostylus sp. 4	Orchidaceae													1			
Pultenaea daphinoides	Fabaceae			1	1												
Pultenaea elliptica	Fabaceae	1	1	1		1		1									
Pultenaea flexilis	Fabaceae													1			
Pultenaea sp.	Fabaceae	1	1														
Pultenaea stipularis	Fabaceae			1	1			1									

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Rapanea variabilis	Myrsinaceae													1			
Restio dimorphus	Restionaceae							1									
Ricinocarpos pinifolius	Euphorbiaceae			1				1									
Rush	?															1	
Sarcopetalum harveyanum	Menispermaceae									1				1			
Scaevola ramosissima	Goodeniaceae					1		1									
Schelhammera undulata	Liliaceae													1			
Schizaea bifida	Schizaeaceae	1		1		1		1									
Schizomeria ovata	Cunoniaceae											1				1	
Schoenus imberbis	Cyperaceae					1											
Schoenus melanostachys	Cyperaceae					1								1			
Schoenus sp. A	Cyperaceae																
Schoenus sp. B	Cyperaceae			1													
Scutellaria mollis	Lamiaceae													1			
Smilax australis	Smilacaceae											1				1	
Smilax glyciphylla	Smilacaceae	1		1				1						1			
Solanum pungetium	Solanaceae									1							
Stackhousia viminea	Stackhousiaceae																
Sticherus flabellatus	Gleicheniaceae			1													
Stipa rudis	Poaceae													1			
Stylidium graminifolium	Stylidiaceae			1													
Stylidium lineare	Stylidiaceae					1		1									
Styphelia sp.	Epacridaceae			1													
Styphelia tubiflora	Epacridaceae			1				1									
Syncarpia glomulifera	Myrtaceae	1	5											1	10		
Synoum glandulosum	Meliaceae													1			
Telopea speciosissima	Proteaceae							1									
Tetrarrhena juncea	Poaceae			1		1											
Tetratheca ericifolia	Tremandraceae					1											
Tetratheca shiresii	Tremandraceae							1									
Thelmytra ixioides	Orchidaceae							1									
Thysanotus juncifolius	Liliaceae					1		1									

Appendix 11 (cont.)

PLANT SPECIES	FAMILY	S		W		K INF.		FR		C		BC		K FERT.		RC	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
Thysanotus tuberosus	Liliaceae					1											
Toona australis	Meliaceae															1	
Tricostularia pauciflora	Cyperaceae					1											
Tylophora barbata	Asclepiadaceae									1							
Vernonia cinerea	Asteraceae													1			
Viola hederacea	Violaceae													1			
Wahlenbergia sp.	Campanulaceae													1			
Wilkiea heugliana	Monimiaceae											1				1	
Woollsia pungens	Epacridaceae					1		1									
Xanthorrhoea arborea	Xanthorrhoeaceae							1						1			
Xanthorrhoea media	Xanthorrhoeaceae					1		1						1			
Xanthorrhoea sp.	Xanthorrhoeaceae			1													
Xanthosia pilosa	Apiaceae	1		1				1									
Xanthosia tridentata	Apiaceae			1		1											
Xyris gracilis	Xyridacae					1											
Ziera pilosa	Rutaceae																
Ziera smithii	Rutaceae									1							

Appendix 12 GALL SPECIES AND GALL MORPHOLOGY AT EACH SITE

SITE	HOST PLANT	GALL SPECIES (OR GROUP)	GALL MORPHOLOGY	KIND OF GALL C = complex S = simple
STRICK- LAND	Acacia brownei (S)	unknown	lumpy stem gall	C
	Allocasuarina torulosa (T)	dipteran	swollen base of branchlet	C
	Allocasuarina torulosa	unknown	small swelling on branchlet	C
	Banksia serrata (T)	Frenchia banksiae	hairy leaf pits	S
	Banksia spinulosa (S)	unknown	stem swelling	C
	Banksia marginata (T/S)	unknown	thickening under main leaf vein	C
	Dillwynia juniperina (S)	Ethone sp.	lumps on stems	C
	Elaeocarpus reticulatus (T/S)	unknown	hairy leaf pits	S
	Eucalyptus gummifera (T)	unknown	large stem swellings	C
	Eucalyptus gummifera	coccoid (? Opisthocellis sp.)	small round rosette both sides leaf	C
	Eucalyptus gummifera	unknown	tiny round galls along leaf edge	C
	Eucalyptus gummifera	unknown	main leaf vein gall, fused leaves	C
	Eucalyptus gummifera	unknown	medium round green leaf gall	C
	Eucalyptus gummifera	wasp (Eurytoma sp.)	small lumps on leaf petiole	C
	Eucalyptus sp. (T)	wasp (Eulophidae)	small round leaf gall	C
	Leptospermum juniperinum (S)	Sphaerococcus turbinata	large oval stem galls	C
	Leptospermum polygalifolium (S)	coccoid	leaf mass	S
	Leptospermum polygalifolium	dipteran	round red gall at end of stem	C
	Leptospermum polygalifolium	Gallinococcus ferrisi	open stem swelling	S
	Leptospermum polygalifolium	Sphaerococcus pirogallus	small oval stem galls	C
	Leptospermum polygalifolium	unknown	leaf rosette	S
	Pomax umbellata (H)	dipteran	swollen stem below umbel	C
	Pultenaea elliptica (S)	dipteran	apical leaf masses	S
	Pultenea sp. (S)	Ethone ? affine	large lumps on stems	C
	Syncarpia glomulifera (T)	psyllid (? Australopsylla sp.)	leaf edge roll	S
	Syncarpia glomulifera	psyllid (Triozidae)	leaf pits, hairy on underside	S
	Syncarpia glomulifera	wasp	round galls under leaves	C
	Syncarpia glomulifera	wasp (Brachyelatus sp.)	large multicelled round stem galls	C
	Syncarpia glomulifera	wasp (Orasemorphia sp.)	stem swelling	C

Appendix 12 (cont.) GALL SPECIES AND GALL MORPHOLOGY AT EACH SITE

SITE	HOST PLANT	GALL SPECIES (OR GROUP)	GALL MORPHOLOGY	KIND OF GALL C = complex S = simple
WATER-FALL	Acacia terminalis (S)	? wasp (Eulophidae)	round reddish galls in leaf axil	C
	Banksia serrata (T)	Frenchia banksiae	hairy leaf pits, leaf rolls	S
	Banksia spinulosa (S)	? dipteran	swelling on back of leaf main vein	C
	Banksia spinulosa	unknown	stem swelling	C
	Ceratopetalum gummiferum (T/S)	unknown	leaf roll	S
	Dodonaea triquetra (S)	unknown	round lumps on main vein new leaves	C
	Dodonaea triquetra	unknown	stem swelling	C
	Eucalyptus gummifera (T)	unknown	flat crimson lump on stem	C
	Eucalyptus gummifera	unknown	white lumps on outer margin of leaf	C
	Eucalyptus gummifera	coccoid (? Opisthocellis sp.)	round galls top leaf, ostiole under	C
	Eucalyptus piperita (T)	Apiomorpha variabilis	large oval stem gall	C
	Eucalyptus sieberi (T)	psyllid (Schedotrioza sp.)	round gall under leaf, open on top	C
	Eucalyptus sieberi	psyllid (Schedotrioza sp.)	tiny thin yellow gall top of leaf	C
	Eucalyptus sieberi	unknown	stem swellings	C
	Eucalyptus sieberi	unknown	tiny round brown galls, under leaf	C
	Eucalyptus sieberi	unknown	round galls on leaf near main vein	C
	Eucalyptus sieberi	unknown	small round white galls leaf	C
	Eucalyptus sieberi	unknown	bent stem gall (at base of petiole)	C
	Isopogon anemonifolius (S)	wasp (Eurytomidae)	lumpy leaf swellings	C
	Leptospermum polygalifolium (S)	? dipteran	small red round gall on end of stem	C
	Leptospermum polygalifolium	Gallinococcus ferrisi	open stem swellings	S
	Pultenaea daphinoides (S)	Ethone sp.	stem swelling	C
	Pultenaea stipularis (S)	Ethone ? affine	large lump on stem	C
KURINGAI INF.	Banksia serrata (T)	Frenchia banksiae	hairy leaf pit, leaf roll from apex	S
	Eucalyptus globoidea (T)	? wasp	tight row flat round galls leaf	C
	Eucalyptus globoidea	? wasp	small round galls near leaf veins	C
	Eucalyptus globoidea	? wasp	multicelled leaf axil gall	C
	Eucalyptus globoidea	coccoid (? Cystococcus sp.)	large round stem gall	C

Appendix 12 (cont.) GALL SPECIES AND GALL MORPHOLOGY AT EACH SITE				
SITE	HOST PLANT	GALL SPECIES (OR GROUP)	GALL MORPHOLOGY	KIND OF GALL C = complex S = simple
KURINGAI	Eucalyptus globoidea	dipteran	pair round galls on top of leaf	C
INF.	Eucalyptus globoidea	psyllid (Synglycaspis sp.)	large round galls under leaf	C
(cont.)	Eucalyptus globoidea	unknown	right angled bend of stem	C
	Eucalyptus globoidea	unknown	inverted-cone shaped galls leaf	C
	Eucalyptus globoidea	unknown	lumpy leaf gall	C
	Eucalyptus globoidea	unknown	stem swelling	C
	Eucalyptus globoidea	unknown	small lumps on stem	C
	Eucalyptus globoidea	unknown	lumpy leaf "blister" gall	S
	Eucalyptus globoidea	wasp (Eulophidae)	multicelled gall nr main leaf vein	C
	Eucalyptus gummifera (T)	coccoid (? Opisthocellis sp.)	lumpy leaf "blister" gall	S
	Eucalyptus haemastoma (T)	? wasp	small swelling on side of leaf	C
	Eucalyptus haemastoma	psyllid (Synglycaspis sp.)	oval leaf gall with sealed ostiole	C
	Eucalyptus haemastoma	unknown	small lumps both sides of leaf	C
	Eucalyptus haemastoma	unknown	stem swelling	C
	Eucalyptus haemastoma	unknown	lumpy swelling on main leaf vein	C
	Leptospermum laevigatum (S)	Gallinococcus ferrisi	open stem swelling	S
	Leptospermum laevigatum	unknown hemipteran	leaf masses	S
	Persoonia lanceolata (S)	coccoid	leaf mass	S
FLAT	Acacia sauveolens (S)	dipteran	rolled edge of phyllode	S
ROCK	Allocasuarina distyla (S)	unknown	multicelled stem swelling	C
	Allocasuarina distyla	unknown	large, single-celled lump on stem	C
	Banksia serrata (T)	Frenchia banksiae	hairy leaf pit galls	S
	Eucalyptus gummifera (T)	unknown	stem swellings	C
	Eucalyptus gummifera	unknown	leaf edge galls	C
	Eucalyptus gummifera	unknown	small round red irreg. stem galls	C
	Eucalyptus gummifera	unknown	small lumpy leaf gall	C
	Eucalyptus haemastoma (T)	dipteran	leaf gall beside main vein	C
	Eucalyptus sieberi (T)	psyllid (Schedotrioza sp.)	large round leaf galls	C

Appendix 12 (cont.) GALL SPECIES AND GALL MORPHOLOGY AT EACH SITE

SITE	HOST PLANT	GALL SPECIES (OR GROUP)	GALL MORPHOLOGY	KIND OF GALL C = complex S = simple
FLAT	Eucalyptus sieberi	unknown	massed small round galls on stem	C
ROCK	Eucalyptus sieberi	unknown	multicelled small round leaf gall	C
(cont.)	Eucalyptus sieberi	unknown	multicelled stem gall	C
	Isopogon anemonifolius (S)	wasp (Eurytomidae)	lumpy leaf swellings	C
	Leptospermum juniperinum (S)	Gallinococcus ferrisi	open stem swellings	S
	Persoonia sp. (S)	unknown	stem swelling	C
	Platysace linearifolia (S)	unknown	apical leaf bud gall	C
CUMBLND.	Ficus sp. (T)	psyllid (? Synglycaspis sp.)	hairy spheres on underside of leaf	C
	Morinda jasminoides (C)	coccoid	leaf pits, top leaf	S
	Morinda jasminoides	dipteran	thickened main leaf vein	C
	Morinda jasminoides	dipteran	leaf roll	S
	Pittosporum undulatum (T)	Phytoliriomyza pittosporocaulis	lumpy stem gall, single celled	C
	Pittosporum undulatum	Phytoliriomyza pittosporophylli	leaf pits ("mine galls")	C
	Pittosporum undulatum	Teuchothrips pittosporiicola	leaf fold, very young leaves	S
BOLA	Cassine australis (T)	dipteran	large lump main leaf vein and stem	C
CREEK	Cayratia clematidae (C)	unknown	stem (or ? leaf bud) gall	C
	Ceratopetalum apetalum (T)	unknown	leaf roll (sides rolled inward)	S
	Citriobatus pauciflorus (S)	wasp	lumpy stem gall	C
	Diospyrus australis (T/S)	unknown	leaf pits	S
	Doryphora sassafras (T)	dipteran	tightly rolled young leaves	S
	Doryphora sassafras	psyllid (? Trioza sp.)	small leaf pits	S
	Doryphora sassafras	unknown	multi-celled blisters on leaf	S
KURINGAI	Syncarpia glomulifera (T)	? wasp	round galls under leaf	C
FERT.	Syncarpia glomulifera	? wasp (Brachyelatus sp.)	large round stem galls	C
	Syncarpia glomulifera	? wasp (Eulophidae)	round galls both sides leaf	C
	Syncarpia glomulifera	? wasp (Orasemorpha sp.)	stem thickenings	C

Appendix 12 (cont.) GALL SPECIES AND GALL MORPHOLOGY AT EACH SITE

SITE	HOST PLANT	GALL SPECIES (OR GROUP)	GALL MORPHOLOGY	KIND OF GALL C = complex S = simple
KURINGAI	Syncarpia glomulifera	psyllid (? Psyllidae)	lumpy leaf edge roll gall	S
FERT.	Syncarpia glomulifera	psyllid (? Trioza sp.)	leaf pits	S
(cont.)	Syncarpia glomulifera	psyllid (? Trioza sp.)	pits on main vein leaf, leaf roll	S
	Syncarpia glomulifera	unknown	leaf roll (young leaves)	S
	Syncarpia glomulifera	unknown	hairy round galls under leaf	C
	Syncarpia glomulifera	unknown	round gall on fruit	C
RED	Ceratopetalum apetalum (T)	psyllid (? Psyllidae)	leaf roll	S
CEDAR	Cryptocaria microneura (T)	unknown	leaf bud gall	C
	Diospyrus australis (T/S)	thrips	leaf roll	S
	Doryphora sassafras (T)	psyllid (? Trioza sp.)	leaf pits	S
	Doryphora sassafras	unknown	stem gall in leaf axil	C

KEY: Letters in brackets in HOST PLANT column indicate plant species growth form (Fairley and Moore 1989, Harden 1991)
T = tree, S = shrub, T/S = tree or shrub, H = herb, C = climber

CHAPTER 4

THE EFFECT OF HOST PLANT TAXON AND GEOGRAPHIC RANGE SIZE ON GALL-FORMING INSECT SPECIES RICHNESS ON AUSTRALIAN EUCALYPTS

4.1 Introduction

Explanations for differences in the size of insect species assemblages on plants usually include references to differences in the geographical area occupied by the host plant species. Area is thought to exert its effect by influencing habitat heterogeneity and/or insect immigration and extinction rates (Strong, Lawton and Southwood 1984). Other important factors not directly related to geographical area are structural complexity of host plants (Lawton 1983) and evolutionary histories of insect and plant taxa (Farrell and Mitter 1993).

