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Variation in foliar nutrients in *Eucalyptus* trees in eastern and Western Australia

J. D. MAJER,[1] H. F. RECHER[2] AND S. GANESHANANDAM[3]
[1]*School of Environmental Biology and* [3]*School of Mathematics and Statistics, Curtin University of Technology, PO Box U1987, Perth, WA 6001, and* [2]*Department of Ecosystem Management, University of New England, Armidale, NSW 2350, Australia*

Abstract Levels of nitrogen, phosphorus and potassium were measured for the foliage of two co-dominant eucalypts at each of two sites, one in eastern Australia and the other in Western Australia. In eastern Australia, foliage was sampled in the canopy and subcanopy for narrow-leaved ironbark *Eucalyptus crebra* and grey box *E. mollucana* and in Western Australia, for jarrah *E. marginata* and marri *E. calophylla*. The Western Australian trees were also sampled for 'young' and 'old' leaves. Both eucalypts in eastern Australia had greater nitrogen and phosphorus levels, but lower potassium, than *E. marginata* or *E. calophylla*. *Eucalyptus calophylla* foliage had greater levels of all three nutrients than *E. marginata* foliage as did *E. crebra* relative to *E. mollucana*. At both sites, foliar nutrient levels were greater in the canopy than subcanopy foliage, and, at least in Western Australia, the younger leaves had greater nutrient levels than the older leaves. The observed differences in foliar nutrient levels are consistent with observed trends in the abundance and diversity of foliage arthropods and the use of the trees as foraging substrates by birds.

INTRODUCTION

The forests and woodlands of the southern part of Australia generally consist of mixed stands of two or more species of *Eucalyptus*. A number of studies have indicated that although the different tree species within a community may have a relatively similar appearance, the usage of these substrates by insectivorous birds may deviate substantially from what would be expected if they did not differentiate between tree species (Recher *et al.* 1991).

The apparent selection of feeding substrates by birds could be associated with differences in tree architecture, which may influence the ease with which food may be obtained, or it could result from a response to differing food availability on the various species of tree. Since 1987 we have been studying the abundance, diversity and spatial distribution of arboreal arthropods within the canopies of two co-dominant eucalypts within one New South Wales and one Western Australian forest (Majer & Recher 1988; Majer *et al.* 1990). In both cases we have found that one of each pair of eucalypts supports a greater abundance (Majer *et al.* 1990) and diversity (J. D. Majer & H. F. Recher unpubl. data) of arthropods than does the other species. Furthermore, abundance and diversity of arthropods is greater on the NSW trees than on those in WA. These trends are consistent with the abundance and species richness of birds being greatest on the NSW site and also with the pattern of usage of trees by insectivorous birds; tree species supporting the highest arthropod levels also experienced the highest foraging rates by birds within both forests that we studied (Recher *et al.* 1991).

At this stage we are not certain why the levels of arthropods are so different on co-dominant *Eucalyptus* species. The abundances of arthropods on trees are known to be influenced by a range of factors. The level of nutrients, particularly nitrogen, within leaves is an important limiting agent for the growth and development of phytophagous arthropods (Mattson 1980), and this could also indirectly affect the abundance and diversity of arthropods from other trophic levels. Some writers believe that plants with less than 1.8% nitrogen are a substandard food resource (Mattson 1980). It has been suggested that, as with many evergreen trees elsewhere in the world (Mattson 1980), Australian forest tree and understorey species tend to exhibit

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low foliar nitrogen levels and may thus present a limiting resource to phytophagous arthropods (Ashton 1975; Fox & Macauley 1977). It may be that our observed differences in arthropod levels are related to small differences in nutrient levels between the various tree species. However at present there is very little experimental evidence to suggest that nitrogen in eucalypts does limit arthropod abundance; only Ohmart's (1991) study of chrysomelids feeding on *Eucalyptus* showed such an effect, but the low levels that he induced experimentally would be unlikely to be manifested in the field.

Secondary plant compounds are also known to vary between tree species and to have deleterious effects on herbivores (Whittaker & Feeny 1971). *Eucalyptus* leaves contain two important groups of such compounds, the essential oils (Penfold & Willis 1961) and the phenolics, including tannins (Hillis 1966). Variations in the amounts and/or diversity of compounds within one or both groups could account for interspecific differences in arthropod levels on the trees which we studied. Once again, the evidence from studies on *Eucalyptus* spp. is that these compounds have no relation to insect performance (e.g. Larsson & Ohmart 1988). It could be that these secondary plant compounds influence the attractiveness of a tree to herbivores but this has not been investigated for *Eucalyptus* spp.

A third factor which could account for differences in arthropod levels on trees is the toughness, or sclerophylly, of the leaf (Morrow 1983). As well as restricting the feeding by many phytophagous arthropods to young foliage (e.g. Ohmart *et al.* 1987; Larsson & Ohmart 1988; Ohmart 1991), this variable could, in the same way that it can for folivorous mammals (Cork & Sanson 1990), account for differences in arthropod abundance between trees.

