Australian Journal of Ecology (1992) **17**, 89–98

The arthropod community of an Australian rainforest tree: Abundance of component taxa, species richness and guild structure

Y. BASSET* AND A. H. ARTHINGTON
Division of Environmental Sciences, Griffith University, Nathan 4111, Australia

Abstract The arthropod community within the crowns of *Argyrodendron actinophyllum* (Sterculiaceae) in a subtropical rainforest near Brisbane, Australia, was investigated during a 2 year study using interception traps and restricted canopy fogging. The total arthropod density was 34 individuals m^{-2} of leaf area. Spiders, psyllids, thrips, psocids and chrysomelids were most abundant. The most diverse families included Curculionidae, Cicadellidae, Staphylinidae, Cerambycidae, Theridiidae, and Chrysomelidae. The arboreal community of *A. actinophyllum* exhibited several features common to arthropod communities from temperate and tropical rainforest trees. Affinity with temperate trees was suggested by the relatively high densities of certain species, by high proportions (in terms of individuals) of sap-suckers and non-insect predators, and by a low proportion of ants. Affinity with tropical rainforest trees was expressed by high proportions of scavenging fauna, particularly wood-eaters and fungal-feeders.

Introduction

Despite great interest in the abundance and species richness of rainforest canopy arthropods, the structure of arboreal arthropod communities remains poorly understood (Erwin 1983a). Such structure may be revealed in at least three ways: through the interactions of the species within the community; through the relationships among species richness, number of individuals and body size (e.g. Morse *et al.* 1988; Bassett & Kitching 1991); and through the guild structure of the community (e.g. Stork 1987a). In this paper we focus on guild structure. This concept has been widely applied in ecology, particularly because guilds can be defined independently of the particular species that comprise them (Terborgh & Robinson 1986). Ultimately, studies of guild structure aim to identify the resources that determine the structure of the community or assess the effects of habitat structure on community characteristics (Terborgh & Robinson 1986).

The study of arthropod communities from the rainforest canopy expanded during the 1980s with the development of canopy fogging techniques (e.g. Erwin & Scott 1980; Erwin 1983b; Adis *et al.* 1984; Stork 1987a,b; Morse *et al.* 1988). Canopy fogging is effective in comparing arboreal faunas from different forest types (e.g. Erwin 1983b; Adis *et al.* 1984) or different stands of the same host (e.g. Hijii 1983, 1986; Majer & Recher 1988). However studies on the composition and abundance of the arthropod fauna associated with a particular rainforest host-tree species are often limited by several factors: (i) the composition and guild structure of the arboreal community depend on the sampling method used and this bias may be considerable (see Basset 1988); few studies have employed several complementary collecting techniques; (ii) sampling is usually restricted to a certain phase of the day and/or to a particular period or season of the year; (iii) catches may depend on the amount of foliage above collecting trays (Barnard *et al.* 1986); (iv) because estimates of arthropod abundance are given per unit collecting surface, results may be difficult to compare between tree species with very different leaf area and foliage compactness; and (v) guild assignment is rarely verified in the field (e.g. herbivores collected are often assumed to feed upon the host-tree sampled).

*Present address: Bishop Museum, 1525 Bernice Street, PO Box 19000A, Honolulu, Hawaii 96817-0916, United States.
Accepted for publication October 1991.

This study was designed to describe population densities, species richness and guild structure of the arthropod community in the crowns of a dominant tree species, *Argyrodendron actinophyllum*, in a subtropical rainforest in Australia. The methods selected aimed to minimize the problems cited above, by using two sampling methods and two time scales. The first technique, use of interception traps, provided a long-term analysis of the arboreal community over two consecutive years, based on continuous arthropod trapping during day and night. The second method, restricted canopy fogging, provided estimates of arthropod abundance per unit leaf area which represent the first published data of this type for a rainforest host.

Study area and methods

Study area and host tree

The study was performed in a 35 ha stand of complex notophyll vine forest (warm subtropical rainforest, Webb *et al.* 1984) at 'Beauty Spot 54' in the Mount Glorious State Forest (27°19′20″S, 152°44′55″E, altitude 700 m), 30 km northwest of Brisbane, Australia. A detailed account of the floristics of the site may be found in Young (1985). The canopy reaches 35–40 m on the site and *Ficus watkinsiana* represents the emergent tree at about 45 m. The Mt Glorious climate can be classified as slightly seasonal humid, with a summer rainfall regime (see Webb *et al.* 1984). Further details about the study site are reported in Basset (1989).

Argyrodendron actinophyllum (Bailey) Edlin (Sterculiaceae), up to 50 m in height (Boland *et al.* 1984), is one of the dominant canopy series of the warm subtropical rainforest (*Argyrodendron* spp. association, McDonald & Whiteman 1979). Distinctive features of this evergreen and monoecious species include plank buttresses, dark, thick and scaly bark, and palmate leaves with conspicuous domatia. In the Mt Glorious area, leaf flush is synchronous among individuals and restricted to summer (October to February; Basset 1991c). Flowering usually occurs from March to May. Detailed accounts of the phenology and distribution of this rainforest species are reported in Boland *et al.* (1984) and Basset (1989).

