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Lipid concentration in the embryo–endosperm fraction of seeds of Australian tropical lowland rainforest trees: relevance to defence and dispersal

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Abstract

The lipid concentration (LC) of the embryo–endosperm fraction was determined for the seeds of 60 species in 22 families from an Australian tropical lowland rainforest. It was negatively related to the mass of the embryo–endosperm across all species, but the relationship was not significant at $P < 0.05$. LC was significantly and positively correlated with N concentration when all species were considered, but not within the families represented by the most species (*Lauraceae*, 13; *Sapindaceae*, 9; *Proteaceae*, 6). LC was significantly and markedly higher in more heavily defended seeds (medians: 27 and 6.9%); there is evidence for the view that seeds rich in either lipid or nitrogen are markedly defended. Lipid concentration was also markedly higher, on average, in seeds taken by the scatter-hoarding *Uromys caudimaculatus* (white-tailed rat) than in seeds of comparable size not taken by *Uromys*, but not known to be protected by any toxin or irritant (medians: 35 and 3.7%, respectively). However, LC was not notably high in one major group of seeds taken by *Uromys* – the largest-seeded species of *Beilschmiedia* and *Endiandra* (*Lauraceae*). The comparisons mostly involved different phyletic lines, and were not consistently supported by contrasts within phyletic lines.

Keywords: Australia, defence, dispersal, lipid concentration, seeds, tropical rainforest

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Introduction

Among species in the tropical lowland rainforest in Australia, those with marked defence of the embryo-cum-endosperm (EE) by fruit or seed tissues have a notably higher concentration of nitrogen (N) in the EE (Grubb *et al*., 1998). In that study it was suggested that an equally strong correlation might be found with the concentration of energy-rich compounds in the EE, but there was no information available on that point. Fats are often found as the means of storage of a relatively large amount of energy in a given volume; they provide 39 kJ g^{-1}, whereas starch yields only 17.5 kJ g^{-1} (Bewley and Black, 1994). This compact store of energy has advantages in terms of maximizing dispersal distance, and also in terms of provisioning for early seedling growth. In a preliminary study, Levin (1974) found that woody species with shade-tolerant juveniles had particularly fatty seeds. In a large-scale study of species from many parts of the world, lipid and nitrogen concentrations were positively correlated among mostly temperate species in a few families (*Asteraceae*, *Boraginaceae*, *Cucurbitaceae*, *Lamiaceae*, *Malvaceae*, *Ranunculaceae*), but in many others they varied independently (Barclay and Earle, 1974). There appears to have been no specific investigation for major tropical families.

The position concerning the *Proteaceae* is especially interesting. Although the *Proteaceae* are found in a variety of rainforests, they are most diverse in the Australian tropical lowland rainforest (24 genera and 47 species; Hyland and Whiffin, 1993). Pate *et al*. (1986) showed that species of *Proteaceae* found in woodlands and heaths on extremely nutrient-poor soils have remarkably high concentrations of N and P in the EE fraction, and forecast that, in contrast, seeds of the rainforest species regenerating under the canopy would not be particularly rich in N or P, but rich in fat. In fact, Grubb *et al*. (1998) showed that a majority of the rainforest *Proteaceae* tested (6 out of 11 species) had notably high concentrations of N

(34–110 mg g dry mass^{-1} in the EE fraction). There is no published information for the variability in lipid concentration for rainforest *Proteaceae*.

Comparisons of N concentrations among species are complicated by the fact that there is a consistent trend toward a lower N concentration in species with larger EE mass values (Grubb and Coomes, 1997; Grubb *et al*., 1998), and sometimes a parallel trend within species (Grubb and Burslem, 1998). Nothing has been published about the relationship between EE mass and lipid concentration in tropical plants.

In Australian lowland rainforests certain large-seeded tree species are notable as being taken by the scatter-hoarding white-tailed rat, *Uromys caudimaculatus* (Watts and Aslin, 1981; Cooper and Cooper, 1994). Grubb (1996) noted that these seeds tend to have a somewhat higher N concentration in the EE relative to what might be expected for their size, and suggested that enrichment in protein might attract the rats, while the relatively thick seed coat prevents all but the rats with larger and stronger jaws from having access. In the deciduous forest of eastern North America, squirrels preferred seeds richer in fat, and the highest fat concentrations were found in seeds that could be broken open only by the squirrels with the strongest jaws (Stapanian, 1986). It seemed to us that the same concept might be true of the relevant species in Australia.