In this paper we describe the foliar nutrient levels of four *Eucalyptus* spp. and relate these to the possibility that leaf nutrients could account for the observed differences in arthropod levels within the canopies of the tree species that we studied in eastern and Western Australia.

METHODS

Sampling was done at Scheyville, NSW (56°05'S, 150°51'E), where we sampled narrow-leaved ironbark (*Eucalyptus crebra*; the NSW co-dominant supporting the highest arthropod levels) and grey box (*Eucalyptus mollucana*), and at Karragullen, WA (32°04'S, 116°07'S), where we sampled marri (*Eucalyptus calophylla*; the WA co-dominant supporting the highest arthropod levels) and jarrah (*Eucalyptus marginata*). The forest at Scheyville was dominated by *E. crebra* (42% of tree foliage, as measured by the composition of foliage above 500 vertical sighting points) and *E. mollucana* (51% of tree foliage) with smaller numbers of forest red gum (*Eucalyptus tereticornis*; 7% of tree foliage) and thin-leaved stringybark (*Eucalyptus eugenoides*; $<1\%$ of tree foliage). Canopy cover was 40–45%, with the canopy averaging 15–18 m in height. Individual trees emerged above the canopy to 25 m. The understorey consisted of eucalypt saplings; grasses and forbs comprised the ground cover. At Karragullen, *E. marginata* (92% of tree foliage) dominated the forest; *E. calophylla* comprised the remaining 8% of tree foliage. Canopy cover was 60%, and mean canopy height was 15–18 m, with individual trees to 30 m. Karragullen had a more diverse understorey than the forest at Scheyville, with a dense subcanopy of eucalypt saplings, sheoak (*Allocasuarina fraserana*) and bull banksia (*Banksia grandis*). The site had a rich herb and shrub layer.

The climate at the Karragullen site falls within Köppen's (1923) mediterranean type, and exhibits cool, wet winters and hot, dry summers. The mean annual rainfall is 1241 mm with most rain falling between May and October. The Scheyville site conforms to Köppen's warm, temperate type and, although spring (August–October) tends to be drier than other seasons, rain falls fairly evenly throughout the year. Mean annual rainfall is 874 mm, summers are warm and winters are cool with occasional frosts.

Foliage was collected from 10 individuals of each tree species at each height range during January 1990, the period when both young and mature leaves were present. At Karragullen we made separate collections of young and mature foliage from each stratum, while the Scheyville collections were mostly mature foliage with some younger leaves. All material was sealed in paper bags, oven dried at 72°C to constant weight and then ground in a Wiley-type mill with a 1 mm sieve for subsequent analysis of nutrients. Two subsamples from each tree and height range were then

analysed for Kjeldahl nitrogen, total phosphorus and total potassium.

Samples for the analysis of potassium and phosphorus were digested using a perchloric acid procedure, and for nitrogen using a Technicon BD-40 digestion procedure (Technicon undated a and b). Potassium levels were then measured on a Varian AA 1475 atomic absorption spectrophotometer. Nitrogen and phosphorus levels were analysed after digestion using a Technicon Autoanalyser II (Technicon undated c). For nitrogen, a phenolic procedure was used and for phosphorus, the molybdenum blue technique was followed.

The statistical analysis was designed to investigate the effects of tree stratum and, in the WA forest, leaf age on foliage nutrients, with an additional assessment of the variation in nutrients between the two eucalypt species within a particular forest. The total variability in the data of three variables, namely Kjeldahl nitrogen, total phosphorus and total potassium, was measured for each foliage sample. The techniques used for the analysis were (i) univariate analysis of variance (ANOVA) and (ii) canonical variate analysis (CVA), both of which were performed using SAS (1989) software.

Initially, three independent comparisons were made for each nutrient variable by means of ANOVA. As the samples for upper and lower foliage were collected on separate trees for each tree species, a factorial model ANOVA was used to analyse the data. This was done separately for WA and NSW trees. The collection of data for young and mature foliage was somewhat different to the above in that the foliage of the two ages was selected from the same tree for a particular stratum. Thus, the investigation of the behaviour of tree species and leaf age on nutrients was performed by means of a nested model ANOVA, with leaf age nested within tree species. Hence, the ANOVA performed were designed to test the effects of (i) species, strata and species*strata interaction, for NSW trees; (ii) species, strata and species*strata interaction, for WA trees; and (iii) species and leaf age within species for WA trees. In order to facilitate these ANOVA, appropriate models were fitted for each of the three response variables, nitrogen, phosphorus and potassium. The appropriate standard deviations are fairly homogeneous (see Tables 1, 2), indicating that transformations are unnecessary (see for example Ott 1988 for more details on factorial and nested design models).

