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Invertebrate communities on Western Australian eucalypts: A comparison of branch clipping and chemical knockdown procedures

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Abstract

*Chemical knockdown and branch clipping procedures were used in wandoo (*Eucalyptus wandoo*) woodland and jarrah (*E. marginata*)/marri (*E. calophylla*) open-forest to sample arboreal invertebrate faunas on three species of Western Australian eucalypts. Jarrah was sampled in both habitats and had significantly lower invertebrate populations and a less diverse fauna than either wandoo or marri. The two procedures provided similar results with respect to the relative abundance of invertebrates on each plant species but the knockdowns sampled a more diverse fauna, including species sheltering in or on bark. Chemical knockdowns underestimated the abundance of sessile invertebrates, such as psyllids. Branch clipping sampled insufficient numbers of large, mobile, or cryptic invertebrates to estimate abundances, but provided a more accurate estimate of the abundance of sessile, leaf-dwelling organisms. Neither procedure provides a complete sample of arboreal invertebrates, but they are complementary. When used in conjunction with each other a more complete estimate of arboreal invertebrate abundance and diversity is obtained. Both procedures can be used concurrently with only a small increase in field time.*

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Introduction

Invertebrates are key components of forest ecosystems. They play important roles in promoting soil structure and nutrient turnover, are major herbivores, seed-feeders and predators, and contribute to the maintenance of plant species diversity. They are also important in pollination and seed-dispersal. In addition, invertebrates are the principal food resource for the majority of forest birds. These are compelling reasons for the need to understand the patterns of abundance, distribution and taxonomic composition of forest invertebrate communities. Before such information can be obtained with acceptable levels of accuracy and repeatability, it is necessary to understand the degree of bias inherent within individual sampling procedures. These problems are typical of those encountered by biologists seeking to estimate the abundance of other forest organisms. Invertebrate sampling, therefore, requires the same attention to detail and comparison of methods as, for example, is used to assess census procedures for birds (see Ralph & Scott 1984 for reviews).

Although in recent years a number of investigators has sampled invertebrates on eucalypts, usually only one procedure has been used. Most commonly a variation of the branch or foliage clipping method has been employed (e.g. Ohmart *et al.* 1983; Bell 1985). Abbott and Van Heurck (1985) used standardized sweep samples with an insect net and Recher *et al.* (1983) applied visual counting procedures. Majer (1986) sampled canopy invertebrates using chemical knockdowns. It is likely that each of these procedures is biased towards particular components of the invertebrate fauna. Both clipping and visual searching procedures probably underestimate the abundance of smaller or more mobile species and do not sample invertebrates sheltering in bark or on branches. Sweep samples and chemical knockdowns may miss sessile animals or those in webs and cocoons. Visual counts and sweep samples probably also suffer from observer variability.

Independently we had begun studies of eucalypt canopy invertebrate communities using clipping (HR) or chemical knockdown (JM) procedures. In this paper, these two methods are compared for estimation of the abundance and spatial patterns of foliage invertebrates. The invertebrate fauna on three species of Western Australian eucalypts are contrasted.

Methods

Invertebrate communities were sampled on wandoo (*Eucalyptus wandoo*) and jarrah (*E. marginata*) at Dryandra State Forest (Grid CU114 on Forests Department Dryandra Map) in March 1986 and on jarrah and marri (*E. calophylla*) in the Victoria Forest block at Karragullen (Grid AZ65 on Forests Department Kelmscott Map) in October 1986. Canopy density and height ranges were 30% and 1–10 m at Dryandra, and 60% and 1–18 m at Karragullen. Chemical knockdown, but not branch clipping, samples were also available from wandoo for March 1984 and March 1985, and from powderbark wandoo (*E. accedens*) for March 1985 in Dryandra State Forest. None of the tree species was in flower at the time of sampling.

Pyrethrum knockdown samples

Between three and five patches of woodland canopy were selected at each site. Each patch was >25 m^2. The canopy was in the height range of 2–8 m above ground and consisted of foliage from 1 to 10 adjacent trees. During early morning the ground layer was cleared and calico sheets of 25 m^2 area were spread on the ground. The canopy was then sprayed with 5 l of 0.5% natural pyrethrum pesticide using a motorized knapsack mistblower. Knockdowns were performed between 1000 and 1200 h and the insecticide reached an approximate height of 7 m. The trees were then left for 30 min to allow silk-attached animals to drop to the ground. At the end of this time the canopy was shaken to dislodge any remaining animals. All animals were then collected from the sheets and placed in vials of 70% ethanol.