Many past analyses of insect diversity and its possible causes utilised data collected for other purposes and so may have been subject to sampling errors. Several recent studies have overcome this difficulty by using data collected specifically to answer questions about the determinants of insect diversity on plants.

Cornell (1985a, 1985b) showed that the geographic range size of oaks (*Quercus*) in North America was an important determinant of regional gall-forming cynipid wasp species richness. In these studies host plant range size was also positively correlated with local insect species richness, so between-site differentiation was not considered to be solely responsible for the species-area effect. In addition, Cornell (1985a) identified a tendency, associated with leaf galls only, for there to be more gall wasp species in oak subgenera that included more plant species.

Studies by Stevens (1986) on wood-boring insects in the eastern United States, and by Lewinsohn (1991) on insects in flower heads of Asteraceae in south-east Brazil, also found that host plant range size influenced regional insect species richness. In both these studies there was no relationship between local insect species richness and host plant range size, so the species-area effect was attributed to between-site differentiation of species.

Lewinsohn (1991) also stressed the importance of insect and plant history, host plant taxon and local competition interactions in the system he studied.

Data collected by Fernandes and Price (1988, 1991) on regional gall species numbers on a selection of shrub species in North and South America showed no evidence of a positive relationship with host plant geographic range size. The same studies identified a pattern of more gall-forming insect species on host plant species in dry environments than in mesic environments.

My study further tests the generality of relationships between insect species richness and host plant characteristics by investigating the fauna of another continent. It is the first quantitative Australian survey specifically designed to identify some of the factors which might influence the species richness of gall-forming insect assemblages on eucalypts.

Eucalyptus is the dominant canopy taxon in Australia. The genus comprises seven subgenera, each divided into sections and series, and contains a total of about 700 species (Brooker and Kleinig 1990). Literature and museum records indicated that *Eucalyptus* is the most gall-prone Australian plant genus (Table 2.1). Eucalypts are host to gall-forming bugs (Psylloidea and Coccoidea), flies (Cecidomyiidae and Fergusoninidae) and wasps (Chalcidoidea) (Appendix 7).

Chapter 3 of this thesis documented a higher level of gall species richness in sclerophyll vegetation on infertile soils, but found that this effect was almost entirely associated with high numbers of gall species on eucalypts, these eucalypts in turn tending to occur on infertile more than on fertile soils. For these reasons it was decided to investigate patterns of gall species richness within the genus *Eucalyptus* in more detail.

In this study I aimed to answer the following questions:

1) Does eucalypt taxon influence gall species richness?

2) Do eucalypt species with large ranges:

a) have more regional gall species,

b) have more local gall species,

c) share fewer gall species between local sites

than eucalypt species with small ranges do?

4.2 Methods

The study area covered coastal regions of eastern Australia from latitude 26° 30′ in Queensland to latitude 36° 52′ in NSW and extended inland into the western slopes and plains regions of NSW. The survey was carried out over a period of 18 months from November 1992 to May 1994. Surveys of this nature are not subject to the same seasonal constraints that surveys of more free-living insects are. Galls remain on perennial hosts long after the insects have gone.

Gall-forming insect species richness was measured on five replicates comprising pairs of closely related eucalypt species. The eucalypt species within each pair were chosen to be as alike as possible except for geographic range size. Each eucalypt pair contained a widespread and a narrowly distributed eucalypt species. The geographic range size of a eucalypt was estimated from the number of mapsheet districts in which it occurred (Gill, Belbin and Chippendale 1985). Each mapsheet district covered 1° latitude by 1.5° longitude (about 136 x 115 kilometres). The eucalypt species selected as having large ranges all occurred in >18 mapsheet districts and those chosen as having small ranges all occurred in $\leqslant$11 mapsheet districts.

To include a broad selection of eucalypt groups one pair came from the subgenus Corymbia, one from the subgenus Monocalyptus, and three from different sections of the subgenus Symphyomyrtus. To minimise habitat differences within pairs the geographic ranges of the members of each pair overlapped. Maps showing the eucalypt species pairs and their geographic ranges are in Appendix 13.

Each eucalypt species was sampled at four sites. The sites were spread as widely as possible over the range of each eucalypt species but always included at least one site in, or close to, the range overlap zone with the other member of the pair. Eucalypt species site locations were obtained from the computer data base, GUMNUT, a compilation of label data of *Eucalyptus* specimens from all major Australian herbaria, held at the National Herbarium, Canberra ACT. Eucalypts were identified in the field using keys and descriptions in Chippendale (1988), Brooker and Kleinig (1990) and Hill (1991).

At each site ten trees were searched for insect induced galls. Preliminary tests showed that no new gall insect species were found at a site after examining seven individual trees. Trees were selected so that juveniles, adults, and small and large individuals were always included. A long-handled pruner was used to cut or pull down branches from high in the canopy of large trees. When tall trees grew on steep slopes the canopy could often be reached by sampling from higher up the slope. At other times high branches were reached by climbing the tree.

Samples of galls on stems and leaves were collected and identified to morphospecies. This method of classification involves identification based primarily on the external and internal morphology of the gall itself but includes classification of gall insects, if present, to at least family level. Morphospecies is commonly used to represent species in gall studies because many gall-forming insects have not been formally described and the gall insect may not be present when the gall is collected. Number of gall morphospecies gives a relatively reliable estimate of species number because gall morphology is usually distinctive for each insect species. For brevity morphospecies will be referred to as species in the rest of this chapter.

Dried voucher specimens of each eucalypt species and its galls were stored in the Herbarium, School of Biological Sciences, Macquarie University, North Ryde, NSW. Wet (ethanol and glycerine) specimens of all insects found in the galls were lodged at the C.S.I.R.O., Institute of Plant Production and Processing, Division of Entomology, Canberra, ACT.

The sum of the different gall species from four sites (an estimate of regional species richness), mean number of gall species at an individual site (local species richness), and mean percentage of gall species shared between individual sites were calculated for each eucalypt species from the field data.

4.3 Results

4.3.1 Host plant taxon and geographic range size

Descriptions of the gall species on each eucalypt species, at each sampling site, are given in Appendix 14. Within each eucalypt pair, larger range species had more total gall-forming species than smaller range eucalypt species (paired t test: $t = 4.1$, $df = 4$, $P < 0.05$). Differences between some eucalypt pairs were substantial, with the Corymbia pair especially carrying distinctly fewer gall species than the Monocalyptus or Symphyomyrtus pairs. As a consequence, if subgenus and section membership had been ignored, no overall difference between large and small geographic range host species would have been apparent (Fig. 4.1, $R^2 = 0.36$, $P > 0.05$).

The extra species on larger range eucalypt hosts came about because of greater differences in gall species composition between sites, rather than from greater numbers of gall species at each site. Evidence of this comes from the absence of any significant effect of eucalypt range size on local gall species richness ($R^2 = 0.17$, $P > 0.05$; paired and independent t tests $P > 0.05$) and from the finding that local sites of wide range eucalypt species shared significantly fewer gall species than did local sites of small range eucalypts (Fig. 4.2).

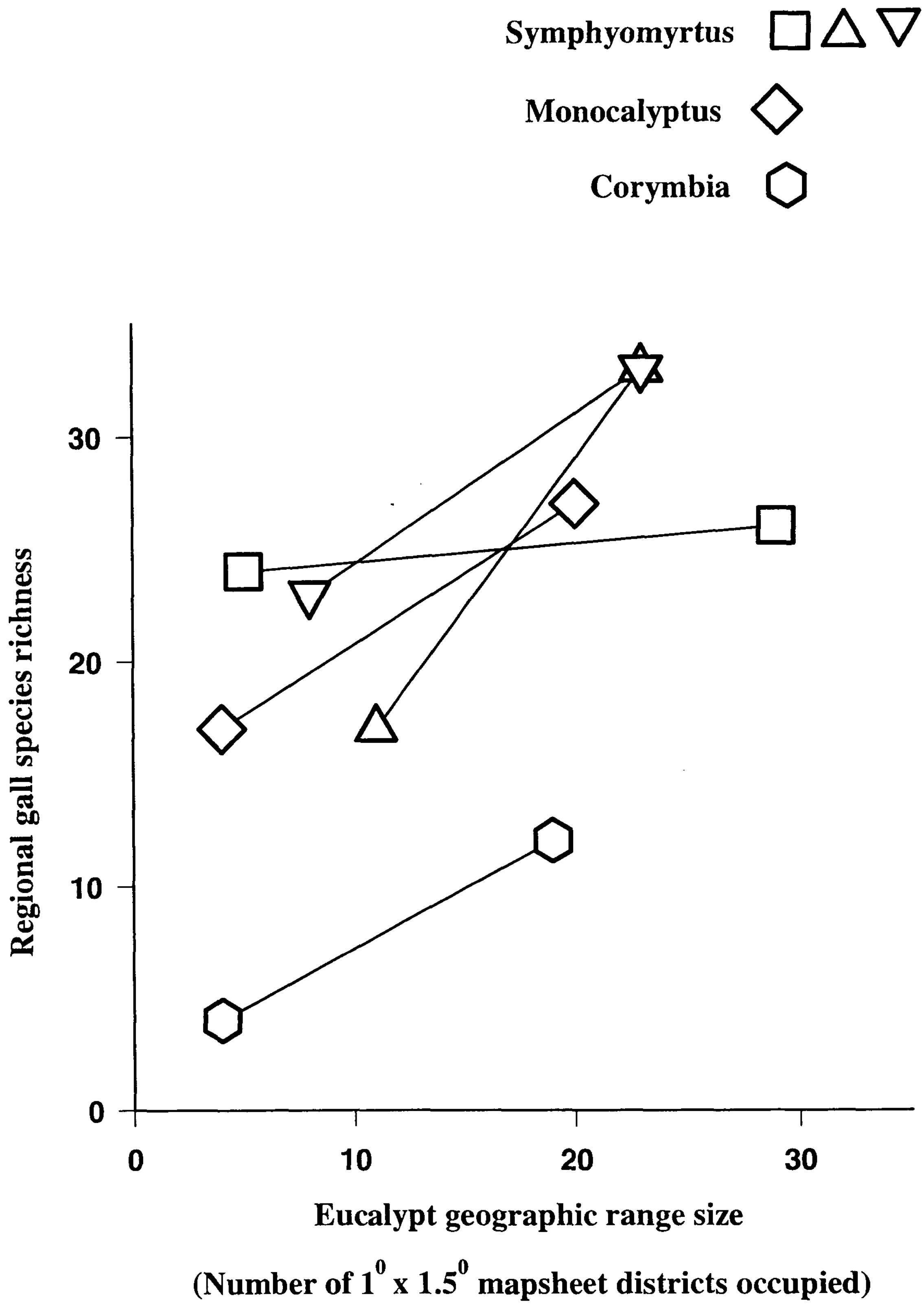


Figure 4.1 Comparison of regional gall species number with eucalypt geographic range size for five eucalypt pairs. (Lines connect pairs).

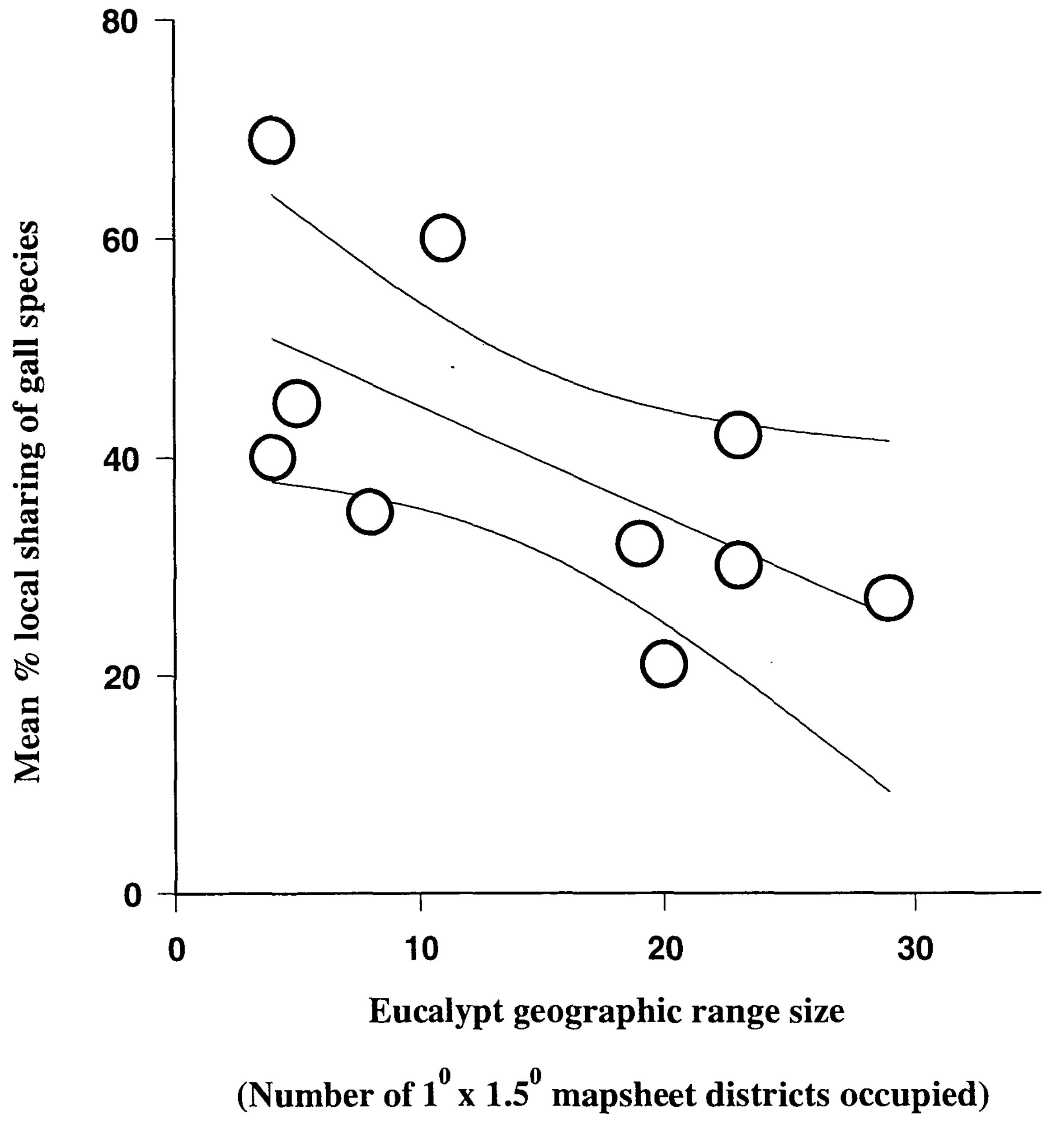


Figure 4.2 Relationship between degree of local sharing of gall species and geographic range size. Each circle represents a different eucalypt species. (±95% confidence limits) ($R^2 = 0.40$, $P < 0.05$).

4.3.2 Host plant geographic range rainfall zone

Although my study was not specifically designed to test for the pattern of higher galling in drier environments, identified by Fernandes and Price (1988, 1991), some indication of such a relationship should be apparent in the results. The members of three of the eucalypt pairs in this study have geographic ranges predominantly in coastal regions. Those of the remaining two pairs have all, or a large proportion of their range, in the drier western slopes and plains regions. To minimise taxonomic effects the three Symphyomyrtus pairs alone were compared (Fig. 4.3). Members of two of these Symphyomyrtus pairs have geographic ranges predominantly in relatively low rainfall regions and the members of the third pair are found in the higher rainfall coastal regions. No clear indication of a trend for more gall species in drier environments was apparent even between the small geographic range eucalypt species where the contrast in environments was most marked.