When interest lies in exploring between-group patterns of differences on more than one response variable, an intrinsically multivariate approach should be used. This approach is desirable either when the individual response variables are of no interest but their aggregate response is, or when no one of the set of response variables shows any distinction between groups whereas a suitable combination of variables clearly distinguishes them, or when a high correlation among the response variables is suspected. The simplest procedure is to construct a linear combination of the variables which clearly separates the groups, if the mean value of this new variable changes considerably from group to group with the value within a group being fairly consistent. One way to choose the coefficients in this linear combination is therefore to maximise the between-group variation while simultaneously minimizing the within-group variation. When this approach is used, it may be possible to determine several linear combinations for separating the groups. These new variates (or dimensions) are usually referred to as canonical variates, where the first variate reflects as much inter-group difference as possible, the second captures as much as possible of the group differences not displayed by the first one, and so on. The first few (one or two) canonical variates are generally sufficient to account for almost all of the group differences. One of the major attractions of this procedure is that if only one or two canonical variates are needed, then a simple graphical representation of the relationship between the various groups can be produced by plotting the values of these variates for sample observations. The canonical variate procedure used here is given a biological treatment by Manly (1986), and an ecological one by Digby and Kempton (1987). Dillon and Goldstein (1984) and Krzanowski (1988) saw canonical variate analysis as an important tool for analysing various types of data.

RESULTS

The F ratios for comparisons from independent ANOVA, together with means and standard deviations for the NSW data are presented in Table 1, while Table 2 shows the results for the WA data. It is evident that the levels of all nutrients differ significantly between tree species within a particular

forest. In all instances, *E. crebra* had greater nutrient levels than *E. mollucana* (Table 1) and *E. calophylla* had higher nutrient levels than *E. marginata* (Table 2). When data from the two tree species were treated together, with the exception of potassium in WA, the concentrations of all three nutrients were significantly greater in the upper than the lower stratum of a particular forest (Tables 1,2). With two exceptions, these trends were mirrored at the individual species level. These were phosphorus, which was slightly greater in the lower foliage than in the upper foliage of *E. mollucana*, reflecting the significance of the interaction effect in Table 1, and the greater potassium concentration in the lower foliage of *E. calophylla* than in the upper foliage, once again confirming the significance of the interaction effect in Table 2. It would be misleading to suggest that there is no overall difference between the potassium concentrations from lower and upper canopies in WA forests. The significance (at 2% level) of the interaction between species and strata may be accounted for by the smaller difference between the lower and the upper canopies of *E. marginata* trees compared to a larger difference among the canopies of *E. calophylla*. As far as the age effects are concerned, the nutrient levels were significantly higher in the younger leaves than the mature foliage of the WA trees (Table 2).

Six sets of canonical variate analyses were performed using all three nutrient response variables. The first CVA was performed to investigate the separation between *E. mollucana* and *E. crebra*, regardless of stratum. The second and third were

Table 1. Means (SD) of nutrient levels (mg g^{-1} dry weight) in lower ($n = 60$) and upper ($n = 50$) canopy foliage of *E. mollucana* and *E. crebra*

	E. mollucana		*E. crebra*		*F* ratios from ANOVA (*P* values)			Residual mean
	Lower	Upper	Lower	Upper	Species	Stratum	Species*stratum	square values
	8.27	10.23	12.06	13.72	184.42	44.78	0.34	3.979
Nitrogen	(3.13)	(1.08)	(1.39)	(1.51)	(0.0001)	(0.0001)	(0.5629)	
	0.57	0.54	0.70	0.93	144.81	22.52	38.38	0.025
Phosphorus	(0.12)	(0.07)	(0.23)	(0.15)	(0.0001)	(0.0001)	(0.0001)	
	2.99	3.44	3.56	3.90	18.68	10.32	0.21	0.798
Potassium	(0.54)	(1.03)	(1.24)	(0.48)	(0.0001)	(0.0015)	(0.6437)	

The means are compared between species and strata using factorial analysis of variance.

Table 2. Means (SD) of nutrient levels (mg g^{-1} dry weight) in lower ($n = 40$) and upper ($n = 40$) canopy foliage, both mature ($n = 40$) and young ($n = 40$), of *E. marginata* and *E. calophylla*

	E. marginata		*E. calophylla*		*F* ratios from ANOVA (*P* values)			Residual mean
	Lower	Upper	Lower	Upper	Species	Stratum	Species*stratum	square values
	6.65	7.88	7.95	9.98	74.40	68.40	4.26	1.551
Nitrogen	(1.18)	(1.01)	(1.22)	(1.52)	(0.0001)	(0.0001)	(0.0408)	
	0.23	0.34	0.36	0.46	35.31	26.32	0.04	0.018
Phosphorus	(0.10)	(0.15)	(0.14)	(0.13)	(0.0001)	(0.0001)	(0.8488)	
	2.95	3.72	6.26	5.74	105.26	0.22	6.21	2.712
Potassium	(1.31)	(1.53)	(2.39)	(1.04)	(0.0001)	(0.6421)	(0.0138)	
	Old	Young	Old	Young	Species		Leaf Age	
	6.70	7.83	8.38	9.55	59.73		13.78	1.933
Nitrogen	(1.08)	(1.16)	(1.65)	(1.58)	(0.0001)		(0.0001)	
	0.19	0.38	0.32	0.50	54.49		62.71	0.011
Phosphorus	(0.06)	(0.13)	(0.10)	(0.13)	(0.0001)		(0.0001)	
	2.06	4.60	4.74	7.26	240.50		107.55	1.187
Potassium	(0.38)	(0.97)	(1.08)	(1.58)	(0.0001)		(0.0001)	

The means are compared between species and strata using factorial analysis of variance, and between leaf age of each species using nested analysis of variance.

