

Nitrogen-Richness and Protection of Seeds in Australian Tropical Rainforest: A Test of Plant Defence Theory

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Nitrogen-richness and protection of seeds in Australian tropical rainforest: a test of plant defence theory

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Some species invest more in protecting their seeds or embryos than others, yet the reasons behind this disparity have not been clearly identified. In order to test the hypotheses that species with marked protection in the fruit have high nitrogen concentration ([N]) in the seeds, and species with marked protection in the seeds have high [N] in the embryo-cum-endosperm fraction (EE), we determined the [N] in the seeds and EE of 194 species from lowland tropical rainforest in NE Queensland. For species in which the fruit provides marked protection of the seed there is a significant negative linear relationship between [N] and log seed mass. There is a similar relationship for 'unprotected' species, but the intercept on the y -axis is significantly and markedly higher for the group of 'protected' species. This relationship holds true when genera rather than species are considered. We are also able to make taxonomically controlled comparisons within six families and within four genera: all six familial comparisons and two of the generic comparisons support the finding for the collection of species as a whole. We then compare the [N] in the EE of species in which the fruit does not offer marked protection, but in which there is a range of investment in the seed wall fraction. Species with > 60% dry mass in the wall have significantly higher [N] than species with less massive walls. Possible advantages of having nitrogen-rich seeds are discussed.

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It is well known that the fruits of many species in tropical rainforests have hard woody walls, sometimes composing a very large proportion of the total fruit mass and sometimes with spines or irritant hairs, while others have walls which are sticky or stinging. Yet others have irritant flesh (e.g. containing raphides of calcium oxalate), or are poisonous. Australian examples are shown in Fig. 1. There seems to have been no attempt in the literature to provide a rationale for the fact that some seeds/embryos are given much greater protection by the fruit than others. Janzen (1969) considered the defences inside the seeds themselves, and forecast that in general small seeds would be found to be non-poisonous (escaping predation more easily)

while many large seeds would prove to be poisonous. Most theory on allocation by plants to defences against animals has concerned leaves (Coley et al. 1985, Edwards 1989), though Loehle (1988) has considered the issue for wood, and Herrera (1982) for vertebrate-dispersed fruits.

In a very general rationale of plant defences, Grubb (1992) suggested that several quite different factors had to be taken into account, one of them being the richness of a plants' parts in nitrogen relative to the richness of its neighbours. He illustrated this point by highlighting the spininess of the relatively few nitrogen-rich plants in the fynbos heathlands of the Cape region of South Africa. Our basic suggestion is that rainforest

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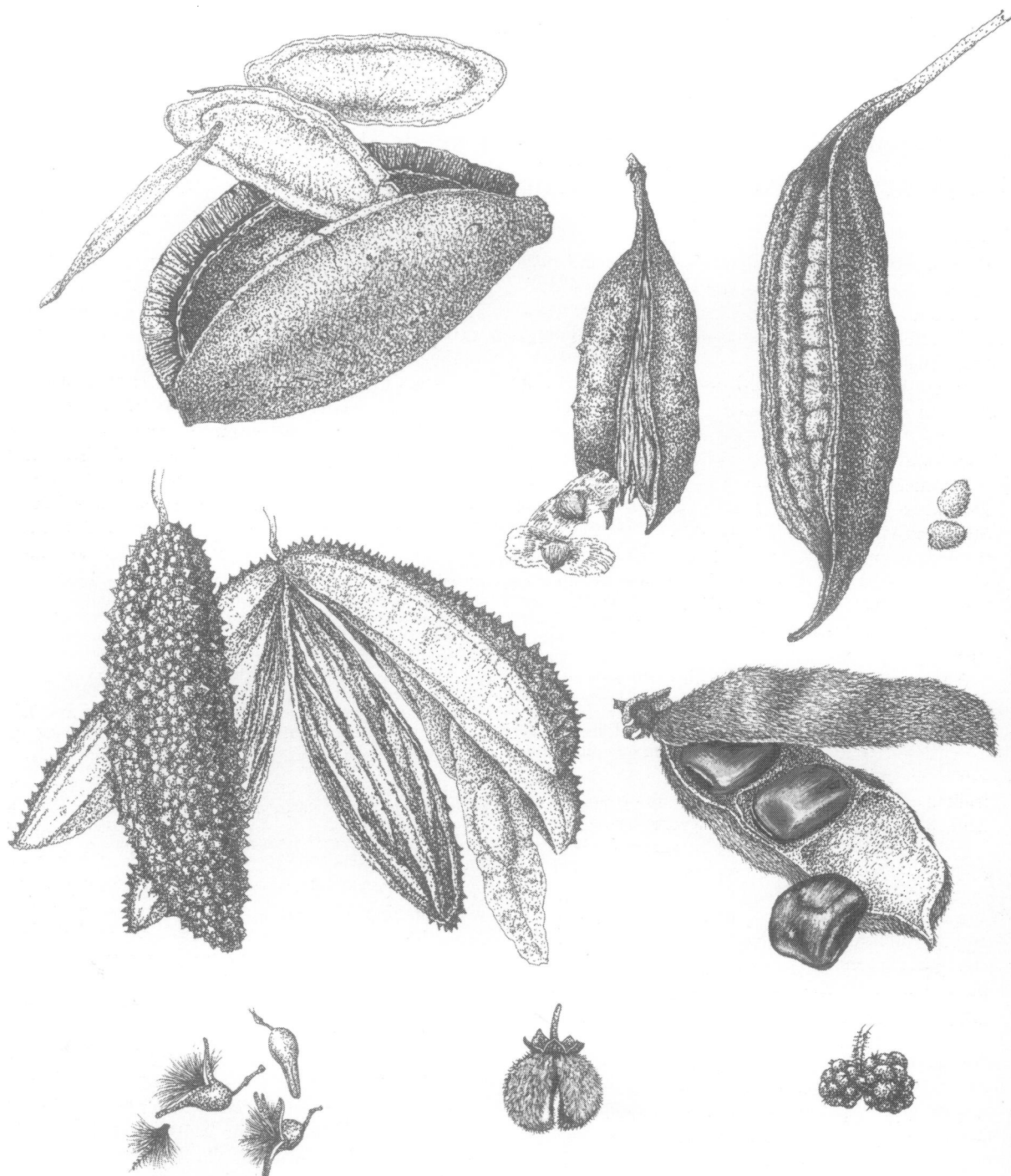


Fig. 1. Species from lowland tropical rainforest in Australia with protective fruit types: top row (left to right) *Cardwellia sublimis* (Proteaceae) woody follicle, *Neosepicea jucunda* (Bignoniaceae) woody capsule, *Brachychiton acerifolius* (Sterculiaceae) woody follicle with irritant hairs on seeds; second row *Flindersia bourjotiana* (Rutaceae) spiny woody capsule, *Mucuna gigantea* (Fabaceae) woody legume covered by irritant hairs; third row *Doryphora aromatica* (Monimiaceae) woody receptacular tissue, *Lethedon setosa* (Thymeleaceae) woody capsule covered by irritant hairs, *Dendrocnide moroides* (Urticaceae) berries with stinging hairs (drawn by Rachel Grubb after Cooper and Cooper 1994).

plants which afford their seeds a particularly high level of protection have notably high concentrations of nitrogen in those seeds. It is impossible to know which animals might have been the main predators during the evolution of the species in our study area, but the selection pressure may be continued now by cockatoos and parrots (e.g. the sulphur-crested cockatoo, *Cacatua galerita*, and the king parrot, *Alisterus scapularis*) and those pigeons with thick-walled gizzards that destroy seeds rather than disperse them (e.g. the white-headed pigeon, *Columba norfolkiensis*). Some insects may also be important. The part played by arboreal mammals in the past is quite unknown; the extant species are folivorous, but a wider range existed in the Tertiary (Archer and Bartholomai 1978), and some of these might have been frugivorous.

Seeds themselves differ greatly in the thickness and hardness of the coat surrounding the embryo-cum-endosperm fraction (EE) (Corner 1976). In the literature thick seed coats have been associated mainly with delay in germination, as a tactic in risk-spreading (Bewley and Black 1982, Grubb 1988, Lee et al. 1991), though Stapanian (1986) suggested that thick coats would protect large walnuts and hickory nuts against predators without the strong jaws of the particular squirrels which are the major dispersal agent. Grubb (1996) made the same point about the seeds of certain tropical trees.

Any hypothesis regarding the nitrogen concentration of the seed or embryo must allow for the fact that there is a very general trend for that concentration to be lower in larger seeds or embryos (Grubb 1996, Grubb and Coomes 1997). In this paper, using original data from tropical lowland rainforest in northern Queensland, we test the two following specific hypotheses.

1. Species with seeds borne in woody or especially thick-walled fruits or which have fruit walls which are sticky, stinging, irritant or poisonous have a high concentration of nitrogen in the seed relative to its size (mass).

2. Species which are not in the above category, but which have an especially thick testa and/or endocarp, have a high concentration of nitrogen in the EE relative to its size (mass).

