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Variation in the guild composition of herbivorous insect assemblages among co-occurring plant species

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Abstract Variation in plant traits among plant species may promote the development of a characteristic functional assemblage of insect herbivores associated with each plant species. However, only a small number of studies have detailed the representation of several herbivore guilds among co-occurring plant species to determine whether the functional structure of herbivorous insect assemblages varies widely and consistently among plant species. The present study provides one of the few published data sets reporting on the density of several guilds of insect herbivores among numerous plant species. Variation in guild associations with plant phenology and season are also described. Insect herbivores were divided into 10 guilds, and the representation of these guilds was examined for 18 co-occurring plant species. Guild densities and assemblage composition varied significantly among plant species, even when variation over time was taken into account. Variation in guild densities and assemblage composition were not strongly related to the taxonomic relationships of the plants. The highest densities of several guilds occurred in spring and summer, although other guilds were not strongly seasonal. Certain guilds were strongly associated with the presence of new leaves, whereas other guilds appeared to prefer mature leaves. This resulted in assemblage differences between samples containing new and mature leaves and samples containing mature leaves only. Even though the timing and duration of leaf and flower production varied among plant species, this did not explain all variation in guild densities among plant species. It is suggested that additional factors, including plant traits, are contributing to the wide and consistent variation in herbivore assemblage composition among plant species.

Key words: arboreal insect assemblages, forest ecology, phytophagous insects, plant–insect interactions.

INTRODUCTION

Variation in herbivorous insect guilds among plant species has been noted in several studies (Moran & Southwood 1982; Stork 1987; Cornell & Kahn 1989; Basset & Burckhardt 1992), challenging the notion of a common functional structure for all arboreal insect assemblages. If guild representation varies widely and consistently among plant species, this may be because of differences in the resources offered by different plant species. One way to investigate the relationship between plant traits and insect guilds is to compare herbivorous insect assemblages among replicate plant species. Cornell and Kahn (1989) found that the species richness of chewing insects increased with host-plant abundance and taxonomic relatedness. Basset and Burckhardt (1992) compared the herbivore guilds of 20 woody and herbaceous plant species in Switzerland and found that variation in herbivore species richness was related to host-plant height, taxonomic relatedness, leaf water content and phenology. The species richness of herbivorous insect guilds associated with several species of *Ficus* in Papua New Guinea has been linked to leaf palatability and leaf production for leaf-chewers, and to tree density and leaf expansion for sap-suckers (Basset & Novotny 1999).

The present study seeks to examine variation in the functional composition of herbivorous insect assemblages among Australian plant species. Several Australian studies have examined the guild composition of insect assemblages associated with plants (Ohmart *et al.* 1983; Yen 1989; Abbot *et al.* 1992; Basset & Arthington 1992; Shuter & Westoby 1992; Recher *et al.* 1996) and have revealed variation among plant species and over time. However, in many cases the guild categories used are quite broad (e.g. predators, herbivores, scavengers, tourists) and many aspects of arboreal insect assemblages, including herbivore guild structure, remain under-studied in Australian systems. The present study aims to provide some preliminary data on the representation of several herbivorous insect guilds in the field.

The present study differs from some previous works by using a finer level of guild resolution, and by considering insect densities rather than only species richness. Previous studies have divided herbivores into suckers and chewers (Schowalter *et al.* 1981; Moran & Southwood 1982; Stork 1987), or endophages and ectophages (Frenzel & Brandl 1998), to distinguish

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broad functional differences within the herbivore guild. However, the use of several guild categories may be more appropriate to describe the wide range of feeding styles and morphology that are present among insect herbivores. This has been acknowledged by studies that describe insect herbivores using several guilds (Root 1973; Lawton 1982; Basset 1992; Root & Cappuccino 1992). Herbivore guilds can be based on feeding method, target plant tissue or morphology, as all three criteria define functional aspects of the insect assemblage. Examples of feeding method guilds include miners and gallers (Opler 1974; McGavin & Brown 1986), while examples of target-tissue guilds are xylem- and mesophyll-feeders (Claridge & Wilson 1976; Novotny & Wilson 1997). Insect morphology in terms of body size and structure can also be related to function (Moran 1986; Bernays & Janzen 1988; Reavey 1993).

Although information on insect species is vital for our understanding of insect assemblage structure, measures of insect density can also be useful. Densities can give an indication of the level of insect preference for and survivorship on a plant species, as well as an estimate of the herbivore pressure on the plant. Information on insect densities can also be used to examine other aspects of forest ecology, such as the availability of food resources for insectivores. However, density measures may be overestimated if the surface area of a sample is very small. In addition, measures of insects per unit branch length have been known to vary widely in space and time among individuals of the one plant species (e.g. 'load' (mg m^{-1}) as defined by Root & Cappuccino 1992)), thus more work is required to determine the suitability of using measures such as load and density to describe the structure of insect assemblages. The present study examines insect assemblages in the field to assess the variation in guild densities among plant species, over time and during periods of leaf flush and flowering.

METHODS

Site description and plant species

The study site in Bunyip State Park, Victoria (approximately 20 000 ha, 37°59′S, 145°48′E), approximately 80 km south-east of Melbourne, is located in tall open eucalypt forest (*sensu* Specht 1970), at an altitude of 120–220 m a.s.l. The climate is temperate (mean winter minimum 2.6°C, mean summer maximum 24.8°C) with a median annual rainfall of 1000 mm. The forest contains many understorey shrub and small tree species representing a range of plant traits. The eastern section of the site encompasses a series of moist, south-facing gullies and spurs, with an overstorey of *Eucalyptus cypellocarpa* L. Johnson, *Eucalyptus obliqua* L'Hérit, *Eucalyptus nitens* Maiden, *Eucalyptus baxteri* (Benth.) Maiden & Blakely and *Eucalyptus sieberi* L. Johnson, whereas the western section is a gentle slope with a drier northerly aspect and an overstorey of *E. baxteri* and *E. sieberi*. These differences are reflected in the distribution of the shrub species, as those with more mesophytic leaves are more common in the eastern section, and those with more sclerophyllous leaves are more common in the western section, although there are exceptions. Of the 18 plant species included in the study, eight were sampled in the western section and the remaining 10 were sampled in the eastern section (Table 1). Thus there are likely to be unavoidable correlations between some plant traits and abiotic factors. However, the species and site selected do provide a comparison of many plant species that are potentially exposed to similar insect species because of their co-occurrence in a relatively small area (approximately 400 ha). Plant species were selected to represent a range of leaf types and to maximize contrasts within families and genera (Table 1). All plant species were evergreen, although they varied in the timing and duration of new leaf production.

Phenology of plant species

Branch samples were placed into phenological categories to compare the insect herbivores associated with various plant organs. These categories were: (i) mature leaves only; (ii) new leaves plus mature leaves; (iii) flowers plus mature leaves; and (iv) flowers plus new and mature leaves. Leaves were considered mature when fully expanded and hardened. Leaves that were less than fully expanded, or fully expanded but not hardened, were considered new. Fruits were rare in branch samples and were ignored when assigning categories.