Collecting methods

Regular access to canopies of 15 trees was provided by single rope techniques (Perry 1978). Arthropods were sampled in two ways. First, five composite interception traps (Basset 1988) were set up permanently in the crowns of five *A. actinophyllum*. Arthropods were collected continuously and removed weekly from February 1986 to February 1988. Second, foliage samples of 0.7 m^2 of leaf area were enclosed and fogged with CO_2 (Basset 1990). Eight such restricted canopy fogging samples were gathered from each of 10 mature trees during January–February 1987. This pilot study allowed the design of a sampling programme for four trees, which took place during three other sampling periods in April–May 1987, November–December 1987 and January–February 1988 (160 samples). For a given sampling event, 16 samples were collected from each tree. They comprised eight samples from the lower crown (15–25 m) and eight samples from the upper crown (25–35 m), which were taken from each of the four possible access points within the crown (four lines oriented N–S–E–W). Access and sampling were restricted, in most cases, to the inner core of tree crowns. All fogging was performed during daylight hours on dry foliage. The description, advantages, limitations and a comparison between the two sampling methods have been discussed elsewhere (Basset 1988, 1989; Basset & Kitching 1991). Collected specimens were stored in 70% ethanol and sorted to families and morphospecies, prior to identification by several taxonomists. Technical difficulties (see Basset 1990) prevented counting of mites and springtails, which were disregarded. Furthermore, most hymenopterans, dipterans and lepidopteran adults were not sorted to species. Vouchers are held at the Queensland Museum, Brisbane. The taxonomic composition of the arboreal fauna associated with *A. actinophyllum* is discussed elsewhere (Basset 1991a).

Population densities and biomass

The leaf area of each fogging sample was determined in the field and averaged 3421.0 ± 64.2 cm^2 ($n = 240$; leaves were considered one-sided for ease of calculations). Arthropod densities were first expressed as number of individuals m^{-2} of fresh foliage (see Basset 1989); then, the number of indi-

viduals kg^{-1} of dry foliage was estimated by regressing fresh leaf area to the dry weight of mature leaves (samples taken from 12 different trees at different locations within the crown):

$$y = 66.6x + 222.8 \ (n = 128;\ F_{1,126} = 330.8;\ P < 0.001;\ r^2 = 0.72)$$

where y = leaf area (cm^2) and x = dry weight of foliage (g) (mean sample size [= 48.0 g DW foliage] × 20.8 = 1 kg DW foliage). Collected specimens were preserved for taxonomic analyses and biomass was estimated from the mean body length and number of individuals of each species collected, using the relationship $W = 0.0305 \times L^{2.62}$ (Rogers *et al.* 1976), where W is the dry weight in milligrams and L the mean body length in millimetres. As far as possible, body length was determined as the mean of 10 length measurements.

Guild system and assignment

In this study, the original guild system of Moran and Southwood (1982) was subdivided further to achieve a finer analysis of the temporal and spatial patterns exhibited by the arboreal fauna. The following guilds and subdivisions were recognized: chewers (including chewers, gall-formers and leaf-miners), sap-suckers (phloem-, xylem- and mesophyll-feeders), epiphyll grazers, scavenging fauna (fungal-feeders, wood-eaters and scavengers), insect predators, other predators, parasitoids, ants, 'tourists' ('tourists' and 'incidentals') and 'uncertains'. The resource shared by each guild is self-explanatory (see Moran & Southwood 1982), with the exception of the following: (i) phloem-, xylem- and mesophyll-feeders include sap-sucking species which insert their stylets in the phloem vessels, xylem vessels and parenchyma tissue, respectively; (ii) epiphyll grazers feed on the surface of the leaves, grazing lichens, algae and fungi; (iii) fungal-feeders include non-active borers, feeding upon fungi growing on and/or under the bark surface; (iv) wood-eaters include active phloem- or xylem-borers; (v) scavengers feed upon dead material of both vegetal and animal origin; (vi) 'tourists' (non-feeding residents) include species that were incidentally associated with the host plant (Nielsen 1975) or those attracted to it for shelter, sun-basking or sexual display (Moran & Southwood 1982); and (vii) 'uncertains' include species whose feeding habits are unknown. Guild assignment was based upon feeding trials, gut content analyses, insect rearings, observations in the field, personal communication with specialists, and the available literature (e.g. Stork 1987a). This information is detailed for each species in Basset (1989).

Results

Totals of 46 000 and 5600 canopy arthropods were collected with interception traps and restricted canopy fogging, respectively. The total arthropod population density was 34 individuals m^{-2} of foliage (Table 1). Spiders were abundant, along with psyllids, thrips, psocids and chrysomelids. The percentage of juvenile specimens collected by traps and fogging, respectively, was: Araneae 87/69%; Blattodea 80/42%; Orthoptera 75/31%; and Coleoptera 8/0.5%. Most of the spiders, cockroaches and grasshoppers collected from the foliage were juveniles, but beetle larvae were usually concealed or active on or under the bark.

A total of 916 species was sorted from the trap collections and 293 species from the fogging collections. Most (87%) of the species collected by fogging were also collected by interception traps. Numbers of phytophagous species collected by interception traps and fogging were 148 and 68, respectively (16 and 23% of the total). Curculionidae, Cicadellidae, Staphylinidae, Cerambycidae, Theridiidae and Chrysomelidae were particularly species-rich (Table 2). The cumulative number of all species sorted from trap collections over time is presented in Fig. 1a. Similar curves plotted for various arboreal guilds (Fig. 1b) suggested that a third year of trapping with interception traps might reveal many 'new' species of predators and fungal-feeders, but fewer phloem-feeders, wood-eaters and chewers. For all of these, the proportion of species, collected 10 weeks before the completion of the sampling programme, amounted to 93.2%, 93.0%, 95.3%, 96.8% and 98.0%, respectively, of the total number of species collected. The curve obtained for all arthropod species from fogging collections (Fig. 1c) suggests that an asymptote is reached sooner when fogging the foliage. In particular, chewing species attained an asymptote sooner than other guilds and most of their common species were obtained after 125