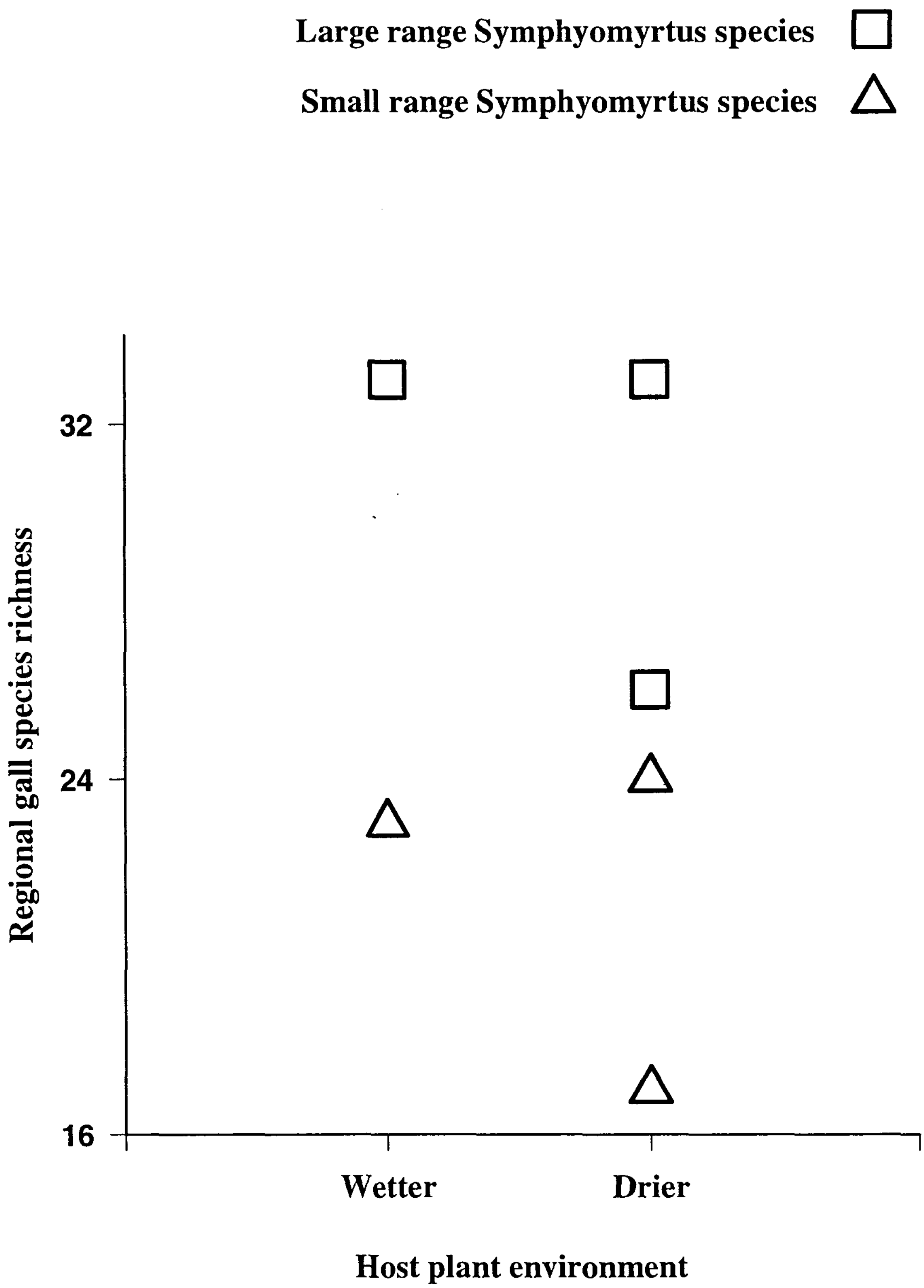


Figure 4.3 Comparison of regional gall species richness on Symphyomyrtus species with geographic ranges in different environments.

4.4 Discussion

4.4.1 Effect of host plant taxon

The presence of a species-area effect only when pairing of eucalypt species was taken into account indicates that differences between host taxa are important determinants of gall-forming insect diversity. This is not surprising considering what is known to date about the host specificity of Australian insect species which gall eucalypts. Those galling groups for which data are available, such as coccoids of the genus *Apiomorpha* (Gullan 1984a), are mostly restricted to a few eucalypt species within a single subgenus. It was proposed in sections 2.2.3 and 2.2.6 that sharing of gall species between host plant species was one way that host species might maintain high numbers of gall species. The specificity of gall-forming insects on eucalypts would tend to limit gall species sharing to host species within the same subgenus. This would mean that eucalypt species from speciose subgenera would tend to have larger gall insect assemblages than those from less speciose subgenera.

Limited gall species sharing may explain why galling on the Corymbia eucalypt species pair was so low. The subgenus Corymbia is the least speciose of the three subgenera surveyed in this study and has fewer species in the area than the other two subgenera (Chippendale and Wolf 1981).

Taxonomic differences may also have been responsible for the absence of a species-area effect in the studies of Fernandes and Price (1988, 1991). Comparisons were not made between closely related host species. The nine shrub species compared for gall species richness in these studies came from eight different families and none were from the same genus.

4.4.2 Effect of host plant geographic range size

Greater regional gall species richness on widespread members of eucalypt pairs came about because local sites were more variable in gall species composition than those of the corresponding small range eucalypt species. This suggests that between-site differentiation is the main mechanism behind the species-area effect that I found. Higher immigration rates usually proposed for larger geographic range host species may have little input into the species-area effect of gall insects on eucalypts because the patchy distribution of most eucalypt species within their geographic ranges (Chippendale and Wolf 1981), and possibly the low dispersal ability of many gall-forming insect species (Gullan and Cockburn 1986), are likely to limit immigration between sites. The size of the individual patches, rather than the total geographic range size of a host eucalypt species, would then influence local extinction rates of insect species and could result in these rates being similar on large and small geographic range host species.

4.4.3 Summary

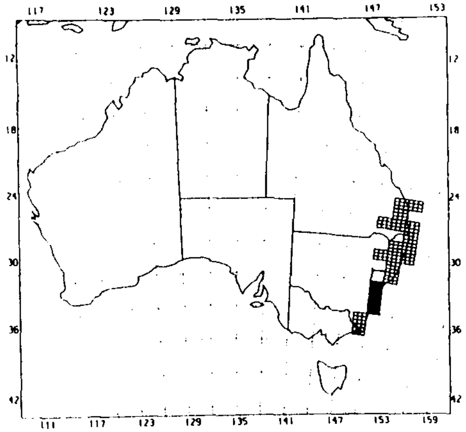
This study has shown that the relationships between gall-forming insect species richness and Australian eucalypt taxon and geographic range size are the similar to those found for insect faunas on other host plant species worldwide. There was no indication that the pattern of higher gall species richness in drier environments applies to eucalypts but further confirmation is required.

Appendix 13 EUCALYPTUS SPECIES PAIRS AND THEIR GEOGRAPHIC RANGES

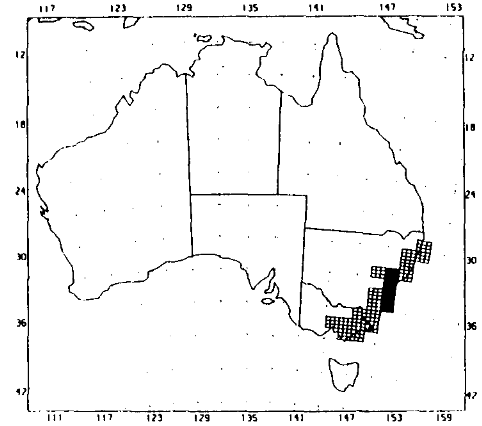
Key: Large geographic ranges - hatched grids
Small geographic ranges - white grids outlined in black
Overlap zones - black grids

Geographic range maps showing number of 1 x 1.5 degree map grids occupied, from Chippendale and Wolf (1981). Eucalyptus species taxon codes from Chippendale and Wolf (1981). The first letter of the code indicates the subgenus, subsequent letters denote subdivisions within the subgenus.
S = Symphyomyrtus, M = Monocalyptus, C = Corymbia.

Eucalyptus gummifera (Sol. ex Gaertner) Hochr.
CAFUF (19 grids)
Eucalyptus eximia Schauer CCA:E (4 grids)

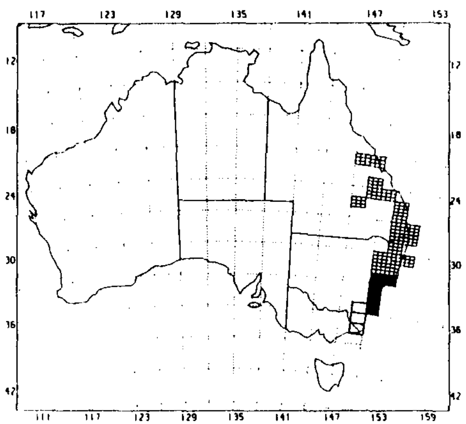


Eucalyptus globoidea Blakely MAHEF (20 grids)
Eucalyptus obstans L. Johnson & K. Hill MAKIE (4 grids)

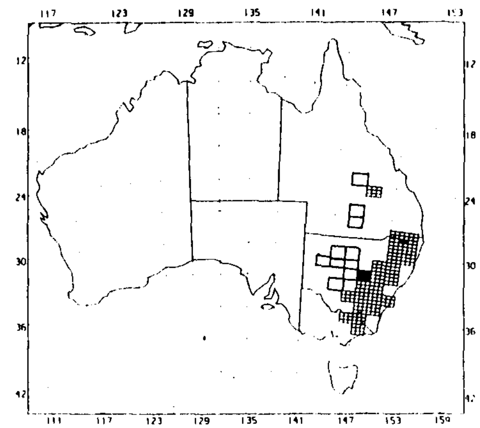


Appendix 13 (cont.)

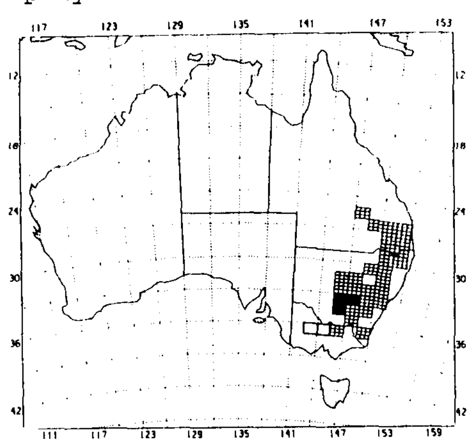
Eucalyptus saligna Smith SECAC (23 grids)
Eucalyptus longifolia Link SECGA (8 grids)



Eucalyptus blakelyi Maiden SNEEFA (23 grids)
Eucalyptus morrisii R. Baker SNEEZ (11 grids)



Eucalyptus sideroxylon sub sp. sideroxylon Cunn. ex Wools SUX:IA (29 grids)
Eucalyptus polybractea R. Baker SUNED (5 grids)



Appendix 14 GALLS ON EUCALYPT SPECIES AT DIFFERENT SITES

Key: 1 in a SITE column indicates the presence of the gall species at that site. 0 indicates absence.
Unless indicated sites in NSW.

EUCALYPT	GALL DESCRIPTION	SITE 1	SITE 2	SITE 3	SITE 4
		Mapleton SF Qld.	Jervis Bay	Castlereigh SF	Raymond Terrace
E. gummifera	swollen leaf vein	1	1	0	1
	green leaf lumps	1	1	1	1
	red stem lumps	1	0	0	0
	stem and petiole swelling	1	0	1	0
	leaf blister	0	1	1	1
	apical stem lump	0	0	0	1
	small round leaf galls	0	0	1	0
	irregular leaf lumps	0	0	1	0
	elongate stem swelling	0	0	1	0
	leaf axil lump	0	0	1	0
	leaf lump both sides	0	0	1	0
	large, flat stem cavity	0	0	0	1
		Galston Gorge	Parr SRA	Bents Basin SRA	15km W Nowra
E. eximia	round leaf lump	1	1	1	1
	small, irregular leaf lumps	1	1	1	1
	main vein leaf lumps	1	1	1	0
	mainveinleaf blisters	1	1	0	0
		Uni. Ecology Res.	27km S Bega	60km S Goulburn	4km N Murrurundi
E. globoidea	leaf blister	1	0	1	0
	purple leaf blotch	0	0	1	0
	main vein leaf pit	0	1	1	0
	pointy lumps	0	1	1	1
	large leaf lump	0	1	1	1
	main vein leaf round sphere	0	0	1	1
	stem gall	1	0	1	1
	curved stem lump	0	0	1	0
	elongate stem swelling	0	0	1	1

Appendix 14 (cont.) GALLS ON EUCALYPT SPECIES AT DIFFERENT SITES					
EUCALYPT	GALL DESCRIPTION	SITE 1	SITE 2	SITE 3	SITE 4
		Uni. Ecology Res.	27km S Bega	60km S Goulburn	4km N Murrurundi
E. globoidea	little round stem swelling	0	0	1	0
(cont.)	little round leaf spheres	0	0	1	0
	Apiomorpha pileata	0	0	1	0
	Apiomorpha sp.1	0	1	1	1
	Apiomorpha spinifer ?	1	0	1	1
	Apiomorpha sp.2	0	0	1	0
	Apiomorpha duplex	0	0	1	0
	leaf mass	0	0	0	1
	end of leaf curl	1	1	0	1
	leaf lump	0	0	0	1
	Apiomorpha sessilis ?	0	0	0	1
	main vein leaf bumps	1	1	0	0
	round leaf galls	0	1	0	0
	round green leaf lump	0	1	0	0
	large leaf edge lump	0	1	0	0
	pointed swelling at petiole base	0	1	0	0
	stem lump	1	0	0	1
	elongate stem swelling	1	0	0	0
		Jervis Bay	Wreck Bay ACT	Beaconhill	Royal NP
E. obstans	round green leaf sphere	1	1	1	1
	leaf blister	1	1	0	1
	fused leaves	0	0	0	1
	irregular red/yellow leaf lumps	1	1	1	1
	leaf dome, blister under	1	0	1	1
	elongate leaf lump	0	0	1	1
	swelling at petiole base	0	0	1	1
	round stem lumps	1	1	0	1
	Apiomorpha pileata ?	0	0	0	1
	Apiomorpha duplex	0	0	0	1
	Apiomorpha minor ?	0	1	0	1
	large multicelled stem swelling	1	1	1	1