Insect collection

Insects were collected by branch sampling, using apparatus (described below) similar to Dempster (1961). This method was selected to enable the collection of sessile and mobile insects, and a more precise identification of the plant organs (and plant species) with which they were associated than that which can be achieved using fogging techniques. These advantages were considered to outweigh the drawbacks of branch sampling, which include small sample sizes and possible evasion by highly mobile insects. Branches of approximately 30 cm were enclosed in a hinged plastic box (26 cm × 18 cm × 19 cm) using a rapid closing action. Both branch and position along the branch (tip or mid-section) were selected haphazardly and care was taken to minimize disturbance of the branch prior to

Table 1. Plant species sampled in the present study, their abbreviations and location within the study site

Family	Species	Authority	Abbreviation	Location
Monimiaceae	*Hedycarya angustifolia*	A. Cunn.	ha	E
Mimosaceae	*Acacia myrtifolia*	(Sm.) Willd.	am	W
	Acacia genistifolia	Link	ag	W
Fabaceae	*Pultenaea muelleri*	Benth.	pj	E
	Pultenaea weindorferi	F. M. Reader	pm	W
Rutaceae	*Boronia muelleri*	(Benth.) E. Cheel	bom	E
	Correa reflexa	(Labill.) Vent.	cr	E
	Phebalium bilobum	Lindl.	pb	E
	Zieria arborescens	Sims	za	E
Rhamnaceae	*Pomaderris aspera*	Sieb. ex DC.	pa	E
	Spyridium parvifolium	(Hook.) F. Muell.	sp	W
Proteaceae	*Banksia marginata*	Cav.	bm	W
	Banksia spinulosa	Sm.	bs	W
	Grevillea barklyana	F. Muell. ex Benth.	gb	E
	Hakea sericea	Schrad. & J. Wendl.	hs	W
	Hakea ulicina	R. Br.	hu	W
	Lomatia fraseri	R. Br.	lf	E
Lamiaceae	*Prostanthera lasianthos*	Labill.	pl	E

E, east; W, west.

collection. The edges of the collecting box were lined with rubber foam, which ensured a tight fit over any protruding plant material. The branch was then clipped from the shrub with secateurs and the box was filled with CO_2 for at least 3 min at 100 kPa. This level of CO_2 treatment was selected after trials with 100 kPa CO_2 for 1.5 min were found to anaesthetize adult *Lucilia cuprina* Wiedemann (Diptera) effectively, and early collections indicated it was also effective for other insects. Following treatment with CO_2 the box was shaken to dislodge animals from the branch. The branch was removed, sealed in a plastic ziplock bag and stored on ice in an insulated container. Animals were collected from the box and immediately preserved in 70% ethanol. On returning to the laboratory, branch samples were weighed fresh and subsamples (one-eighth of the total sample fresh weight) were taken for microscope examination to collect animals that had remained attached, and to note the presence of leaf mines and galls.

Samples were collected on 12 occasions over 16 months from October 1994 to January 1996 (October, November, December 1994; January, February, May, July, August, September, October, November 1995; January 1996). Thus the insect fauna of six seasons were represented: spring and summer 1994; autumn, winter, spring and summer 1995. On each occasion, three branches were sampled from three individuals of each plant species. Sampled plants were tagged with flagging tape to ensure that they would not be sampled twice. Sampling took place during daylight hours and in dry weather only.

Insect herbivores were identified to morphospecies in many instances, although resolution was limited to family level for most Coccoidea, Aleyrodoidea, Cicadelloidea, Fulgoroidea and lepidopteran larvae; suborder level for Thysanoptera; and order level for dipteran and coleopteran larvae. Insects were placed in herbivore guilds on the basis of published diet descriptions. Where only one stage of the life cycle is herbivorous, the non-herbivorous stage was not included in analyses, for example adult Lepidoptera. The term herbivore, as used here, includes insects eating above-ground plant tissues, but excludes insects that specialize on pollen, nectar or fruit.

Feeding guilds

Guild categories are as shown in Table 2. The concept of guild used here follows that of Root (1967). The guilds applied in the present study represent one example of many categories that could be used to define functional groups of insect herbivores (Cornell & Kahn 1989; Basset & Burckhardt 1992; Root & Cappuccino 1992) and were based on insect morphology, feeding method and target-tissues as reported in CSIRO (1991), Novotny and Wilson (1997), Sadof and Neal (1993), Washington and Walker (1990), and Lewis (1973). It is acknowledged that the guild system used here is likely to have many flaws, and the assignation of member taxa may be incorrect because of our incomplete knowledge of the biology of arboreal insects associated with Australian plant species. The guild system used here also departs from some conventional guild systems in several ways, and has been formulated specifically for the analysis of the insects collected in the present study.

Table 2. Guild categories

Category	Code	Contents
Mobile phloem feeders	pm	Hemiptera: Psylloidea, Aphidoidea, Fulgoroidea, Cicadelloidea (excluding Cicadellidae)
Sessile phloem feeders	ps	Hemiptera: Coccoidea, Aleyrodoidea
Mobile mesophyll feeders	mm	Hemiptera: Heteroptera
Sessile mesophyll feeders	ms	Hemiptera: Diaspididae
Xylem feeders	x	Hemiptera: Cercopoidea.
Cicadellids	cic	Hemiptera: Cicadellidae.
Shallow suckers/chewers	ssc	Thysanoptera; Diptera: larvae; grubs of unknown order.
External chewers	xc	Lepidoptera: all herbivorous larvae except miners; Coleoptera: herbivorous adults (excluding Curculionoidea) and all larvae
Internal chewers	ic	Lepidoptera: mining larvae; miners of unknown order
Rostrum chewers	rc	Coleoptera: Curculionoidea (adults)

Although the categories of mesophyll-, phloem- and xylem-feeders have been used, the family Cicadellidae has been put into an additional guild for two reasons. First, different tribes within the Cicadellidae may target phloem, mesophyll or xylem (Novotny & Wilson 1997). Cicadellids collected in the present study were usually not identified beyond family and thus the plant tissues targeted by individuals are unknown. Furthermore, unlike many Hemiptera, cicadellids probably do not use salivary enzymes for leaf penetration (based on the work of Pollard 1968). Suckers were divided into those that probably use salivary enzymes (insects grouped into meso-, phloem- and xylem-feeders), and those that do not (cicadellids) so that the association of these two groups with certain leaf mechanical and structural features can be compared in the future.

Some guilds were formed to examine the potential ecological effects of morphological differences and their interaction with feeding strategies. For this reason chewers were divided into three guilds, internal, external and rostrum. Internal leaf feeding may place constraints on an insect's morphology and feeding method that do not apply to externally feeding chewers. In addition, the rostrum chewer guild was formed to investigate whether the distinct head capsule morphology of adult weevils results in feeding capabilities that are different from those chewers that do not possess a rostrum. It should be pointed out that some curculionids have very short rostra and may be morphologically similar to taxa grouped as external chewers. However, very few of these were encountered in the present study. Phloem and mesophyll feeders were also further divided into sessile and mobile groups to examine the potential effects of mobility on host-plant and phenological associations.

Thysanopterans are designated as shallow suckers/chewers as their mouthparts can pierce plant cells and suck their contents, but also have a limited capacity to crush and rasp plant tissue (Lewis 1973). In addition, the short stylets of most thysanopterans allow penetration of plant epidermal and mesophyll layers, but they rarely reach vascular tissue (Lewis 1973). The shallow sucker/chewer guild also includes dipteran larvae and other small grub-like larvae, which were unidentified to order, as it is assumed that these animals also have a capacity to chew and suck, but that penetration into the plant is limited because of their small mouthparts.

Orthopterans and gall-makers were encountered very rarely in the present study, whereas phasmids were not collected at all. Hence these groups do not feature in the guild system used.

Sample surface area

Total surface area of leaves and stems was measured for six branch samples of each plant species using the image analysis software BIOSCAN 3.1 (Monash University). Leaves and stems were measured separately and the surface area of a cylinder was used to calculate the surface area of stems and of terete leaves. Regression lines of sample surface area versus sample fresh weight were calculated for each plant species and all were statistically significant ($F = 8.99$–1307.57, $P = 0.04$–< 0.001). The resultant equations were used to estimate the total surface area of each sample from its fresh weight. Insect densities are presented as per unit surface area.