The present study was designed to answer the following questions for species of Australian tropical lowland rainforest: (1) Is the lipid concentration generally lower in seeds with a larger EE mass value in either intraspecific or interspecific comparisons? (2) Is lipid concentration positively or negatively correlated with N concentration in the EE fraction in rainforest species in general, and the *Proteaceae* in particular? (3) Is the EE fraction of heavily defended seeds notably rich in lipid as well as nitrogen? (4) Is the EE fraction notably rich in lipid in seeds that are chosen by rats? We analysed only the EE fraction of any species. When we refer to 'seed' we normally mean a single, mature, fertilized ovule, including the testa plus the fibrous inner part of the fruit wall, where present; in the case of *Elaeocarpus* there is often more than one fertilized ovule in a single 'seed'.

Materials and methods

Most of the seeds used were collected by E.A.A. and P.J. Grubb, D.J. Metcalfe, A.K. Irvine and J.M.G. Bloor between October 1992 and December 1999 at a variety of rainforest sites in north-east Queensland, Australia. Seeds of *Flindersia brayleyana* were purchased from the Department of Forestry. The method of lipid analysis (see below) prevented us from using seeds less than *c*. 100 mg dry mass. Granted that constraint, we analysed a wide range of the more widespread species in the rainforest of north-east Australia: 60 species spanning 22 families. They came from sites with a range of altitudes, precipitation values and soil types (cf. Grubb *et al*., 1998). All species are tall or short trees except for *Austrobaileya scandens*, which is a tall vine (see Table 1). All species other than *Aleurites moluccana*, *Elaeocarpus grandis* and *E. ruminatus* are shade-tolerant at the stage of establishment. Nomenclature follows Henderson (1997).

The seeds were stored air-dry at room temperature between collection in Australia and analysis in Cambridge in 1999 or 2000. The procedure for lipid extraction was based on suggestions from Christie (1982). A 20-ml Soxhlet extractor was used to remove the lipids from the EE fraction. Oven-dried seeds were blended into a fine meal, and a sample of known mass was placed in a cellulose extraction thimble of diameter 18 mm and depth 55 mm. A 54-ml mixture of methanol and chloroform (1:2 by volume), heated to boiling point, was used as the solvent. The extraction was run for 2 h, the time determined experimentally for the thimble to reach constant mass. The thimble was dried at room temperature for 48 h before weighing. The mass difference of the thimble before and after extraction was assumed to be the lost lipid fraction, and was determined to 0.1 mg. A minimum of two replicates was analysed for each species (mostly 3–12). Repeatable results for per cent lipid concentration were obtained with samples as small as 400 mg, but not smaller. Therefore, in the case of small-seeded species, the EE fraction from several seeds had to be combined for one run. Approximately 4 g is the upper limit on sample size for the thimble size used. Heavier seeds were blended completely, and a representative portion used for the analysis.

For most species the nitrogen concentration in the EE fraction was obtained from Grubb *et al*. (1998); for the few species included in this study but not analysed by Grubb *et al*. (1998), N concentration was determined using the same method. In the case of *Cardwellia sublimis*, the embryos analysed were from a new seed collection with appreciably smaller seeds than those used by Grubb *et al*. (1998). When exploring the relationship between per cent lipid in the EE and EE dry mass within a species, single seeds of a wide range of sizes for *Castanospora alphandii*, *Diploglottis bracteata* and *Triunia erythrocarpa* were used, but in the case of *Cardwellia sublimis* we had to combine two embryos most similar in dry mass for each run.

