Latitude, seed predation and seed mass

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Abstract

Aim We set out to test the hypothesis that rates of pre- and post-dispersal seed predation would be higher towards the tropics, across a broad range of species from around the world. We also aimed to quantify the slope and predictive power of the relationship between seed mass and latitude both within and across species.

Methods Seed mass, pre-dispersal seed predation and post-dispersal seed removal data were compiled from the literature. Wherever possible, these data were combined with information regarding the latitude at which the data were collected. Analyses were performed using both cross-species and phylogenetic regressions.

Results Contrary to expectations, we found no significant relationship between seed predation and latitude ($\log_{10}$ proportion of seeds surviving predispersal seed predation vs. latitude, $P = 0.63$; $R^2 = 0.02$; $n = 122$ species: $\log_{10}$ proportion of seeds remaining after postdispersal seed removal vs. latitude, $P = 0.54$; $R^2 = 0.02$; $n = 205$ species). These relationships remained non-significant after variation because of seed mass was accounted for. We also found a very substantial ($R^2 = 0.21$) relationship between seed mass and latitude across 2706 species, with seed mass being significantly higher towards the tropics. Within-species seed mass decline with latitude was significant, but only about two-sevenths, as rapid as the cross-species decline with latitude. Results of phylogenetic analyses were very similar to cross-species analyses. We also demonstrated a positive relationship between seed mass and development time across ten species from dry sclerophyll woodland in Sydney ($P < 0.001$; $R^2 = 0.77$; Standardized Major Axis slope $= 0.14$). These data lend support to the hypothesis that growing period might affect the maximum attainable seed mass in a given environment.

Main conclusions There was no evidence that seed predation is higher towards the tropics. The strong relationship between seed mass and latitude shown here had been observed in previous studies, but had not previously been quantified at a global scale. There was a tenfold reduction in mean seed mass for every *c.* 23° moved towards the poles, despite a wide range of seed mass within each latitude.

Keywords
predispersal seed predation, postdispersal seed predation, seed size, seed development time.

INTRODUCTION

Because temperatures are higher or more continuously favourable towards the tropics, it has been widely expected that herbivory and predation might be more sustained threats there. Considerable evidence supports this. For example, collation of data from seventeen studies showed significantly higher rates of herbivory towards the tropics (Coley & Aide, 1991), as did a meta-analysis of the

relationship between winter browsing intensity and latitude across six species of woody plants (Swihart & Bryant, 2001). Similarly, rates of predation on crabs (Dudley & Vermeij, 1978; Heck & Wilson, 1987), marine gastropods (Dudley & Vermeij, 1978), wasps (Jeanne, 1979) and across seventy-eight species of herbivorous insects (Hawkins *et al.*, 1997) have been shown to be higher towards the tropics.

Herbivore species diversity, as well as herbivore density and activity, might contribute to greater herbivore pressure experienced by plants towards the tropics. Indeed, there is evidence that many important guilds of herbivores are more diverse towards the tropics, including hemipterans

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(N. Andrew, unpubl. data), Papilionid butterflies (Sime & Brower, 1998), and small mammals (Hansson, 1992). However, evidence regarding patterns in herbivore density with latitude is sparse and inconsistent. One study showed hemipterans to be more abundant closer to the equator, but found no particular relationship between the abundance of Coleoptera and latitude (N. Andrew, unpubl. data). There was no relationship between latitude and the abundance of small mammals trapped over a 5-year period in Sweden (Hansson, 1992).