Statistics

Insect densities, morphospecies richness and sample surface areas were compared with one-way ANOVAs and post hoc Tukey's tests, with data transformed when necessary to conform with assumptions. The Kruskal–Wallis test was used to detect differences in feeding guilds among plant species, as these data did not comply with ANOVA assumptions. Relationships between sample surface area, morphospecies richness

and insect density were tested by using Pearson correlation. Pearson's χ^2 tests were used to test the association between sample type or season and peak guild densities or individuals.

Non-metric multidimensional scaling (NMDS) using Bray–Curtis similarity was used to examine similarities in insect assemblages among plant species. Analysis of similarity (ANOSIM; Clarke 1993; Clarke & Warwick 1994) was used to test hypotheses of differences in insect assemblages among plant species. Data are sometimes fourth-root transformed prior to NMDS and ANOSIM to downweight highly abundant taxa. However, all multivariate analyses presented here were performed on the raw data to illustrate assemblage differences in terms of guild abundance as well as guild composition.

Univariate tests were undertaken using SYSTAT 7.0 for Windows (SPSS Inc.), and multivariate tests were performed using PRIMER 4.0 beta (Plymouth Marine Laboratory, UK). Probability levels were not adjusted (Stewart-Oaten 1995), with the α level for all tests being $P < 0.05$.

RESULTS

Variation in assemblage composition among plant species

Results from ANOSIM analysis revealed significant dissimilarity in guild composition among most plant species, even when variation among seasons was taken into account (Fig. 1). Assemblage composition based on herbivore guilds was distinctive for each plant species (Fig. 2). Although densities of suckers were generally higher than densities of chewers, the per cent representation of individual guilds within these broad groupings differed among plant species. The herbivore assemblages of some species, such as *Pultenaea muelleri, Boronia muelleri, Acacia genistifolia* and *Phebalium bilobum* were dominated by phloem feeders (Fig. 2d,f,b,h), whereas mesophyll feeders were also a prominent component of assemblages associated with *Lomatia fraseri, Spyridium parvifolium, Hedycarya angustifolia* and *Grevillea barklyana* (Fig. 2q,k,a,n). Shallow suckers/chewers were dominant on *Correa reflexa* (Fig. 2g).

	ha	ag	am	pm	pw	bom	cr	pb	za	pa	sp	bm	bs	gb	hs	hu	lf	pl
ag	-																	
am	-	+																
pm	-	-	-															
pw	-	-	-	-														
bom	-	+	+	-	-													
cr	-	-	-	-	-	-												
pb	+	-	-	-	+	-	-											
za	-	-	+	-	-	+	-	-										
pa	-	-	-	-	+	-	-	+	+									
sp	+	-	+	-	-	-	-	-	-	-								
bm	+	-	-	-	-	-	-	+	-	-	-							
bs	+	-	+	-	+	-	-	+	+	+	+	+						
gb	-	-	+	-	-	-	-	-	-	-	-	-	-					
hs	-	-	+	-	-	-	-	-	-	-	-	-	-	-				
hu	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-			
lf	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-		
pl	+	-	-	-	+	-	-	+	-	+	-	+	+	-	-	-	-	
	5	2	7	0	4	3	0	6	4	5	4	4	9	2	1	1	1	6

Fig. 1. Similarity matrix of ANOSIM results for plant species, using season totals of guild densities as replicates ($n = 6$). +, significant similarity in insect assemblage composition between species; –, significant dissimilarity. Figures below the matrix are the total number of plant species with similar insect assemblages. Plant species abbreviations are indicated by the codes in Table 1.

Mean densities of guilds were significantly different among plant species and sometimes varied widely in magnitude (Fig. 3). Family trends in guild densities were generally not evident, except perhaps the moderate to high densities of external chewers on Rhamnaceae species (Fig. 3h) and rostrum chewers on Rutaceae and Rhamnaceae species (Fig. 3i). Insect densities also varied widely within plant species over the sampling period, as is indicated by the often large error bars (Fig. 3).

The NMDS plot of assemblage composition confirms some of the similarities in guild representation already observed (Fig. 4). Although densities of all guilds were used to generate the NMDS plot, suckers contribute largely to the distribution of points because of their generally high densities. The clustering of Proteaceae species and their proximity to *C. reflexa* is largely due to the generally low densities of phloem feeders associated with these species (Fig. 4a–c). Both *Acacia* species were associated with high densities of mobile phloem feeders and low densities of sessile phloem feeders (Fig. 4a–c). The remaining plant families overlap more, reflecting the sometimes large differences in assemblage composition among confamilial plant species. *Pultenaea muelleri, B. muelleri* and *A. genistifolia* all have high densities of mobile phloem feeders, but they vary in the representation of other sucking guilds (Fig. 4), whereas *H. angustifolia* and *C. reflexa* are distinguished by high densities of sessile suckers and shallow suckers/chewers, respectively (Fig. 4a,c-e). The similarity of insect assemblages did not appear to be influenced by the part of the site where the plant species was sampled (i.e. east *vs* west; Fig. 4f).

The NMDS plot (Fig. 4a) also tends to support the similarities of assemblages portrayed by ANOSIM results (Fig. 1), even though the NMDS was based on total densities for each plant species whereas the ANOSIM used six seasonal replicates for each plant species. For example, the distinctiveness of the *C. reflexa* and *P. muelleri* assemblages indicated in the NMDS plot (Fig. 4a) is supported by their dissimilarity to those of all other plant species shown by the ANOSIM results (Fig. 1).

Total insect density and morphospecies richness

Mean insect density differed significantly among plant species ($F = 3.81$, $P < 0.001$, Fig. 5a), with the lowest mean densities recorded on *Hakea sericea* and the highest on *P. muelleri*. High mean densities on some plant species may be largely attributed to high densities of certain insect taxa, such as aleyrodid scales on *P. muelleri* and coccoid scales on *H. angustifolia*. Large error bars are indicative of highly seasonal or spatially clustered taxa, such as psyllid nymphs on *A. genistifolia*.

The morphospecies richness of insect herbivores also differed significantly among plant species ($F = 8.02$, $P < 0.001$, Fig. 5b), with *Pomaderris aspera* having the highest mean number of morphospecies and *A. genistifolia, Acacia myrtifolia* and *G. barklyana* having the lowest. Calculation of morphospecies richness was highly conservative, as many individuals were identified to family level only, and thus true species richness was underestimated.

Results of pairwise tests indicated that levels of herbivore density and morphospecies richness were generally not significantly different among members of the