Our classification of markedly defended against and not markedly defended is slightly different from that given by Grubb *et al*. (1998) because we have no data for whole-seed lipid concentration values. Grubb *et al*. (1998) considered the relationship between N

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concentration in the whole seed and defence of the whole seed, while we are focusing on the relationship between the lipid concentration in just the EE fraction and its defence. Many defences protect both the seed and the EE, but in some cases seed tissues, such as a thick fibrous testa, protect the EE in the absence of whole-seed defences provided by the fruit. Marked defence is provided by toxin or poison (*Castanospermum, Idiospermum, Phaleria, Semecarpus, Triunia*), by fruit with walls that are woody (*Cardwellia, Castanospermum, Darlingia, Flindersia, Opisthiolepis*) or leathery (*Aleurites, Diploglottis bracteata*), by tough cone scales (*Lepidozamia*) or by the fibrous wall of the 'seed' making up more than 60% of the 'seed' mass (*Aleurites, Athertonia, Fontainea, Pouteria* and some species of *Elaeocarpus*) (Grubb *et al*., 1998).

Following Grubb *et al*. (1998), we recognize a small group of species intermediate in degree of defence: *Beilschmiedia bancroftii, Endiandra insignis, E. palmerstonii* and *Macadamia whelanii*. Data are presented for lipid concentrations for these species, but they are not included in our analysis of more- and less-defended seeds.

Our classification according to whether seeds were taken or not taken by *Uromys* was determined as follows. Hyland and Whiffin (1993) mention large-scale destruction by *Uromys* for nine species: *Aleurites moluccana** (*Euphorbiaceae*), *Athertonia diversifolia**, *Eidothea zoexylocarpa, Macadamia* cf. *hildebrandtii* (*Proteaceae*), *Beilschmiedia bancroftii**, *Cryptocarya pleurosperma**, *Endiandra palmerstonii** (*Lauraceae*), *Elaeocarpus bancroftii** and *E. stellaris* (*Elaeocarpaceae*). Harrington *et al*. (1997) confirmed the use of four of these species by *Uromys*, and added two more: *Endiandra insignis** (*Lauraceae*) and *Pouteria castanosperma** (*Sapotaceae*). The experience of one of us (P.J.G.) spread over 7 years, supplemented by the experience of A.K. Irvine for more than 20 years, confirms the use by *Uromys* of all the species listed, and adds three more: *Fontainea picrosperma**, *Hylandia dockrillii* (*Euphorbiaceae*) and *Elaeocarpus grandis** (*Elaeocarpaceae*). The species marked with an asterisk are the ten from which the EE fraction was analysed.

A number of other species with relatively large seeds (mean dry mass mostly greater than 1000 mg), generally with notably thinner seed coats than those characteristically taken by *Uromys*, are regularly eaten by smaller rats and the musky rat-kangaroo (*Hypsiprymnodon moschatus*), and appear to be eaten occasionally by *Uromys*: some *Aglaia* and *Dysoxylum* spp. (*Meliaceae*), *Austrobaileya scandens* (*Austrobaileyaceae*), *Castanospora alphandii, Diploglottis bracteata* (*Sapindaceae*), *Corynocarpus cribbianus* (*Corynocarpaceae*), *Oraniopsis appendiculata* (*Arecaceae*), *Prumnopitys* spp. (*Podocarpaceae*) and *Prunus turneriana* (*Rosaceae*) (Cooper and Cooper, 1994; Harrington *et al*., 1997; Mr S. Comport, personal communication). The EE fraction from all these was analysed, but they have not been included in the 'eaten by *Uromys*' category.

Ten species in our 'eaten by *Uromys*' category were compared with ten species of seeds of comparable size, not recorded as being eaten by *Uromys* and not recorded as being toxic or irritant: *Beilschmiedia tooram, B. volkii, Endiandra sankeyana, E. sideroxylon* (*Lauraceae*), *Syzygium cormiflorum, S. gustavioides, S. kuranda* (*Myrtaceae*) [most of these being included in the comparative study of Harrington *et al*. (1997)] as well as *Baileyoxylon lanceolatum* (*Flacourtiaceae*), *Niemeyera prunifera* (*Sapotaceae*) and *Polyalthia michaelii* (*Annonaceae*).

One further large-seeded species was analysed to increase the range of families (*Mammea touriga, Clusiaceae*), but this could not be assigned confidently among the three groups recognized with respect to white-tailed rats. There is some uncertainty about the eaten/not eaten categories, and so our discussion concentrates on those species for which there are the most data, and which fall on either extreme of desirability to the rats.