Table 1. Population intensities of some taxa and guilds from the foliage of *A. actinophyllum*, compared with other studies

Group	Individuals m^{-2} leaf area				Individuals kg^{-1} DW* foliage			
	A	O	W	J	A	O	L	F
Araneae	8.6	2.4–5.4	3.2	7–20	123	13.7–28.2	–	–
Clubionidae	1.6	–	–	–	23	–	–	–
Theridiidae	2.7	–	–	–	39	–	–	–
Coleoptera	5.3	–	1.2	–	76	–	–	–
Chrysomelidae	1.9	0.4–0.8	–	–	27	2.2–3.2	–	–
Corylophidae	1.7	–	–	–	24	–	–	–
Curculionidae	0.8	0.4–0.9	–	–	11	2.5–4.8	–	–
Homoptera	8.1	–	–	–	116	–	–	–
Cicadellidae	1.6	0.9–2.7	–	–	23	5.0–13.9	–	–
Psylloidae	6.0	'scarce'	0.2	–	86	–	–	–
Hymenoptera	2.7	–	0.4	–	39	–	–	–
Formicidae	0.8	–	0.1	–	11	–	–	–
Lepidoptera (larvae)	0.6	0.7–1.6	0.2	–	9	4.0–8.0	–	–
Psocoptera	2.8	–	0.3	–	40	–	–	–
Thysanoptera	3.3	–	0.2	–	47	–	–	–
All arthropods	34.0	6.0–14.0	10.0	–	485	34.0–73.0	–	–
Chewers	2.5	1.7–2.9	–	–	36	9.6–15.1	17.4	1.3–30.6
Phloem-feeders	7.7	–	–	–	110	–	–	–
Mesophyll-feeders	1.2	–	–	–	17	–	–	–
All herbivores	11.4	–	–	–	163	–	–	–
Epiphyll grazers	3.0	–	–	–	43	–	–	–
Fungal-feeders	2.2	–	–	–	31	–	–	–
Parasitoids	1.8	–	–	–	26	–	–	–
Predators	10.2	–	–	–	146	–	–	–
Uncertains	2.6	–	–	–	37	–	–	–
Mines†	30.6	–	–	–	437	–	–	–
Galls†	3.0	–	–	–	43	–	–	–

Sources: A = *Argyrodendron actinophyllum*, present study; O = Ohmart *et al.* (1983), Australia, *Eucalyptus* spp.; W = Woinarski and Cullen (1984), Australia, non-eucalypt trees; J = Jennings and Dimond (1988), USA, fir-spruce forests; L = Larsson and Tenow (1980), Sweden, *Pinus silvestris*; F = Futuyma and Gould (1979), USA, deciduous forest (caterpillars and sawflies only).

*Dry weight; †Active and inactive.

samples (about 43 m^2 of leaf area sampled on different trees, see Basset 1989).

Most of the individuals collected by interception traps were represented by tourists, along with phloem-feeders, fungal-feeders and predators (Fig. 2a; Appendix 1). Chewers accounted for less than 6% of the individuals. The traps yielded very few 'incidentals', gall-formers, xylem-feeders and no leaf-miners (all these guilds represent <0.5% of the total individuals collected per trap; they are not included in Fig. 2). However fogging collections were dominated by predators and phloem-feeders, followed by epiphyll grazers, chewers, fungal-feeders and parasitoids. Ants and tourists were relatively scarce on foliage of *A. actinophyllum*. Very few gall-formers and incidentals were collected and no leaf-miners and xylem-feeders at all (these guilds represent <0.4% of the total individuals). The biomass in interception traps comprised predators (including several species of predatory Gryllacrididae and one of Tettigoniidae), tourists (including all the lepidopteran adults) and chewers (Fig. 2b; Appendix 1). The biomass collected with fogging was dominated by chewers, predators, phloem-feeders and scavengers (Fig. 2b). In terms of number of species, predators, wood-eaters and tourists were prevalent in trap collections, whereas predators, chewers and phloem-feeders dominated the fogging collections (Fig. 2c; Appendix 1).

Discussion

Population densities of foliage arthropods

It should be emphasized that our comparisons between the arthropod community of *A. actinophyllum* and communities associated with other trees remain tentative because many authors have used different sampling techniques that are not always directly comparable. With respect to quan-

Table 2. Number of species sorted from interception traps (operated continuously from February 1986 to February 1988 in five trees) and fogging collections (160 foliage samples of leaf area 0.7 m^2 sampled from 4 trees in April–May 1987, November–December 1987 and January–February 1988), presented for the 20 most diverse arthropod families.

Interception traps			Restricted canopy fogging		
Taxa	Order	No. spp.	Taxa	Order	No. spp.
Curculionidae	Col.	70	Curculionidae	Col.	18
Cicadellidae	Hom.	33	Theridiidae	Ar.	14
Staphylinidae	Col.	31	Araneidae	Ar.	12
Cerambycidae	Col.	26	Chrysomelidae	Col.	10
Clubionidae	Ar.	22	Salticidae	Ar.	10
Miridae	Het.	22	Phlaeothripidae	Thys.	10
Theridiidae	Ar.	21	Cicadellidae	Hom.	9
Scolytidae	Col.	19	Formicidae	Hym.	8
Pselaphidae	Col.	19	Thomisidae	Ar.	8
Encyrtidae	Hym.	18	Psylloidae	Hom.	7
Lauxaniidae	Dipt.	18	Caeciliidae	Psoc.	6
Chrysomelidae	Col.	17	Ectopsocidae	Psoc.	6
Dolichopodidae	Dipt.	15	Pseudocaeciliidae	Psoc.	6
Tenebrionidae	Col.	14	Clubionidae	Ar.	5
Drosophilidae	Dipt.	13	Staphylinidae	Col.	5
Lygaeidae	Het.	12	Miridae	Het.	5
Coccinellidae	Col.	11	Thripidae	Thys.	5
Elateridae	Col.	11	Coccinellidae	Col.	4
Carabidae	Col.	10	Geometridae	Lep.	4
Empididae	Dipt.	10	Peripsocidae	Psoc.	4