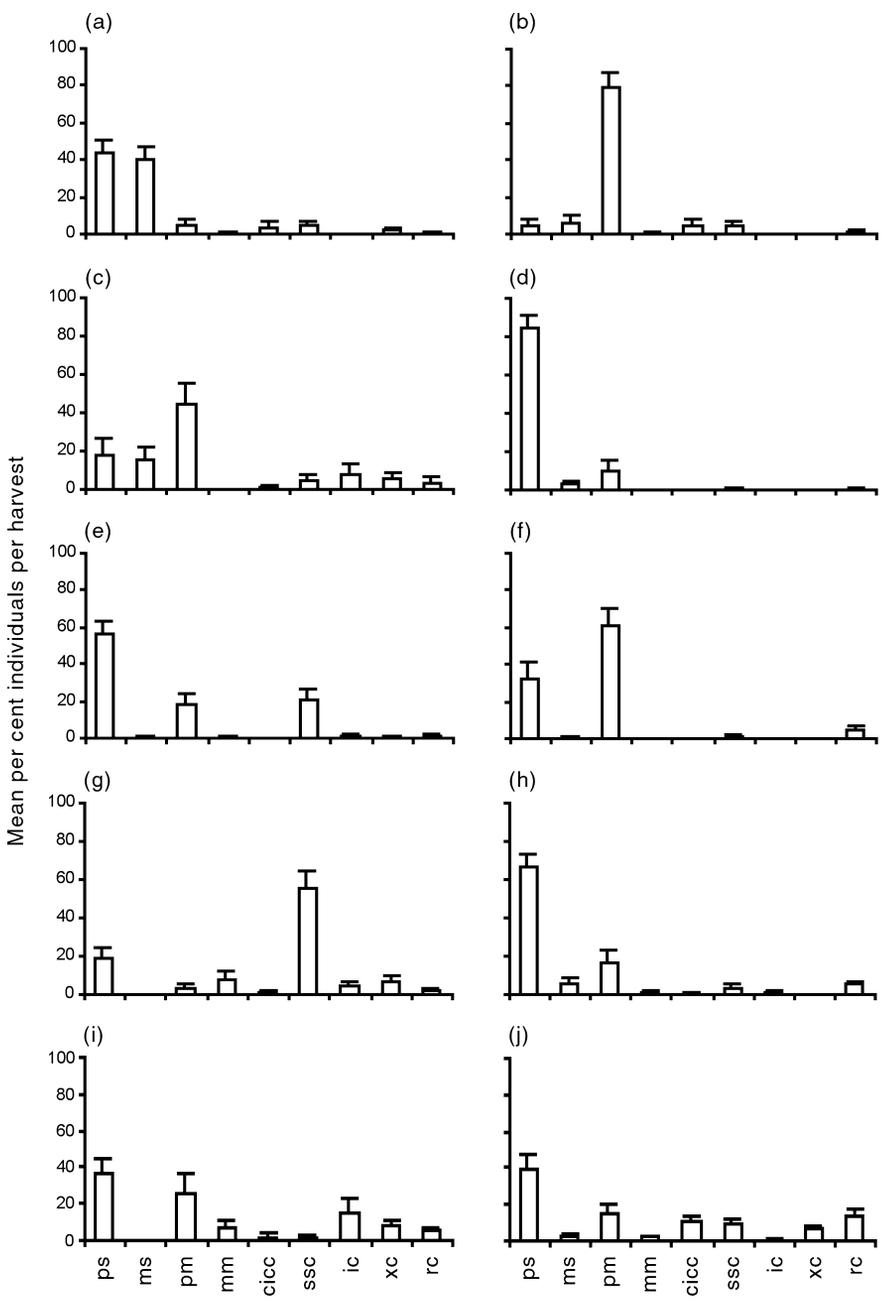


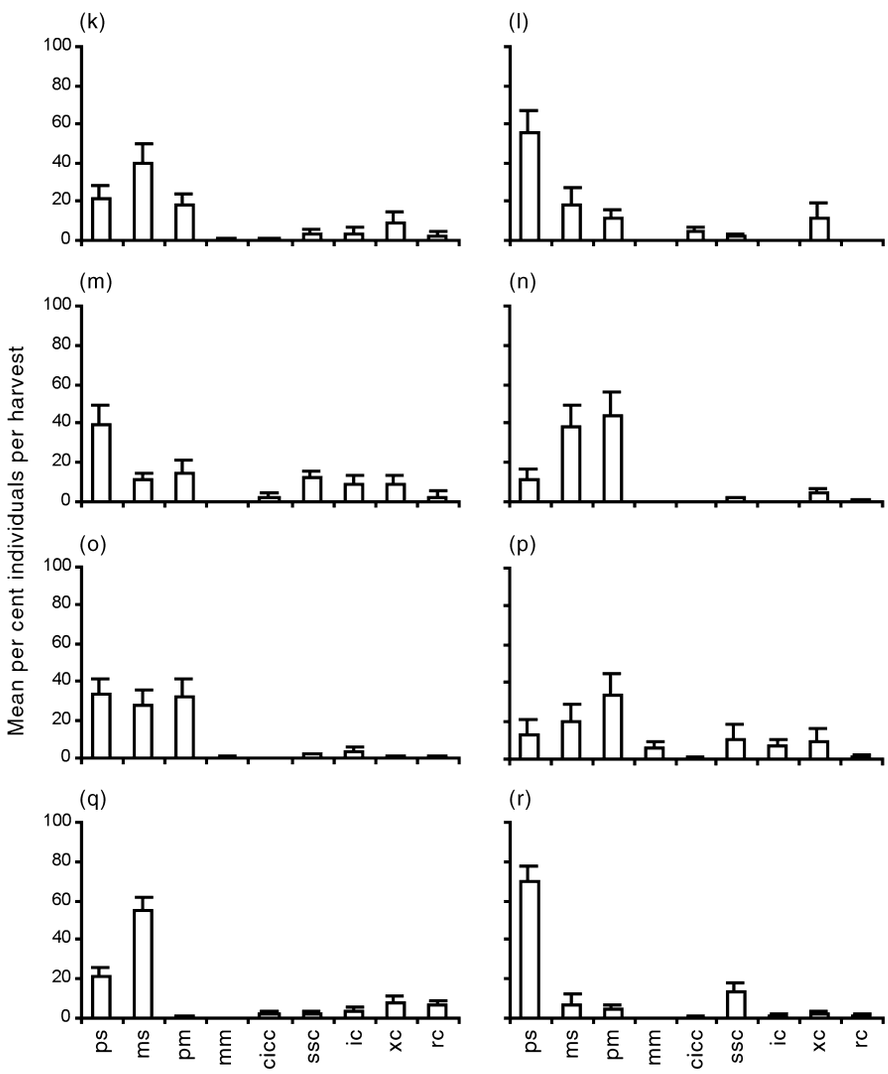
Fig. 2. Representation of herbivorous insect guilds on each plant species, expressed using mean percent individuals per harvest ($n = 12$). Error bars are one standard error of the mean. Codes for guilds as in text. Xylem feeders are not depicted because of their scarcity. (a) *Hedycarya angustifolia*; (b) *Acacia genistifolia*; (c) *Acacia myrtifolia* (d) *Pultenaea muelleri*; (e) *Pultenaea weindorferi*; (f) *Boronia muelleri*; (g) *Correa reflexa*; (h) *Phebalium bilobum*; (i) *Zieria arborescens*; (j) *Pomaderris aspera*; (k) *Spyridium parvifolium*; (l) *Banksia marginata*; (m) *Banksia spinulosa*; (n) *Grevillea barklyana*; (o) *Hakea ulicina*; (p) *Hakea sericea*; (q) *Lomatia fraseri*; (r) *Prostanthera lasianthos.*

same plant family (Fig. 5a,b). Some general trends were suggested for related plant species, such as low densities on Proteaceae species, low morphospecies richness for *Acacia* species and high morphospecies richness for the Fabaceae and Rutaceae.

Mean sample surface area varied significantly among plant species ($F = 77.61$, $P < 0.001$; Fig. 5c). Sample surface area was greatest for *Banksia spinulosa, Hakea ulicina* and *P. muelleri* and smallest for *A. genistifolia, A. myrtifolia*, *L. fraseri* and *S. parvifolium* (Fig. 5c). Although differences in sample size among plant species may have influenced the number of morphospecies collected, sample surface area was found to be a poor predictor of morphospecies richness ($r^2 = 0.10$). Sample surface area was not significantly correlated with insect density ($r^2 = 0.18$). However, the high insect densities recorded for certain plant species (e.g. *A. genistifolia*) may have been influenced by the small surface area size of individual branch samples.

Plant phenology

The plant species sampled in the present study displayed a variety of phenological patterns (Fig. 6). Some species had a brief period of leaf flush (e.g. *Banksia marginata*), while others produced new leaves continually (e.g. *P. aspera*). The timing and duration of flowering also varied among species. On some species, flowers were scarce or restricted to the upper canopy (above the maximum branch sampling height of 2 m), and were rarely or never collected in branch samples. These factors resulted in uneven sample sizes for the different phenological categories, both among and within species (Table 3).