Pearson's rank correlation coefficient (r) is reported to gauge the relatedness of EE dry mass, lipid and N concentrations. The median lipid concentrations in EEs that are defended, undefended, taken and not taken were compared using the Mann–Whitney U-test for non-parametric distributions. The Mann–Whitney statistic (W) is reported for each comparison.

Results

For none of the four species, of which nine or more replicates were analysed, was there a significant intraspecific relationship between lipid concentration and the mass of the EE fraction. There was a marginally non-significant negative correlation between the mean lipid concentration and the dry mass of the EE (Table 1, Fig. 1) when comparisons are made among all species analysed ($r = -0.231$, $P = 0.075$).

There was a significant positive correlation between lipid concentration and N concentration in the collection of species for which we have both values ($n = 58$, $r = 0.443$, $P = 0.001$). The relation for all species is shown in Fig. 2. There was no significant relationship within either of the families with the most species (*Lauraceae* and *Sapindaceae*). The *Proteaceae* analysed (Table 1) showed a spectrum of results from outstanding richness in lipid (*Athertonia*) to outstanding richness in N (*Opisthiolepis*), but there was no correlation between the variables.

Considering the whole collection of species, there

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Table 1. Embryo–endosperm dry mass, lipid and N concentrations in the embryo–endosperm of 60 species from lowland tropical rainforest, Australia. Growth form is indicated by the following letters: TT, tall tree (>15 m tall); ST, short tree (>6 m, ⩽15 m tall); TV, tall vine. The column *n* indicates the number of replicate samples used in the determination of lipid concentration. n/a in the EE [N] column indicates that these data were unavailable. Species in which the embryo is markedly defended are indicated as follows in the 'Def.' column: C, tough cone scales; L, leathery fruit walls; P, toxin or poison; T, fibrous wall of the seed making up more than 60% of the 'seed' mass; W, woody fruit walls; I, species that are intermediate with respect to defence. Classification according to whether or not taken by *Uromys* is indicated as follows in the Taken/not taken column: U, species that are taken regularly by *Uromys*; NU, species of comparable size that are not taken; r, species occasionally taken by *Uromys* and regularly taken by smaller rats and the musky rat-kangaroo