On return to the laboratory the resulting catch was separated and counted in broad taxonomic groups. The animals were placed in filter paper funnels for 12 h to drain off the preservative and then weighed. It was assumed that this weight approximated the live wet-weight of the animals. Ants were weighed separately since they were usually the most abundant animals.

Branch clipping

Trees were selected with foliage between 1.5 and 4 m above ground. From each tree a single sample of leaves, twigs and small branches (<10 mm in diameter) was clipped from the outer foliage of a single branch. Samples were selected which weighed 150–250 g and contained a minimum of 40 leaves. Branches with large numbers of seed capsules were avoided. Samples below 2.5 m were inserted into a plastic bag prior to clipping while higher samples (2.5–5 m) were bagged as rapidly as possible. No animals were observed leaving the samples before bagging. The bagged material was sprayed with a rapid knockdown household insecticide and the bag sealed until processed.

In the laboratory, bags were opened after weighing and the sample vigorously shaken prior to removal. The bag was then inspected for invertebrates dislodged by shaking; these invertebrates were identified and counted. Forty leaves were then taken randomly from the sample and inspected on both surfaces for sessile invertebrates and those in webs or cocoons. If present these were identified and counted. Invertebrate numbers obtained from these bags were then expressed as numbers/g of sample so that comparisons could be made between tree species. The average area of a single leaf for each species at each site was estimated from the mean of a randomly selected sample of 150–200 leaves. Abundances of sessile and web-spinning invertebrates plus those in cocoons were then compared between tree species using equal sized leaf areas (i.e. numbers cm^{-2} leaf area). Numbers were halved to allow for the presence of invertebrates on both the upper and lower surface of the leaf. A Li-Cor portable area meter was used.

TABLE 1. Numbers and biomass of invertebrates collected in pyrethrum knockdown samples of jarrah (*Eucalyptus marginata*) and wandoo (*Eucalyptus wandoo*) canopy in Dryandra State Forest during March 1986

Taxon	*Eucalyptus marginata*						*Eucalyptus wandoo*						
	1	2	3	4	5	$\bar{x}$ ± s.d.	1	2	3	4	5	$\bar{x}$ ± s.d.	Sig.
Arachnida													
Pseudoscorpionida	1	–	–	1	–	0.4 ± 0.5	–	–	–	2	1	0.6 ± 0.9	n.t.
Araneae	27	10	14	35	27	22.6 ± 10.3	34	39	54	90	50	53.4 ± 22.0	‡
Crustacea Isopoda	1	–	–	–	2	0.6 ± 0.9	–	–	–	–	1	0.2 ± 0.5	n.t.
Collembola	–	–	–	–	–	–	–	–	–	–	1	0.2 ± 0.4	n.t.
Insecta													
Thysanura	–	1	3	4	–	1.6 ± 1.8	–	1	7	1	1	2.0 ± 2.8	NS
Blattodea	6	6	22	5	11	10.0 ± 7.0	29	46	21	36	21	30.6 ± 10.6	‡
Mantodea	1	–	–	4	–	1.0 ± 1.7	–	–	–	–	–	–	n.t.
Dermaptera	2	–	–	–	–	0.4 ± 0.9	–	–	3	5	1	1.8 ± 2.2	n.t.
Orthoptera	–	1	3	–	–	0.8 ± 1.3	1	–	–	3	2	1.3 ± 1.3	NS
Phasmatodea	–	–	–	5	–	1.0 ± 2.2	–	–	–	–	–	–	n.t.
Psocoptera	1	1	–	3	1	1.2 ± 1.1	1	1	21	3	1	5.4 ± 8.8	NS
Hemiptera	54	11	20	41	26	30.4 ± 17.1	36	16	39	33	31	31.0 ± 8.9	NS
Thysanoptera	–	–	–	–	–	–	13	3	6	4	3	5.8 ± 4.2	‡
Neuroptera adults	–	–	–	–	–	–	–	–	1	1	2	0.8 ± 0.8	n.t.
Coleoptera adults	25	25	33	35	24	28.4 ± 5.2	123	79	65	126	85	95.6 ± 27.4	‡
Coleoptera larvae	–	–	4	–	4	1.6 ± 2.2	4	3	4	2	2	3.0 ± 1.0	NS
Diptera adults	9	1	2	3	34	9.8 ± 13.9	15	6	30	28	32	22.2 ± 11.2	‡
Lepidoptera adults	2	–	1	1	3	1.4 ± 1.1	2	3	7	5	4	4.2 ± 1.9	NS
Lepidoptera larvae	7	1	1	7	1	3.4 ± 3.3	–	2	5	7	4	3.6 ± 2.7	NS
Hymenoptera ants	192	36	39	59	23	69.8 ± 69.5	224	78	22	16	158	99.6 ± 89.9	NS
Hymenoptera others	4	14	6	10	23	11.4 ± 7.5	14	18	22	40	14	21.6 ± 10.8	NS
Total invertebrates	332	107	148	213	179	195.8 ± 85.6	496	295	307	402	414	382.8 ± 83.1	‡
Total invertebrates excluding ants	140	71	109	154	156	126.0 ± 36.0	272	217	285	386	256	283.2 ± 62.9	‡
Biomass (g)	2.4	1.6	1.6	1.7	0.7	1.6 ± 0.6	2.8	1.8	5.5	3.3	2.4	3.2 ± 1.4	‡