Table 3. Percentage variance represented by the first or first and second canonical variates of the six canonical variate analyses. The correlations between nutrient levels and the canonical variates of the samples are also shown

Groups separated	Canonical variate	% of variation explained	Correlation coefficients between the nutrient variables and the canonical variate (*P* values) Nitrogen	Phosphorus	Potassium	Plots of canonical variate scores
E. mollucana, *E. crebra* ($n = 220$)	1	99.70	0.88 (0.0001)	0.81 (0.0001)	0.38 (0.0001)	Fig. 1
E. mollucana ($n = 110$)	1	99.27	0.88	−0.35	0.62	Fig. 2a
Lower			(0.0001)	(0.0001)	(0.0001)	
Upper						
E. crebra ($n = 110$)	1	99.09	0.75	0.76	0.25	Fig. 2b
Lower			(0.0001)	(0.0001)	(0.0072)	
Upper						
E. marginata, *E. calophylla* ($n = 160$)	1	99.55	0.69 (0.0001)	0.57 (0.0001)	0.88 (0.0001)	Fig. 3
E. marginata ($n = 80$)	1	96.35	0.65	0.88	0.95	Fig. 4a
Lower & mature			(0.0001)	(0.0001)	(0.0001)	
Lower & young						
Upper & mature						
Upper & young						
E. calophylla ($n = 80$)	1	58.42	0.28	0.64	0.99	Fig. 4b
Lower & mature			(0.0113)	(0.0001)	(0.0001)	
Lower & young	2	38.63	0.88	0.69	−0.03	
Upper & mature			(0.0001)	(0.0001)	(0.7849)	
Upper & young						

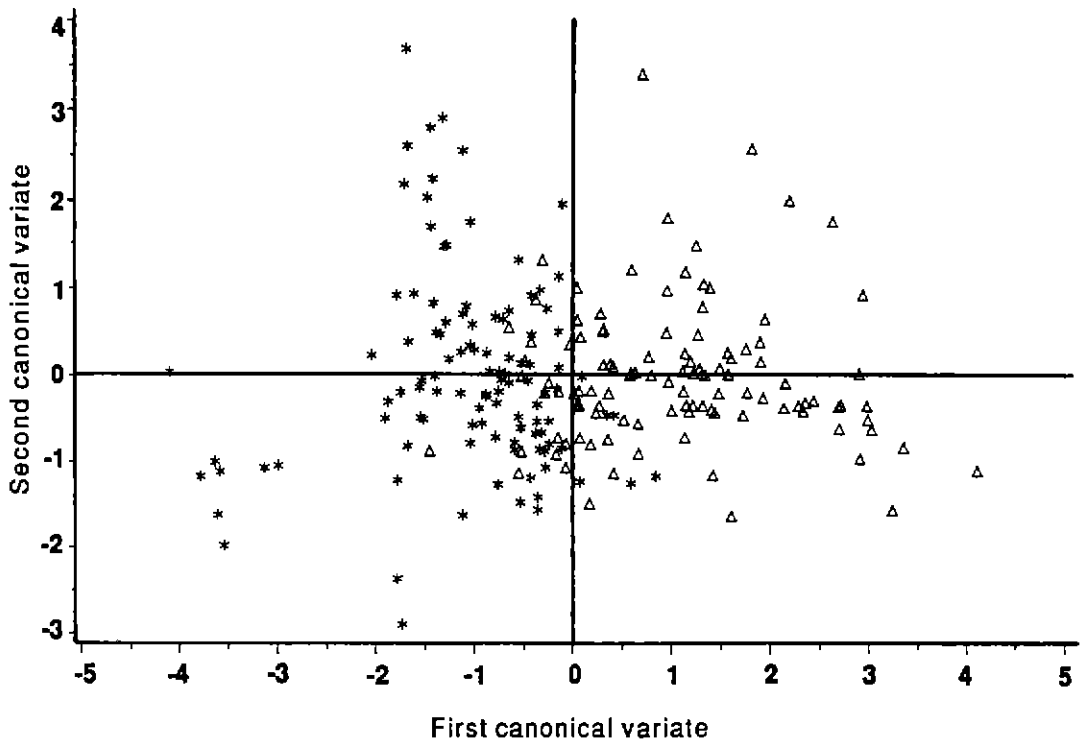

Fig. 1. Individual NSW foliage sample data, plotted against first and second canonical variates as axes, derived using the nitrogen, phosphorus and potassium data. (*) *E. mollucana*; (△) *E. crebra*.