Family	Species	Growth form	EE dry mass (mg)	Mean lipid conc. (%)	*n*	EE [N] (mg/g)	Def.	Taken/ not taken
Anacard.	*Semecarpus australiensis*	TT	2000	24 ± 1.2	3	17	P	
Annon.	*Polyalthia michaelii*	TT	2500	19 ± 0.58	3	14		NU
Arec.	*Oraniopsis appendiculata*	TT	1800	6.2 ± 0.38	3	8.8		r
Arec.	*Wodyetia bifurcata*	TT	3800	8.5 ± 0.30	2	8.1		
Austrobailey.	*Austrobaileya scandens*	TV	380	39 ± 2.3	3	35		r
Clus.	*Mammea touriga*	TT	12000	3.9 ± 1.3	3	0.66		
Corynocarp.	*Corynocarpus cribbianus*	TT	7700	8.1 ± 0.49	3	26		r
Elaeocarp.	*Elaeocarpus elliffii*	TT	25	12 ± 1.0	3	n/a	T	
Elaeocarp.	*Elaeocarpus grandis*	TT	73	44 ± 1.4	3	19	T	U
Elaeocarp.	*Elaeocarpus ruminatus*	TT	82	27 ± 1.5	2	9.4	T	
Elaeocarp.	*Elaeocarpus foveolatus*	TT	180	34 ± 1.2	3	9.5	T	
Elaeocarp.	*Elaeocarpus bancroftii*	TT	180	39 ± 1.3	2	22	T	U
Euphorb.	*Fontainea picrosperma*	ST	490	39 ± 1.2	2	21	T	U
Euphorb.	*Aleurites moluccana*	TT	3400	53 ± 5.6	3	47	L, T	U
Fab.	*Castanospermum australe*	TT	13000	5.8 ± 0.62	3	15	P,W	
Flacourt.	*Baileyoxylon lanceolatum*	TT	800	13 ± 1.6	2	42		NU
Idiosperm.	*Idiospermum australiense*	TT	59000	9.9 ± 0.29	3	10	P	
Laur.	*Cryptocarya onoprienkoana*	TT	740	9.2 ± 0.69	4	8.3		
Laur.	*Endiandra bessaphila*	TT	920	9.4 ± 1.0	4	11		
Laur.	*Beilschmiedia recurva*	TT	1300	1.7 ± 0.82	4	16		
Laur.	*Cryptocarya angulata*	TT	1500	7.3 ± 1.0	4	14		
Laur.	*Endiandra monothyra*	TT	1600	7.9 ± 2.7	3	9.3		
Laur.	*Cryptocarya pleurosperma*	TT	2400	7.3 ± 0.40	3	10		U
Laur.	*Endiandra sideroxylon*	TT	3300	4.9 ± 0.70	4	6.9		NU
Laur.	*Beilschmiedia tooram*	TT	4500	2.4 ± 0.20	4	6.1		NU
Laur.	*Endiandra sankeyana*	TT	5200	1.7 ± 0.18	4	7		NU
Laur.	*Endiandra insignis*	TT	12000	3.7 ± 0.51	3	12	I	U
Laur.	*Endiandra palmerstonii*	TT	16000	1.9 ± 0.20	4	8.6	I	U
Laur.	*Beilschmiedia volckii*	TT	20000	0.89 ± 0.30	3	8.1		NU
Laur.	*Beilschmiedia bancroftii*	TT	23000	6.7 ± 0.68	3	14	I	U
Meli.	*Aglaia australiensis*	ST	770	6.2 ± 0.24	3	22		r
Meli.	*Dysoxylum latifolium*	TT	2200	6.0 ± 0.55	3	31		r
Myrt.	*Syzygium wilsonii*	TT	58	0.10	2	n/a		
Myrt.	*Syzygium boonjee*	ST	1800	0.30 ± 0.22	3	4.5		
Myrt.	*Syzygium cormiflorum*	TT	6600	5.9 ± 0.42	3	4.2		NU
Myrt.	*Syzygium kuranda*	TT	7500	1.1 ± 0.13	4	2.6		NU
Myrt.	*Syzygium gustavioides*	TT	47000	2.1 ± 0.13	4	3.6		NU
Podocarp.	*Prumnopitys amara*	TT	490	12 ± 1.9	3	11		r
Prot.	*Darlingia darlingiana*	TT	150	46 ± 7.3	2	66	W	
Prot.	*Opisthiolepis heterophylla*	TT	150	16 ± 0.51	3	110	W	
Prot.	*Cardwellia sublimis*	TT	270	27 ± 0.85	9	82	W	
Prot.	*Triunia erythrocarpa*	ST	850	5.4 ± 0.52	10	10	P	
Prot.	*Athertonia diversifolia*	TT	1700	67 ± 2.4	6	22	T	U
Prot.	*Macadamia whelanii*	TT	5500	26 ± 1.0	5	14	I	
Ros.	*Prunus turneriana*	TT	1800	9.0 ± 1.3	3	14		r
Rut.	*Flindersia brayleyana*	TT	42	53 ± 2.6	3	33	W	
Rut.	*Flindersia bourjotiana*	TT	120	48 ± 2.8	3	51	W	
Sapind.	*Diploglottis diphyllostegia*	TT	65	1.8 ± 0.31	5	12		
Sapind.	*Sarcotoechia lanceolata*	TT	140	1.0 ± 0.35	2	31		
Sapind.	*Arytera pauciflora*	ST	210	4.7 ± 0.64	3	10		