Where possible the data are compared using the Mann-Whitney U-test: ‡$P<0.05$; NS, not significant; n.t., not tested.

TABLE 2. Numbers and biomass of invertebrates collected in pyrethrum knockdown samples of powderbark wandoo (*Eucalyptus accedens*) and wandoo (*Eucalyptus wandoo*) canopy in Dryandra State Forest during March 1985

Taxon	*Eucalyptus accedens* 1	2	3	4	5	$\bar{x} \pm$ s.d.	*Eucalyptus wandoo* 1	2	3	$\bar{x} \pm$ s.d.	Sig.
Arachnida											
Pseudoscorpionida	–	–	–	–	–	–	1	–	–	0.3 ± 0.6	n.t.
Acarina	2	25	–	–	8	7.0 ± 10.6	–	2	–	0.7 ± 1.2	n.t.
Araneae	43	65	113	99	79	79.8 ± 27.6	119	90	89	99.3 ± 17.0	NS
Crustacea Isopoda	–	–	1	–	–	0.2 ± 0.5	–	–	–	–	n.t.
Collembola	1	–	1	–	–	0.4 ± 0.6	–	–	–	–	n.t.
Insecta											
Thysanura	11	1	1	1	6	4.0 ± 4.5	5	2	–	2.3 ± 2.5	NS
Blattodea	10	37	14	12	18	18.2 ± 10.9	46	13	23	27.3 ± 16.9	NS
Mantodea	–	1	4	1	–	1.2 ± 1.6	1	4	–	1.7 ± 2.1	n.t.
Dermaptera	16	16	–	–	–	6.4 ± 8.8	4	–	3	2.3 ± 2.1	n.t.
Orthoptera	1	3	4	4	–	2.4 ± 1.8	–	1	11	4.0 ± 6.1	NS
Phasmatodea	–	–	–	–	–	–	–	–	1	0.3 ± 0.6	n.t.
Psocoptera	1	–	–	–	–	0.2 ± 0.5	1	2	–	1.0 ± 1.0	n.t.
Hemiptera	33	58	16	14	46	33.4 ± 19.0	28	21	12	20.3 ± 8.0	NS
Thysanoptera	3	8	16	30	3	12.0 ± 11.4	3	4	–	2.3 ± 2.1	NS
Neuroptera adults	1	1	–	–	–	0.4 ± 0.6	–	–	–	–	n.t.
Neuroptera larvae	2	–	1	–	–	0.6 ± 0.9	–	–	–	–	n.t.
Coleoptera adults	54	94	68	60	98	74.8 ± 20.0	74	68	54	65.3 ± 10.2	NS
Coleoptera larvae	2	1	–	–	1	0.8 ± 0.8	2	2	–	1.3 ± 1.2	n.t.
Diptera adults	7	5	8	9	9	7.6 ± 1.7	8	6	–	4.7 ± 4.2	NS
Diptera larvae	–	–	–	–	5	1.0 ± 2.2	–	–	–	–	n.t.
Lepidoptera adults	–	2	1	3	2	1.6 ± 1.1	2	2	–	1.3 ± 1.2	NS
Lepidoptera larvae	2	2	2	3	7	3.2 ± 2.2	4	8	7	6.3 ± 2.1	NS
Hymenoptera ants	93	126	143	86	44	98.4 ± 38.4	327	232	133	230.7 ± 97.0	NS
Hymenoptera others	11	10	16	32	3	14.4 ± 10.9	6	11	4	7.0 ± 3.6	NS
Total invertebrates	293	455	409	354	329	368.0 ± 64.4	631	468	337	478.7 ± 147.3	NS
Total invertebrates excluding ants	200	329	266	268	285	269.6 ± 46.4	304	236	204	248.0 ± 51.1	NS
Biomass (g)	3.7	4.4	5.0	3.9	4.0	4.2 ± 0.5	5.0	4.6	3.1	4.2 ± 1.0	NS