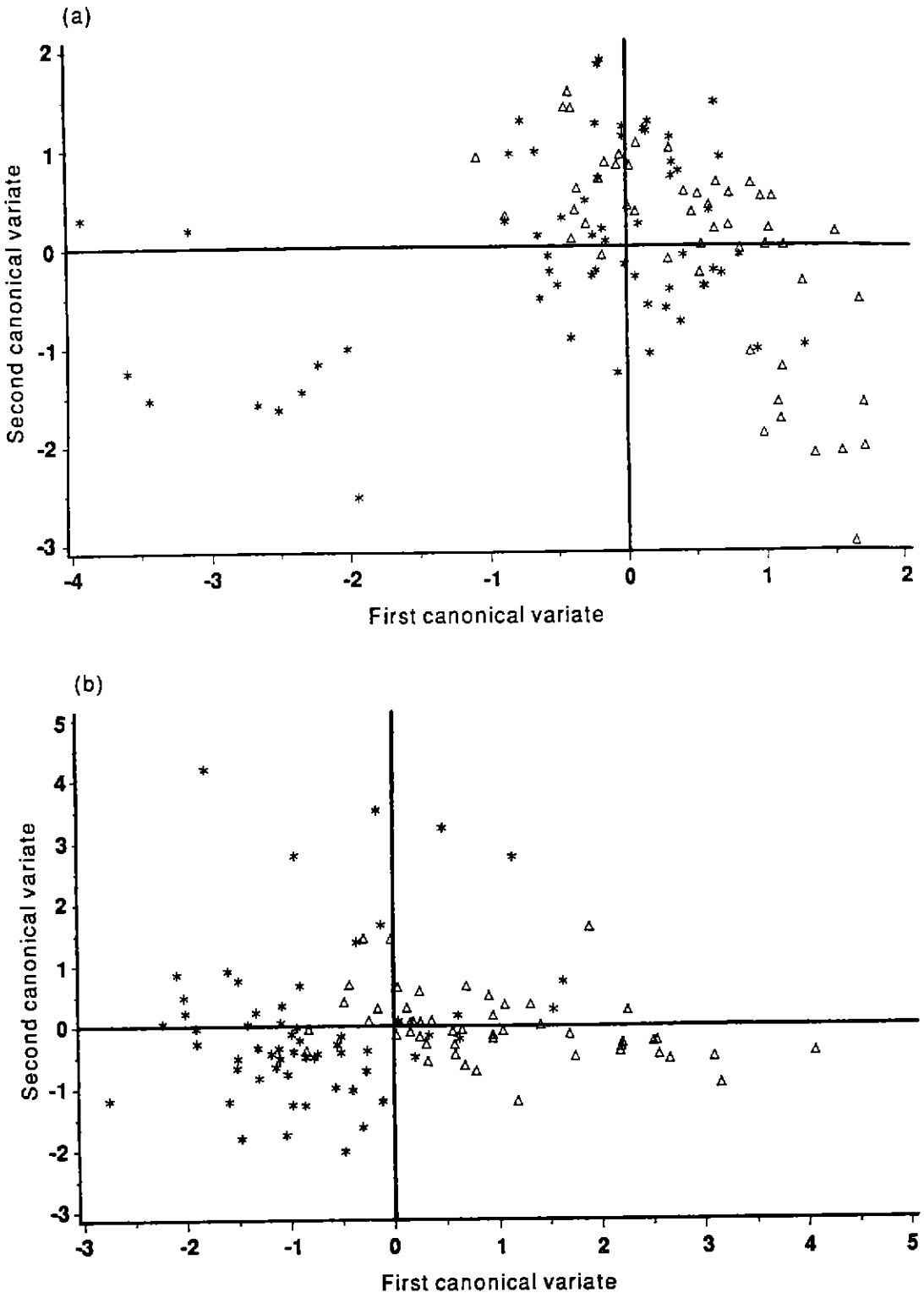

Fig. 2. Individual (a) *E. mollucana* and (b) *E. crebra* data from upper and subcanopy strata, plotted against first and second canonical variates as axes, derived using the nitrogen, phosphorus and potassium data. (*) subcanopy; (△) upper canopy.

performed to differentiate the effects of lower and upper canopy separately for both *E. mollucana* and *E. crebra*. The last three CVA were carried out on the WA data, first with *E. marginata* and *E. calophylla* trees as groups, the next two to differentiate the effects of both stratum and foliage age separately on *E. marginata* and on *E. calophylla* foliar nutrient levels. The first five CVA indicated that the first canonical variate was sufficient to explain nearly all the variation among the respective