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Table 1. *Continued*

Family	Species	Growth form	EE dry mass (mg)	Mean lipid conc. (%)	*n*	EE [N] (mg/g)	Def.	Taken/ not taken
Sapind.	*Cupaniopsis flagelliformis*	TT	220	2.3 ± 0.22	2	12		
Sapind.	*Sarcotoechia serrata*	ST	280	6.1 ± 1.7	3	13		
Sapind.	*Harpullia pendula*	ST	320	6.9 ± 1.1	9	13		
Sapind.	*Diploglottis smithii*	TT	450	2.2 ± 0.47	6	11		
Sapind.	*Castanospora alphandii*	TT	1700	14 ± 1.2	11	11		r
Sapind.	*Diploglottis bracteata*	TT	3200	2.0 ± 0.34	12	12	L	r
Sapot.	*Pouteria castanosperma*	TT	1400	30 ± 0.59	4	29	T	U
Sapot.	*Niemeyera prunifera*	TT	8500	9.8 ± 0.29	3	5		NU
Thymelae.	*Phaleria clerodendron*	TT	4400	11 ± 0.98	3	29	P	
Zam.	*Lepidozamia hopei*	TT	13000	7.3 ± 0.29	3	28	C	

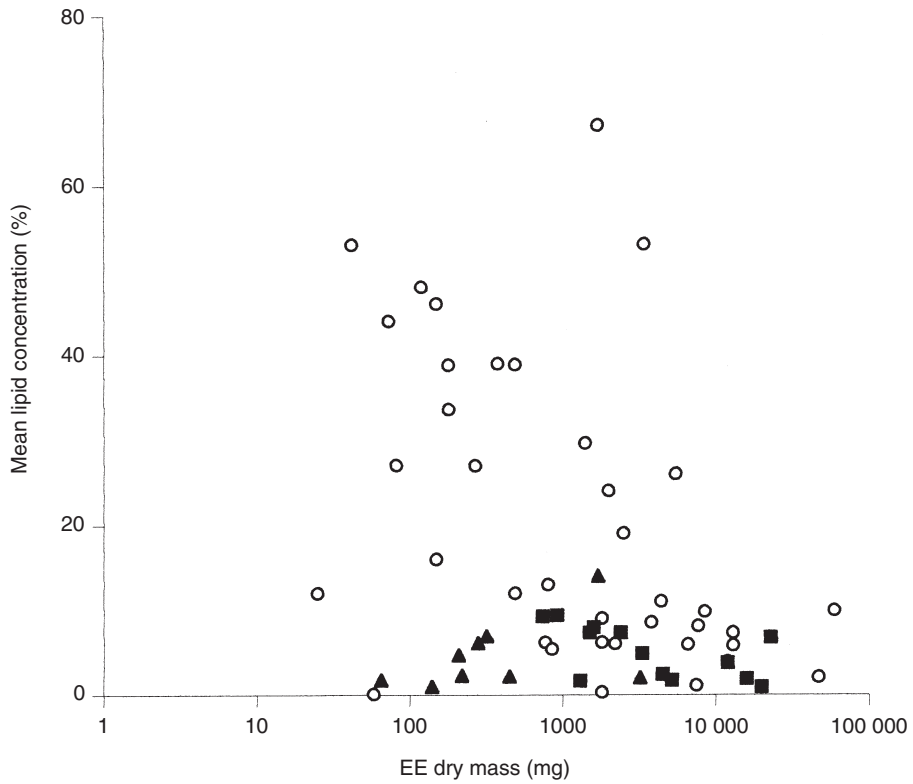

Figure 1. The lipid concentration (% dry mass) in the embryo–endosperm fraction as a function of the mean dry mass of that fraction per seed (log scale); each circle represents one species. The values for the *Lauraceae* are shown by filled squares, and those for the *Sapindaceae* by filled triangles.

was a significant and notably higher concentration of lipid in the EE of species with markedly defended seeds (medians: 27% lipid in defended seeds and 6.9% in undefended seeds; $W = 863.5$, $P < 0.001$). In some cases, this result arose chiefly from systematic differences between phyletic lines. Most *Lauraceae*, *Myrtaceae* and *Sapindaceae*, which lack marked defence of the EE fraction, were relatively low in lipid (less than 10%). In contrast, the taxa with marked defence that we studied were mostly in the *Anacardiaceae*, *Elaeocarpaceae*, *Euphorbiaceae*, *Fabaceae*, *Idiospermaceae*, *Proteaceae*, *Rutaceae*, *Thymelaeaceae* and *Zamiaceae*, and most were rich in lipid. The one intrafamilial contrast that can be made was consistent with the overall trend; in the *Sapotaceae*, *Pouteria* is markedly defended and had 30% lipid, while *Niemeyera*, which is not markedly defended, had 9.8% lipid. However, the one intrageneric contrast that could be made does not