Where possible the data are compared using the Mann-Whitney U-test: NS, not significant; n.t. not tested.

Results

Dryandra State Forest

Total invertebrates, numbers of invertebrates exclusive of ants, and invertebrate biomass sampled by chemical knockdown were all significantly greater on wandoo than on jarrah (Mann-Whitney U-test; $P<0.05$; Table 1). Eighteen of the 21 taxa recorded were more abundant on wandoo. Of these, spiders (Araneae), cockroaches (Blattodea), thrips (Thysanoptera), adult beetles (Coleoptera) and adult flies (Diptera) were significantly more abundant on wandoo than jarrah (Mann-Whitney U-test; $P<0.05$). The ratios of both abundance and invertebrate biomass were each 1:2 in favour of wandoo. Despite these differences, approximately the same number of taxa at ordinal level were found on the two species. In a comparison of the invertebrate fauna on wandoo and powderbark wandoo (*E. accedens*) sampled by chemical knockdown in 1985, total numbers of invertebrates, invertebrate biomass and the abundance of individual taxa did not differ between the species (Table 2).

The biomass of invertebrates on wandoo was similar in 1984, 1985 and 1986 (Table 3). However, total invertebrates were significantly different between years (Kruskall-Wallis analysis of variance; $P<0.05$). This was due to ground-living ants foraging in greater numbers on trees during the warmer years; if ants were excluded from the invertebrate count there is no significant difference in numbers between years (Table 3).

Similar differences between wandoo and jarrah were obtained by the branch clipping procedures, but fewer taxa were encountered (Table 4). The ratio of abundance of invertebrates on jarrah versus wandoo was 1:5 for the bagged samples (Table 4a) and 1:13 if the samples were standardized for leaf area (Table 4b). The majority of invertebrates sampled by the clipping procedures consisted of sessile groups such as psyllids (Hemiptera: Psylloidea) or web-spinning animals such as moth (Lepidoptera) larvae. Fifty-two per cent of the invertebrates recovered from the bagged sample and 74% of those recorded on leaves were in these categories.

Karragullen

At the time of sampling there was an outbreak of a psyllid, *Eucalyptolyma* sp., on marri. The total number of invertebrates and the number excluding ants was therefore significantly greater on marri than jarrah (Mann-Whitney U-test; $P<0.05$; Table 5). If both ants and psyllids are excluded, the ratio of total invertebrate abundance between jarrah and marri was 1:4, but numbers between individual trees were variable and the difference between tree species was not significant. Silverfish (Thysanura) were significantly more abundant on jarrah, but psyllids, beetle larvae and adult flies were significantly more abundant on marri (Mann-Whitney U-test; $P<0.05$). Biomass was also variable and, though greater on marri, the difference was not significant. There was no difference in the diversity of taxa at the ordinal level on the two eucalypts.

The abundance of *Eucalyptolyma* on marri was reflected in the branch clip results (Table 6). Apart from ants, which were more abundant on jarrah, the numbers and kinds of invert-

TABLE 3. Numbers and biomass ($\bar{x} \pm$ s.d.) of invertebrates collected in pyrethrum knockdown samples of wandoo (*Eucalyptus wandoo*) canopy in Dryandra State Forest during March, 1984, 1985 and 1986

	1984	1985	1986	Sig.
Sample size	5	5	3	
Total invertebrates	176.0 ± 80.9	478.7 ± 147.3	382.8 ± 83.1	*
Total invertebrates excluding ants	156.4 ± 83.8	248.0 ± 51.1	283.2 ± 62.9	NS
Invertebrate wet-weight (g) excluding ants	2.9 ± 2.2	4.2 ± 1.0	3.2 ± 1.4	NS
Ant wet-weight (g)	0.1 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	*
Mean minimum temperature (°C)	9.3	16.5	11.2	
Mean maximum temperature (°C)	23.5	33.3	26.8	
Total March rainfall (mm)	24	6	14	

The invertebrate data are compared using the Kruskal-Wallis one-way analysis of variance: $P<0.01$; NS, not significant.