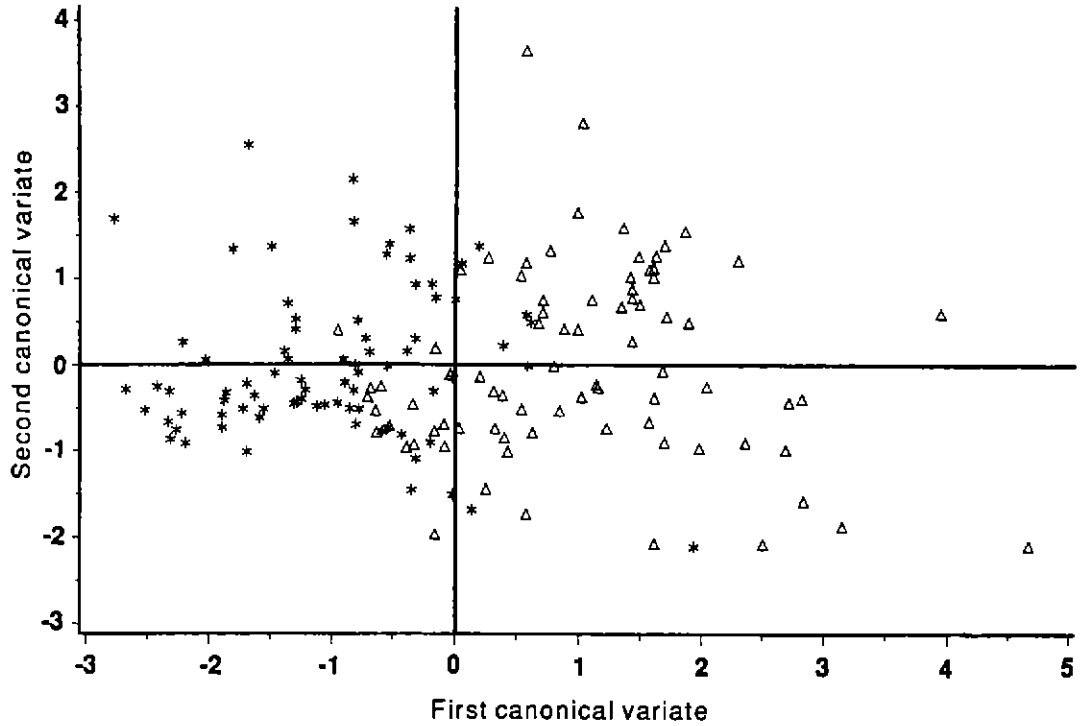

Fig. 3. Individual WA foliage sample data, plotted against first and second canonical variates as axes, derived using the nitrogen, phosphorus and potassium data. (*) *E. marginata*; (△) *E. calophylla*.

groups (Table 3). The final CVA, which investigated the impact of stratum and foliage age on *E. calophylla* foliar nutrients, produced a result in which the first two canonical variates accounted for 97% of the variation among groups (Table 3). In all six CVA, the sample observations were plotted against their values for the first two canonical variates to illustrate the nature of the separation (Figs 1–4). In order to provide further insight into the reasons for the separations of samples on the CVA diagram, the correlation coefficients between the nutrient variables and the associated canonical variate of that sample were calculated. The correlation coefficients are shown in Table 3.

There is only a slight overlap between samples from *E. mollucana* and *E. crebra* (Fig. 1). Inspection of the correlation coefficients between nutrient levels and canonical variates (Table 3) indicates that nitrogen and phosphorus are the most important nutrients in the discrimination of foliage from these two tree species. The plots of *E. mollucana* and *E. marginata* foliage from different strata (Figs 2a,b, respectively) also produced a separation between samples and from the two strata, although not as clear as in Fig. 1. Levels of nitrogen were consistently associated with this separation of samples, although phosphorus only appeared to be important with *E. crebra* and potassium with *E. mollucana*. The weak negative correlation of phosphorus with the canonical variate for *E. mollucana* was associated with the lower foliage containing slightly greater quantities of this nutrient than the upper foliage (Table 1).

The results for the WA trees are presented in Figs 3 and 4. Once again, samples from *E. calophylla* and *E. marginata* are well separated along canonical variate 1, with little overlap in samples from the two tree species. In this CVA, potassium, and to a lesser extent nitrogen, are strongly correlated with the canonical variates of the corresponding samples. The plots of *E. marginata* and *E. calophylla* samples from different strata and foliage ages are shown in Fig. 4a,b, respectively. In the case of *E. marginata*, there is a clear separation of samples from mature lower foliage to the left of the diagram through to young upper canopy foliage to the right; the other two categories of foliage are positioned in the middle of the diagram but are still well separated from each other. In this case both potassium, phosphorus, and to a lesser extent nitrogen, are highly correlated with the first canonical variate (Table 3). The situation for *E. calophylla* is slightly more complicated in that young and mature foliage separated on canonical variate 1 while upper and lower foliage separated out on canonical variate 2 (Fig. 4a). This is