titative studies of arthropod abundance, few data are available on all insect species present at endemic levels (i.e. not in outbreak situations) on the foliage of any host-plant sampled (Ohmart *et al.* 1983). Our study is difficult to compare with those of Ohmart *et al.* (1983) and Woinarski and Cullen (1984), who used branch clipping as the main sampling technique. The latter authors considered only arthropods with a body length >3 mm, whereas most arboreal arthropods are smaller than this (e.g. Morse *et al.* 1988; Basset & Kitching 1991). In addition, relative abundances presented as number of individuals per kg of foliage are not easy to compare between host-plants of very different specific leaf weight (such as heavy eucalypt leaves and the far lighter *A. actinophyllum* leaves). The abundance of foliage arthropods expressed as number of individuals per unit leaf area is easier to compare among species.

Our results (Table 1) probably underestimate the actual abundance of taxa associated with the foliage of *A. actinophyllum* in the Mt Glorious rainforest, but are more comprehensive than any other study of rainforest trees reported to date. Although generally low, arthropod densities on the foliage of *A. actinophyllum* fell within the ranges reported in other studies. Most of the taxa examined were more abundant on *A. actinophyllum* foliage than that reported for eucalypt foliage (e.g. spiders, psyllids, thrips and psocids), but these differences may have arisen from differences in sampling methodology. Some insects, such as two chrysomelids (*Rhyparida* sp. and *Longitarsus* sp.), one lathridiid (*Cortinicara* sp.) and two psyllids (*Aconopsylla* sp. and *Protyora* sp.), were within the range of abundance recorded on some of the eucalypts sampled by Ohmart *et al.* (1983). The dominance of a few herbivorous species is often characteristic of temperate trees (e.g. Nielsen 1975). Herbivore load, as represented by mean herbivore biomass (mg DW) 100 g^{-1} DW of consumable plant material, amounted to 27 mg DW. This was much lower than that reported by Root (1973) for *Brassica oleracea* grown in the USA (40–340 mg DW), but fell into the range of values indicated by Schowalter *et al.* (1981) for several tree species growing in an undisturbed watershed in the USA (11.5–50.8 mg DW).

Species richness

The species richness of arthropods on *A. actinophyllum* was compared with similar data from temperate trees (Martin 1966; Klomp & Teerink

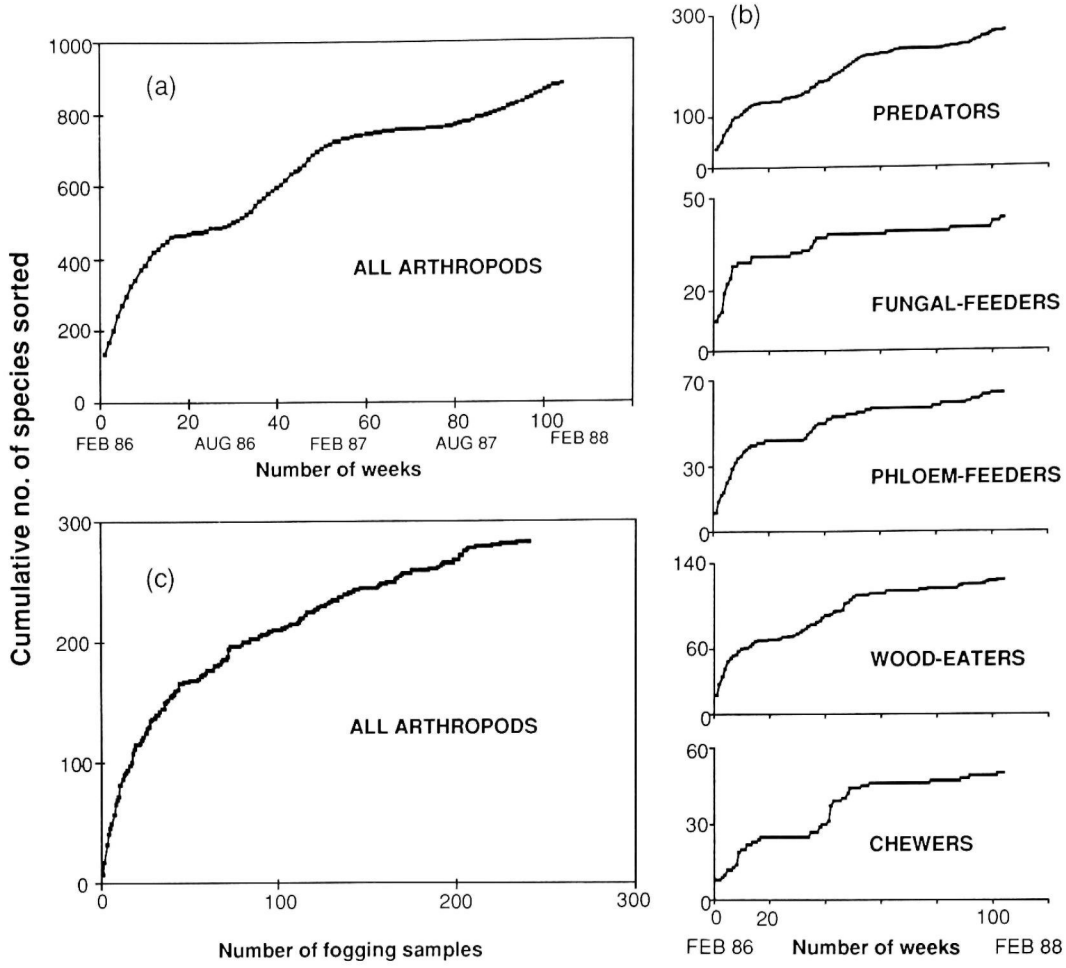

Fig. 1. Cumulative number of species sorted for (a) all arthropods in trap collections; (b) various guilds in trap collections; and (c) all arthropods in fogging collections.