Many of the seed mass values have been given by Grubb and Metcalfe (1996). Nine species with 'protected' seeds, and 40 species with 'unprotected', are used in this study in addition to those used in the brief preliminary account given by Grubb (1998).

Materials and methods

We have collected fruits from representatives of almost all the families with marked defence of the seeds in tropical north-eastern Queensland (NEQ), and from as

many as possible of the other families. Our total sample includes 75 out of the 155 in the list of native 'rainforest' plants recorded for NEQ (including Cape York Peninsula) by Hyland et al. (1994). We restricted our sampling to forest types 1 and 5a (complex mesophyll vine forest and complex notophyll vine forest) of Tracey (1982). We collected from sites in the range from sea level to 850 m, and from very wet – annual rainfall ca 4 m yr⁻¹ and on average no 'dry month' sensu Walter (1971) – to the dry edge of 'rainforest' near Atherton where the annual rainfall is only ca 1.4 m yr⁻¹ – on average four 'dry months' per year. Most of the species we collected are found on a variety of soils derived from basalt, granite or nutrient-poor metamorphic rocks. Our collection sites were at 145–146°E and 16–18°S.

Nomenclature follows Henderson (1997). We collected seeds (under permit numbers 1685, 1995 and FO/000782/95/SAB from the Queensland National Parks and Wildlife Service [now Dept of Environment], and permit numbers 489, 824 and 948 from Queensland Dept of Primary Industries Forest Service [now Dept of Natural Resources]) between September 1992 and August 1993, and between December 1994 and March 1997.

Definitions

We define a 'seed' as a single mature fertilized ovule, including the testa plus the fibrous inner part of the fruit wall where present. We removed any fleshy part of the fruit wall, or any aril or sarcotesta except where the latter is very thin and difficult to remove (as in *Melicope vitiflora*). Likewise we removed any wing or plume from dry-seeded species. For true seeds of mean dry mass > 40 mg we separated the wall (testa) and the EE fraction. For pyrenes and samaras of > 40 mg we separated the wall and the true seed, except that where the testa and endocarp are fused, we separated the compound wall and the EE fraction.

We treat a seed as 'markedly protected by its fruit' if it has notable protection up until the time that it leaves its parent. We have classified species as 'protected' according to the descriptions in Everist (1974), Hyland and Whiffin (1993) and Cooper and Cooper (1994). The assignment of fruits to types follows Flora of Australia, where the relevant volumes have been published, otherwise Floyd (1989) or Hyland and Whiffin (1993). We recognize the following protective fruit types; the families and genera listed are those included in our study.

1. Capsules, follicles and legumes with woody walls, thick relative to the size of the fruit: Apocynaceae (*Alstonia*, also said to be toxic; *Parsonsia*), Bignoniaceae (*Neosepicea*, Fig. 1), Elaeocarpaceae (*Peripen-*

tadenia; *Sloanea*, also has stiff bristles on the fruit), Fabaceae (*Castanospermum*; *Mucuna*, also has irritant hairs on the fruit, Fig. 1), Hamamelidaceae (*Ostrearia*), Mimosaceae (*Acacia*, *Archidendron*), Proteaceae (*Cardwellia*, Fig. 1; *Darlingia*, *Grevillea*, *Lomatia*, *Macadamia*, *Opisthiolepis*, *Stenocarpus*), Rutaceae (*Flindersia*, most species have spiny capsules, Fig. 1), Sapindaceae (*Elattostachys*, *Lepiderema*, *Toechima*), Sterculiaceae (*Brachychiton*, also has irritant hairs inside the fruit, Fig. 1) and Thymelaeaceae (*Lethedon*, also has irritant hairs on the fruit, Fig. 1).

2. Gymnospermous cones with tough scales: Zamiaceae (*Bowenia*, *Lepidozamia*).

3. Capsules with thick leathery walls (≥ 3 mm thick): Euphorbiaceae (*Aleurites*; *Omphalea*, very thick walls but only the exocarp leathery), Meliaceae (*Chisocheton*, *Dysoxylum*), and Sapindaceae (*Diploglottis bracteata*).

4. Drupe with almost woody, densely granular endocarp based on sclereids: Celastraceae (*Siphonodon*).

5. 'Perianth tube' (actually receptacular tissue) enclosing seeds becomes woody, splitting when ripe: Monimiaceae (*Daphnandra*, *Doryphora*, Fig. 1).

6. Persistent calyx tube with very sticky wall enclosing single seed: Nyctaginaceae (*Pisonia*).

7. Berries or drupes with irritant or stinging hairs: Davidsoniaceae (*Davidsonia*, irritant hairs on pericarp), Urticaceae (*Dendrocnide*, stinging hairs on berries, and especially on pedicels, Fig. 1).

8. Berries with flesh that contains abundant raphides: Araceae (*Rhaphidophora*).

9. Berries with flesh reported to give a 'burning sensation': Pandanaceae (*Pandanus*).

10. Berries or drupes or other fruits in which the flesh is reported to be toxic to humans and/or livestock: Anacardiaceae (*Semecarpus*), Apocynaceae (*Cerbera*, *Melodinus*, *Neisosperma*), Araceae (*Alocasia*), Idiiospermaceae (*Idiospermum*), Lauraceae (*Cryptocarya pleurosperma*), Solanaceae (*Solanum*), Thymelaeaceae (*Phaleria*, *Wikstroemia*). The Arecaceae might be included on the basis of *Oraniopsis* fruit being described as toxic by Cooper and Cooper (1994), which would be consistent with the evidence for *Orania* in South-east Asia (Whitmore 1973), but we know of no strong evidence for *Oraniopsis* and treat it as non-toxic.

Of these taxa with protection in the wall, a few also have seeds reported to be poisonous to humans or livestock. They fall into three groups.

1. Follicle or legume with woody wall: *Castanospermum* and *Mucuna* (testa thin), and *Macadamia* (testa thick and hard).

2. Capsule with thick leathery wall: *Aleurites* (also testa thick and very hard).

3. Gymnospermous cone: *Bowenia*, *Lepidozamia*.

We treat seeds as 'unprotected' (not markedly protected by their fruits) if they fall into one of the following types.

1. Capsules with thin walls, not markedly woody or leathery: Euphorbiaceae (*Codiaeum*, *Glochidion*, *Macaranga*, *Mallotus*), Myrtaceae (*Xanthostemon*), Onagraceae (*Ludwigia*), Phyllodraceae (*Helmholtzia*), Pittosporaceae (*Pittosporum*), Rhamnaceae (*Alphitonia*), Rubiaceae (*Wendlandia*), Rutaceae (*Melicope*), Sapindaceae (*Arytera*, *Cupaniopsis*, *Diploglottis* apart from *D. bracteata*, *Guioa*, *Harpullia*, *Mischocarpus*, *Rhyso-toechia*, *Sarcotoechia*, *Synima*), Zingiberaceae (*Alpinia*).

2. Capsule with a sub-fleshy wall: Sapindaceae (*Castanospora*).

3. Dry, winged fruits dispersed as such: Cunoniaceae (*Gillbeea*), Sterculiaceae (*Argyrodendron*; *Francisco-dendron*).

4. Thin-walled adhesive fruits on spikes: Piperaceae (*Peperomia*).

5. Berries or drupes with no latex or other obvious protective compounds: various genera in Actinidiaceae, Agavaceae, Annonaceae, Araliaceae, Arecaceae, Austrobaileyaceae, Boraginaceae, Burseraceae, Caprifoliaceae, Cardiopteridaceae, Elaeagnaceae, Elaeocarpaceae, Erythroxylaceae, Euphorbiaceae, Flacourtiaceae, Gesneriaceae, Grossulariaceae, Icacinaceae, Lauraceae, Liliaceae, Loganiaceae, Melastomataceae, Meliaceae, Menispermaceae, Myrsinaceae, Myrtaceae, Piperaceae, Podocarpaceae, Proteaceae, Rosaceae, Rubiaceae, Rutaceae, Theaceae, Verbenaceae and Vitaceae.

6. Berries or drupes with abundant latex when immature, but with little or none at the time of dispersal: Clusiaceae (*Calophyllum*, *Garcinia*, *Mammea*), Moraceae (*Ficus*, *Maclura*), and Sapotaceae (*Chrysophyllum*, *Niemeyera*, *Planchonella*, *Pouteria*).

7. Berries said to be inedible when immature (perhaps with cucurbitacins): Cucurbitaceae (*Trichosanthes*).

There are a few species which are intermediate between our 'protected' and 'unprotected' groups, most notably certain Lauraceae with large fruits (ca 5 cm diameter) and thick mesocarps with a not very fleshy texture: *Beilschmiedia bancroftii*, *Endiandra insignis* and *E. palmerstonii*. We include data for these three species in Table 1, but do not use them in our statistical analyses.

In respect of our second hypothesis we separate species according to the percentage of the 'seed' dry mass found in the coat as opposed to the embryo-cum-endosperm fraction. We recognize three groups: > 60 , $30-60$ and $< 30\%$.