Guild associations with phenology and seasonality

The phenological category associated with the highest (or 'peak') guild density was noted for all plant species and the number of peak densities was tallied for all plant species (Fig. 7a). For the sessile guilds, the highest numbers of individuals feeding on new versus mature leaves was tallied (Fig. 7a). The abundance of most

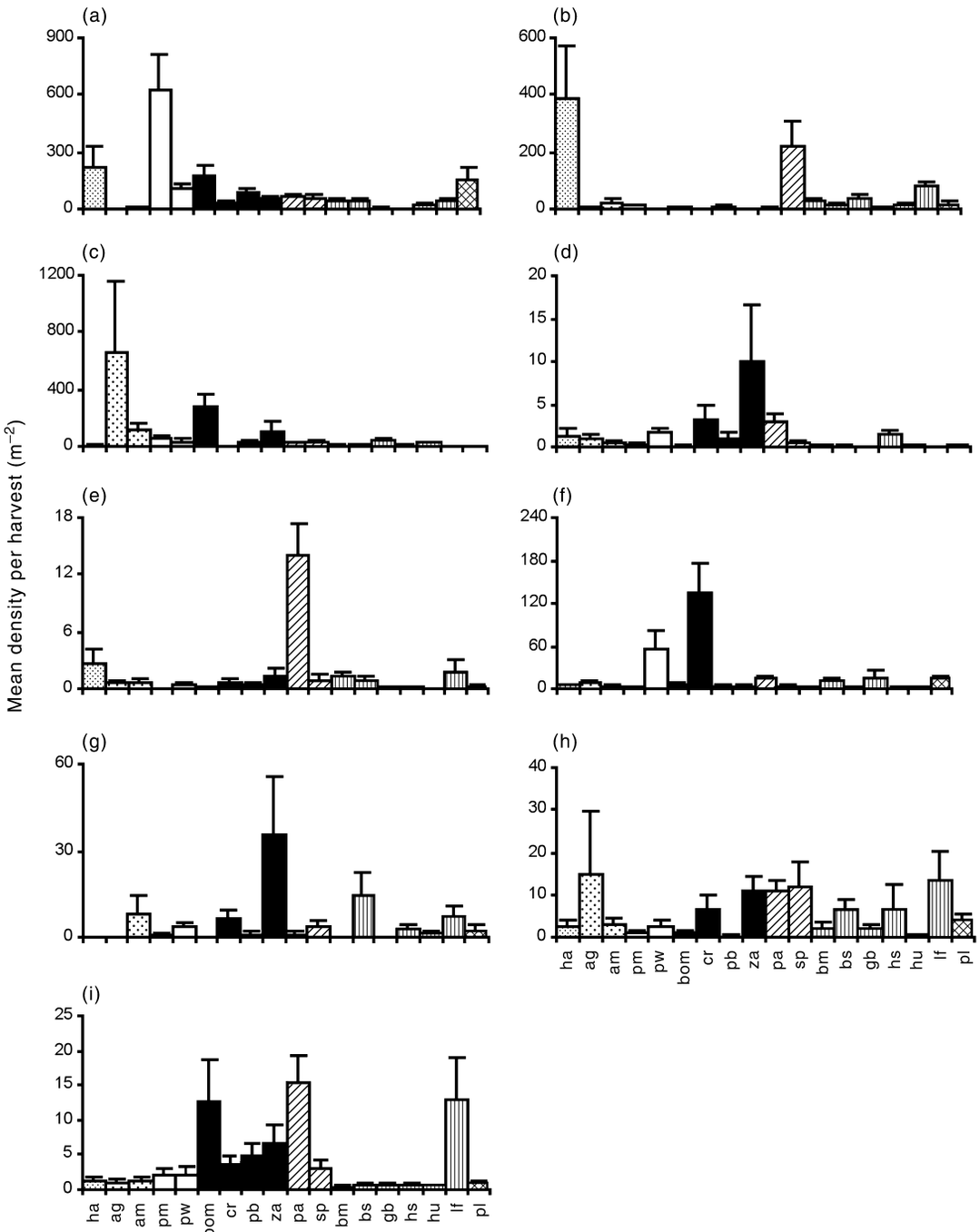


Fig. 3. Mean densities (+ SE) per harvest ($n = 12$) of insect feeding guilds associated with each plant species. Plant families are denoted by shading; KW and P denote Kruskal-Wallis results. Note different scales on y-axes. Key to plant species as in Table 1. (a) Sessile phloem-feeders, KW = 127.54, $P < 0.001$; (b) sessile mesophyll-feeders, KW = 91.06, $P < 0.001$; (c) mobile phloem-feeders, KW = 69.49, $P < 0.001$; (d) mobile mesophyll-feeders, KW = 53.61, $P < 0.001$; (e) Cicadellids, KW = 58.45, $P < 0.001$; (f) shallow suckers/chewers, KW = 65.51, $P < 0.001$; (g) internal chewers, KW = 30.27, $P = 0.024$; (h) external chewers, KW = 45.63, $P < 0.001$; (i) rostrum chewers, KW = 64.68, $P < 0.001$. (⊡), Monimiaceae; (⊡), Mimosaceae; (□), Fabaceae; (■), Rutaceae; (▨), Rhamnaceae; (▥), Proteaceae; (⊠), Lamiaceae.

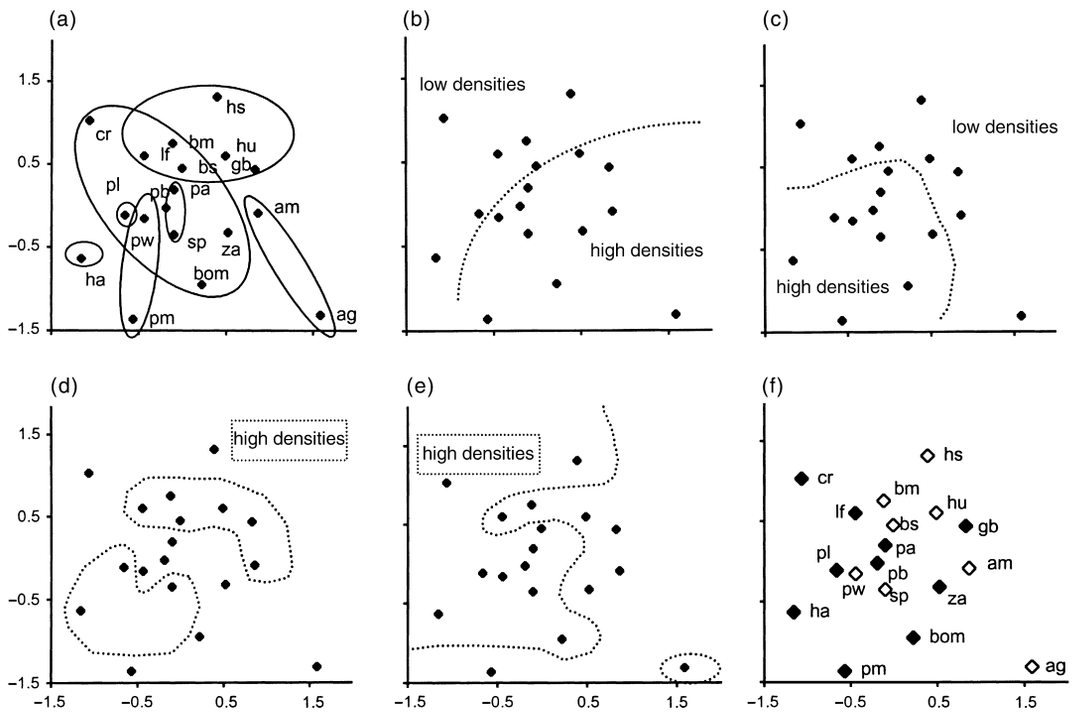


Fig. 4. NMDS plots of plant species based on total guild densities for all sample types. The degree of similarity in the guild composition of the insect assemblages among plant species is indicated by the distance between points. (a) Plant species grouped by family. (b–e) High and low total densities of individual guilds as defined by rank densities: (b) mobile phloem feeders, (c) sessile phloem feeders, (d) sessile mesophyll feeders, (e) shallow suckers/chewers. (f) Plant species grouped by site section. (◇), West; (◆), east. Plant species abbreviations are in Table 1.