1973; Nielsen 1975; Ohmart & Voigt 1981; Moran & Southwood 1982; Hijii 1983, 1986; Basset 1985a,b), tropical and rainforest trees (Moran & Southwood 1982; Erwin 1983b; Adis *et al.* 1984; Stork 1987a), and eucalypt trees (Ohmart *et al.* 1983; Yen 1989). The most diverse arthropod families sampled are similar in species richness to those recorded in other rainforest studies, particularly beetles, for which more comparative data are available (Erwin & Scott 1980; Erwin 1983b; Bourlière 1983; Monteith & Davies 1984; Stork 1987b). The proportion of parasitoid and tourist species was low because most hymenopterans, dipterans and lepidopteran adults were not sorted to species.

On *A. actinophyllum*, the proportion of scavenging species was high (particularly wood-eaters, Fig. 2c), consistent with the findings of Stork (1987a) in Bornean rainforest trees. Rainforest trees usually have a high proportion of dead wood in their crowns, which, coupled with high rainfall, may provide more suitable habitats for scavenging fauna than do temperate trees. A substantial proportion of species richness was due to the occurrence of wood-eating taxa (e.g. Curculionidae, Cerambycidae, Scolytidae), predatory species (e.g. Staphylinidae, several spider families) and, to a lesser extent, herbivorous species (e.g. Cicadellidae, Chrysomelidae) (Fig. 2c). Since most wood-eating and predatory species are rarely restricted to a single tree species (e.g. Hamilton 1978; Jermy 1988), this suggests that the species richness of the arboreal community on *A. actinophyllum* depends substantially on vagile species unlikely to be restricted to this tree species. In fact, predators, wood-eaters and fungal-feeders appeared to be influenced more by the surrounding rainforest community than by the various habitats provided by *A. actinophyllum*.