TABLE 4. Invertebrates sampled by branch clipping procedures on jarrah (*Eucalyptus marginata*) and wandoo (*Eucalyptus wandoo*) at Dryandra State Forest

Variable	*Eucalyptus marginata*	*Eucalyptus wandoo*
a. Total number of invertebrates recovered from bagged samples		
Number of samples	60	64
Sample weight (g) ($\bar{x}$ ± s.d.)	227 ± 97	248 ± 100
Invertebrates		
Arachnida Araneae	9	19
Insecta		
Homoptera psyllids	8	96
Homoptera others	0	10
Coleoptera	9	9
Diptera	7	7
Lepidoptera	10	15
Hymenoptera ants	5	24
Others	4	46
Total	45	226
Invertebrate numbers g^{-1} of sample × 10^3	3	14
b. Total numbers of invertebrates recorded on samples of 40 leaves		
Number of samples	64	64
Mean leaf area (cm^2)	32.0	16.5
Invertebrates		
Insecta		
Homoptera psyllids	5	19
Homoptera others	1	1
Hymenoptera ants	0	6
Others	0	17
Total	6	43
Invertebrate numbers cm^{-2} leaf surface × 10^5	4	51

ebrates collected from the bagged samples were greater on marri than jarrah. Psyllids in particular were much more abundant on marri with nearly 2000 recovered from the bags. Although psyllids formed 98% of the invertebrates from the bagged marri samples, only 94 (70%) were collected from the bagged jarrah samples (Table 6a). A total of 11 psyllids were recorded on all the jarrah leaves inspected ($n = 1280$) whereas there was an average of 4.2 psyllids per individual marri leaf (Table 6b).

Discussion

Of the eucalypts sampled at both Dryandra and Karragullen, jarrah supported the smallest numbers and the lowest biomass of arboreal invertebrates. These differences are reflected in the use of the various tree species as foraging substrates by birds. At Dryandra few birds occurred in jarrah and most species foraged in wandoo or powderbark wandoo (H. F. Recher, unpubl. data). Abbott and Van Heurck (1985) measured arthropod abundance on jarrah and marri and compared the use of these trees by forest birds. They sampled arthropods using a sweep net technique and found similar biomass and arthropod taxa on both marri and jarrah, although the numbers of arthropods were higher on the jarrah than the marri. This discrepancy with the data from the present study could result from the fact that these authors sampled lower in the canopy than we did. Although their sample sizes were small, the three species of foliage-gleaning acanthizid warblers on their study area foraged more frequently on marri than jarrah relative to expected frequency based on the proportion of each tree species in the forest.

Reasons for different invertebrate abundance levels on eucalypts are obscure although it could be linked to the presence of secondary plant compounds, the nutrient level of the foliage, or to the structure of the leaves. Selection of tree species by herbivorous marsupials has been related to the presence of

…and biomass of invertebrates collected in pyrethrum knockdown samples of jarrah (*Eucalyptus marginata*) and marri (*Eucalyptus calophylla*) canopy at Karragullen during October 1986