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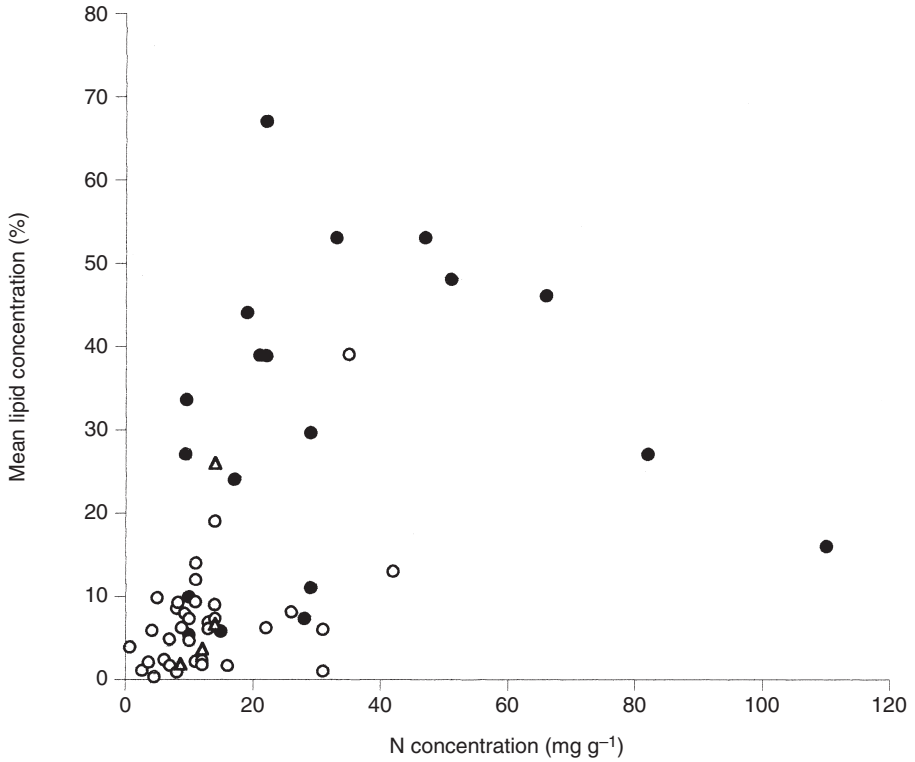

Figure 2. The relationship between the concentrations of lipid and nitrogen in the embryo–endosperm fractions for 58 species. The filled circles are for species with markedly defended embryos, the empty circles for species with embryos not markedly defended, and empty triangles are for the four species intermediate with respect to defence.

support the trend: in *Diploglottis* (*Sapindaceae*), *D. bracteata* is markedly defended and had 2.0% lipid. It did not differ appreciably from *D. diphyllostegia* and *D. smithii*, which are not markedly defended.

The lipid concentration of the EE was significantly and markedly higher in the species regularly taken by *Uromys* (n = 10, median = 35%) than in the collection of species with seeds of similar size and not known to be eaten by *Uromys* (n = 10, median = 3.7%; W = 73.0, P = 0.02). The species taken occasionally by *Uromys* and mainly by smaller rats and the musky rat-kangaroo were much lower in lipid (n = 9, median = 8.1%) than those regularly taken by *Uromys*, although this difference was not statistically significant. However, the difference between the species taken regularly by *Uromys* and those taken not at all or only occasionally was significant (medians 35% and 6.2%; W = 237.0, P = 0.03). As in the comparison of markedly defended seeds and seeds not markedly defended, the contrasted groups involved mainly different families. Moreover, when the large-seeded *Lauraceae* taken by *Uromys* were compared with those *Lauraceae* that have relatively large seeds but which are not taken by *Uromys* (see Table 1), there was no significant difference and only a slight trend: 3.7% and 2.1%. Within the *Sapotaceae*, however, *Pouteria* is taken while *Niemeyera*, which was much lower in lipid, is not taken.