Appendix 14 (cont.) GALLS ON EUCALYPT SPECIES AT DIFFERENT SITES

EUCALYPT	GALL DESCRIPTION	SITE 1 Jervis Bay	SITE 2 Wreck Bay ACT	SITE 3 Beaconhill	SITE 4 Royal NP
E. obstans	irregular leaf lumps	1	0	1	0
(cont.)	*Apiomorpha sp.*	0	1	0	0
	round stem lump	0	1	0	0
	little red spheres on leaf	1	0	0	0
	main vein leaf blister	1	0	0	0
		Dalrymple-Hay NR.	Wattagan SF	Collins Gap Qld	7km NW Ebor
E. saligna	curled leaf edge forming flat lump	1	1	0	1
	apical leaf mass	1	0	1	1
	fused leaves at midrib	0	0	0	1
	leaf curl from apex	0	0	0	1
	main leaf vein & stem, round sphere	1	1	1	1
	little lumps top of leaf, pits under	1	1	1	1
	little leaf lumps, both sides	0	0	0	1
	large leaf blister	1	1	1	1
	multicelled lump under main leaf vein	1	0	1	1
	irregular lumps, top of leaf	0	0	0	1
	irregular, thin, both sides leaf	1	1	1	1
	multicelled, leaf edge lumps	1	0	0	1
	round sphere leaf edge, both sides	1	0	0	1
	small lumps, petiole & main vein leaf	1	0	1	1
	little leaf blisters	1	1	1	1
	thickened main vein leaf	0	1	0	1
	leaf & stem 'pyramids'	0	1	0	1
	rough stem swelling	0	1	0	1
	spines under leaf, main vein, stems	1	1	1	0
	coccoid stem lump	1	0	1	0
	tube (? coccoid) on leaf	0	0	1	0
	black spots both sides leaf	0	1	1	0
	elongate stem swelling	1	1	1	0
	stem blisters	0	0	1	1
	elongate stem lump	0	1	1	0

Appendix 14 (cont.) GALLS ON EUCALYPT SPECIES AT DIFFERENT SITES

EUCALYPT	GALL DESCRIPTION	SITE 1	SITE 2	SITE 3	SITE 4
		Dalrymple-Hay NR.	Wattagan SF	Collins Gap Qld	7km NW Ebor
E. saligna (cont.)	small, roundish stem lumps	1	0	1	1
	large, one-celled leaf sphere	0	1	0	0
	side of leaf curl	0	1	0	0
	elongate stem pits	1	1	0	1
	lumps both sides of leaf near edge	1	1	1	0
	large, flat leaf edge lumps	0	1	0	0
	green leaf sphere, coccoid	0	1	1	0
	thin lumps both sides leaf, side veins	1	0	0	0
		27km S Bega	7km W Bodalla	Mogo	Appin
E. longifolia	tiny round leaf spheres	0	0	0	1
	leaf lumps, both sides	1	1	1	1
	leaf mass	0	1	1	1
	tiny leaf dome	0	0	0	1
	leaf blister	0	0	0	1
	side of leaf curl	0	0	1	1
	rough, round leaf galls	1	0	0	1
	round gall, one side leaf	1	1	1	1
	peaked leaf galls	0	1	1	1
	little round stem swellings	1	1	0	1
	stem swelling	0	1	1	1
	coccoid stem sewlling	1	0	0	0
	very large stem swelling	1	1	0	0
	round stem lumps	0	1	1	1
	long, thin stem galls	0	0	0	1
	large round leaf gall	1	0	0	0
	Apiomorpha karschii ?	1	0	1	0
	Apiomorpha sp.	0	1	1	0
	round leaf gall	0	1	1	0
	main vein leaf lumps	0	1	1	0

Appendix 14 (cont.) GALLS ON EUCALYPT SPECIES AT DIFFERENT SITES

EUCALYPT	GALL DESCRIPTION	SITE 1	SITE 2	SITE 3	SITE 4
		27km S Bega	7km W Bodalla	Mogo	Appin
E. longifolia	black lines on leaf veins	1	0	0	0
(cont.)	pink leaf lumps	1	0	0	0
	small, brown leaf blister	1	0	0	0
		30km S Tentfld.	3km W Qbeyan.	Goonoo SF	12km S Wyalong
E. blakelyi	fused leaves	1	1	1	1
	leaf base lump	0	1	0	1
	pale green spheres, main leaf vein	1	1	1	1
	small blotches, both sides leaf	0	0	0	1
	small, round, red leaf spheres	1	0	1	1
	leaf lumps	0	1	1	1
	rounded leaf 'pillars', near main vein	0	0.	0	1
	side of leaf roll	0	1	0	1
	woody leaf blister	0	0	1	1
	lump, main vein leaf	1	0	1	1
	rough, roundish stem gall	1	0	1	1
	elongate stem swelling	1	1	1	1
	Apiomorpha sp.1	1	0	1	1
	Apiomorpha subconica ?	1	0	1	1
	swellings, main vein leaf	0	0	1	0
	large coccoid leaf blister	0	0	1	0
	small wasp leaf blister	0	1	0	0
	round stem & petiole lumps	0	0	1	0
	peaked lump, main vein leaf	1	0	1	0
	round galls, leaf edge	0	0	1	0
	small, round stem galls	1	0	1	0
	little stem 'knobs'	0	1	0	0
	tiny red leaf spheres	0	1	0	0
	tiny leaf lumps, both sides	0	1	0	0
	irreg. red leaf folds, both sides	0	1	0	0
	round stem swelling	1	1	0	0
	double round stem swelling	1	0	0	0

Appendix 14 (cont.) GALLS ON EUCALYPT SPECIES AT DIFFERENT SITES

EUCALYPT	GALL DESCRIPTION	SITE 1	SITE 2	SITE 3	SITE 4
		30km S Tentfld.	3km W Qbeyan.	Goonoo SF	12km S Wyalong
E. blakelyi	*Apiomorpha sp.2*	1	0	0	0
(cont.)	round stem lump (? Maskellia)	1	0	0	0
	large leaf lumps	1	0	0	0
	massed small stem lumps	1	0	0	0
	lumpy, green stem rosettes	1	0	0	0
	large leaf lump	1	0	0	0
		Yathong	Girilambone	near Buckeroo Mt	5 km W Nymagee
E. morrisii	leaf mass	0	0	0	1
	small leaf spheres	1	1	1	1
	woody leaf patch	0	1	1	1
	leaf pits	1	0	0	1
	small leaf blisters	1	1	1	1
	lumps, both sides leaf	0	1	1	1
	little peaked leaf lumps	1	1	1	1
	little leaf columns	1	1	1	1
	sphere, main vein leaf & petiole	0	1	1	1
	swelling main vein with leaf curl	0	1	1	1
	main vein leaf lump	1	1	1	1
	large stem lump	0	0	0	1
	elongate stem swelling	1	1	1	1
	open stem swelling	1	0	0	1
	leaf curl pouches	0	1	1	0
	round, rough leaf axil gall	0	1	1	0
	Apiomorpha sp.	1	0	0	0
		Cocoparra NP	9km S Inglewd. Qld.	Castlereigh SF	9 km W Nymagee
E. sideroxylon	sphere on one side leaf	0	0	0	1
	blisters between leaf veins	0	0	0	1
	spheres, leaf margins	1	0	0	1
	tiny 'craters' on leaf	0	0	0	1

Appendix 14 (cont.) GALLS ON EUCALYPT SPECIES AT DIFFERENT SITES					
EUCALYPT	GALL DESCRIPTION	SITE 1 Cocoparra NP	SITE 2 9km S Inglewd. Qld.	SITE 3 Castlereigh SF	SITE 4 9 km W Nymagee
E. sideroxylon	main vein leaf lump	1	1	1	1
(cont.)	pits, both sides leaf	0	1	1	1
	leaf blisters, both sides	1	0	1	1
	multicelled leaf lumps	0	1	0	1
	large leaf spheres	0	1	1	1
	fold in leaf	0	0	0	1
	leaf roll	1	0	1	1
	peaked blister on leaf	0	0	0	1
	petiole swelling	0	0	0	1
	large round stem lumps	1	0	1	1
	elongate stem swelling	1	0	1	1
	large stem swelling	0	1	0	1
	Apiomorpha sp.1	0	0	1	0
	'pimples' under bark	0	0	0	1
	'star' psyllid on leaf	0	0	1	0
	psyllid gall on leaf	0	0	1	0
	little leaf lumps	0	1	1	0
	coccoid stem gall	1	1	0	0
	little leaf spheres	1	1	0	0
	Apiomorpha urnalis	1	0	0	0
	Apiomorpha munita	1	0	0	0
	Apiomorpha sp.2	1	0	0	0
		1km SW W Wyalong	8km W W Wyalong	10km S W Wyalong	W Wyalong
E. polybractea	leaf lumps, both sides	0	1	1	1
	leaf blister	0	1	0	1
	side of leaf blister causing curl	0	1	1	1
	leaf curl	1	1	1	1
	main vein leaf lump	1	1	1	1
	green leaf lump	1	1	1	1
	round stem lump	0	1	1	1
	elongate stem swelling	1	1	1	1

Appendix 14 (cont.) GALLS ON EUCALYPT SPECIES AT DIFFERENT SITES

EUCALYPT	GALL DESCRIPTION	SITE 1 1km SW W Wyalong	SITE 2 8km W W Wyalong	SITE 3 10km S W Wyalong	SITE 4 W Wyalong
E. polybractea	stem swellings at stem junctions	0	1	1	1
(cont.)	*Maskellia sp. ?*	1	0	1	1
	green cone on leaf	0	1	1	0
	small round stem spheres	1	1	1	0
	Apiomorpha sp.1	0	1	1	0
	Apiomorpha sp.2	1	1	0	0
	Apiomorpha munita	0	1	1	0
	Apiomorpha urnalis	1	0	1	0
	leaf pit & lump	1	1	0	0
	round leaf galls	1	0	0	0
	little peaked leaf gall	1	0	0	0
	leaf bud gall	1	0	0	0
	Apiomorpha sp. 3	1	0	0	0
	large stem lump	1	0	0	0
	round, peaked, main vein & petiole	1	0	0	0
	flat, round leaf spots	1	0	0	0

CHAPTER 5

THE EFFECT OF HOST PLANT TAXON, GEOGRAPHIC RANGE SIZE AND RAINFALL ZONE ON GALL-FORMING INSECT SPECIES RICHNESS ON AUSTRALIAN ACACIAS

5.1 Introduction

This study was designed to determine the effect of host plant taxonomic group, geographic range size, and rainfall zone on the number of gall-forming insect species associated with an acacia species. The study arose from the previous study of gall insect species richness on *Eucalyptus* (Chapter 4) and was set up to discover whether the relationships obtained for *Eucalyptus* applied to other Australian plant genera.

The study on *Eucalyptus* identified a positive relationship between regional gall species richness and eucalypt geographic range size when host plant taxonomic group was taken into account. Local gall species richness was not related to host plant geographic range size in that study, so the species-area effect was due to between-site differentiation only. There were insufficient data available from the eucalypt study to test whether the rainfall zone in which the host plant was found affected gall species richness. There was no apparent trend for gall species richness to be higher on eucalypts from drier areas than on eucalypts from wetter areas.

Acacia was chosen as the host genus on which to test whether the patterns found for *Eucalyptus* generalized to a different radiation of gall species because *Acacia* appeared to be another gall-prone Australian plant genus (Table 2.1). Australian acacias are known to be galled by flies (Cecidomyiidae), wasps (Chalcidoidea) and thrips (Phlaeothripinae) (Appendix 1).

Acacia comprises over 750 species in Australia (Morrison and Davies 1991). Acacias are shrubby or tree-like plants. Some Australian acacia species have bipinnate adult leaves but most have phyllodes, modified petioles, in place of true leaves.

I addressed the following questions:

1) Does acacia taxon influence the size of gall insect assemblages?

2) Do acacia species with large ranges:

a) have more regional gall species

b) have more local gall species

c) share fewer gall species between local sites

than acacia species with small ranges do?

3) Do acacia species with geographic ranges predominantly in low rainfall regions:

a) have more regional gall species

b) have more local gall species

c) share fewer gall species between local sites

than acacia species with geographic ranges predominantly in high rainfall regions do?

To answer these questions I surveyed gall species richness, in the field, on closely related pairs of large and small range acacia species from both low and high rainfall regions of NSW, Australia.

5.2 Methods

The study area covered regions of N.S.W. from latitude 29° 30' to latitude 35° 50' and extended from the coast and adjacent tablelands inland to the western slopes and plains. The median annual rainfall on the coast and tablelands ranges from 600 mm to 1600 mm. On the western slopes and plains areas included in this study the median annual rainfall range is from 200 mm to 600 mm (Parkinson 1986).

The survey was carried out from October 1993 to November 1994. Surveys of gall species on perennial plants are not subject to the same seasonal constraints as surveys of more ephemeral free-living insects would be. Gall insects leave relatively long-lasting evidence of their occupancy of such a host plant.

Gall-forming insect species richness was measured on 16 acacia species. The geographic range size of an acacia species was estimated as the number of mapsheet districts in which it occurred (Maslin and Pedley 1982). Each mapsheet district covered

1^0 latitude by 1.5^0 longitude (about 136 x 115 kilometres). Eight acacia species were selected as having small ranges (< 10 mapsheet districts) and eight were selected as having large ranges (≥ 10 mapsheet districts). Within each range size category four acacia species were selected with ranges predominantly in regions of > 600 mm median annual rainfall and four with ranges predominantly in regions of < 600 mm median annual rainfall (Parkinson 1986).

In order to cover a broad cross-section of acacia types, each group of four acacia species comprising each range size/rainfall region category was chosen so that representatives from Botrycephalae, Phyllodineae, Plurinerves and Juliflorae *Acacia* sections (as defined by B. Maslin (pers. comm.)) were included. Acacias from section Botrycephalae have bipinnate adult leaves, those from the other sections are phyllodinous acacias. Maps showing the acacia species pairs and their geographic ranges are in Appendix 15.

Each acacia species was sampled at two sites. Acacia species site locations were obtained from labels on voucher specimens held at the Royal Botanical Gardens Herbarium, Sydney, NSW. The sites were as widely separated as possible within each acacia's range. Two sites per species is obviously too few to give a comprehensive coverage of regional gall species richness, but I chose to sample many acacia species at two sites each, rather than fewer species at many sites, because the power of the study to test for effects of geographic range size and rainfall zone depended on the number of species, rather than on the number of sites examined within each species. Time constraints prevented sampling of many acacia species at many sites. Acacias were identified in the field using keys and descriptions in Morrison and Davies (1991) and Cunningham, Mulham, Milthorpe and Leigh (1992).

At each site 10 individuals were searched for insect induced galls. Juvenile as well as adult plants were always included. Preliminary searches had shown that no new gall species were encountered after sampling about eight acacia plants. Samples of all galls encountered were collected and identified to morphospecies. In most cases the morphology of a gall is distinctive for a gall insect species. Consequently morphospecies has become an accepted substitute for species among those who study gall-forming insects. For brevity morphospecies will be referred to as species in the rest of this chapter.

Dried voucher specimens of each acacia species and its galls were stored in the Herbarium, School of Biological Sciences, Macquarie University, North Ryde, NSW. Wet (ethanol and glycerine) specimens of all insects found in the galls were lodged at the C.S.I.R.O., Institute of Plant Production and Processing, Division of Entomology, Canberra, ACT.

The sum of the different gall species from two sites (a measure of regional richness), mean number of gall species per site (local species richness), and mean percentage of gall species shared between individual sites were calculated for each acacia species from the field data. In addition, the different kinds of gall species on an acacia were classified according to whether they occurred on flowerbuds, seed-pods, stems (including phyllodes), or true leaves. The mean number of each kind of gall per acacia species was calculated for each taxon group.