Taxon	*Eucalyptus marginata* 1	2	3	4	$\bar{x}$ ± s.d.	*Eucalyptus wandoo* 1	2	3	4	$\bar{x}$ ± s.d.	Sig.
Arachnida											
Pseudoscorpionida	–	–	–	–	–	–	–	–	1	0.2 ± 0.5	n.t.
Acarina	1	–	–	1	0.5 ± 0.5	4	–	21	29	13.5 ± 13.7	NS
Araneae	23	22	28	22	23.8 ± 2.9	36	25	52	76	47.2 ± 22.1	NS
Crustacea Isopoda	3	–	–	–	0.8 ± 1.5	–	–	–	–	–	n.t.
Collembola	1	–	6	–	1.8 ± 2.9	9	–	–	2	2.8 ± 4.3	n.t.
Insecta											
Thysanura	87	23	23	61	48.5 ± 31.3	13	9	5	–	6.8 ± 5.6	‡
Blattodea	12	7	8	5	8.0 ± 2.9	18	–	16	25	14.8 ± 10.6	NS
Mantodea	–	–	–	–	–	–	–	1	–	0.2 ± 0.5	n.t.
Dermaptera	2	–	–	–	0.5 ± 1.0	2	–	–	–	0.5 ± 1.0	n.t.
Orthoptera	–	3	1	1	1.2 ± 1.2	8	2	3	2	3.8 ± 2.9	NS
Phasmatodea	1	–	–	1	0.5 ± 0.6	–	4	3	1	2.0 ± 1.8	NS
Hemiptera psyllids	–	–	–	–	–	4300	1500	700	3200	2425.0 ± 1628.0	‡
Hemiptera others	47	18	35	37	34.2 ± 12.0	26	60	60	176	80.5 ± 65.7	NS
Psocoptera	26	2	–	32	15.0 ± 16.4	5	5	2	1200	303.0 ± 598.0	NS
Thysanoptera	–	–	–	–	–	–	–	–	7	1.8 ± 3.5	n.t.
Neuroptera adults	3	–	–	–	0.8 ± 1.5	–	3	12	1	4.0 ± 5.5	n.t.
Neuroptera larvae	–	1	1	–	0.5 ± 0.6	–	–	–	–	–	n.t.
Coleoptera adults	112	34	25	31	50.5 ± 41.2	274	97	503	111	246.3 ± 189.1	NS
Coleoptera larvae	–	1	–	–	0.2 ± 0.5	15	9	2	105	32.8 ± 48.5	‡
Mecoptera	–	–	–	–	–	–	2	2	7	2.8 ± 2.9	n.t.
Diptera adults	86	31	27	24	42.0 ± 29.5	245	119	107	426	224.2 ± 148.3	‡
Diptera larvae	–	–	–	–	–	–	–	–	30	7.5 ± 15.0	n.t.
Trichoptera	–	–	–	–	–	–	6	6	5	4.2 ± 2.9	n.t.
Lepidoptera adults	18	9	6	2	8.8 ± 6.8	19	8	14	7	12.0 ± 5.6	NS
Lepidoptera larvae	15	9	4	17	11.3 ± 5.9	17	6	56	58	34.2 ± 26.7	NS
Hymenoptera ants	16	142	37	16	52.8 ± 60.3	40	1	94	76	52.8 ± 41.2	NS
Hymenoptera others	25	1	11	4	10.2 ± 10.7	2	21	15	117	38.8 ± 52.8	NS
Hymenoptera larvae	–	–	–	–	–	–	–	18	32	12.5 ± 15.5	n.t.
Total invertebrates	478	303	211	254	311.5 ± 117.2	5033	1877	1692	5694	3574 ± 2085	‡
Total invertebrates excluding ants	462	161	174	238	258.7 ± 139.6	4993	1876	1598	5618	3521 ± 2079	‡
Total invertebrates excluding ants & psyllids	462	161	174	238	258.7 ± 139.6	693	376	898	2418	1096 ± 907	NS
Biomass (g)	6.7	3.9	1.4	0.6	3.2 ± 2.8	5.1	2.1	10.9†	8.4†	6.6 ± 3.8	NS

Where possible the data are compared using the Mann-Whitney U-test: ‡$P<0.05$; NS, not significant; n.t. not tested.
†Excluding the large sawfly (Hymenoptera) larvae, which weighed 13.0 and 7.3 g respectively in marri samples 3 and 4.

TABLE 6 Invertebrates sampled by branch clipping procedures on jarrah (*Eucalyptus marginata*) and marri (*Eucalyptus calophylla*) at Karragullen