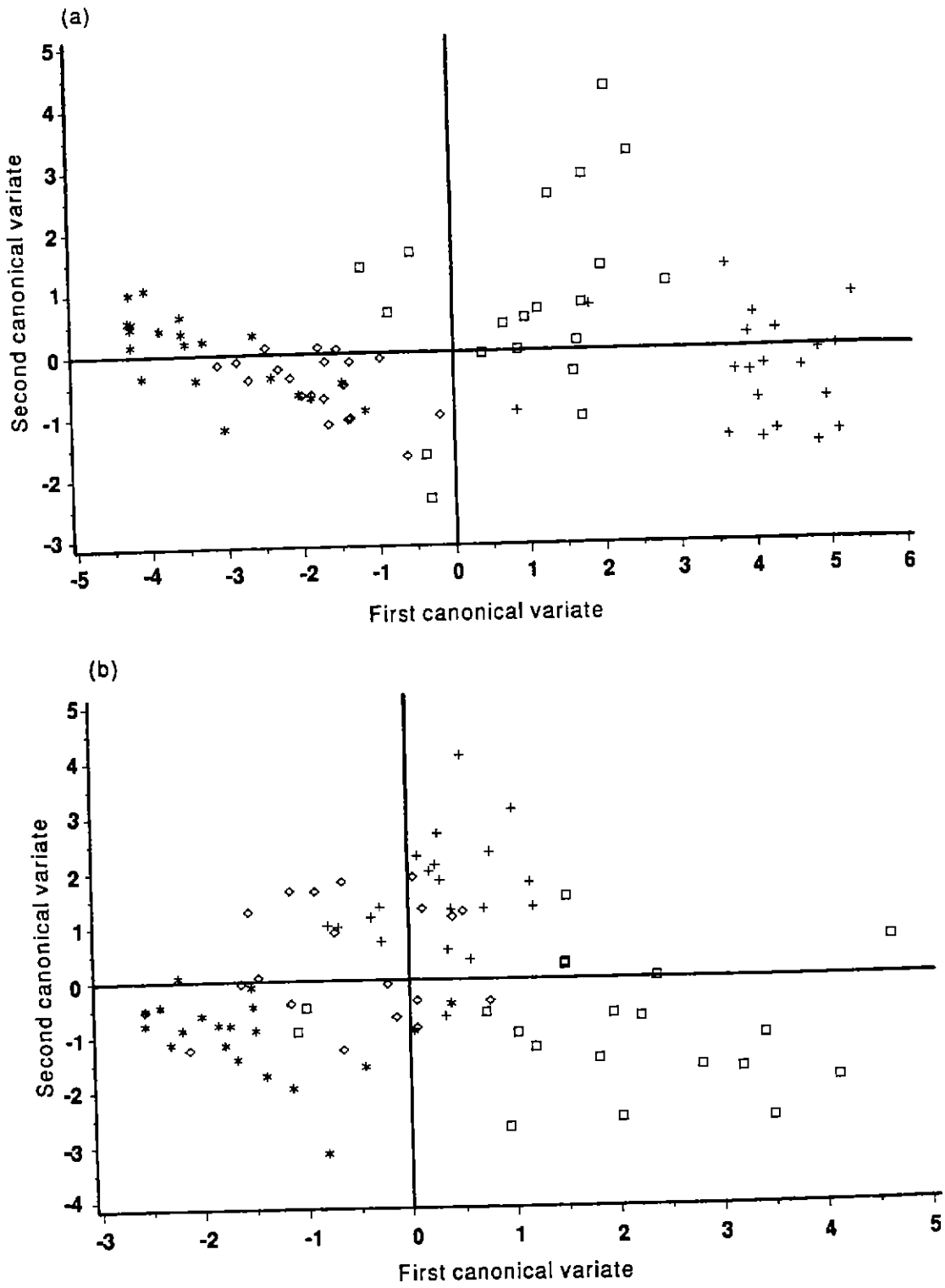

Fig. 4. Individual (a) *E. marginata* and (b) *E. calophylla* data from upper and subcanopy strata, plotted against first and second canonical variates as axes, derived using the nitrogen, phosphorus and potassium data. (*) subcanopy mature foliage; (◇) upper canopy mature foliage; (□) subcanopy young foliage; (+) upper canopy young foliage.

consistent with the fact that two canonical variates were required to explain the bulk of the variation in the data (Table 3). Potassium, and to a lesser extent phosphorus are correlated with canonical variate 1 and hence contribute towards the separation of young and mature foliage, while nitrogen and phosphorus are highly correlated with the second canonical variate and are therefore responsible for the discrimination of foliage from different strata.

DISCUSSION

There are large differences in the levels of all three nutrients which were measured on trees from the NSW and WA forests. All nutrient levels were higher on *E. crebra* than *E. mollucana*, higher on *E. calophylla* than *E. marginata*, higher on upper than lower foliage (except for phosphorus on *E. mollucana*) and, at least in the case of the WA forest, higher on young than on mature foliage. Apart from the exception mentioned above, all three nutrients tended to follow the same trends, although the correlations between specific nutrient levels and canonical variates (Table 3) suggest that certain nutrients vary more strongly than others within a particular comparison. Apart from nitrogen showing up as the most important determinant in the separation of foliage in most of the comparisons, the ranking of the degree of importance of the three nutrients within a particular comparison revealed no consistent trends.