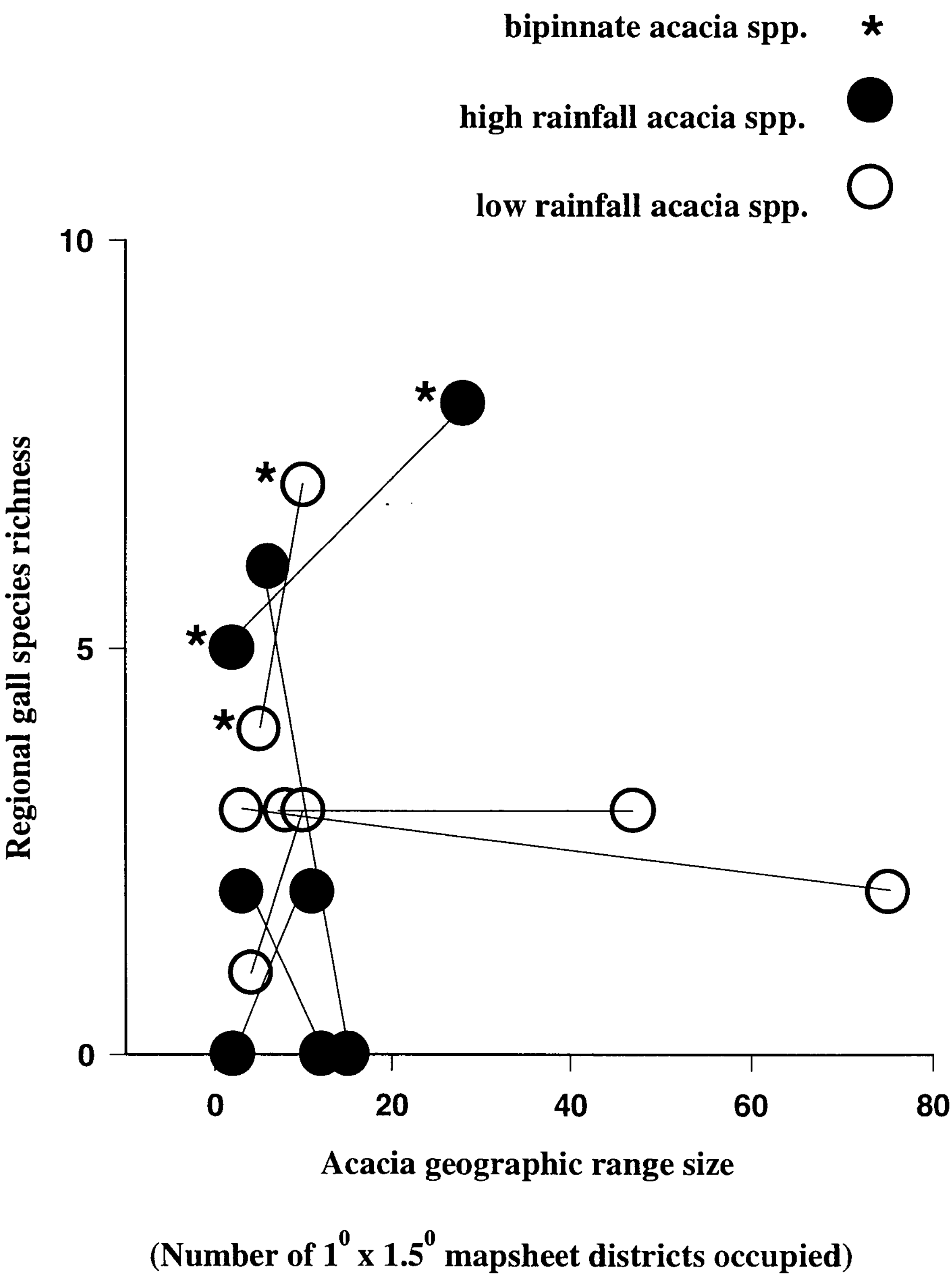


Figure 5.1 Regional gall species richness on pairs of closely related acacia species (pairs are joined by lines) with ranges in high or low rainfall zones. Each pair comprises a small and a large range acacia species.

5.3 Results

Descriptions of the gall species on each acacia species, at each sampling site, are given in Appendix 16. Acacias were far less gall-prone than eucalypts. The number of gall species at a site for the acacia species of this study varied from zero to seven (mean = 2.3, S.D. ± 1.9). Eucalypt species in my previous study (Chapter 4) had from two to twenty one gall species per site (mean = 11.1, S.D. ± 4.9).

Inspection of regional gall species richness for the 16 acacia species (Fig. 5.1) suggests that section Botrycephalae (bipinnate acacia species) had more gall species than the other acacia taxa but that there were no consistent relationships with host geographic range size or rainfall zone.

Table 5.1 One-way analysis of variance with regional gall species richness as the dependent variable and acacia taxon group as the treatment variable.

Source	Sums-of-squares	df	Mean-square	F-ratio	P
taxon	47.19	3	15.73	4.52	0.02
error	41.75	12	3.48		

One-way analysis of variance with taxon as the only factor showed that the effect of taxon on regional gall species richness was significant (Table 5.1). As Fig. 5.2 indicates, galling in section Botrycephalae was outstandingly higher than in sections Plurinerves and Phyllodineae. Section Juliflorae was in the overlap zone between Botrycephalae and the other two sections.

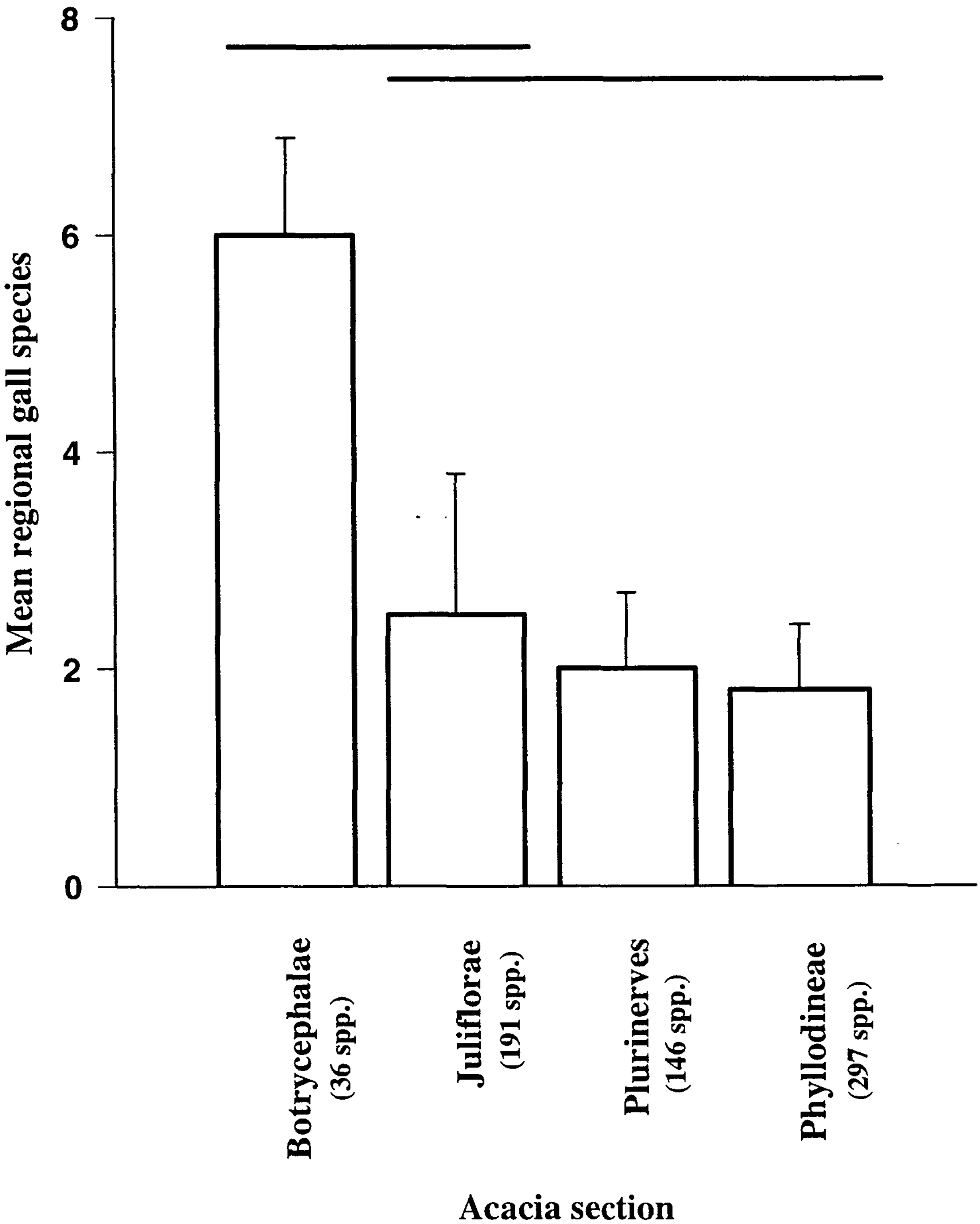


Figure 5.2 Comparison of mean regional gall species richness between the four acacia taxa of the study. Lines above graph bars connect taxa that were not significantly different (Tukey HSD, $P > 0.05$). Error bars are SE. Number of described species in each acacia section B. Maslin (pers. comm.)

Table 5.2 Different kinds of gall species on acacias from four *Acacia* sections. Acacia species in section Botrycephalae are bipinnate, the others are phyllodinous. Galls were grouped according to galling site on the plant. The category of 'stem' includes stems and modified petioles (phyllodes).

	Mean number of gall species/acacia species			
Acacia section	Flowerbud	Seed-pod	Stem	True Leaf
Botrycephalae	0.5	0.75	2	2.75
Phyllodineae	0.5	0	0.5	-
Plurinerves	0.25	0.25	1.5	-
Juliflorae	0.25	0.25	2	-

Table 5.2 lists the mean number of gall species per acacia species in each category (flowerbud, seed-pod, stem, or leaf) for each acacia taxon group. It shows that a large proportion of the galls on bipinnate acacias were on true leaves, the habitat that is absent on phyllodinous acacias, and that the bipinnate acacias did not have notably more gall species than the phyllodinous acacias on other plant parts.

For the purpose of testing the interaction effects of host plant taxon, geographic range size and rainfall zone on gall species richness the replicates were the acacia species, not the sites. As there was only one species in each cell of the 2 x 2 x 4 design, no sum of squares (SS) for the three-way interaction among taxon, range size and rainfall zone could be estimated separately from the error SS. None of the separate factors or interactions significantly influenced regional gall species richness (Table 5.3).

Similar analyses of the effect of host plant taxon, range size and rainfall zone on local gall species richness (Table 5.4), and on the degree of gall species sharing between local sites (Table 5.5), were performed. These tests were done to distinguish between area or rainfall zone per se, and between-site differentiation, as causes of regional species-area or species-rainfall zone effects respectively. None of the effects were strong enough to be statistically significant.

Table 5.3 Three-way analysis of variance with regional gall species richness as the dependent variable and acacia taxon group, geographic range size and rainfall zone as the treatment variables. The three-way interaction term was used as the error.

Source	Sum-of-squares	df	Mean-square	F-ratio	P
taxon	47.19	3	15.73	3.33	0.18
size	0.06	1	0.06	0.01	0.92
zone	0.56	1	0.56	0.12	0.75
taxon*size	16.19	3	5.40	1.14	0.46
taxon*zone	7.69	3	2.56	0.54	0.69
size*zone	3.06	1	3.06	0.65	0.48
error	14.19	3	4.73		

Table 5.4 Three-way analysis of variance with mean local gall species richness as the dependent variable and acacia taxon group, geographic range size and rainfall zone as the treatment variables. The three-way interaction term was used as the error.

Source	Sum-of-squares	df	Mean-square	F-ratio	P
taxon	27.05	3	9.02	3.71	0.16
size	0.39	1	0.39	0.16	0.72
zone	0.14	1	0.14	0.06	0.83
taxon*size	9.42	3	3.14	1.29	0.42
taxon*zone	7.67	3	2.56	1.05	0.48
size*zone	3.52	1	3.52	1.45	0.32
error	7.30	3	2.43		

Table 5.5 Three-way analysis of variance with % of gall species shared between local sites as the dependent variable and acacia taxon group, geographic range size and rainfall zone as the treatment variables. The three-way interaction term was used as the error.

Source	Sum-of-squares	df	Mean-square	F-ratio	P
taxon	504.50	3	168.17	0.09	0.96
size	1560.25	1	1560.25	0.85	0.43
zone	1600.00	1	1600.00	0.87	0.42
taxon*size	3214.25	3	1071.42	0.58	0.67
taxon*zone	1999.50	3	666.50	0.36	0.79
size*zone	1980.25	1	1980.25	1.08	0.38
error	5524.25	3	1841.42		

It is hard to explain why the effect of host plant taxon on regional gall species richness should have been significant in the one-way anova (Table 5.1) but not in the three-way anova (Table 5.3). Such a difference can only come about when in the three-way analysis, interaction terms involving taxon take up, by chance, substantial variation that was allocated to error in the one-way analysis. Considering the obvious difference between bipinnate and phyllodinous acacias in Fig. 5.1, the small absolute number of gall species on phyllodinous acacia taxa, and the fact that the interaction terms involving taxon have no credible biological interpretation, I am inclined to believe that host taxon does influence gall species richness as suggested by the one-way anova.

5.4 Discussion

5.4.1 Host plant taxon

The influence of host plant taxon on gall species richness was recognised by Cornell (1985a) who showed that white oaks have richer gall assemblages (on leaves) than primitive oaks, which have richer gall assemblages than black oaks. He attributed this result to a corresponding pattern among these *Quercus* subgenera in which the white oak subgenus is more speciose than the primitive oak subgenus, which in turn is more speciose than the black oak subgenus.

My work on eucalypts (Chapter 4) also showed the importance of taxonomic effects on gall species numbers. The species-area effect was only present when eucalypt subgroup was taken into account. There were indications that the number of species in a eucalypt subgenus, and the number of close relatives of a eucalypt species that occurred in the study region, were positively related to the size of the gall assemblages on a eucalypt.

In my study of acacias the section which had the most galls, Botrycephalae, is not the most speciose of the four acacia sections (Fig. 5.2) and has fewer species in the study area than the other sections (Maslin and Hnatiuk 1987). The influence of acacia taxon on gall species richness must be different from that of oak and eucalypt taxa. The effect of acacia taxon is likely to be due to the major structural difference, presence or absence of true leaves, between bipinnate and phyllodinous acacia groups. Both kinds of acacia can have galls on flowerbuds, seed-pods and stems (including modified stems, petioles, that have become phyllodes) but only bipinnate acacias can support insect species that gall true leaves. Although phyllodes appear to be functional substitutes for true leaves, and often look like true leaves, they are apparently not equivalent to leaves as galling sites. Phyllodinous acacias probably lack whole suites of leaf-galling insect species which attack bipinnate acacias.

5.4.2 Host plant geographic range size

The positive relationship between host plant range size and regional gall species richness, found within subgenus groups of Australian eucalypts and for gall assemblages in other parts of the world (Chapter 4) did not apply to the acacias in this study. As no regional species-area effects were detected by my study, the absence of any effects of host range size on local gall species numbers, or on degree of sharing between local sites, was to be expected.

Ideally, a greater contrast in geographic range size, which may have more readily demonstrated an effect of range size on gall species richness, would have been obtained for all acacia species pairs. However, as Fig. 5.1 shows, even out of the three cases where the difference in geographic range size between the small and large range acacia species was substantial, with the larger range species occupying ≥ 28 regions, only one of the contrasts showed the predicted pattern.

A factor perhaps more likely to have masked a species-area effect was the low absolute numbers of gall insect species on phyllodinous acacia species (only one of the 12 species having more than three gall species) and the proportionately high chance variation. It is notable that for the bipinnate acacias, where regional numbers of gall species were four to eight per acacia species, both pairs showed the predicted relationship with geographic range size.