Discussion

Limitations of the data

The lipid extraction method used would have removed a wide range of compounds other than fats. However, fats constitute the overwhelmingly important fraction of the lipids in seeds (Mayer and Poljakoff-Mayber, 1989), and therefore it is almost certain that where relatively high lipid concentrations (over 10%) are recorded, they reflect chiefly a high concentration of storage triglycerides. There is an analogous problem with the N concentrations, which might reflect non-protein amino acids in some species, but very probably reflect protein concentrations in most. In the following discussion we use the conventional multiplier of 6.25 to convert from N to probable protein concentration (Allen, 1974).

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Trends in lipid and protein concentrations

Although not statistically significant in the case of lipids, the general trends toward lower concentrations of both lipid and protein in larger seeds are not easily explained. Presumably both types of compounds are especially valuable relative to carbohydrates; lipids supply more energy per unit mass, and nitrogen is likely to be in short supply for any seedling facing competition from established plants. On the other hand, both require an extra input of energy at the stage of synthesis, relative to carbohydrates, and this extra input may be worthwhile only where the total mass of reserves for the seedling is small – leaving aside the attraction of demanding dispersers, to which we return below.

Across all species, there was a positive correlation between protein and lipid concentrations, but the situation is confused by the fact that this correlation was not found within any of the three families with the most species studied. This likely arises from the fact that the largest numbers of seeds available to us happened to be from families in which there is little variation in the concentration of seed oil. The data show that in some families, there is considerably more variation in the concentration of lipid than there is in the *Lauraceae* and *Sapindaceae*. Further studies of the families for which there does appear to be a substantial variation in the fat concentration, such as the *Elaeocarpaceae*, *Proteaceae* and *Sapotaceae*, would be useful.

Lipid concentration and defence

The lipid concentration in the EE was notably higher, on average, in species with marked defence, and lipid concentration was correlated with protein concentration in the collection of species as a whole. Therefore, we suggest that *either* a high lipid concentration *or* a high protein concentration will have led to selection for increased defence. This interpretation is supported by the results in Fig. 2. Most *Lauraceae*, *Myrtaceae* and *Sapindaceae*, which lack marked defence of the EE fraction, were relatively low in lipid (less than 10%) and protein (less than 10 mg g^{-1}) in the EE. In contrast, species of *Elaeocarpus* and *Fontainea*, with marked defence of the EE fraction, were fairly rich in both lipid (39–44%) and protein (up to 22 mg g^{-1}), while *Flindersia* was even richer in both, and *Pouteria* was relatively richer in protein than lipid. Among the *Proteaceae*, the poisonous fruits of *Triunia* had unexpectedly low concentrations of both lipid and protein.

Lipid concentration and choice by rats

Many researchers have focused on the role of seed contents in germination, cotyledon functional morphology or early seedling growth, e.g. Levin (1974), Kitajima (1996) and Ichie *et al*. (2001). However, our study and that of Stapanian (1986) suggest that seed contents may be selected for in relation to the need for successful dispersal by scatter-hoarding rodents. The three species analysed here that are not shade tolerant at the seedling stage (*Aleurites*, *Elaeocarpus grandis* and *E. ruminatus*) all had high lipid concentrations, suggesting that a store of lipid could be useful in buffering against prolonged shade or for supporting rapid height growth, of value in competition in high-light conditions.

In the *Elaeocarpaceae*, *Euphorbiaceae*, *Proteaceae* and *Sapotaceae*, the seeds taken by *Uromys* were substantially higher in fat than those that are not. The seeds in the *Lauraceae* taken by the rats were not particularly high in fat, suggesting that there may be a desirable nutrient other than protein or fat that is supplied by these seeds.

Future work

New studies of lipid and protein concentrations are needed for prominent fruit types that provide protection for the seeds, but which are not found in the Australian tropics, e.g. the woody thick-walled pyxidia of the *Lecythidaceae* in South America. Likewise, we need analyses of fats and proteins in the seeds known to be attractive to squirrels in various parts of Africa (Gautier-Hion *et al*., 1985; Dowsett-Lemaire, 1988). These data, along with more accurate estimates of the mean and variance for rates of dispersal and predation for the seeds of a large number of species, will permit a more comprehensive synthesis of the ecological significance of seed contents.

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