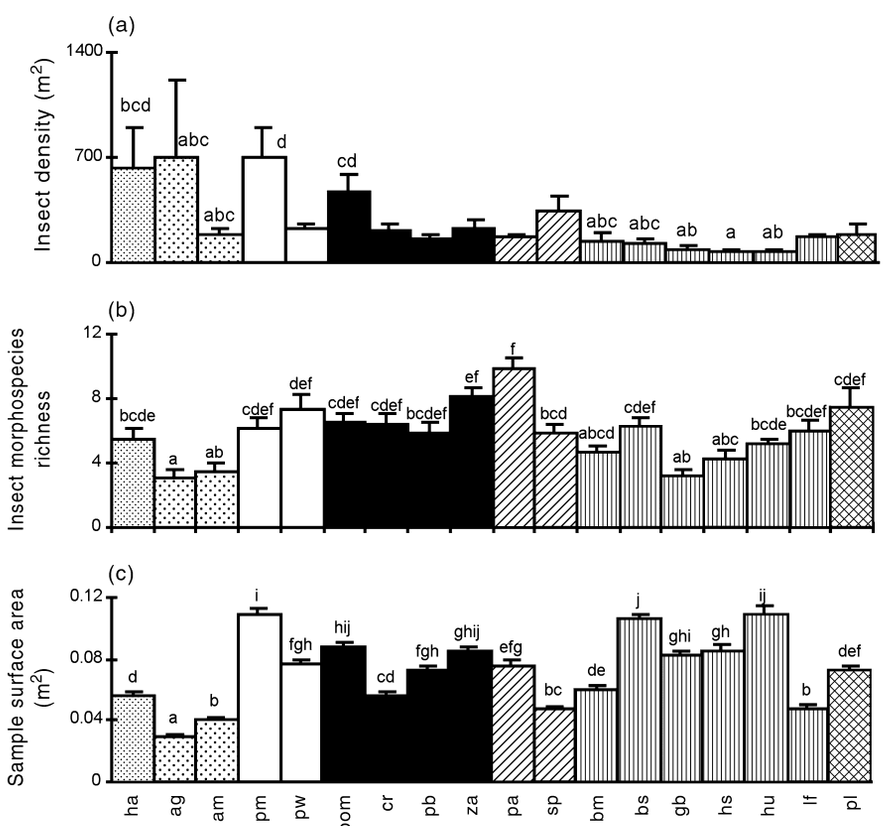


Fig. 5. Values for each plant species (means + SE) of (a) density of insect herbivores per harvest ($n = 12$); (b) morphospecies richness of insect herbivores per harvest ($n = 12$); (c) surface area for branch samples of each plant species ($n = 108$). Data were transformed for analysis, but the raw data are presented here. Columns sharing the same letters are not significantly different. Shading denotes plant family: Plant species abbreviations are in Table 1. (▨), Monimiaceae; (⬚), Mimosaceae; (□), Fabaceae; (■), Rutaceae; (▨), Rhamnaceae; (▥), Proteaceae; (▩), Lamiaceae.

guilds was not independent of sample type (Fig. 7a). Peak densities of many guilds were associated with samples containing new leaves, although this trend was less distinct for rostrum chewers and mobile mesophyll feeders (Fig. 7a). Peak individuals of all sessile guilds were strongly associated with mature leaves (Fig. 7a).

Table 3. Number of branch samples in each phenological category

Plant species	Phenology			
	New and mature leaves	Mature leaves only	Flowers and mature leaves	Flowers, new and mature leaves
Hedycarya angustifolia	87	19		2
Acacia genistifolia	45	35	20	8
Acacia myrtifolia	45	43	15	5
Pultenaea muelleri	46	44	6	12
Pultenaea weindorferi	53	33	7	15
Boronia muelleri	39	28	39	2
Correa reflexa	64	26	9	9
Phebalium bilobum	56	34	6	12
Zieria arborescens	36	44	4	24
Pomaderris aspera	89	17		2
Spyridium parvifolium	55	26	15	12
Banksia marginata	17	91		
Banksia spinulosa	43	65		
Grevillea barklyana	51	48	6	3
Hakea sericea	40	47	21	
Hakea ulicina	42	58	8	
Lomatia fraseri	26	82		
Prostanthera lasianthos	76	26	1	5

Sample size for seasons was the same for all plant species: spring 1994, 18; summer 1994, 27; autumn 1995, 9; winter 1995, 18; spring 1995, 27; summer 1995, 9.

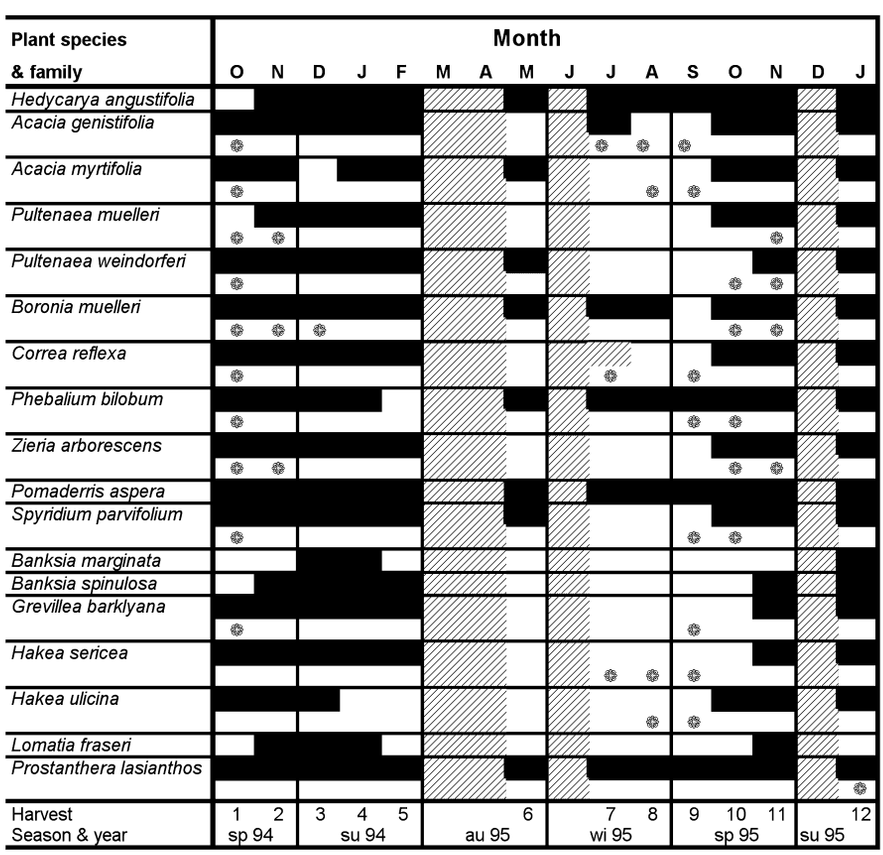


Fig. 6. Main leaf flush and flowering periods for all plant species, as indicated by the presence of new leaves or flowers in branch samples. Shading for new leaves and flowers indicates the presence of these organs in at least one-third of branch samples from a harvest. Season abbreviations: sp, spring; su, summer, au, autumn; wi, winter. (■), New leaves; (flower symbol), flowers; (▨), not sampled.