5.4.3 Host plant geographic range rainfall zone

Fernandes and Price (1988, 1991) have collected evidence which shows that there are greater numbers of gall species on vegetation in dry environments than in mesic environments. Their study of gall populations in Minas Gerais, Brazil and Arizona, United States suggested that xeric sites provide relatively disease and enemy free habitats for gall-forming insects compared with mesic sites (Fernandes and Price 1992). This finding led them to propose the difference in the impact of pathogens, parasitoids, and possibly gall eating herbivores, as the mechanism responsible for the observed difference in gall species richness between the two kinds of environment.

The emerging pattern of greater gall-forming insect diversity in drier regions did not appear to apply to Australian eucalypts (section 4.3.2) and did not apply to the acacias studied here. The low absolute numbers of gall species on phyllodinous acacias is unlikely to be responsible for this result because the expected relationship between gall species richness and rainfall zone was not evident even in the bipinnate acacias. In both the small range size bipinnate acacia pair and the large range size pair it was the species from the high rainfall environments which had the most gall species (Fig. 5.1).

The absence of a species-rainfall zone effect may indicate that the proposed reduction of disease and enemies in dry environments does not occur in dry Australian environments. Alternatively, other effects may counteract any tendency, driven by these factors, for larger gall species assemblages in low rainfall areas.

The Australian environment is characterised by soils of low fertility (Bowen 1981, White 1986). This has resulted in predominantly sclerophyllous vegetation (plants with hard, tough leaves) even in many high rainfall areas. Fernandes and Price (1991) included sclerophylly among plant characteristics which may favour galling. They suggest that the aspects of sclerophylly which promote galling are related to increased longevity of leaves and high levels of secondary compounds. In Australia, the favourable effect of sclerophylly in high rainfall areas may override the proposed disadvantages of more enemies and diseases of gall insects in such environments.

Another potentially important effect is related to the reliability of rainfall and its influence on acacia growth patterns. Many gall-forming insects require actively growing plant tissue for gall initiation. Although some acacias sprout readily in response to fire or other damage, most have only one reliable growth flush per year (New 1984). This usually occurs after flowering which is stimulated by rain. If rainfall does not always occur at a suitable time (as is more likely in the low rainfall areas of this study (Parkinson 1986)) then the flowerbuds, fruits and other actively dividing plant parts required for gall initiation will not be available each year. This could counteract the proposed favourable effect of reduced pressure of enemies and diseases in dry areas.

5.4.4 Summary

This study of Australian acacias has confirmed the importance of the influence of host plant taxon on gall species numbers identified for Australian eucalypts. It shows that taxon size, in terms of both absolute species richness and number of co-occurring species, which seemed to be responsible for differences in galling between some eucalypt subgenera, does not effect gall species richness in acacias. Instead, it is the difference in a particular characteristic, the presence or absence of true leaves, which best explains the difference in galling between acacia taxa.

In contrast to the study on eucalypts, host plant geographic range size had no detectable effect on gall species richness on acacias. It seems likely that this outcome was due more to the small absolute numbers of gall species on most acacias in the study, resulting in large stochastic effects relative to the mean, than a real absence of a species-area effect.

Both my eucalypt and my acacia studies failed to provide any evidence that dry environments favour galling in Australia. The reasons for this lack of correspondence with patterns elsewhere may relate to the predominantly sclerophyllous nature of Australian vegetation in both low and high rainfall areas and the less reliable rainfall in drier areas.

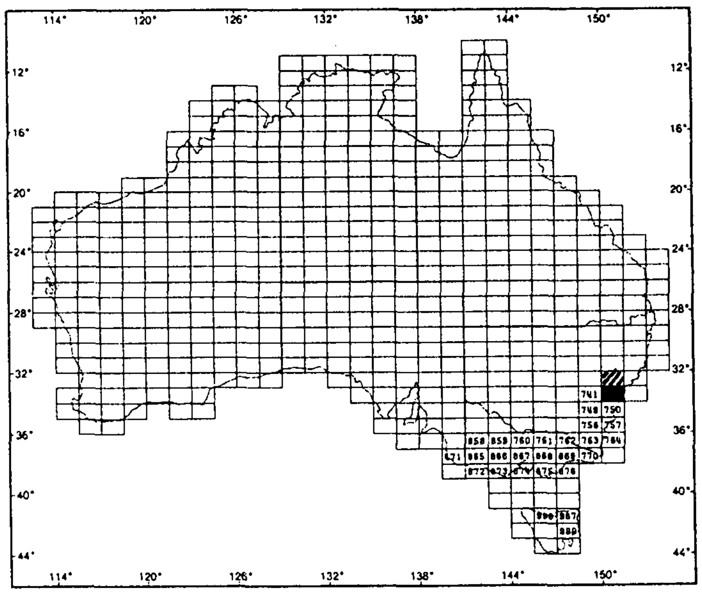
Appendix 15 ACACIA SPECIES AND THEIR GEOGRAPHIC RANGES

Key: Large geographic ranges - numbered grids
(three digit number grid designation (Brook 1977)
Small geographic ranges - striped grids
Overlap zones - black grids

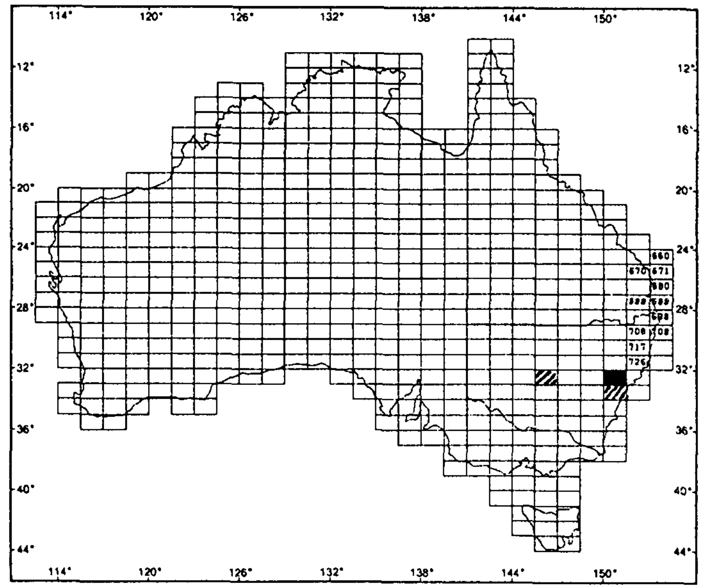
Geographic range maps showing number of 1 x 1.5 degree map grids occupied, modified from Maslin and Pedley (1982).
Acacia species section classifications from B. Maslin (pers. comm.).

HIGH RAINFALL ZONE ACACIA SPECIES

SECTION Botrycephalae
Acacia mearnsii De Wild. (28 grids)
Acacia schinoides Benth. (2 grids)



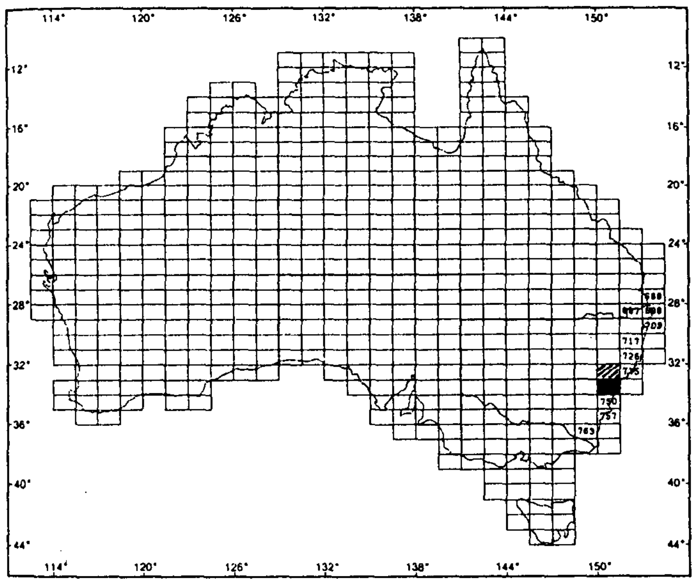
SECTION Phyllodineae
Acacia quadrilateralis D.C. (12 grids)
Acacia prominens A. Cunn. ex G. Don (3 grids)



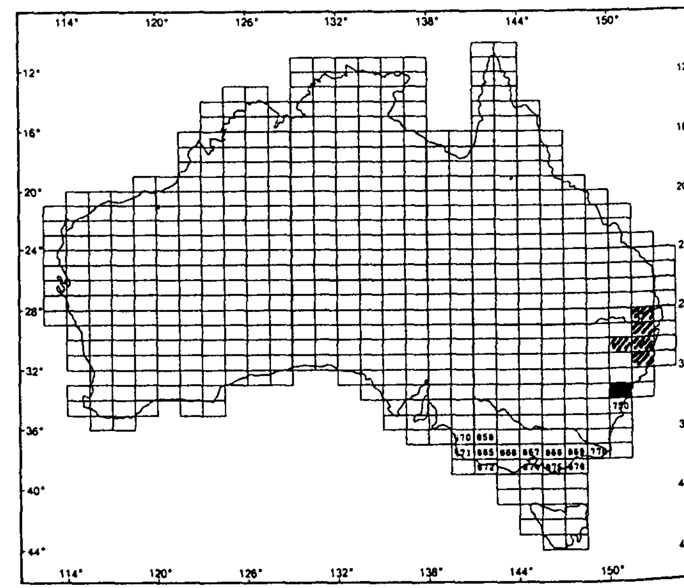
Appendix 15 (cont.) ACACIA SPECIES AND THEIR GEOGRAPHIC RANGES

HIGH RAINFALL ZONE ACACIA SPECIES (cont.)

SECTION Plurinerves
Acacia binervata D.C. (11grids)
Acacia trinervata Sieber ex D.C. (2 grids)



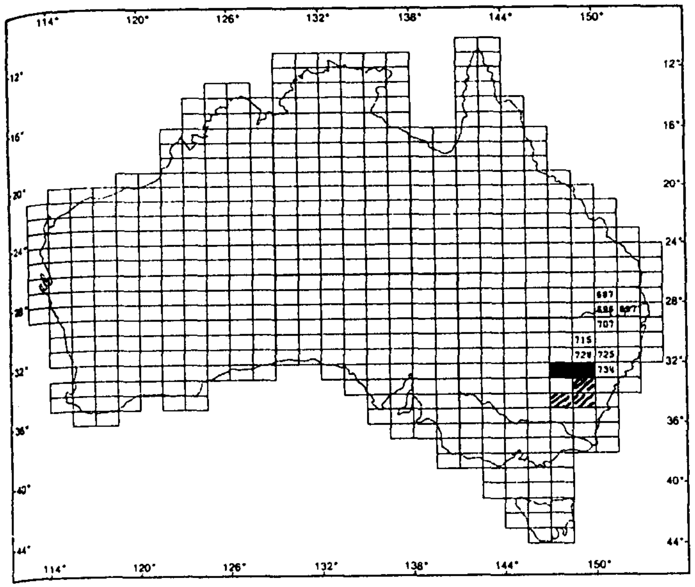
SECTION Juliflorae
Acacia oxycedrus Sieber ex D.C. (15 grids)
Acacia diphylla Tindale (6 grids)



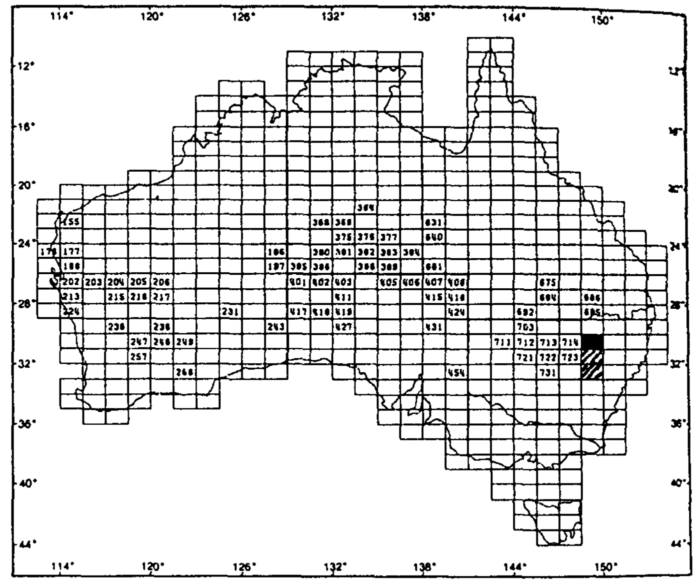
Appendix 15 (cont.) ACACIA SPECIES AND THEIR GEOGRAPHIC RANGES

LOW RAINFALL ZONE ACACIA SPECIES

SECTION Botrycephalae
Acacia polybotria Benth. (10 grids)
Acacia mollifolia Maiden & Blakely (5 grids)



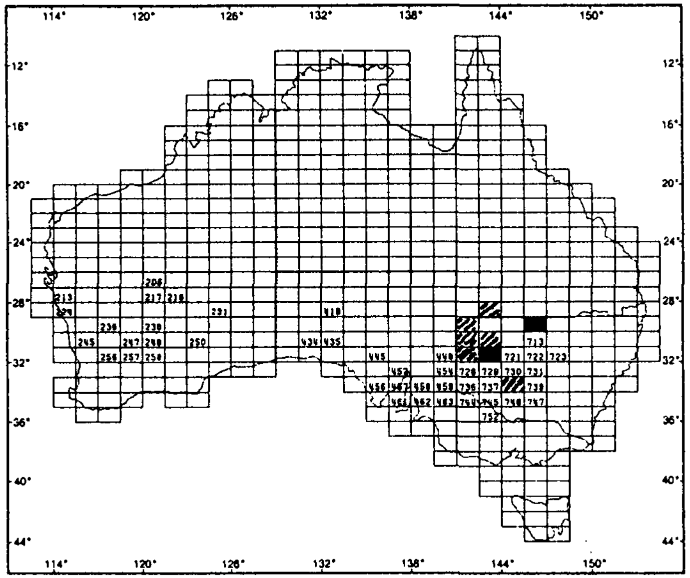
SECTION Phyllodineae
Acacia murrayana F. Muell. ex Benth. (75 grids)
Acacia pilligaensis Maiden (3 grids)



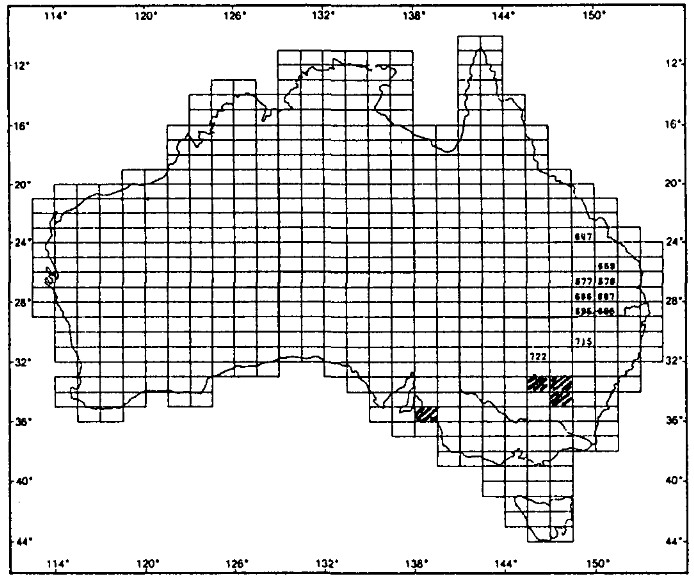
Appendix 15 (cont.) ACACIA SPECIES AND THEIR GEOGRAPHIC RANGES

LOW RAINFALL ZONE ACACIA SPECIES *(cont.)*

SECTION Plurinerves
Acacia colletioides Benth. (47 grids)
Acacia cana Maiden (8 grids)



SECTION Juliflorae
Acacia burrowii Maiden (10 grids)
Acacia rhigiophylla F. Muell. ex Benth. (4 grids)



Appendix 16 GALLS ON ACACIA SPECIES AT DIFFERENT SITES

Key: 1 in a SITE column indicates the presence of the gall species at that site. 0 indicates absence. All sites in NSW.