Sampling and analyses

Sampling was often from one individual. Our basic sample for seed mass was of ten seeds or ten fruits, taken haphazardly across the whole size range

Table 1. Seed mass, embryo-cum-endosperm fraction (EE) dry mass and proportion of total seed mass in EE, and nitrogen concentration [N] in seeds and EE of 197 species from lowland tropical rainforest, Australia. The letters after species names indicate life-form: S, shrub or very short tree (≤ 6 m tall); ST, short tree (> 6 m, ≤ 15 m tall); TT, tall tree (> 15 m tall); SV, short vine; TV, tall vine; E, epiphyte; HE, hemiepiphyte; H, herb. Species in which the fruit provides marked defence of the seed are indicated: W, capsules, follicles and legumes with woody walls, and woody perianth tubes; C, gymnospermous cones with tough scales; L, capsules with thick leathery walls; G, densely granular fruit based on sclereids; S, sticky, persistent calyx; I, irritant or stinging hairs; R, flesh causing 'burning' sensation; P, toxic or poisonous flesh. Values are given to two significant figures; values in columns have been independently rounded off and so do not necessarily multiply.

Family	Species	Seed dry mass (mg)	Seed [N] (mg/g)	EE dry mass (mg)	EE [N] (mg/g)	% Seed in EE	Defence
Gesneriaceae	<i>Cyrtandra baileyi</i> S	0.0085	28				
Rubiaceae	<i>Wendlandia basistaminea</i> S	0.017	27				
Grossulariaceae	<i>Abrophyllum ornans</i> ST	0.049	17				
Actinidiaceae	<i>Saurauia andreana</i> S	0.057	25				
Melastomataceae	* <i>Melastoma affine</i> S	0.071	36				
Piperaceae	* <i>Piper umbellatum</i> var. <i>subpeltatum</i> S	0.073	28				
Moraceae	* <i>Ficus racemosa</i> TT	0.13	24				
Phyllodraceae	<i>Helmholtzia acrifolia</i> H	0.14	12				
Araceae	<i>Rhaphidophora australasica</i> TV	0.18	39				
Moraceae	<i>Ficus leptoclada</i> ST	0.21	25				R
Piperaceae	<i>Peperomia blanda</i> var. <i>floribunda</i> H	0.22	22				
Moraceae	<i>Ficus fraseri</i> ST	0.23	23				
Moraceae	<i>Ficus virens</i> TT + HE	0.23	8				
Piperaceae	<i>Peperomia nervis</i> H + E	0.25	21				
Solanaceae	* <i>Solanum aviculare</i> S	0.29	24				
Moraceae	<i>Ficus microcarpa</i> TT + HE	0.34	15				
Moraceae	<i>Ficus destruens</i> TT + HE	0.40	9.1				
Verbenaceae	<i>Callicarpa longifolia</i> S	0.41	17				
Moraceae	<i>Ficus obliqua</i> TT + HE	0.44	18				
Moraceae	<i>Ficus crassipes</i> TT + HE	0.45	20				
Onagraceae	<i>Ludwigia octovalvis</i> H	0.45	21				
Loganiaceae	<i>Geniostoma rupestre</i> S	0.48	20				
Moraceae	<i>Ficus superba</i> TT + HE	0.55	11				
Urticaceae	* <i>Dendrocnide moroides</i> S	0.65	27				I
Verbenaceae	<i>Callicarpa pedunculata</i> S	0.66	9.1				
Rosaceae	<i>Rubus moluccanus</i> S	0.85	13				
Loganiaceae	<i>Fagraea berteriana</i> ST + E	1.2	30				
Piperaceae	<i>Piper rothianum</i> TV	1.2	24				
Araliaceae	<i>Polyscias mollis</i> ST	1.5	14				
Solanaceae	<i>Solanum viridifolium</i> ST	1.5	26				P
Liliaceae	<i>Molineria capitulata</i> H	1.7	26				
Caprifoliaceae	<i>Sambucus australasica</i> S	1.7	21				
Solanaceae	<i>Solanum dallachii</i> S	2.1	35				P
Araliaceae	<i>Polyscias purpurea</i> S	2.4	17				
Apocynaceae	<i>Alstonia spectabilis</i> TT	2.5	31				WP
Araliaceae	<i>Schefflera actinophylla</i> ST + E	2.7	22				
Araliaceae	<i>Polyscias murrayi</i> TT	2.8	18				
Araliaceae	<i>Schefflera elliptica</i> ST + E	3.1	8.2				
Myrtaceae	<i>Xanthostemon whitei</i> TT	3.2	6.0				
Moraceae	* <i>Ficus pleurocarpa</i> TT + HE	3.3	4.5				
Rubiaceae	<i>Mymecodia</i> sp. H + E	3.6	34				
Rutaceae	* <i>Acronychia crassipetala</i> ST	4.0	19				

Table 1. (continued)

Family	Species	Seed dry mass (mg)	Seed [N] (mg/g)	EE dry mass (mg)	EE [N] (mg/g)	% Seed in EE	Defence
Araliaceae	<i>Cephalalaria cephalobotrys</i> SV	4.0	18				
Moraceae	<i>Maclura cochinchinensis</i> 1† TV	4.0	31				W
Monimiaceae	<i>Daphnandra repandula</i> TT	4.7	34				
Araliaceae	<i>Polyscias australiana</i> ST	5.7	26				
Liliaceae	<i>Dianella caerulea</i> H	7.1	31				
Euphorbiaceae	<i>Breynia cernua</i> ST	7.7	26				W
Apocynaceae	<i>Parsonsia straminea</i> TV	7.8	39				
Rubiaceae	<i>Morinda jasminoides</i> SV	8.4	17				
Araliaceae	<i>Polyscias elegans</i> TT	8.7	12				
Pittosporaceae	<i>Pittosporum ferrugineum</i> ST	9.9	17				
Araceae	<i>Alocasia brisbanensis</i> H	10	22				P
Monimiaceae	<i>Doryphora aromatica</i> TT	10	23				W
Cardiopteridaceae	<i>Cardiopteris moluccana</i> TV	11	24				
Agavaceae	<i>Cordylone canifolia</i> S	12	21				
Mimosaceae	<i>Acacia aulacocarpa</i> TT	13	58				W
Euphorbiaceae	<i>Glochidion harveyanum</i> ST	13	20				
Rutaceae	<i>*Sarcamelicope simplicifolia</i> ST	13	16				WI
Thymelaeaceae	<i>Leihedon setosa</i> ST	14	33				
Euphorbiaceae	<i>Mallotus paniculatus</i> ST	14	16				
Zingiberaceae	<i>Alpinia modesta</i> H	15	15				
Cunoniaceae	<i>Gillbeea adenopetala</i> TT	15	13	3.2	25	21	
Moraceae	<i>*Maclura cochinchinensis</i> 2 TV	15	29				
Pandanaceae	<i>Pandanus monicola</i> S	17	51				B
Rhamnaceae	<i>Alphitonia philippinensis</i> TT	18	21				
Rutaceae	<i>Melicope vitiflora</i> TT	19	16				P
Thymelaeaceae	<i>Wikstroemia indica</i> S	19	45				W
Bignoniaceae	<i>*Neosepicea jucunda</i> TV	20	41				
Vitaceae	<i>*Cayratia saponaria</i> SV	23	25				W
Proteaceae	<i>Grevillea baileyana</i> TT	24	71	22	76	92	W
Euphorbiaceae	<i>Lomatia fraxinifolia</i> TT	25	29				
Euphorbiaceae	<i>Codiaeum variegatum</i> S	29	15				W
Euphorbiaceae	<i>Macaranga involucreta</i> ST	33	16	15	25	46	W
Apocynaceae	<i>*Parsonsia latifolia</i> TV	33	38				
Piperaceae	<i>*Piper caninum</i> TV	33	15				
Menispermaceae	<i>*Legnephora moorei</i> TV	36	12				
Sapindaceae	<i>*Mischocarpus lachnocarpus</i> TT	40	20				W
Proteaceae	<i>Stenocarpus sinuatus</i> TT	43	43	26	69	61	
Sapindaceae	<i>Guioa lasioneura</i> ST	49	25	39	29	80	
Erythroxylaceae	<i>Erythroxylum ecarinatum</i> TT	52	16	7.8	26	15	
Rutaceae	<i>Flindersia brayleyana</i> TT	54	32	42	33	78	W
Sapindaceae	<i>Guioa acutifolia</i> ST	54	17	47	18	87	
Apocynaceae	<i>Melodinus australis</i> TV	65	13	20	18	31	P
Myrsinaceae	<i>Ardisia brevipedata</i> S	73	8.6	50	11	69	
Sapindaceae	<i>Diploglottis diphylostegia</i> TT	76	13	74	12	97	
Sapindaceae	<i>Elatostachys megalantha</i> ST	82	33	67	37	82	W
Cucurbitaceae	<i>Trichosanthes</i> sp. TV	86	32	28	66	33	
Sapindaceae	<i>Toechina erythrocarpum</i> TT	90	28	65	25	72	W

Table 1. (continued)