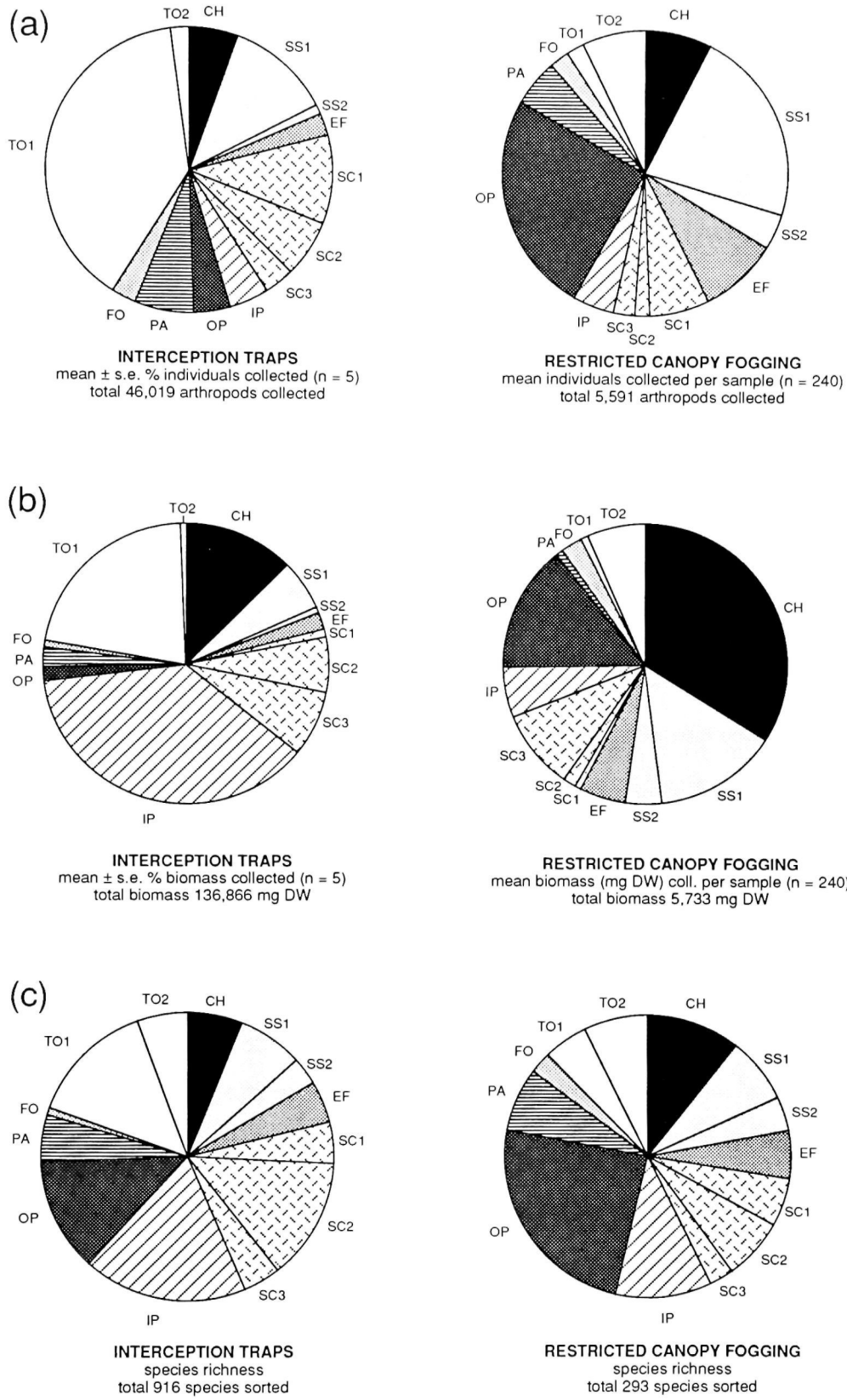

Fig. 2. Guild structure of *A. actinophyllum* arthropods, expressed as (a) number of individuals, (b) biomass and (c) species richness. Interception trap data on left, fogging data on right. Key: CH = chewers, SS1 = phloem-feeders, SS2 = mesophyll-feeders, EF = epiphyll grazers, SC1 = fungal-feeders, SC2 = wood-eaters, SC3 = scavengers, IP = insect predators, OP = other predators, PA = parasitoids, FO = ants, TO1 = tourists, TO2 = uncertains.

Guild structure

Guild structure may be expressed as number of individuals, biomass or species. From their guild analysis of various temperate and tropical trees, Moran and Southwood (1982) concluded that there is proportional constancy in the number of species (but not in number of individuals) within the guilds closely associated with trees. For rainforest trees, Stork (1987a) concluded that, in some instances, the trophic structure of arboreal communities would perhaps be appraised more meaningfully by considering the number of individuals or the biomass rather than the number of species. In addition, the ratio of certain guilds based on their relative species richness may depend on sampling effort and when sampling is performed (see plots of Fig. 1b). For these reasons, the guild structure of the arthropod community associated with *A. actinophyllum* was examined primarily with regard to the number of individuals and biomass. Since guild composition expressed as number of individuals is subject to seasonal and annual changes (Root 1973; Basset 1985b; Hendrix *et al.* 1988; Yen 1989), discrete sampling in time of arboreal faunas must be interpreted with caution.

We compared the guild structure of *A. actinophyllum* arthropods with similar data available (Moran & Southwood 1982; Ohmart *et al.* 1983; Basset 1985a,b; Hijii 1986; Stork 1987a; Yen 1989). Moran and Southwood (1982) proposed that a high proportion of chewing species on a tree is correlated with a low proportion of sap-sucking taxa and vice-versa. On *A. actinophyllum*, the ratio of chewing to sap-sucking individuals was low (traps: 0.5; fogging: 0.3). Mucilage cells abundant in the leaves of *A. actinophyllum* and mucilage canals (Metcalfe & Chalk 1957) abundant at the base of the petiole may interfere more with chewers than with sap-suckers, particularly because sap-suckers are able to insert their stylets between cells and nearly always bypass mucilage canals unless they are very dense or totally enclose the phloem vessels (Dixon 1975). The ratio of predators to other guilds was high, particularly when number of species was considered (Fig. 2c), and this seems characteristic of rainforest ecosystems (e.g. Elton 1973). However this ratio expressed in biomass was much lower (Fig. 2b), particularly when heavy-bodied tettigoniids were omitted from interception trap catches. Arboreal ants, which were relatively scarce on *A. actinophyllum*, may be limited by host phenology and the concomitant low productivity of herbivores at Mt. Glorious during the dry season (Majer 1990; Basset 1991b), and may be supplanted by spider predators. The proportion of scavenging fauna (excluding Collembola) appears higher in tropical trees (9.9–13.3%) than in temperate ones (2.6%). *A. actinophyllum* supported a high percentage of scavenging fauna (traps 27%; fogging 9%) and particularly of fungal-feeders (Fig. 2a). The proportion of tourists sampled was quite variable in the published work examined, probably due to different sampling methods and differences in guild assignment (see Stork 1987a).

The arboreal community of *A. actinophyllum* exhibits several features common to temperate and tropical rainforest trees. Affinity with temperate trees is indicated by the high population densities of certain phytophagous species, by the abundance of sap-suckers and non-insect predators and the low proportion of ants (Moran & Southwood 1982; Basset 1985b; Hijii 1986; Stork 1987a). This contrasts with predators and scavengers, and particularly with wood-eaters and fungal-feeders, which were diverse and abundant, as in other rainforest trees.

Sampling methods had a marked influence on the perception of arboreal community structure (see also Basset & Kitching 1991). Continuous and non-attractive trapping ensures a meaningful picture of arboreal community structure because the phenology of certain rainforest trees, including *A. actinophyllum*, may be important in structuring rainforest herbivore communities (Basset 1991c,d). Although the study of the rainforest canopy and its arthropod inhabitants is demanding, the use of simple and complementary methodologies, such as those developed in this study, should increase the number of comparative data sets.

Acknowledgements

We thank R. L. Kitching for his support during the study. N. D. Springate, D. Burckhardt and I. Löbl commented on the manuscript. The Queensland Department of Forestry allowed Y. Basset to carry out the research in the Mt Glorious State Forest and the Australian Museum contributed to travel expenses. The research was funded by a Griffith University Postgraduate Research Scholarship to

Y. Basset, and a small contribution from the Centre for Catchment and In-Stream Research, Division of Environmental Sciences.

References

Adis J., Lubin Y. D. & Montgomery G. G. (1984) Arthropods from the canopy of inundated and Terra firma forest near Manaus, Brazil, with critical considerations on the Pyrethrum-fogging technique. *Stud. Neotrop. Fauna Envir.* **19**, 223–36.