ACACIA SPECIES	GALL DESCRIPTION	SITE 1	SITE 2
		Termeil	Tomago River
Acacia mearnsii	stem pits	1	0
	pinnule mass	1	0
	round pinnule gall	1	1
	small black-centred pinnule gall	1	0
	'star' gall	1	1
	round stem swelling	1	1
	enlarged flower	1	1
	seed pod gall	0	1
		Brown's Field, Wahroonga	Wattagan SF
Acacia schinoides	swollen phyllode base	1	1
	'star' gall	1	1
	round phyllode lump	1	1
	swollen glands on rachis	0	1
	large stem lump	0	1
		Near old Nabiac airfield	22km NW Grafton
Acacia quadrilateralis	No galls found on this acacia	0	0
		Mooney Mooney Creek	15km S Bulga
Acacia prominens	fused apical phyllodes	1	1
	black phyllode blisters	0	1
		Near old Nabiac airfield	2km S Woolgoolga
Acacia binervata	flat phyllode lump	1	0
	round phyllode lump	1	0

Appendix 16 (cont.) GALLS ON ACACIA SPECIES AT DIFFERENT SITES

ACACIA SPECIES	GALL DESCRIPTION	SITE 1	SITE 2
		3km SW Wallacia	Colo Heights
Acacia trinervata	No galls found on this acacia	0	0
		Brooklyn	Peats Ridge
Acacia oxycedrus	No galls found on this acacia	0	0
		Baker's Creek Falls LO	21km NW Gloucester
Acacia diphylla	phyllode lump	1	1
	deformed seed pod	1	0
	flower bud gall	1	0
	swollen phyllode	1	1
	swollen branchlets	1	1
	elongate stem swelling	0	1
		15km N Coonabarabran	Coghill Creek
Acacia polybotrya	'cotton wool' gall	1	1
	tiny black pinnule lumps	1	0
	pinnule 'star' gall	1	1
	'witches broom' leaf mass	1	1
	elongate stem swelling	0	1
	swollen leaf petiole	0	1
	round stem swelling	0	1
Acacia mollifolia		Between Trewillga & Molong	Between Orange & Parkes
	round stem swelling	1	1
	elongate stem swelling	1	0
	seed pod gall (wasp)	1	0
	seed pod gall (fly)	0	1

Appendix 16 (cont.) GALLS ON ACACIA SPECIES AT DIFFERENT SITES

ACACIA SPECIES	GALL DESCRIPTION	SITE 1	SITE 2
		7km SE Nyngan	27km NE Byrock
Acacia murrayana	elongate stem swelling	1	1
	large round stem galls	1	0
		Goonoo SF	55km S Narrabri
Acacia pilligaensis	stem swelling	1	0
	phyllode lump	1	1
	flower bud gall	0	1
		Cobar	Shuttleton, W Nymagee
Acacia colletioides	phyllode lump	1	1
	flower bud gall	1	1
	lumpy phyllode	1	1
		70km NW Wilcannia	60km NW White Cliffs
Acacia cana	minute phyllode lumps	1	0
	stunted seed pods	1	1
	flat phyllode lump	1	0
		2km SE Narrabri	60km NW Coonabarabran
Acacia burrowii	phyllode lump	1	1
	swollen, bent stems	1	0
	tiny, black-centered phyllode spots	1	1
		1km S Alleena	6km SW West Wyalong
Acacia rhigiophylla	large round stem swelling	1	0

CHAPTER 6

GENERAL DISCUSSION

The intimate nature of the relationship between specialist organisms, like gall-forming insects, and the plants that they rely on for food and shelter, means that the characteristics of a host plant species have the potential to strongly affect the diversity of the gall insect species that the plant supports. This thesis has investigated several plant features that are likely to have an impact on how favourable a plant species is for galling in Australia. Evidence was drawn from the data base derived from literature and museum records; from the comparative field study of gall diversity on native vegetation at sites of low and high fertility near Sydney, NSW; and from wider scale field surveys of gall species richness, on eucalypts and acacias, throughout NSW and southern Queensland.

The conclusions of the thesis are outlined below and compared with patterns found for gall insect/host plant associations in other countries. Other potentially important plant characteristics are then examined. Finally, a summary of the factors likely to influence gall-forming insect species diversity in this country is presented in the form of a profile of a gall-prone Australian plant species.

6.1 Australian gall insects

The literature and museum records indicated that, as in other countries, gall induction in Australia is confined to a few insect taxa. The taxonomic composition of the gall insect fauna and the relative importance of each gall insect group varies in different parts of the world. In Australia cecidomyiid flies and chalcidoid wasps are the most prevalent gall inducers, psyllids and coccoid bugs are common gallers, and galls caused by other flies, thrips, beetles and lepidopterous insects are least common (sections 2.1.3, 2.1.4).

6.2 Factors tested in the thesis

This section discusses the main conclusions of the four thesis surveys and compares them with the findings of other studies. The evidence regarding the factors influencing gall species richness is summarised in Table 6.1.

Table 6.1 Potential determinants of gall-forming insect species richness

Sources of evidence regarding the influence of soil fertility, host plant taxon, host plant geographic range size and host plant geographic range rainfall zone on gall species richness. Code: xxx = a strong, clear-cut effect, xx = a weaker but still significant effect, x = effect suggestive, but marginal or not significant, 0 = no effect. Not applicable (n/a) indicates that the survey did not test that factor.

		SOURCE		
FACTOR	Data base	Soil fertility field study	Eucalypt field survey	Acacia field survey
Host plant taxon	xxx	*xxx	xxx	xx
Soil fertility	0	**xxx	n/a	n/a
Range size	xx	n/a	xxx	x
Rainfall zone	0	n/a	0	0

*Study not designed to test for this factor. The conclusion was strong but a posteriori.

**Effect of soil fertility was strong but via host plant taxon

6.2.1 Host plant taxon

Host plant taxon emerged as an important determinant of gall-forming insect species richness in all three of the thesis surveys, respectively comparing eucalypts to other plants, subgenera within *Eucalyptus*, and subtaxa within *Acacia*. More than 75% of known Australian gall insect species are on plant species from only four genera (Table 2.1). As outlined in section 6.2.2 below, the effect of soil fertility on galling was an indirect one, via host plant taxon.

Concentration of galling in only a few plant groups is a world-wide phenomenon (section 2.1.7). Some notably gall-prone genera are *Quercus,* in the United Kingdom (Askew 1961) and North America (Cornell 1985a), *Populis* and *Salix* in North America (Price 1992) and *Rosa* in North America (Felt 1940).

One way in which the assemblages of gall species on host plant species may be augmented is by sharing of gall species between closely related host species. Within the most gall-prone Australian plant genus, *Eucalyptus*, plant species with the most gall species were from the more speciose subgenera, (sections 2.2.3, 2 2.6 and 4.4.1) and from subgenera with many species in a region (section 4.4.1). These findings concur with those of Cornell (1985a) who identified a positive relationship between *Quercus* subgenus size and number of cynipid wasp species galling leaves. Taxon size has also been shown to influence galling at the family level. Fernandes (1992) found a positive relationship between gall species richness and plant family size in Indonesia.

On the other hand, the effect of taxon size did not appear to be responsible for differences in gall species richness between the A*cacia* species surveyed in this thesis (section 5.4.1). Instead, the striking structural difference between taxon groups, the presence or absence of true leaves, was the major factor affecting gall species richness in this plant genus. Other structural, chemical and phenological differences between host plant taxa are likely to affect galling within a plant genus but to date these have not been investigated for other plant genera.

6.2.2 Soil fertility

Data base information, presented in sections 2.2.2.and 2.2.6, on galling within the genus *Eucalyptus,* gave no indication of a relationship between lower soil fertility and higher numbers of gall species.

The comparison of gall species richness at relatively infertile and fertile soil sites, described in Chapter 3, indicated that soil fertility affected galling through its effect on the composition of the plant assemblages at a site. There were more myrtaceous tree species, especially eucalypts, on less fertile soil sites. Myrtaceous trees were more susceptible to galling than other categories of plant.

Myrtaceous tree species at infertile sites did not have higher gall species richness than those at fertile sites (Fig. 3.3) and many plant groups at the infertile sites were sclerophyllous but did not have many galls (Appendix 11). Thus the evidence suggests that the attributes of sclerophyllous vegetation proposed to favour galling, long-lived parts

(Fernandes and Price 1988, 1991) and high concentrations of protective secondary compounds (Cornell 1983, Taper and Case 1987), do not by themselves explain patterns of galling in Australia. However, the fact that gall-prone myrtaceous trees had high proportions of complex galls, likely to require long-lived parts and long-term protection from enemies, suggests that these factors play some part in determining gall species richness.

The importance of leaf longevity and plant secondary compounds needs to be tested more directly by measurement of these characteristics and their comparison with gall diversity. Ideally these would be phylogenetically independent comparisons between plant lineages with many gall species and those with few, or no gall species. The time at which secondary compounds become abundant in developing plant tissues could be included in such studies. Having high concentrations of protective chemicals in young as well as older plant tissue, as described for eucalypt leaves in section 3.4, may promote galling more than just having such protection in older tissues.

In Australia there are often long dry periods even in regions with a relatively high annual rainfall (Linacre and Hobbs 1977). Many plants wilt during prolonged dryness, causing photosynthesis to slow or stop. This could have an adverse effect on insects inhabiting galls. Unlike external insect herbivores which are able to utilise suitable existing plant tissue at many sites on a plant, gall-forming insects may require constant replenishment of nutrients, at the gall site, to maintain an adequate food supply. The rigid nature of sclerophyllous leaves helps prevent their collapse during drying and so allows photosynthesis to continue (Turner 1994). Plants which continue to photosynthesise during dry periods would provide a continuous flow of nutrients, and thus are likely to be better hosts for gall insects, than plants which cut off the food supply. The impact of this aspect of sclerophylly on gall-forming insects would be worth further investigation.

Fernandes and Price (1991) have suggested that the high concentration of nutrients in high nutrient status plants may be toxic to gall-forming insects. If correct, this could be another reason to expect more gall species on infertile soil vegetation than on fertile soil vegetation. So far the little evidence available on this question does not support the hypothesis. Fertilising host plants does not result in an increase in nutrients in galls (Hartley

1990, Hartley and Lawton 1992). Gall insects seem to be able to manipulate levels of nutrients in the gall to their own advantage.

6.2.3 Host plant geographic range size

Information from the thesis database, section 2.2.4, suggested that gall-forming insect species richness was limited in eucalypts with small geographic ranges but that eucalypts with large ranges could have large or small gall species assemblages. Subsequently, a significant species-area effect was obtained from the more reliable data of the *Eucalyptus* survey, (section 4.3.1) after *Eucalyptus* subgenus was taken into account. Although no significant species-area effect was detected in the *Acacia* survey it seems likely, as discussed in section 5.4.2, that this result was due to the low level of galling on most acacia species rather than the real absence of an effect of host range size. The presence of a species-area effect in the bipinnate acacia pairs of the survey supports this idea.

Host plant geographic range size has been shown to influence the species richness of wood-boring beetles on host plant species from several genera (Stevens 1986); insects on the flower heads of Asteraceae (Lewinsohn 1991); and cynipid wasps on oaks (Cornell 1985a, 1985b); but not gall assemblages on a selection of shrub species from several genera (Fernandes and Price 1988, 1991).

Lewinsohn (1991) included host plant taxon as a factor in the analysis of the species-area effect for insects in the flower heads of Asteraceae but Cornell (1985a) demonstrated a species-area effect for all (leaf plus non-leaf) gall species on oaks, without taking oak taxon into account. Cornell (1985a) suggested that the reason he was able to ignore taxonomic effects may have been because oaks constitute a very homogeneous host group. (Although there is no explanation suggested as to why taxon was important when leaf galls alone were considered (section 6.2.1). Presumably the requirements of leaf galling insect species on oak are more specific than the requirements of non-leaf galling insect species and so, for leaf gallers, even the small differences between the very similar oak subgenera are significant).

In contrast to oaks, eucalypt subgenera are distinctly different from each other and some may eventually be elevated to genus level (L. Johnson pers. comm.). This may explain why subgenus had to be taken into account before the species-area effect was apparent in the survey of gall species on eucalypts (section 4.3.1).

The fact that host plant taxa were from a mixture of lineages, and the insect species host specific, may also explain the absence of the species-area effect in the studies by Fernandes and Price (1988, 1991) which did not consider host plant taxon differences in the analysis. In the case of wood-boring beetles, although the host plant species were diverse, which might be expected to mask the species-area effect, the requirements of the beetles were less specific than those of gall insects. Many of the beetle species were broadly polyphagous (Stevens 1986). It seems that for specialists, like gall-forming insects, the degree of diversity of host plant taxa will usually need to be taken into account when species-area effects are being measured.

6.2.4 Host plant geographic range rainfall zone

None of the findings of the thesis surveys were consistent with the pattern, found by Fernandes and Price (1988, 1991), of more gall-forming insect species in drier environments than in mesic environments. The geographic ranges of the most gall-prone eucalypt species in the database were in a variety of rainfall zones and microhabitats (sections 2.2.5 and 2.2.6); there was no clear difference in galling between eucalypt species from low rainfall regions and those from high rainfall regions (section 4.3.2); and no significant effect of geographic range rainfall zone on gall species richness on acacias (section 5.4.3). Part of the explanation for the absence of a difference in galling between dry and wet environments in Australia may be related to adaptations of eucalypts and acacias to features of the Australian environment.

Fernandes and Price (1992) suggest that one reason for the xeric/mesic pattern is that gall insect mortality, caused by endophytic fungi, is reduced in plants in dry environments. This is because the water status of such plants is lower than that of plants growing in wetter environments. Some eucalypt species in dry environments have deep roots capable of tapping ground water supplies (Grieve 1956, Nulsen, Bligh, Baxter, Solin and Imrie 1986). The water status of these plant species could therefore be as high as the water status of species in wet environments. This would mean that the chance of attack by endophytic fungi on such plant species would be the same in dry and wet environments.

The way in which the greater variability of rainfall in the drier regions of Australia may prevent the production of new growth on acacias, and consequently reduce the availability of reliable sites for galling, has been discussed in section 5.4.3. This would act in the opposite direction to pressures which tend to increase gall species richness in drier regions.

The factor likely to have the biggest impact in removing any potential difference in galling, due to differential enemy attack between dry and wet environments in Australia, is the characteristic low fertility of most Australian soils (Bowen 1981). Low soil fertility has produced widespread sclerophyllous vegetation in wet as well as dry environments. This means that the long-lived plant parts favourable for galling are also likely to be available on susceptible plant species in wet environments. Even if, as proposed by Fernandes and Price (1992), fungi, other micro-organisms and herbivores are more numerous in wet environments, the protection from these afforded by high levels of secondary compounds in gall-prone sclerophyllous plant species could prevent higher numbers of enemies from reducing gall species richness.

6.3 Additional factors

This section discusses other plant characteristics, not included in the original design of the thesis surveys, which have the potential to affect gall-forming insect species diversity.

6.3.1 Meristem availability

The requirement of most gall-forming insect species for meristematic tissue in which to induce gall formation (section 1.1) suggests that the number of such sites in space and time may have an impact on gall insect species diversity. Several studies have shown that having many meristematic sites favours gall insect abundance (Washburn and Cornell 1981, Craig, Price and Itami 1986, Price and Clancy 1986, Waring and Price 1990) but none have measured the relationship between the number of such sites and gall species richness.