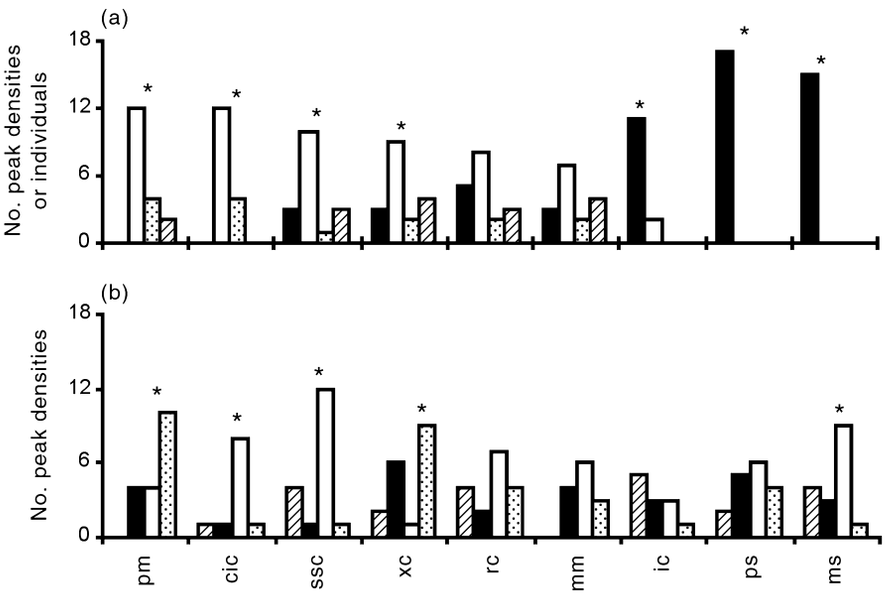


Fig. 7. (a) Number of peak densities in each branch sample category (m, mature leaves only ($n = 18$); n, new and mature leaves ($n = 18$); f, flowers and mature leaves ($n = 13$); fn, flowers, new and mature leaves ($n = 13$)) has been shown for pm, cic, ssc, xc, rc and mm. For sessile guilds (ps, ms and ic) the number of highest tallies for individuals feeding on new versus mature leaves has been shown. (■), m; (□), n; (▨), fn; (▨), f. Codes for guilds are in text. (b) The number of peak densities for each season for each guild: (▨), autumn 1995; (■), winter 1995; (□), spring 1995; (▨), summer 1995. Asterisks denote a significant association between (a) peak densities or individuals and sample category, or (b) peak densities and season detected using Pearson's χ^2 test of independence.

Peak densities were tallied in a similar way for four of the six seasons sampled (Fig. 7b) and the abundance of most guilds was not independent of season (Fig. 7b). Cicadellids, shallow suckers/chewers and sessile mesophyll feeders were associated with spring, whereas mobile phloem feeders were associated with summer (Fig. 7b). Seasonal associations of the remaining guilds were less distinct (Fig. 7b).

An NMDS plot comparing the guilds associated with new and mature leaf samples revealed a loose clustering of samples containing new and mature leaves, and another cluster of samples containing mature leaves only, although there was also overlap between these groups (Fig. 8).

The percentage of samples containing new leaves and flowers varied among plant species (Table 3). As the presence of new leaves and flowers was associated with peak densities of certain guilds, differences in the representation of new leaves and flowers among plant species may be contributing to differences in assemblage composition among plant species. Correlations were used to determine whether a relationship existed between the percentage of samples that contained new leaves and flowers, and log (mean guild density + 1.5), using plant species as replicates. No significant correlation was found for any guild.

While peak densities of certain guilds were strongly associated with the presence of new leaves, it is important to note that densities associated with the new leaves of one species may still be less than densities associated with the mature leaves of another plant species (Fig. 9a,b). The reverse is true for sessile mesophyll feeders, which tend to have peak densities associated with mature leaves only (Fig. 9c). This suggests that the resources offered by leaves of a similar age may differ among plant species. Furthermore, similarities in guild density between the new leaves of one species and the mature leaves of another may indicate that the resources offered by the new leaves of one plant species may be equivalent to those offered by the mature leaves of another plant species.

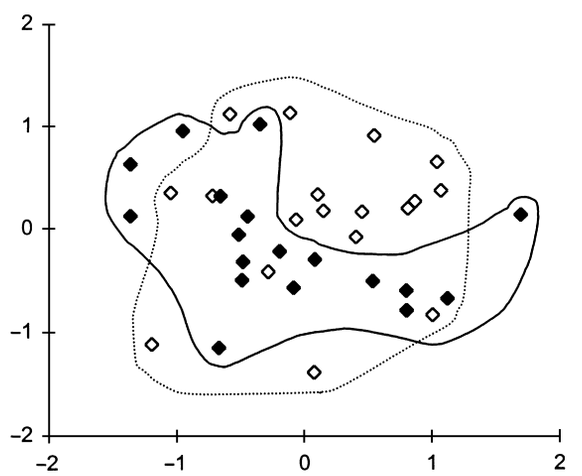


Fig. 8. NMDS plot of plant species based on total densities of guilds. Each plant species has been divided into samples containing (◇) new and mature leaves, and (◆) mature leaves only. The degree of similarity in the guild composition of the insect assemblages associated with each sample type is indicated by the distance between points. Mean stress = 0.19.

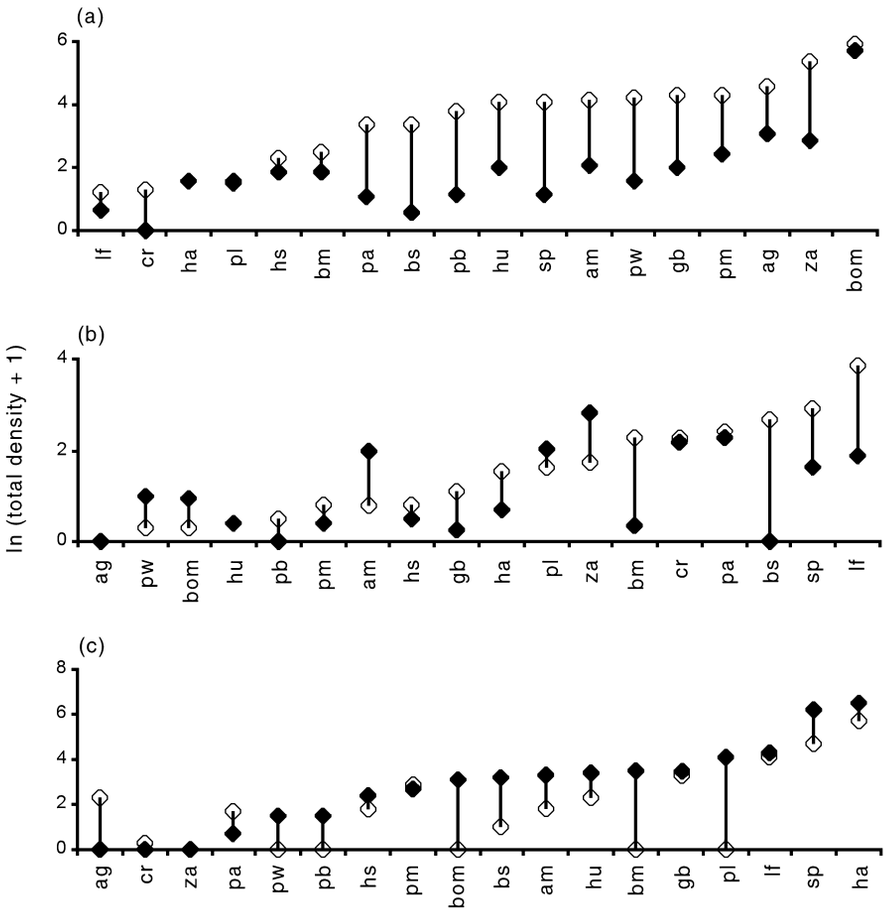


Fig. 9. Total densities of selected herbivore guilds associated with samples containing new and mature leaves (◇) and samples containing mature leaves only (◆). (a) Mobile phloem feeders; (b) external chewers; (c) sessile mesophyll feeders.