Family	Species	Seed dry mass (mg)	Seed [N] (mg/g)	EE dry mass (mg)	EE [N] (mg/g)	% Seed in EE	Defence
Boraginaceae	* <i>Cordia dichotoma</i> TT	97	9.9	21	44	22	
Hamamelidaceae	<i>Ostrearia australiana</i> TT	100	29	51	58	51	W
Sterculiaceae	* <i>Argyrodendron trifoliolatum</i> TT	110	14	61	12	55	
Elaeocarpaceae	<i>Sloanea machrydei</i> TT	130	17	60	26	46	W
Rutaceae	<i>Flindersia bourjoiana</i> TT	130	48	120	51	92	W
Araliaceae	<i>Delarbrea michiana</i> ST	150	17	65	21	43	
Elaeagnaceae	* <i>Elaeagnus triflora</i> TV	150	28	110	33	70	
Sterculiaceae	* <i>Francisodendron laurifolium</i> TT	160	30	140	33	84	
Sapindaceae	* <i>Sarcotoechia lanceolata</i> TT	160	29	140	31	86	
Sterculiaceae	<i>Brachychiton acerifolius</i> TT	170	55	120	78	71	WI
Icacinaceae	<i>Apodytes brachystylis</i> TT	180	14	110	17	61	
Sterculiaceae	<i>Argyrodendron peralatum</i> 1 TT	180	13	54	13	30	
Lauraceae	* <i>Neolitsea dealbata</i> TT	180	13	140	14	79	
Proteaceae	* <i>Opisthiolepis heterophylla</i> TT	180	88	150	110	87	W
Proteaceae	<i>Darlingia darlingiana</i> TT	200	53	150	66	75	W
Nyctaginaceae	<i>Pisonia umbellifera</i> TT	210	50	200	52	95	S
Icacinaceae	<i>Irvingbaileya australis</i> TT	220	11	23	25	11	
Sapindaceae	* <i>Arytera pauciflora</i> ST	250	11	210	10	84	
Sapindaceae	<i>Cupaniopsis flagelliformis</i> TT	250	11	220	12	88	
Lauraceae	* <i>Cryptocarya melanocarpa</i> TT	270	9.2	160	12	58	
Sapindaceae	<i>Synina macrophylla</i> ST	280	15	250	14	89	
Rutaceae	<i>Euodia haplophylla</i> ST	290	32	100	76	35	
Lauraceae	<i>Litsea bindoniana</i> TT	290	16	270	17	93	
Arecaceae	<i>Pythosperma elegans</i> ST	300	9	290	8.9	97	
Sapindaceae	<i>Sarcotoechia serrata</i> ST	300	14	280	13	93	
Icacinaceae	<i>Citronella smythii</i> TT	310	17	200	23	63	
Elaeocarpaceae	<i>Elaeocarpus largiflorens</i> TT	310	7.1	84	13	27	
Meliaceae	<i>Dysoxylum papuanum</i> TT	320	16	300	15	94	
Sapindaceae	<i>Rhysoetochia robertsonii</i> TT	320	20	290	20	91	
Meliaceae	<i>Dysoxylum parasiticum</i> TT	350	30	330	28	94	L
Sapindaceae	<i>Harpullia pendula</i> ST	350	13	320	13	91	
Arecaceae	<i>Calamus australis</i> TV	410	12	410	12	100	W
Sapindaceae	<i>Lepiderema largiflorens</i> S	420	26	370	29	88	
Sapotaceae	<i>Planchonella obovoidea</i> TT	420	7.3	110	22	8.5	
Davidsoniaceae	* <i>Davidsonia pruriens</i> ST	440	12	200	12	45	I
Mimosaceae	<i>Archidendron lucyi</i> ST	480	54	450	50	35	W
Sapindaceae	<i>Diploglottis smithii</i> TT	510	11	450	11	88	
Meliaceae	<i>Dysoxylum pettigrewianum</i> TT	530	32	500	32	94	L
Meliaceae	<i>Melia azedarach</i> TT	530	5.6	14	48	2.6	
Theaceae	<i>Ternstroemia cherryi</i> TT	570	14	340	20	60	
Sterculiaceae	<i>Argyrodendron</i> sp. [Boonjie B.P. Hyland RfK 2139] TT	590	17	230	19	39	
Lauraceae	<i>Litsea leefeana</i> TT	600	16	580	15	97	
Elaeocarpaceae	* <i>Elaeocarpus foveolatus</i> TT	610	4.8	180	9.5	28	
Burseraceae	<i>Canarium vitense</i> TT	650	5.7	43	47	6.6	
Lauraceae	<i>Cinnamomum laubatii</i> TT	650	16	610	17	94	
Rutaceae	<i>Acronychia vestita</i> TT	660	2.0	8.6	30	1.3	

Table 1. (continued)

Family	Species	Seed dry mass (mg)	Seed [N] (mg/g)	EE dry mass (mg)	EE [N] (mg/g)	% Seed in EE	Defence
Austrobaileyaceae	<i>Austrobaileya scandens</i> TV	660	23	380	35	58	
Sterculiaceae	<i>Argyrodendron perlatum</i> 2† TT	700	10	390	9.1	56	
Annonaceae	<i>Polyaulax</i> sp. ST	720	15	660	15	91	
Verbenaceae	<i>Gmelina fasciculiflora</i> TT	730	2.6	19	42	2.6	G
Celastraceae	<i>Siphonodon membranaceus</i> TT	740	5.9	56	31	7.6	W
Proteaceae	<i>Cardwellia sublimis</i> TT	770	72	660	82	86	W
Elaeocarpaceae	<i>Peripentadenia mearsii</i> ST	780	26	430	43	55	W
Icacinaceae	<i>Gomphandra australiana</i> TT	830	11	620	13	75	
Elaeocarpaceae	<i>Aceratium sericoleopsis</i> TT	930	4.2	70	16	7.5	
Lauraceae	* <i>Cryptocarya onoprienkoana</i> TT	930	7.6	680	8.3	73	
Clusiaceae	<i>Garcinia</i> sp. [Davies Ck. J. G. Tracey 14745] TT	990	5.1	960	4.8	97	P
Apocynaceae	<i>Neisosperma poweri</i> ST	1 000	13	190	37	19	
Lauraceae	<i>Cryptocarya grandis</i> TT	1 000	8.6	350	15	35	
Lauraceae	* <i>Endiandra bessaphila</i> TT	1 100	11	640	11	58	
Proteaceae	* <i>Triunia erythrocarpa</i> ST	1 200	9.5	1 000	10	86	
Proteaceae	* <i>Turillia bleasdalei</i> ST	1 200	8.1	580	15	49	
Euphorbiaceae	<i>Fontainea picrosperma</i> ST	1 300	12	490	21	38	
Podocarpaceae	<i>Prumnopitys amara</i> TT	1 300	7.0	490	11	38	
Lauraceae	<i>Beilschmiedia recurva</i> TT	1 400	17	1 300	16	93	
Lauraceae	<i>Cryptocarya angulata</i> TT	1 600	14	1 500	14	94	
Flacourtiaceae	<i>Baileyxylon lanceolatum</i> TT	1 700	23	800	42	47	
Areaceae	* <i>Oraniopsis appendiculata</i> TT	1 800	6.0	1 500	8.8	84	
Lauraceae	* <i>Endiandra monothrya</i> TT	1 900	9.8	1 000	9.3	53	
Myrtaceae	<i>Syzygium boonjee</i> ST	1 900	5.1	1 600	4.5	84	
Sapindaceae	<i>Castanospora alphanthii</i> TT	2 000	11	1 700	11	85	
Meliaceae	<i>Dysoxylum latifolium</i> TT	2 200	31	2 200	31	100	C
Zamiaceae	<i>Bowenia spectabilis</i> H	2 300	34	2 200	36	96	
Lauraceae	* <i>Cryptocarya corrugata</i> TT	2 400	6.7	2 100	6.0	87	
Lauraceae	* <i>Endiandra longipedicellata</i> TT	2 500	8.2	1 900	8.5	75	
Sapotaceae	<i>Chrysophyllum</i> sp. [Mt Lewis A. K. Irvine 1402] TT	2 600	7.8	2 400	7.6	92	
Meliaceae	<i>Dysoxylum</i> sp. aff. <i>klanderii</i> TT	2 600	28	2 300	29	89	L
Sapindaceae	* <i>Diploglottis bracteata</i> 1 TT	2 800	15	2 500	14	87	L
Rosaceae	<i>Prunus turneriana</i> TT	3 000	9.0	1 800	14	60	
Sapindaceae	* <i>Diploglottis bracteata</i> 2† TT	3 500	12	3 200	12	90	L
Meliaceae	<i>Chisocheiton longistipitatus</i> TT	3 600	13	3 300	13	92	L
Lauraceae	* <i>Endiandra montana</i> TT	3 700	5.4	3 100	5.1	85	
Lauraceae	* <i>Endiandra sideroxylon</i> TT	4 000	7.0	3 300	6.9	83	
Lauraceae	* <i>Endiandra sankeyana</i> 1† TT	4 200	8.1	3 400	7.3	80	
Fabaceae	<i>Mucuna gigantea</i> TV	4 700	32	3 700	38	79	WI
Anacardiaceae	<i>Semecarpus australiensis</i> TT	5 000	12	2 000	17	40	P
Sapotaceae	<i>Pouteria castanosperma</i> TT	5 200	8.9	1 400	29	27	
Corynocarpaceae	<i>Corynocarpus cribbianus</i> 1 TT	5 500	18	3 800	25	69	
Clusiaceae	<i>Calophyllum costatum</i> TT	5 600	4.8	2 500	9.0	45	
Lauraceae	<i>Cryptocarya oblata</i> 1† TT	5 600	6.4	4 900	6.1	88	
Sapindaceae	<i>Diploglottis bracteata</i> 3 TT	5 600	11	5 200	11	93	L
Lauraceae	* <i>Beilschmiedia tooram</i> TT	5 800	6.3	2 700	6.1	47	
Thymelaeaceae	<i>Phaleria clerodendron</i> ST	5 900	23	4 400	29	75	P