Variable	*Eucalyptus marginata*	*Eucalyptus calophylla*
a. Total number of invertebrates recovered from bagged samples		
Number of samples	32	32
Sample weight (g) ($\bar{x}$ ± s.d.)	139.0 ± 67.0	118.0 ± 56.0
Sample height (m) ($\bar{x}$ ± s.d.)	2.5 ± 0.8	2.5 ± 1.1
Invertebrates		
Arachnida Araneae	3	6
Insecta		
Orthoptera		
Homoptera psyllids	0	1
Homoptera others	94	1884
Coleoptera	0	1
Diptera	0	1
Lepidoptera	0	8
Hymenoptera ants	37	3
Total	134	>1904
Invertebrate numbers g^{-1} of sample × 10^2	3	>50
b. Total number of invertebrates recorded on samples of 40 leaves		
Number of samples	32	32
Mean (± s.d.) leaf area (cm^2)	20.6 ± 5.1	20.4 ± 3.6
Mean (± s.d.) weight of 40 leaves (g)	24.2 ± 4.5	31.5 ± 7.2
Invertebrates		
Insecta		
Homoptera psyllids	11	5378
Total	11	5378
Invertebrate numbers cm^{-2} leaf surface × 10^5	21	10294

secondary compounds and/or to differences in foliage nutrient levels (Ullrey *et al.* 1981; Braithwaite *et al.* 1984). Herbivorous insects may respond in a similar manner with the higher levels of abundance or smaller amounts of secondary compounds. We have found no information on secondary plant compounds in wandoo or powderbark wandoo, although Gildemeister and Hoffman (1961) and Hingston (1961) respectively have produced data on the levels of essential oils and polyphenols in marri and jarrah. While there is little difference in the overall oil concentration in the leaves of the two species, the polyphenol value is 2.6 times greater in the jarrah than in the marri leaves. This could account for the lower levels of invertebrates on the former species.

There are few data available on nutrients in the foliage of Western Australian eucalypts. Hingston *et al.* (1980/81) found that jarrah leaves had lower levels of nutrients (nitrogen, phosphorus and potassium), as well as smaller amounts of various trace elements, than marri. However, both species appeared to have low nutrient levels compared to some eucalypts from eastern Australia. J. Marshall (*in litt.*) points out that it is difficult to draw conclusions on the nutrient status of eucalypt foliage based on samples taken from different locations or at different seasons. However, some data provided by Marshall (unpubl. data) suggest that marri and wandoo foliage have higher nutrient levels than jarrah. This could also account for the lower usage of jarrah foliage by invertebrates.

The anatomy of the leaves of these eucalypts may also influence their use by herbivores. In comparison with wandoo and marri, jarrah leaves are thinner. Also, the thickness of leaf cuticle is greater on jarrah than on marri (Ridge *et al.* 1984). Thus, jarrah leaves may be more difficult to chew or penetrate than marri and the nutritive reward per unit area of jarrah leaf would be less than that of either wandoo or marri.

Regardless of reasons for different invertebrate abundance on the eucalypts sampled, both knockdown and branch clipping procedures provided information on relative abundance; namely, jarrah has a poorer invertebrate fauna than either marri or wandoo. This observation is consistent with the use of these species as foraging substrates by small, foliage-gleaning birds. The knockdown data collected over 3 years, for wandoo at least, suggest that invertebrate abundance and biomass does not vary much from year to year for a given season. Work is currently in progress to determine the seasonal variation in invertebrate abundance and diversity on some of these tree species.

Each procedure samples a different part of the arboreal invertebrate fauna. The knockdowns sample a much wider array of invertebrates and include many insects which live in, or take refuge on, bark. Bark-dwelling invertebrates include pseudoscorpions (Pseudoscorpionida), slaters (Isopoda), springtails (Collembola), cockroaches and booklice (Psocoptera). The greater abundance of silverfish on jarrah than on marri is probably related to the fibrous and deeply furrowed bark of jarrah providing a better habitat for these animals than the hard, shallowly furrowed bark of marri. Clipping sampled sessile or web-spinning animals almost exclusively. Less common invertebrates, mobile animals and bark-dwellers were unrepresented in clipped samples. Nonetheless the two procedures complement each other and can be used concurrently with little additional field effort. By producing greater numbers of invertebrates, the knockdown samples produce data which are easier to analyse statistically than are those data from the branch clipping samples. Both methods undersample those species which are only present on foliage at night.

It was possible to perform two knockdowns per day (restricting samples to between 1000 and 1200 h) with the help of six people. An additional two person hours was required to take 16 branch clip samples, but this work could generally be fitted into the knockdown routine without extending field time. Sorting and laboratory analysis for the two methods required four person hours for each knockdown and one person hour for each four to five clip samples. Eight knockdowns therefore required 32 person hours, and 64 branch clips took 12–15 person hours. In comparison with performing chemical knockdowns alone, both sampling techniques may be performed together with little additional field time and a 38–47% increase in laboratory time.

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