Barnard P. C., Brooks, S. J. & Stork N. E. (1986) The seasonality and distribution of Neuroptera, Raphidioptera, and Mecoptera on oaks in Richmond Park, Surrey, as revealed by insecticide sampling. *J. Nat. Hist.* **20**, 1321–31.

Basset Y. (1985a) Les peuplements d'arthropodes sur *Pinus mugo* Turra dans les tourbières du Haut-Jura neuchâtelois. *Bull. Soc. Neuchâtel. Sci. Nat.* **108**, 63–76.

Basset Y. (1985b) Aspects de la répartition des peuplements d'arthropodes dans les couronnes de *Pinus mugo* Turra. *Mitt. Schweiz. Ent. Ges.* **58**, 263–74.

Basset Y. (1988) A composite interception trap for sampling arthropods in tree canopies. *J. Aust. Ent. Soc.* **27**, 213–19.

Basset Y. (1989) The temporal and spatial distribution of arboreal arthropods associated with the rainforest tree *Argyrodendron actinophyllum*. PhD thesis, Griffith University, Brisbane.

Basset Y. (1990) The arboreal fauna of the rainforest tree *Argyrodendron actinophyllum* as sampled with restricted canopy fogging: Composition of the fauna. *Entomologist* **109**, 173–83.

Basset Y. (1991a) The taxonomic composition of the arthropod fauna associated with an Australian rainforest tree. *Aust. J. Zool.* **39**, 171–90.

Basset Y. (1991b) The seasonality of arboreal arthropods foraging within an Australian rainforest tree. *Ecol. Entomol.* **16**, 265–78.

Basset Y. (1991c) Leaf production of an overstorey rainforest tree and its effects on the temporal distribution of associated insect herbivores. *Oecologia* (in press).

Basset Y. (1991d) Influence of leaf traits on the spatial distribution of insect herbivores associated with an overstorey rainforest tree. *Oecologia* **87**, 388–93.

Basset Y. & Kitching R. L. (1991) Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. *Ecol. Entomol.* (in press).

Boland D. J., Brooker M. I. H., Chippendale G. M., Hyland B. P. M., Johnston R. D., Kleining D. A. & Turner J. D. (1984) *Forest Trees of Australia*. Nelson — CSIRO, Canberra.

Bourlière F. (1983) Animal species diversity in tropical forests. In: *Ecosystems of the World 14a: Tropical Rain Forest — Structure and Function* (ed. F. B. Golley) pp. 77–91. Elsevier, Amsterdam.

Dixon A. F. G. (1975) Aphids and translocation. In: *Encyclopedia of Plant Physiology. Vol. 1: Phloem Transport* (eds M. H. Zimmerman and J. A. Milburn) pp. 154–70. Springer, Berlin.

Elton C. S. (1973) The structure of invertebrate populations inside Neotropical rain forest. *J. Anim. Ecol.* **42**, 55–104.

Erwin T. L. (1983a) Tropical forest canopies: The last biotic frontier. *Bull. Ent. Soc. Am.* **29**, 14–19.

Erwin T. L. (1983b) Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In: *Tropical Rain Forest: Ecology and Management* (eds S. L. Sutton, T. C. Whitmore and A. C. Chadwick) pp. 59–76. Blackwell, Oxford.

Erwin T. L. & Scott J. C. (1980) Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: The fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. *Coleopts Bull.* **34**, 305–22.

Futuyma D. J. & Gould F. (1979) Associations of plants and insects in a deciduous forest. *Ecol. Monogr.* **49**, 33–50.

Hamilton W. D. (1978) Evolution and diversity under bark. In: *Diversity of Insect Faunas* (eds L. A. Mound and N. Waloff) pp. 89–104. Blackwell, Oxford.

Hendrix S. D., Brown V. K. & Dingle H. (1988) Arthropod guild structure during early old field succession in a new and old world site. *J. Anim. Ecol.* **57**, 1053–65.

Hijii N. (1983) Arboreal fauna in a forest. I. Preliminary observation on seasonal fluctuations in density, biomass and faunal composition in a *Chamaecyparis obtusa* plantation. *Jap. J. Ecol.* **33**, 435–44.

Hijii N. (1986) Density, biomass, and guild structure of arboreal arthropods as related to their inhabited tree size in a *Cryptomeria japonica* plantation. *Ecol. Res.* **1**, 97–118.

Jennings D. T. & Dimond J. B. (1988) Arboreal spiders (Araneae) on balsam fir and spruces in East-Central Maine. *J. Arachnol.* **16**, 223–35.

Jermy T. (1988) Can predation lead to narrow food specialization in phytophagous insects? *Ecology* **69**, 902–4.

Klomp H. & Teerink B. J. (1973) The density of the invertebrate summer fauna on the crowns of pine trees. *Pinus sylvestris*, in the central part of the Netherlands. *Beitr. Ent.* **23**, 325–40.

Larsson S. & Tenow O. (1980) Needle-eating insects and grazing dynamics in a mature scotch pine forest in central Sweden. *Ecol. Bull.* **32**, 269–306.

Majer J. D. (1990) The abundance and diversity of arboreal ants in Northern Australia. *Biotropica* **22**, 191–9.

Majer J. D. & Recher H. F. (1988) Invertebrate communities on western Australian eucalypts: A comparison of branch clipping and chemical knockdown procedures. *Aust. J. Ecol.* **13**, 269–78.

Martin J. L. (1966) The insect ecology of red pine plantations in Central Ontario. IV. The crown fauna. *Can. Ent.* **98**, 10–27.