Table 1. (continued)

Family	Species	Seed dry mass (mg)	Seed [N] (mg/g)	EE dry mass (mg)	EE [N] (mg/g)	% Seed in EE	Defence
Lauraceae	<i>Endiandra sankeyana</i> 2 TT	7 000	7.7	5 200	7.0	74	
Euphorbiaceae	<i>Aleurites moluccana</i> TT	7 900	22	3 400	47	43	L
Lauraceae	* <i>Endiandra xanthocarpa</i> 1† TT	8 600	6.6	5 500	6.3	64	
Sapotaceae	<i>Niemeyera prunifera</i> TT	8 800	5.8	8 500	5.0	97	
Lauraceae	<i>Cryptocarya oblata</i> 2 TT	9 700	6.5	8 500	6.1	88	
Proteaceae	* <i>Athertonia diversifolia</i> TT	11 000	4.1	1 100	22	14	
Corynocarpaceae	<i>Corynocarpus cribbianus</i> 2† TT	11 000	19	7 700	26	70	
Lauraceae	<i>Cryptocarya pleurosperma</i> TT	11 000	4.5	2 400	10	22	P
Elaeocarpaceae	* <i>Elaeocarpus bancroftii</i> TT	11 000	4.3	180	22	1.6	
Lauraceae	<i>Endiandra xanthocarpa</i> 2 TT	11 000	5.4	8 000	5.5	74	
Proteaceae	* <i>Macadamia whelanii</i> TT	11 000	6.3	5 500	14	50	W
Apocynaceae	* <i>Cerbera inflata</i> TT	13 000	3.4	1 200	26	9.2	P
Clusiaceae	<i>Mammea touriga</i> TT	14 000	5.2	11 000	5.4	79	
Fabaceae	<i>Castanospermum australe</i> TT	14 000	14	13 000	15	93	W
Euphorbiaceae	<i>Onphalea queenslandiae</i> TV	16 000	26	13 000	30	81	L
Lauraceae	<i>Endiandra insignis</i> 1 TT	18 000	7.7	11 000	12	61	
Zamiaceae	<i>Lepidozamia hopei</i> TT	18 000	22	17 000	28	94	C
Proteaceae	<i>Eidothea zoxylocarya</i> TT	18 000	12	5 200	34	29	
Lauraceae	* <i>Endiandra insignis</i> 2 TT	19 000	8.6	10 000	11	54	
Lauraceae	* <i>Beilschmiedia volckii</i> TT	24 000	8.5	20 000	8.1	82	
Lauraceae	* <i>Endiandra palmerstonii</i> TT	28 000	7.7	13 000	8.6	47	
Lauraceae	* <i>Beilschmiedia bandroftii</i> TT	43 000	16	29 000	14	68	
Myrtaceae	<i>Syzygium gustavioides</i> TT	48 000	4.5	47 000	3.6	98	
Idiospermaceae	<i>Idiospermum australiense</i> TT	82 000	10	81 000	10	99	P

* Collections used in this study in addition to those given in the preliminary account given by Grubb (1998).

† Collection used in statistical analyses and in Fig. 1, where more than one collection for a species has been made. The chosen collection has been randomly selected.

available. We often increased the sample to 20–50 seeds for species with mean seed dry mass < 50 mg and always for species with mean seed dry mass < 100 µg. We collected only apparently healthy seeds. We cleaned them, and dried them for at least 48 h at 80°C, and determined dry mass values for single seeds or known numbers of seeds on an electronic balance to a precision of 0.1 mg. We quote the mean values rounded off to two significant figures. In most species for which we determined dry mass values of single seeds the largest had a value two to three times the smallest. As recorded in Grubb and Metcalfe (1996), in a wider-ranging study of seed size in NEQ, we have made two collections of 10 seeds at different sites or different times for each of 24 species. For two species the collections differed in mean dry mass by a factor of three to four (both in Table 1); in the other 22 cases the difference between the first mean and the overall mean was $14 \pm 2.5\%$ (SE; range 0–37%).

For each species with a seed dry mass value > 40 mg we determined the concentrations of N, P, K, Ca and Mg in the embryo-cum-endosperm (EE) and wall fractions using standard methods reported by Grubb et al. (1994). We analysed the largest and smallest seeds from each collection, and one seed near the mean, because Oladokun (1989) and Grubb and Burslem (1998), working in West Africa and Malaysia respectively, had found for a number of species evidence of a trend to lower concentrations in larger seeds within a given seed crop. For most species with a mean seed dry mass ≤ 40 mg we analysed whole seeds; 2–3 samples for those of mean dry mass > 3 mg but only one for smaller seeds. We report in this paper only the data for nitrogen concentrations, but refer briefly to the data for P, K, Ca and Mg.

Where we analysed > 1 sample, the largest seed had a higher concentration of nitrogen (by a margin of 10% or more) than the smallest seed in 37 cases, a lower concentration in 36, and a difference of < 10% in 52. We quote the mean nitrogen concentration, [N], rounded off to two significant figures.

Statistical analyses

Unless stated otherwise, data were analysed by regression analysis using GLIM (Baker 1987). The most parsimonious models were generated using real [N] values and log-transformed seed dry mass data, and then applying a gamma error structure. Gamma errors are appropriate as the sample variance was not constant even after taking the log of the response variable (Crawley 1993, cf. Taylor 1961). A log-link function was used throughout. Significance was taken as $P \leq 0.05$. In comparing genera we have used arithmetic means for the [N] values and logarithmic means for the mean seed dry mass values.

Results

Comparisons of species with differing degrees of defence in the fruit wall

Comparison of the 'protected' and 'unprotected' species is complicated by the 'protected' seeds being significantly larger than the 'unprotected' seeds (Fig. 2; $P < 0.05$, Mann-Whitney *U*-test).

For both 'protected' and 'unprotected' seeds there is a significant negative linear relationship between [N] and log seed dry mass ('protected' $F = 10.5$, d.f. 52, $P < 0.005$; 'unprotected' $F = 61.7$, d.f. 138, $P < 0.001$, Fig. 3). The intercepts on the *y* axes ('protected' 49.4, 'unprotected' 20.8) are significantly different ($P < 0.001$), although the two lines have a common slope (-1.23). There is also a significant negative linear relationship between [N] and log seed dry mass when the mean values for genera are considered ('protected' $F = 9.03$, d.f. 43, $P < 0.005$; 'unprotected' $F = 48.5$, d.f. 100, $P < 0.001$, Fig. 4). For the genera as for the species, the intercepts on the *y* axes are significantly different ('protected' 50.1, 'unprotected' 22.6; $P < 0.001$) and the two groups of genera share a common slope (-1.25). The intercepts and slopes of the lines for species and for genera do not differ significantly when either 'protected' or 'unprotected' taxa are considered ($P > 0.05$, *t*-test).

In making taxonomically controlled contrasts (TCCs) we use a regression line for [N] on log seed dry mass for the whole collection of species ($y = 25.6 - 1.16x$, $F = 21.0$, 192 d.f., $P < 0.001$). We consider the actual [N] values in the 'protected' and 'unprotected' species relative to those forecast by the common regression line.

There are six families in which we can make TCCs, and all of these support the conclusion drawn from the collection of species as a whole (Fig. 5). There are four genera in which we can make TCCs independent of those considered in the intrafamilial comparisons, using the same regression equation (Fig. 6). Two of these (*Dysoxylum* and *Solanum*) support the conclusion drawn from the collection of species as a whole, but the other two (*Cryptocarya* and *Diploglottis*) do not.