We are not certain why nutrient levels differ between tree species within a particular forest, although such differences have been reported frequently elsewhere (e.g. Fox & Macauley 1977). The within-forest differences reported here are unlikely to result from differences in soil nutrient status because the trees we compared grew in close proximity to each other. One possibility is that the trees possess differing root physiologies or symbionts and hence may differ in the efficiency with which they are able to extract nutrients from the rhizosphere. Another is that the various species may possess different internal storage strategies; species with lower foliar nutrient levels may sequester nutrients in other parts of the plant. In view of the fact that the species within each comparison are from different subgenera (*E. crebra* and *E. mollucana* — *Symphyomyrtus*, *E. marginata* — *Monocalyptus*, *E. calophylla* — *Corymbia*), they could well exhibit differences in the ways in which nutrients are taken up and stored. Comparison of the nutrient data between the two forests indicated that nitrogen and phosphorus, but not potassium, were higher in foliage of the NSW than the WA trees (*cf.* Tables 1,2). This could be due to differences in the levels of nutrients within the soils of the two forests (Braithwaite 1986; Braithwaite *et al.* 1983; Landsberg *et al.* 1990).

Nitrogen and phosphorus are generally mobile nutrients within the plant, and their within-plant concentrations are usually highly correlated. Levels of these nutrients decrease as the leaf matures because these nutrients are reallocated to new leaves or to reproductive activities (Garten 1978; Grove 1990). Leaves which are higher in the canopy tend to receive more sunlight than those in the subcanopy and may thus exhibit higher photosynthetic rates and more leaf production. Since nitrogen and phosphorus levels are respectively related to the amounts of protein and nucleic acid in tissues, and since potassium is related to enzymatic activity, the elevated levels of these nutrients may reflect higher metabolic activity in the more insolated upper foliage.

Arthropods have been sampled from equal volumes and areas of foliage within the canopy (7.1–20 m) and subcanopy (1–7 m) of the four species during early 1987 by a chemical knockdown procedure (see Majer & Recher 1988). The results, given in Majer *et al.* 1990 and Recher *et al.* 1991, indicate higher levels of arthropods at Scheyville than at Karragullen, higher levels of arthropods from many taxa in the upper canopy than in the subcanopy and, within a particular forest, highest levels of arthropods on *E. crebra* and on *E. calophylla*. Arthropod sampling has subsequently continued at 3 monthly intervals for a further year at Scheyville and 2 years at Karragullen and these trends have been confirmed (J. D. Majer & H. F. Recher, unpubl. data). The trends in nutrient levels in leaves are consistent with our observations on the abundance and diversity of arthropods on the different tree species. Within each of the two forests, the tree species with highest foliar nutrient levels supported the greatest abundance and diversity of arthropods (Majer *et al.* 1990; Recher *et al.* 1991; J. D. Majer & H. F. Recher, unpubl. data). This trend could be a direct response to nutrient levels since the levels of herbivory on trees are sometimes correlated with the dietary quality of the foliage (Landsberg 1990). Those arthropods which are higher in the food chain may in turn reach levels which reflect the abundance of herbivores on which they may feed.

Usually it is the levels of nitrogen which correlate with herbivore levels, presumably because this reflects the protein content of the diet (see references in White 1969; Morrow 1983). Phosphorus and potassium levels may also represent some aspects of the nutritional quality of the foliage. However, determination of the relative im-

portance of nitrogen, phosphorus and potassium to arthropod levels on vegetation is hindered by the fact that they each tend to follow similar trends between tree species, strata and leaf ages (*cf.* data in Tables 1,2).

We have already mentioned that nutritional quality of the foliage is not the only influence on herbivore levels. Polyphenol levels are 2.6 times higher in *E. marginata* than in *E. calophylla* foliage (Hingston 1961) and this could have contributed to the observed differences in the levels of arthropods. Leaf toughness has also been shown to be negatively correlated with the amount of feeding or with the levels of herbivorous arthropods on Australian trees (Lowman & Box 1983; Ohmart *et al.* 1987; Ohmart *et al.* 1991). As yet, we have no data on the secondary plant compounds in the foliage of the NSW trees which we studied, nor on the leaf toughness of leaves of any of the four tree species. It may well be that a whole suite of factors interplay to influence the levels of arthropods on these tree species.

The higher levels of nutrients in the upper foliage could also account for our observation that a number of arthropod taxa are more abundant in the upper than lower foliage of all tree species. Admittedly there may also be some direct effect on the arthropods, such as a response to higher insolation or possibly to associated higher canopy temperatures, but higher nutritional quality of the upper foliage is likely to be an important factor.

Although our arthropod sampling methods did not differentiate between levels of animals on young and mature foliage, visual inspections of the foliage during sampling periods indicate that they were greater on the former. Once again, this could have been accounted for in terms of nutritional quality of foliage, although the increasing toughness of older leaves is also known to reduce the feeding and abundance of certain animals (Larsson & Ohmart 1988; Ohmart *et al.* 1983).

Despite the fact that there is no consensus of evidence in Australia about the relative importance of leaf nutrients, secondary plant compounds and physical structure to arthropod abundance, our comparisons between forest sites, tree species, tree strata and leaf age suggest that, at least for the trees which we studied, levels of foliar nutrients are particularly important in determining the levels of arthropods on trees. Since many components of the avifauna are at least in part dependent on arthropods in their diet, our observations on the differences in bird usage of eucalypt forests (Recher *et al.* 1991) are consistent with the distribution of nutrients in the forest trees where much of their feeding takes place.

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