DISCUSSION

The results suggest wide variation in the functional composition of herbivore assemblages among co-occurring plant species, and that a more or less characteristic herbivore fauna is associated with each plant species. However, there are limitations to the present study. Associations between plants and insects may not mean the insect is feeding on the plant; feeding observations are necessary to resolve this. Sampling was restricted to daylight hours and night sampling may alter the observed pattern. Other studies have shown significant variation in insect assemblages for plant species at different sites (Lawton 1982; Woinarski & Cullen 1984; Root & Cappuccino 1992). Sampling of these plant species at additional sites is required to establish the generality of the patterns reported here. The sampling regime in the present study may not have detected rare insect species, as surveying 18 plant species meant that relatively low numbers of branch samples could be collected from each plant species. However, it is still meaningful to compare the guild composition and densities of the more common insects among plant species. Insect abundances are known to vary significantly over time and outbreaks may last longer than the sampling period of the present study (Root & Cappuccino 1992). Thus the dominance of some guilds in the present study may result from short-term fluctuations in insect numbers. Some insect assemblages associated with plants are reported to have no fixed pattern of organization (Abbott *et al.* 1992), whereas others retain a predictable structure (in terms of the rank abundances of species), even when there is considerable temporal variation in the abundance of some insect species (Lawton 1984; Root & Cappuccino 1992).

The variation in assemblage composition among plant species was not only due to different levels of chewers and suckers, as has been noted in other studies (Moran & Southwood 1982; Stork 1987; Majer *et al.* 1990), but was also due to variation in the densities of different types of chewers and suckers among plant species. This variation in guild representation among plant species concurs with the findings of Cornell and Kahn (1989) and Basset and Burckhardt (1992), although their guild comparisons were based on numbers of insect species. In contrast, Basset and Novotny (1999) reported little variation in the rank numbers of species in each herbivore guild (chewers, phloem-feeders, xylem-feeders and mesophyll feeders) for 14

species of *Ficus* in Papua New Guinea. The herbivorous insect assemblage of the rainforest tree *Argyrodendron actinophyllum* (Sterculiaceae) appears to be most similar to the assemblages of *P. aspera* and *Zieria arborescens* described in the present study, based on rank abundances of chewers, phloem-feeders and mesophyll-feeders (Basset & Arthington 1992). *Pomaderris aspera* and *Z. arborescens* tend to grow in moist gullies and their leaves are among the largest and most mesophytic of those collected in the present study, most closely resembling the leaves of *A. actinophyllum.*

Total densities of insect herbivores varied among plant species. This was not because of variation in sample surface area. Densities (65–754 m^{-2}) were generally greater than those recorded for other Australian forests, for example, a density of 4 m^{-2} for insect herbivores on *Eucalyptus* (Ohmart *et al.* 1983) and 11.4 m^{-2} on *A. actinophyllum* (Basset & Arthington 1992). In vegetation similar to that of the present study, densities of all arthropods were approximately 8 m^{-2} on *Eucalyptus* species and 10 m^{-2} on non-eucalypt species (Woinarski & Cullen 1984). The greater densities reported in the present study may result from collecting methods. All three previous studies concentrated on free-living invertebrates (greater than 3 mm body length in Woinarski and Cullen (1984)) and none used dissecting microsopes to inspect branches. Thus many small insects and insects remaining attached to the branches were probably underestimated. Basset and Arthington (1992) may have recorded higher densities by using one-sided leaf area to estimate sample surface area, in contrast to two-sided leaf area as used by Woinarski and Cullen (1984) and the present study (details of surface area estimation are not stated in Ohmart *et al.* (1983)). All three studies calculated surface area for leaves only, whereas the present study measured both leaves and stems. Thus it is difficult to determine how densities found in the present study compare with those of other Australian plant species.

The taxonomic affinities of plant species were not strongly related to the similarity of their insect assemblages based on guild densities. Taxonomic relatedness may not be the same as phylogenetic relatedness for these species, which may obscure the influence of plant phylogeny on these assemblages. In addition, plant taxonomic affinities may be more closely linked to the taxonomic composition of the insect assemblages, rather than the guild composition, as selection takes place at the species level.

Although the eastern and western parts of the study site were clearly different in terms of abiotic conditions, there were no assemblage differences between east and west. This suggests that the influence of abiotic conditions was not as strong as that of other factors. Alternately, if the composition of insect assemblages was influenced by microclimate, this may have been at a scale different from that examined by east/west comparisons.

Changes in herbivorous insect abundance are known to coincide with phenological changes of their host plants (Wolda 1979; Lowman 1982; White 1984; Woinarski & Cullen 1984; Basset 1991; Abbott *et al.* 1992). However, although some guilds were associated with the presence of new leaves and flowers, the abundance of these organs did not explain differences in guild densities among plant species. This indicates that assemblage structure is not simply a product of phenological differences among plant species, although phenology is clearly linked to temporal fluctuations of many insect herbivores.

Factors other than (or additional to) plant phylogeny, phenology, site microclimate and sample size are probably contributing to assemblage composition. These may include different pressures from predators and parasites among plant species, leading to different herbivore fauna (Price 1980).

Additional plant traits may also influence herbivorous insect assemblages, simply in terms of the variation in resources offered by different plant species. Differences in the insect assemblages associated with 'new and mature leaf' samples, and 'mature leaf only' samples indicate that many guilds are responding to differences in leaf quality or some other factor related to leaf age. Variation in leaf structural, chemical and nutritional properties may underlie associations with new or mature leaves (Feeny 1970; Rhoades & Cates 1976; Scriber & Slansky 1981; Coley 1983; White 1984). Previous studies have indicated that mobile suckers and many external chewers prefer new leaves (Fowler & Lawton 1984; Sutton 1984; Larsson & Ohmart 1988), perhaps because of nutritional quality (Scriber & Slansky 1981; White 1984) or toughness (Feeny 1970; Hoffman & McEvoy 1986). Mobile phloem feeders may also prefer new leaves because of the potentially superior phloem sap quality or higher translocation rates associated with actively growing meristems (Canny 1984; Douglas 1993). The apparent mature leaf preference of sessile insects may be a sampling artefact, in that the longer a leaf persists on a plant, the more likely it is to be colonized by a sessile insect. Conversely, a sessile vascular feeder may have the best long-term return by commencing to feed on a leaf just after leaf expansion (Hartnett & Bazzaz 1984), as this is when the leaf begins a net export of sugars and amino acids via the phloem (Dickson & Larson 1981; Canny 1984). The mobilization of nitrogenous compounds during leaf senescence may also make feeding on mature leaves attractive to sucking insects (White 1984).

Just as differences in plant traits may explain assemblage variation between new and mature leaves, they may also explain assemblage variation among plant species. The plant species surveyed in the present study

vary widely in anatomy, mechanical properties, nutritional value, chemistry and physiology. These gradients of variation may explain much about assemblage composition. The overlap in guild densities between the new leaves of one plant and the mature leaves of another also indicates that they may offer equivalent resources. Future work will examine correlations between leaf traits and guild densities by comparing leaves of different ages and of different plant species.

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