Comparisons of species without marked protection in the fruit wall but with differing degrees of defence in the 'seed'

Only three species with < 30% dry mass in the wall fraction had a somewhat high [N] in the EE fraction for their size: *Guioa lasioneura* (Sapindaceae), *Sarcotoechia lanceolata* (Sapindaceae) and *Franciscodendron* (Sterculiaceae); the other 42 species all had [N] values < 20 mg g⁻¹ (Fig. 7). Those with 30–60% allocation to wall did not have significantly higher [N] than those with < 30% allocation ($P > 0.05$). However, although the species with > 60% in the wall show a very wide range of [N],

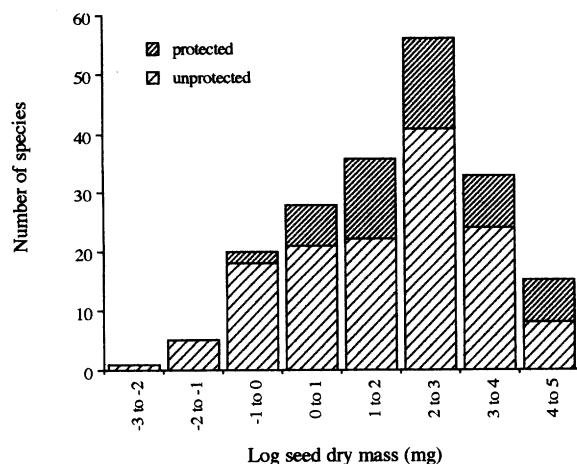


Fig. 2. The numbers of species in different seed-size classes in the 'protected' and 'unprotected' species analysed. The 'protected' species have significantly larger seeds than the 'unprotected' species ($P < 0.05$).

they had significantly higher [N] than the other two classes ($P < 0.001$). The species with $> 60\%$ wall also tended to have smaller seeds than those with less investment in the wall fraction, although the highest [N] were not found in the smallest seeded-species. Also, the highest values for [N] in the EE fraction of species with $> 60\%$ wall were high even in comparison with values for some species with marked protection in the fruit wall. In summary, the results show that species with relatively high [N] in the EE fraction have marked physical protection, but that some species with thick seed walls do not have particularly high [N].

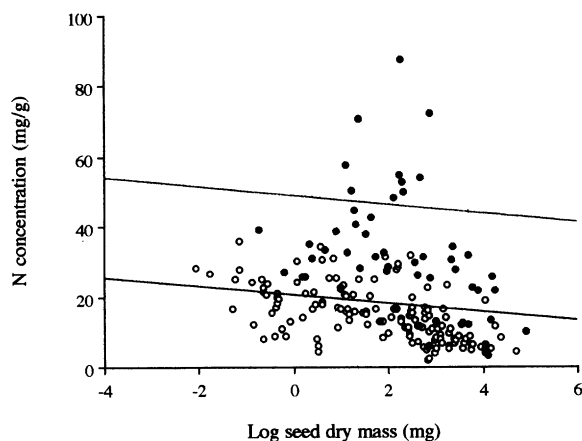


Fig. 3. Regression of N concentration on log seed dry mass for species with marked protection in the fruit (filled circles) and species without marked protection (open circles). The intercept on the y -axis of the upper line ('protected' species) is significantly greater than that of the lower line ('unprotected' species; $P < 0.001$). The slopes of the two lines are not significantly different.

Nutrients other than nitrogen

Our data for P, K, Ca and Mg will be given elsewhere as part of a wider survey of nutrient concentrations in seeds and fruits in our study area. Our analyses show that the concentrations of P, Ca and Mg were also significantly and markedly higher in species with 'protected' seeds than in those with 'unprotected' seeds; intercepts on y -axes 5.8 ('protected') and 2.7 ('unprotected'), $P < 0.001$; 12.0 and 8.9, $P < 0.05$, and 3.8 and 2.6, $P < 0.001$ respectively. There was no such difference for K. For none of these elements are the gradients of the slopes for 'protected' and 'unprotected' species significantly different. This result differs slightly from that reported for a smaller data set (Grubb 1998), where there were no significant differences between the groups of species in terms of Ca and Mg concentrations.

Discussion

Limitations of the data

In most cases we have analysed only one collection for each species, but for eight species where we have two or more collections the [N] in the seed is similar in all collections, even where the seed mass is appreciably different. Here we give first the quotient of the higher value for mean seed dry mass over the lower, and then the quotient of the mean concentration in the seeds of the collection with larger mass over that in the smaller seeds: *Argyrodendron peralatum* 3.9, 0.82; *Cryptocarya oblata* 1.7, 1.0; *Corynocarpus cribbianus* 2.0, 1.0; *Diploglottis bracteata* 2.0, 0.77; *Endiandra insignis* 1.1,

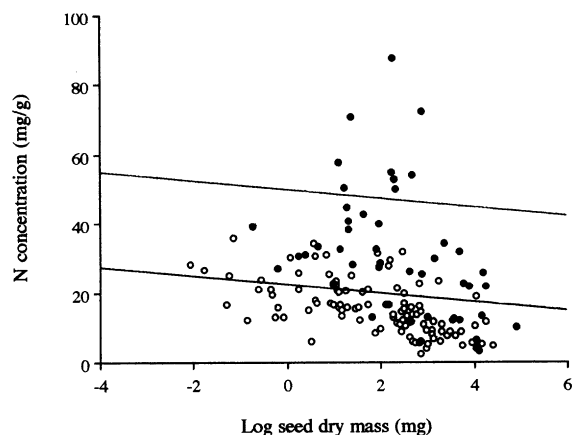


Fig. 4. Regression of N concentration on log seed dry mass for genera with marked protection in the fruit (filled circles) and species without marked protection (open circles). The intercept on the y -axis of the upper line ('protected' species) is significantly greater than that of the lower line ('unprotected' species; $P < 0.001$). The slopes of the two lines are not significantly different.

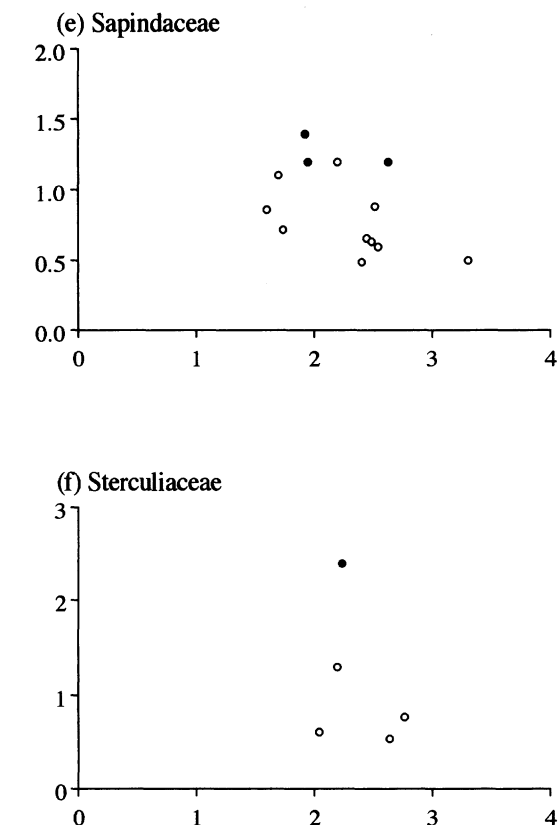
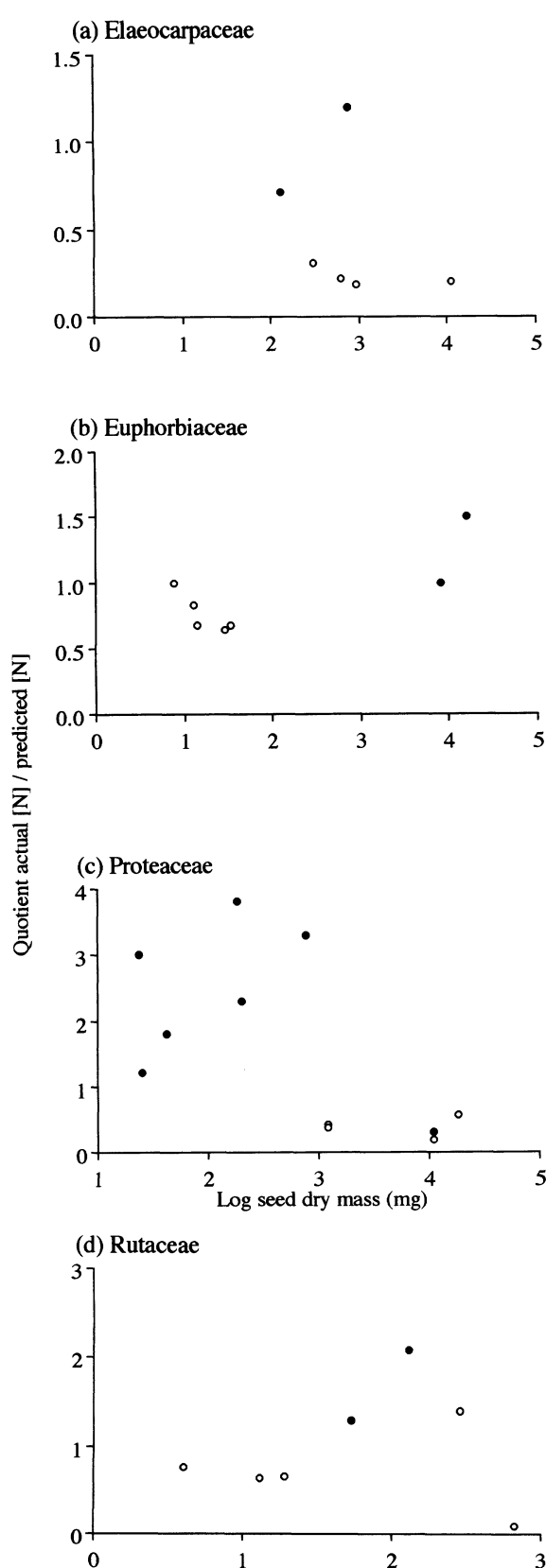