The number of resprouts is a measure of the availability of meristem. Many plant groups known to be gall-prone are also capable of producing numerous resprouts. This is especially true of some species of *Eucalyptus* which not only possess four distinct locations at which meristem is available, providing a range of spatial niches, but also have numerous growth flushes per year, allowing for many temporal niches (section 3.4). The influence of meristem availability, in space and time, on the number of gall species on eucalypts, could be inferred from measurements of the relationship between gall species richness and interspecific variation in the number of locations at which resprouts occur and the number of resprouting events per year.

Perhaps even more importantly, the propensity of many eucalypts to resprout, in response to defoliation by fire, frost, severe drought or insect herbivore attack, also indicates a tendency to respond more readily to the gall initiating stimulus of a gall insect. Investigation of this idea would be facilitated by an understanding of the mechanism of gall induction by insects. This knowledge is not yet available.

6.3.2 Plant architecture

Just as the size of the geographic range of a host plant can influence insect species richness, by affecting immigration and extinction rates and habitat diversity, the growth form of a plant species is likely to influence the number of gall species associated with it. Lawton and Schröder (1977), Lawton (1979) and Lawton (1983) presented evidence of a general pattern of increasing insect species richness with increasing size and complexity of host plant growth form. The three main plant groups they identified, in order of increasing size and complexity, were herbs, shrubs and trees. In contrast, studies by Fernandes and Price (1988, 1991), found no evidence of a pattern between host plant growth form and insect species richness for gall-forming insects.

My study of the effect of soil fertility on galling in Australia (Chapter 3), although not designed to look for such a pattern, does provide support for its existence. More gall species occurred on trees than on shrubs, on both fertile and infertile soils (Fig. 6.1). On infertile soils more gall species occurred on shrubs than on herbs and climbers.

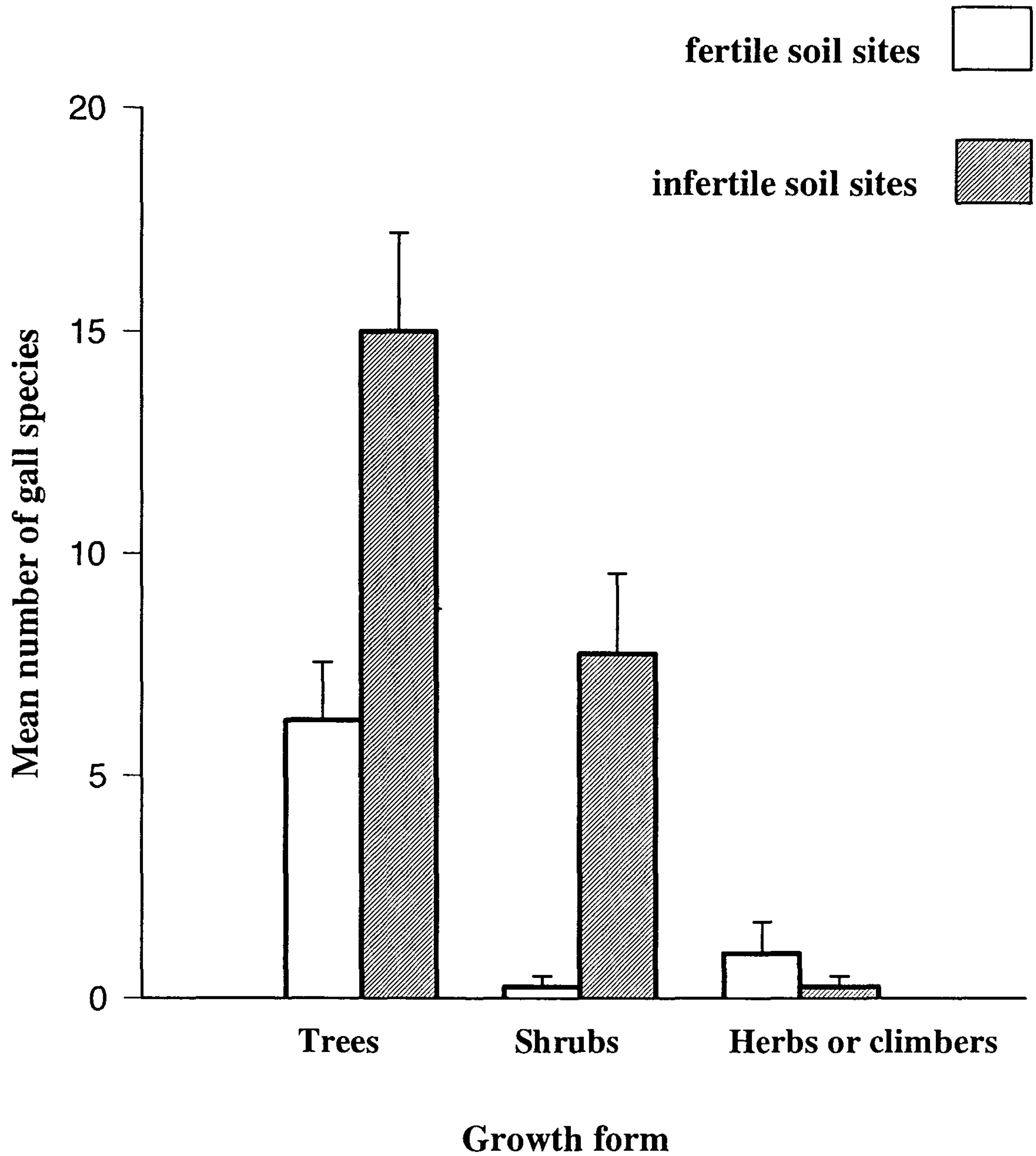


Figure 6.1 Relationship between galling and plant growth form at infertile and fertile sites. Data from Appendix 12. Error bars are SE. Plants that can be shrubs or trees are included with Trees. Differences between growth forms within each soil fertility category were all significant ($P < 0.05$) except for shrubs and herbs/climbers at fertile soil sites. (Comparing mean number of gall species with all plant species, or with the number of galled plant species, in each growth form category, gave the same result.)

The principles underlying the geographic scale species-area effect and the smaller scale plant growth form effect may also extend to even smaller scale interspecific differences in adult plant size and in the form and size of the plant parts utilised by insects. Evidence for such interspecific effects is sparse and inconclusive.

Lawton and Price (1979) found more species of Agromyzidae miner on larger species of British Umbelliferae than on smaller species but concluded that leaf form, which was correlated with plant size, was the more important of the two plant attributes. Plant species with broad, undivided leaves had larger insect faunas than those with finely divided leaves.

Cornell and Washburn (1979) noted that cynipid gall species richness on oak shrub species did not appear to differ consistently from that on oak tree species. This suggests that, at the scale of within-genus comparisons, plant size does not have a significant influence on gall species numbers. However, it seems likely that this conclusion would not be supported by a more rigorous examination of interspecific variation in plant size and galling. In a study of intraspecific variation in oak tree height and cynipid gall species richness, Cornell (1986) obtained a positive relationship between these two variables.

Bipinnate Australian acacia species would be suitable subjects for a within-genus comparison of plant size and gall species richness. My survey of *Acacia*, Chapter 5, has identified bipinnate acacias as a relatively gall-prone group; there are 36 described Australian species (Maslin and Hnatiuk 1987); and species range from tall trees to low spreading shrubs (Morrison and Davies 1991).

Larger plant parts may have larger potential resource fluxes available for insects than smaller plant parts. Studies of gall insect species on host species of *Populus, Salix and Rosa,* summarised in Price (1991a) indicated that large leaves, buds and shoots are more favourable than smaller plant parts for gall insects. These studies were all within-species host plant comparisons. Except for indications from the study of agromyzid miners by Lawton and Price (1979), already mentioned, evidence for within-genus differences in insect species richness between plant species with parts of different size and/or complexity is not available.

Asphondylia species (Waring and Price 1990), and *Atriplex* species (Hawkins, Goeden, and Gagné 1986) are examples of plant species which have small leaves but relatively large gall insect faunas. The high levels of galling on these species suggests that leaf size may not be a significant determinant of gall species number. However, many of the gall species on these plant species are on stems. Comparison of leaf size and form with number of leaf gall species on plant species from the same genus would give a better indication of the importance of leaf architecture to galling.

An Australian plant genus which exhibits a wide range of leaf types, from minute scales to broad blades 20cm long (Bodkin 1986), is the genus *Melaleuca*. This genus comprises about 215 species in Australia (Wilson 1991). It also appears to be relatively gall-prone (Appendix 2). These features suggest that *Melaleuca* would be an appropriate genus in which to investigate relationships between galling and leaf architecture.

6.3.3 Plant geographic range latitude

Price (1991b) describes preliminary findings of an eventual global survey of the distribution of galling species along latitudinal gradients. Data collection for this purpose is still in progress (P. Price pers. comm.). So far the data indicate that there is a peak in gall species richness in the warm temperate zone (25^0 - 45^0 north or south) and a trend for the highest number of gall species to be associated with sclerophyllous vegetation. The data for my comparison of gall species diversity on vegetation at low and high fertility sites were collected in a similar way to the data in Price (1991b). The sites are in the temperate zone (section 3.2). Gall species richness at the infertile sites was of the same order as galling on sclerophyllous vegetation at temperate sites reported in Price (1991b) and so fits with the emerging pattern. There are no published data on galling at other latitudes in Australia.

6.4 An Australian scenario

The diagram in Fig. 6.2 summarises the characteristics, identified in this thesis, which seem to favour galling. Some are unique to Australian plants, others apply worldwide. As pointed out in Fig. 6.2, there is good evidence for the influence of some of these characteristics on gall species richness, but others require further research to substantiate their roles.

The Australian environment is characterised by widespread low soil fertility and aridity. Some of the ways in which plant species have adapted to this regime make them favourable hosts for gall-forming insects. Low soil fertility plays a major role by selecting for sclerophyllous characteristics which have the potential to promote galling. Sclerophylly also causes nett primary production to accumulate as fuel rather than decomposing rapidly. This combines with aridity to increase the incidence and severity of fire. One response to defoliation caused by aridity, or fire, is to have readily available meristem. Large geographic range size, large complex growth form and perhaps large complex plant parts and a temperate latitude, enhance these primary characteristics.

Thus the most gall-prone Australian plant species is likely to be a large tree from a speciose genus and subgenus. It will be widely distributed, possibly in warm temperate latitudes. It will have well developed sclerophyllous features including rigid leaves, high concentrations of secondary compounds in young as well as older tissues, and long-lived parts. Its leaves may be large, it responds to defoliation by resprouting readily from numerous sites, and it has several growth flushes throughout the year. Most of the gall-forming insect species on this hypothetical plant species will be cecidomyiid flies, chalcidoid wasps, psyllids and coccoid bugs.

This thesis has identified host plant taxon and geographic range size as important factors affecting gall-forming insect species richness in Australia. Arguments have been presented for the relevance of soil fertility, host plant meristem availability and plant architecture to gall diversity and suggestions made on how these could be investigated further. Apparent conformity with an emerging global latitudinal pattern has been noted. Reasons for the lack of impact of host plant geographic range rainfall zone on gall species numbers in Australia have been discussed. Galling in Australia can be seen as similar in many respects to galling elsewhere but with some additional features produced by the overriding effect of widespread low soil fertility.

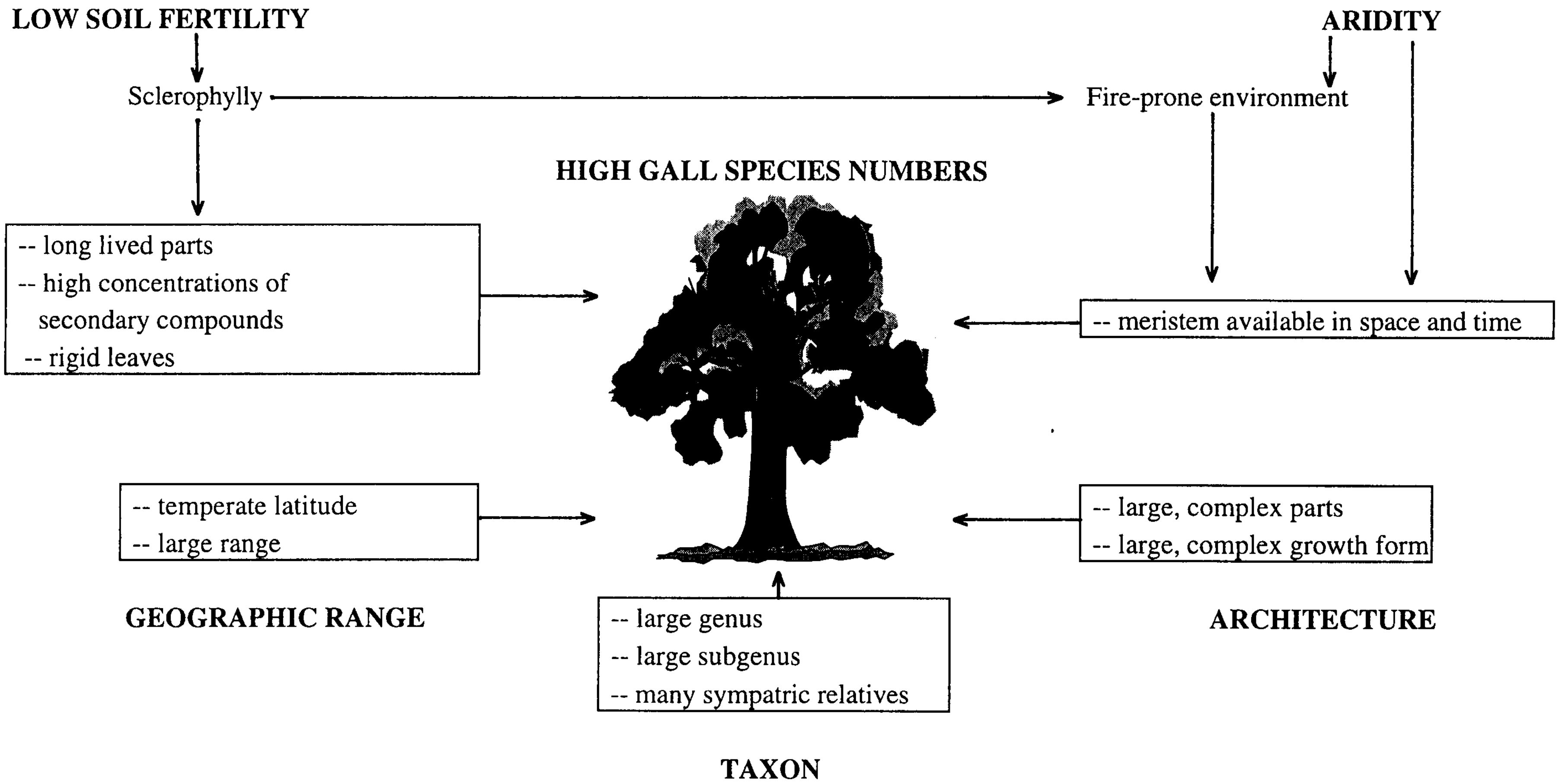


Figure 6.2 Profile of a gall-prone Australian plant species - plant characteristics promoting galling
Evidence for the importance of plant taxon and geographic range size, and to some extent for sclerophylly and growth form, comes from this thesis. Future work needs to address the effect of sclerophyllous characteristics and plant architecture more directly, and to investigate the impact of meristem availability and range latitude.

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