McDonald W. J. F. & Whiteman W. G. (1979) *Explanatory Booklet for Murwillumbah Sheet. Moreton Region Vegetation Map Series*. Queensland Department of Primary Industries, Brisbane.

Metcalfe C. R. & Chalk L. (1957) *Anatomy of the Dicotyledons: Leaves, Stems and Wood in Relation to Taxonomy with Notes on Economic Use*. Clarendon Press, Oxford.

Monteith G. B. & Davies V. T. (1984) Preliminary account of a survey of arthropods (insects and spiders) along an altitudinal rainforest transect in tropical Queensland. In: *Australian National Rainforest Study Report, Vol. 1. Proceedings of a workshop on the past, present and future of Australian rainforests* (eds G. L. Werren and A. P. Kershaw) pp. 402–14. Geography Department, Monash University, Melbourne.

Moran C. V. & Southwood T. R. E. (1982) The guild composition of arthropod communities in trees. *J. Anim. Ecol.* **51**, 289–306.

Morse D. R., Stork N. E. & Lawton J. H. (1988) Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecol. Entomol.* **13**, 25–37.

Nielsen B. O. (1975) The species composition and community structure of the beech canopy fauna in Denmark. *Vidensk. Meddr. Dansk Naturh. Foren.* **138**, 137–70.

Ohmart C. P., Stewart L. G. & Thomas J. R. (1983) Phytophagous insect communities in the canopies of three *Eucalyptus* forest types in south-eastern Australia. *Aust. J. Ecol.* **8**, 395–403.

Ohmart C. P. & Voigt W. G. (1981) Arthropod communities in the crown of the natural and planted stands of *Pinus radiata* (Monterey pine) in California. *Can. Ent.* **113**, 673–84.

Perry D. R. (1978) A method of access into the crowns of emergent and canopy trees. *Biotropica* **10**, 155–7.

Rogers L. E., Hinds W. T. & Buschbom R. L. (1976) A general weight vs length relationship for insects. *Ann. Ent. Soc. Am.* **69**, 387–9.

Root R. B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* **43**, 95–124.

Schowalter T. D., Webb J. W. & Crossley Jr D. A. (1981) Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology* **62**, 1010–19.

Stork N. E. (1987a) Guild structure of arthropods from Bornean rain forest trees. *Ecol. Entomol.* **12**, 69–80.

Stork N. E. (1987b) Arthropod faunal similarity of Bornean rain forest trees. *Ecol. Entomol.* **12**, 219–26.

Terborgh J. & Robinson S. (1986) Guilds and their utility in ecology. In: *Community Ecology: Pattern and Process* (eds J. Kikkawa and D. J. Anderson) pp. 65–90. Blackwell, Oxford.

Webb L. J., Tracey G. & Williams W. T. (1984) An ecological framework of Australian rainforest. ii. Floristic classification. *Aust. J. Ecol.* **9**, 169–98.

Woinarski J. C. Z. & Cullen J. M. (1984) Distribution of invertebrates on foliage in forests of south-eastern Australia. *Aust. J. Ecol.* **9**, 207–32.

Yen A. L. (1989) Overstorey invertebrates in the Big Desert, Victoria. In: *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management* (eds J. C. Noble and R. A. Bradstock) pp. 285–99. CSIRO, Canberra.

Young P. A. R. (1985) *Vegetation and Flora: Brisbane Forest Park.* Brisbane Forest Park Administration Authority, Brisbane.

Appendix 1. Guild structure of arthropods foraging within *A. actinophyllum* crowns (details of values used in Fig. 2)

	No. individuals		Biomass		No. species	
Guild	IT*	RCF†	IT‡	RCF§	IT	RCF
Chewers	5.65	1.73	12.53	8.26	55	31
	(0.98)	(0.15)	(1.60)	(3.00)		
Phloem-feeders	11.04	5.24	5.88	3.52	65	22
	(0.81)	(0.62)	(0.51)	(0.28)		
Mesophyll-feeders	1.79	0.83	0.42	0.92	28	11
	(0.59)	(0.08)	(0.07)	(0.36)		
Epiphyll grazers	2.60	2.07	1.84	1.26	44	16
	(0.41)	(0.20)	(0.31)	(0.34)		
Fungal-feeders	9.74	1.48	0.88	0.18	42	16
	(0.83)	(0.20)	(0.07)	(0.02)		
Wood-eaters	6.47	0.40	6.31	0.31	124	20
	(2.05)	(0.05)	(1.38)	(0.15)		
Scavengers	3.81	0.61	7.60	2.26	38	8
	(0.62)	(0.06)	(1.99)	(0.36)		
Insect predators	4.34	1.10	37.07	1.43	165	32
	(0.24)	(0.20)	(2.99)	(0.30)		
Other predators	4.03	5.87	1.73	3.48	117	72
	(0.26)	(0.29)	(0.16)	(0.36)		
Parasitoids	6.58	1.23	2.23	0.17	48	21
	(0.75)	(0.94)	(0.67)	(0.02)		
Ants	2.68	0.51	0.82	0.62	8	7
	(1.45)	(0.08)	(0.40)	(0.09)		
Tourists	39.12	0.38	21.42	0.13	126	15
	(2.77)	(0.05)	(1.14)	(0.02)		
Uncertains	1.85	1.76	0.75	1.74	56	22
	(0.48)	(0.17)	(0.06)	(0.20)		

IT = interception traps RCF = restricted canopy fogging

*mean (s.e.) % individuals collected (n = 5)

†mean (s.e.) individuals collected per sample (n = 240)

‡mean (s.e.) % biomass collected (n = 5)

§mean (s.e.) biomass (mg DW) collected per sample (n = 240)