Fig. 5. The concentration of N in the seeds of taxa with protection by the fruit (filled circles) and without (open circles) in intrafamilial contrasts. The regression line is the line derived for the whole collection of seeds; within each fruit type the taxa are listed in order of increasing mean seed dry mass. Within each intrafamilial contrast the genera with protected seeds have higher values for [N], relative to those predicted from their mass than the unprotected, except for *Macadamia* (see Discussion). (a) Elaeocarpaceae: *Sloanea* and *Peripentadenia* with woody capsules containing arillate seeds vs *Elaeocarpus largiflorens*, *E. foveolatus*, *Aceratium* and *E. bancroftii* with fleshy drupes. (b) Euphorbiaceae: *Aleurites* and *Omphalea* with capsules which have thick leathery walls vs *Glochidion*, *Mallothus*, *Codiaeum* and *Macaranga* which have capsules with relatively thin walls, *Breynia* with a berry, and *Fontainea* with a drupe. (c) Proteaceae: *Grevillea*, *Lomatia*, *Stenocarpus*, *Darlingia*, *Opisthiolepis*, *Cardwellia* and *Macadamia* with thick-walled woody follicles vs *Triunia*, *Turillia*, *Athertonia* and *Eidothea* with drupes. (d) Rutaceae: *Flindersia* spp. with thick-walled woody capsules vs *Acronychia crassipetala* and *Melicope* with thin-walled capsules and *Sarcomelicope*, *Euodia* and *Acronychia vestita* with drupes. (e) Sapindaceae: *Elatostachys*, *Toeckia* and *Lepiderema* which have capsules with woody walls vs *Mischocarpus*, *Guioa lasioneura*, *G. acutifolia*, *Sarcotoechia lanceolata*, *Cupaniopsis*, *Synima*, *Sarcotoechia serrata*, *Rhysotoechia*, *Harpullia* and *Castanospora* which have capsules with relatively soft leathery walls. (f) Sterculiaceae: *Brachychiton* which has a thickly woody follicle lined with irritant hairs vs three *Argyrodendron* spp. and *Franciscodendron* with samaras.

1.1; *E. sankeyana* 1.7, 0.95 *E. xanthocarpa* 1.3, 0.82 and *Maclura cochinchinensis* 3.8, 0.93 (Table 1). The general trend is toward a somewhat lower value in the larger

seeds, which was not our finding for the collection as a whole (see above). However, the trend is consistent with the findings of Grubb and Burslem (1998) for seeds of different size within a single collection.

It is important to note that the nitrogen measured in the seeds may not all have been in protein, and of potential value to predators (Pate et al. 1986). It is known that in the legumes a large proportion of the seed N can be present as toxic amino acids (Janzen 1969). However, this feature has not been demonstrated in many families, and we treat the [N] as generally a useful indication of value to animals whose growth is limited by the N supply.

It is possible but improbable that richness in P, Ca or Mg makes the seeds with marked protection especially attractive to predators. There is no body of evidence suggesting that the growth rates of animals are generally related to the supplies of these nutrients. A more serious possibility is that seeds with marked protection also have especially energy-rich seeds, e.g. rich in lipids, and that the protection on that ground is as important as in respect of the protein-richness, or even more important. This possibility remains to be tested.

Seed nitrogen concentration and defence in the fruit wall or the seed

Our first hypothesis was supported by our results. The analysis is complicated because of the difference in seed size between the 'protected' and 'unprotected' species. However, the regression lines for [N] on log mean seed dry mass were significantly and markedly different. We were also able to test our hypothesis by making comparisons within six families and four genera; in 6/6 and 2/4 cases it received support.

Ten species from six families with 'protected' seeds had strikingly high [N] values, i.e. values above the regression line for that group, and well above the cloud of points for the 'unprotected' species: *Acacia* and *Archidendron* (Mimosaceae), *Cardwellia*, *Darlingia*, *Grevillea* and *Opisthiolepis* (Proteaceae), *Flindersia bourgotiana* (Rutaceae) and *Brachychiton* (Sterculiaceae), all with capsules, follicles or legumes; *Pisonia* (Nyctaginaceae, with a sticky persistent calyx) and *Pandanus* (Pandanaceae, with a noxious berry).

Our second hypothesis was also supported by our results. Despite a very wide range of [N] values in the seeds of species with > 60% of dry mass in the wall, the mean was significantly greater in these species than in those that had < 60%. All species with a particularly high [N] in the EE fraction had a high proportion of the total seed mass in wall. Our hypothesis failed to predict the existence of several species which have a very thick endocarp or testa and a not very high [N], but the idea of a thick coat being valuable in delaying germination, so spreading the risk in seedling survival, was already well established (Bewley and Black 1982,

Grubb 1988). Most of the species whose seeds we analysed are shade-tolerant at the stage of establishment. Our finding that 23/92 of the shade-tolerant species allocate > 60% of seed mass to wall is consistent with the observation that many of them take many months or years to germinate (Hyland 1983, 1989, Hopkins and Graham 1987). Ng (1978) similarly found considerably delayed germination in 53/180 shade-tolerant species studied in Malaysia.

Our specific hypotheses were derived from the more general plant defence theory of Grubb (1992), and go some way toward supporting that. Our results are also broadly in agreement with the theory of McKey (1979) who argued that a plant's allocation to defence should be concentrated in those tissues which are most critical for the fitness of the species.

It was not feasible, using our data, to make a test of the hypothesis that poisonous seeds have particularly high [N] values because most of the species in our collection with poisonous seeds also have marked protection by the fruit. However, the few species without marked protection of the 'seed' by the fruit but with poisonous seeds in fleshy drupes do not support the hypothesis. While *Melia* (which also has a very thick endocarp) does have a notably high [N], *Fontainea* and *Triunia* (with a not especially thick coat) do not, and nor do the possibly toxic species of *Endiandra* and *Turrillia*. Our list of poisonous seeds may be incomplete, as there is a paucity of knowledge on the toxicity of Australian rainforest fruits generally, and uncertainty about where the toxins are in fruits known to contain a toxic principle. Also, 'toxicity' is recorded for humans and livestock, and the extent of toxicity to native animals is unknown. The most puzzling group of species in our whole collection in respect of defence is that of the Proteaceae with poisonous seeds in drupes (*Triunia*, *Turrillia*) or poisonous seeds in drupe-like one-seeded follicles (certain species of *Macadamia*). Possibly they are protected because of their especially high concentrations of lipids (cf. Pate et al. 1986).

The advantage to seeds of having a high nitrogen concentration

The value might come at the stage of dispersal or the stage of establishment. Grubb (1996) suggested that the high [N] in the embryos of a number of one-seeded fruits with thick endocarp lay in attracting the few dispersers with teeth and jaws able to pierce the wall, much as Stapanian (1986) suggested that richness in energy would attract the specialized dispersal agents of certain north temperate trees.

Whether or not this hypothesis is true for the plants described by Grubb (1996), it cannot be true for the wind-dispersed seeds which receive such massive protec-

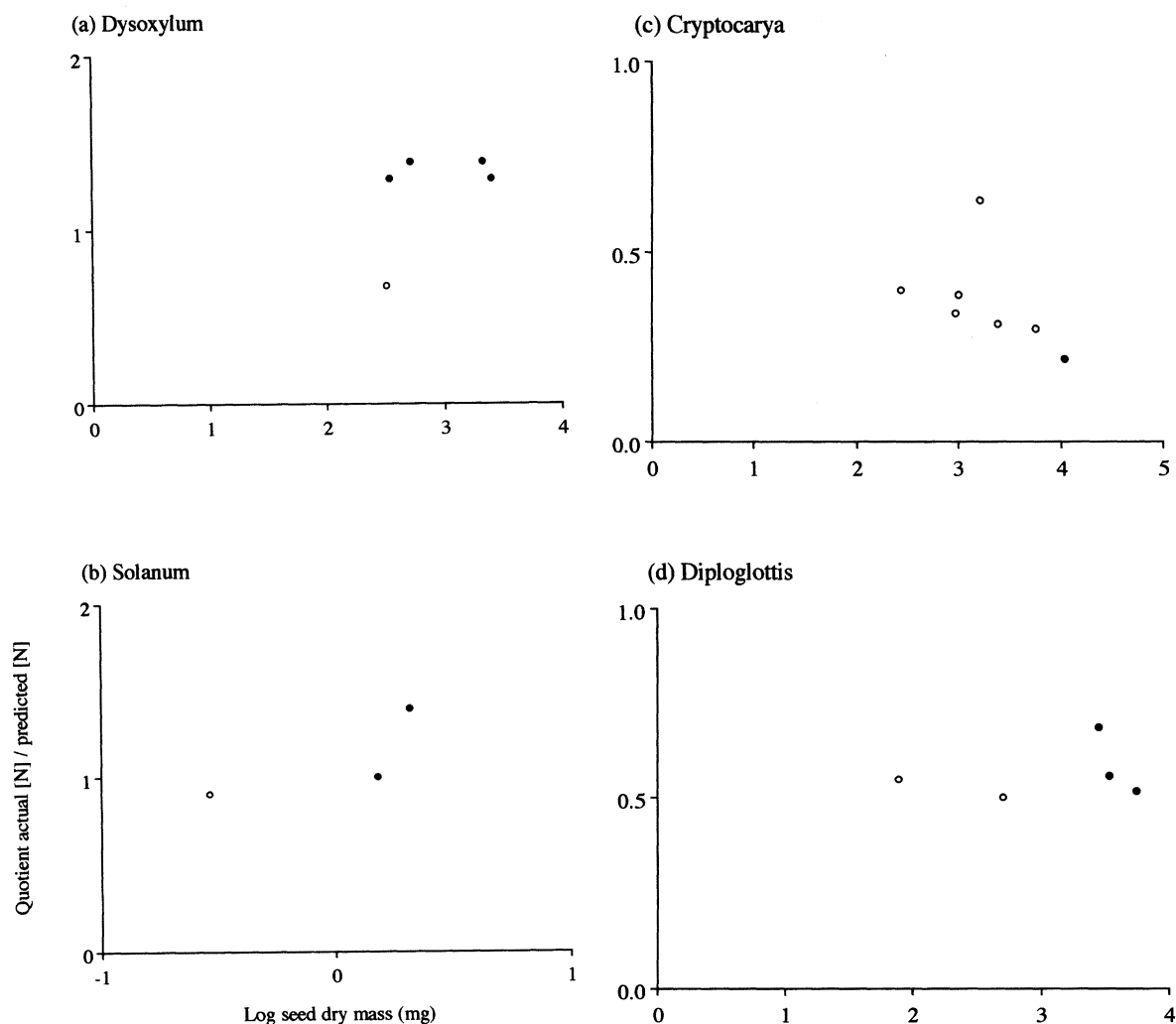


Fig. 6. The concentration of N in the seeds of species with protection by the fruit (filled circles) and without (open circles) in intrageneric contrasts. The regression line is the line derived for the whole collection of seeds; within each fruit type the taxa are listed in order of increasing mean seed dry mass. Only in the first two of the intrageneric contrasts do the species with protected seeds have higher values for [N], relative to those predicted from their mass, than the unprotected. (a) *Dysoxylum*: *D. sp. aff. klanderi*, *D. latifolium*, *D. parasiticum* and *D. pettigrewianum* which have capsules with leathery walls vs *D. papuanum* which has a thin-walled capsule. (b) *Solanum*: *S. dallachii* and *S. viridifolium* which have berries with poisonous flesh vs *S. aviculare* which has an edible berry. (c) *Cryptocarya*: *C. pleurosperma* which has toxic fruit vs six species with unprotected fruit. (d) *Diploglottis*: Three collections of *D. bracteata* which has a capsule with thick leathery walls vs *D. diphyllostegia* and *D. smithii* which have capsules with thin walls.

tion in the Apocynaceae, Bignoniaceae, Proteaceae, and Rutaceae-Flindersioideae, or the seeds which fall from their capsules to the ground and do not have thick walls able to be penetrated only by specialist predators, as in the *Lethedon*-type of Thymelaeaceae, many legumes, Meliaceae, Sapindaceae and *Brachychiton*-type of Sterculiaceae. Thus we look for an advantage at the stage of establishment.

The first point to make in this connection is that there is no correlation between [N] of the EE fraction and that of the leaves of saplings. Some of the species with high [N] in the EE fraction maintain high [N] in their tissues throughout their lives, while in others there is a marked change in status from being rich in N at the

seed stage to being poor in N at the sapling stage. We have established this point by determining the [N] values in healthy mature leaves of shade-grown saplings of 44 species of tree and shrub which are shade-tolerant at the stage of establishment, plus leaves of light-grown saplings of 5 species that are light-demanding at the stage of establishment (needing > 4% diffuse site factor; cf. Grubb and Metcalfe 1996). They were all sampled in an area of ca 1 km² of primary forest on basalt-derived soil near Mt Bartle Frere (complex mesophyll vine forest – type 1b sensu Tracey (1982); rainfall ca 3.5 m yr⁻¹; 820 m a.s.l.; 145°43'E, 17°23'S). The mean [N] was 23 mg g⁻¹ (± 1.6), which is in the middle of the range (21–25 mg g⁻¹) reported for tropical lowland

rainforests on relatively rich soils reported by Vitousek and Sanford (1986). The various species listed below all had high [N] in the seeds.

We consider a species to have a 'high' foliar [N] if that is above the mean plus 2 SE for our reference collection, and 'low' if it is below the mean minus 2 SE. By these criteria *Elattostachys megalantha* (26 mg g⁻¹), *Rhaphidophora australasica* (26), *Acacia aulacocarpa* (28), *Doryphora aromatica* (28), *Wikstroemia indica* (28), *Daphnandra repandula* (32), *Pisonia umbellifera* (32), *Bowenia spectabilis* (33), *Aleurites moluccana* (43) and *Solanum dallachii* (55) are high, and *Cardwellia sublimis* (9), *Flindersia bourjotiana* (10), *Idiospermum australiense* (10), *Ostrearia australiana* (12), *Pandanus monticola* (12), *Darlingia ferruginea* (13), *Alstonia scholaris* (16) and *Brachychiton acerifolius* (17) are actually notably low. Those not especially high or low are *Opisthiolepis heterophylla* (19 mg g⁻¹) and *Phaleria clerodendron* (21 mg g⁻¹). There is also evidence that *Dysoxylum* has [N] values higher than most of the species coexisting with it: in New Guinea (Grubb and Edwards 1982), and in New Zealand (Grubb unpubl.).

Particular interest attaches to the species which have a high [N] in the seed but not in the leaves. For some of them a specific advantage can be suggested. The provision of a substantial initial capital for setting up specialized root systems that are expensive in N (and P?) to establish, as in the nitrogen-fixing nodules of the Leguminosae and coralloid roots of the Zamiaceae. There is convincing evidence of the need for 'starter nitrogen' for legumes (Sprent and Thomas 1984). We suggest here the same explanation for the Proteaceae, because there is similar evidence that proteoid roots form more readily where there is a modest capital of available N and P than on a totally impoverished substratum (Lamont 1972). It is particularly striking that the foliar concentrations of N and P in seedlings

and saplings of the Proteaceae in our study area are decidedly low relative to most coexisting plants (see above). It seems most likely that the seed N and P move mainly into the roots (or perhaps the stems).

The literature on the significance of large seeds coupled with high concentrations of N and P in the dominant Proteaceae of many heath communities in Australia and South Africa has not taken into account the existence of notably high N and P concentrations in contemporary rainforest Proteaceae. It is widely accepted that the heathland Proteaceae are derived from rainforest types (Beadle 1966, Hill and Christophel 1988) and it is tempting to suggest that the possession of high N and P values in the embryo evolved in rainforest taxa, and constituted a pre-adaptation to life in fire-prone communities on extremely poor soils. The suggestion by Pate et al. (1986) that among the Proteaceae taxa becoming established in forest shade have high concentrations of lipid while taxa becoming established in high light on extremely poor soils have high concentrations of N and P is clearly not correct, even though there certainly are shade-tolerant Proteaceae with oil-rich seeds of the type referred to (*Macadamia*, *Triunia*, *Turillia*, and perhaps *Helicia*).

For the taxa without specialized root systems the only suggestion we can make is that having seeds rich in N, the nutrient known to limit growth of seedlings in root-filled soil in forest on at least the older basalt-derived type of soil in our study area (PJ and EAA Grubb unpubl.), is that it may reduce the effect of root competition. Parrish and Bazzaz (1985) showed that among seedlings of the old-field annual *Abutilon theophrasti* derived from seeds of a given range of dry mass, those with higher [N] values were more competitive when grown on a N-poor substratum. We need new experiments of this type with seedlings of rainforest trees.

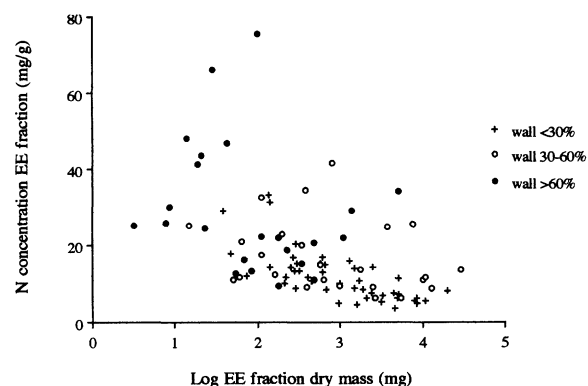


Fig. 7. The concentration of N in the embryo-cum-endosperm (EE) fraction of species in which the fruit does not provide marked protection, but in which there is a differing degree of defence in the 'seed'. Species with > 60% dry mass in the wall fraction have significantly greater N concentrations than species in the other two classes ($P < 0.001$).

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