The relationship between latitude and seed predation

Both the generality of the above mechanism, and the wide range of taxa displaying latitudinal gradients in predation or herbivory, suggest that levels of seed predation might be higher towards the tropics. However, the only paper we are aware of that investigates this relationship is by Garcia *et al.* (2000), who found no correlation between predispersal seed predation and latitude across thirty-one populations of *Juniperus communis* at latitudes from 37°06′ N to 68°13′ N. The paucity of information on the relationship between seed predation and latitude is troubling, as pre- and post-dispersal seed predation are known to be important selective filters. It is not uncommon for plants to lose 90–100% of a given seed crop to seed predators (Louda, 1989; Crawley, 1992; Hulme, 1998), and these losses can result in significantly reduced seedling establishment (Brown *et al.*, 1979; Inouye *et al.*, 1980; De Steven & Putz, 1984; Hobbs, 1985; Louda, 1989; Heske *et al.*, 1993; Asquith *et al.*, 1997; Cornett *et al.*, 1998; Feller & Klinka, 1998).

In this paper we compile the available evidence to assess whether pre- and post-dispersal seed predation are greater towards the tropics.

The relationship between latitude and seed size

There are usually around six orders of magnitude of variation in seed mass within a given habitat (Leishman *et al.*, 2000). In addition to this huge range of variation in seed mass within habitats, there are also significant differences in seed mass between different habitats. One variable that seems to be associated with shifts in seed mass between different habitats is latitude. The relationship between seed mass and latitude has been investigated at various taxonomic levels. Within species, most studies have shown either significantly larger seeds towards the tropics (thirty-six species), or non-significant relationships between seed mass and latitude (forty-one species), with only two species showing significantly larger seeds towards the poles (Table 1). Within genera, Crouch & Vander Kloet (1980) have shown a trend for larger seeds towards the tropics across eight species of *Vaccinium* section *Cyanococcus* (blueberries), and B.R. Murray, A.D.H. Brown, J.P. Grace (unpubl. data) showed a similar trend for larger seeds towards the tropics across all thirty-eight Australian taxa in the genus *Glycine*. Levin (1974) showed that seeds of species from the temperate zone were significantly smaller than those from subtropical

regions, which were smaller than seeds from the tropics; this was across 802 species of herbs, 204 species of shrubs and 280 species of trees. Suggestive trends in the same direction were also found for sixty-two species of vines and eighty-eight species of shrubby trees in the Fabaceae (Levin, 1974). Lord *et al.* (1997) also showed that mean seed mass was greater at a tropical site than at a subtropical than at a temperate site in Australia, both across all species in the communities, and within growth-forms, dispersal syndromes and families.

Although these previous studies have clearly indicated a relationship between seed mass and latitude, important details regarding the nature of this relationship at a broad scale remain unclear, including details of the amount of variation in seed size that is associated with changes in latitude, and the slope of the relationship at a global scale. Thus, the second main aim of the present study was to quantify the slope and predictive power of the relationship between seed size and latitude across a wide range of species from a diverse array of ecosystems from around the world. We also investigated whether the shifts in seed mass within species were similar in magnitude to the shifts in seed mass observed among species.

Relationships between seed mass, seed predation and latitude

The relationships between seed mass and rates of pre and postdispersal seed predation are described in a separate paper (A.T. Moles and M. Westoby, unpubl. data). The major findings of that work were (1) no particular relationship between seed mass and rates of predispersal seed removal and (2) a weak negative relationship between postdispersal seed removal and diaspore mass. In the present paper, we investigated the hypothesis that the slight negative relationship between seed predation and seed mass might be interacting with the positive relationship between seed mass and latitude to cancel out or weaken relationships between seed predation and latitude.

Seed development time

Several mechanisms might contribute to the relationship between seed mass and latitude, including greater habitat shadiness in the tropics, a greater prevalence of vertebrate dispersal agents in the tropics and a higher proportion of plants of larger growth forms (e.g. trees) towards the equator (reviewed in Lord *et al.*, 1997). Another hypothesis suggests that the shorter growing seasons experienced by plants nearer the poles might constrain the maximum size of seeds that can be produced at a given latitude (Stebbins, 1974). This mechanism could only contribute to the relationship between seed mass and latitude if larger seeds did take longer to complete their development than small seeds. Although this seems plausible, we are not aware of any previous study of the relationship between seed mass and development time. For this reason, we gathered data to assess the slope and predictive power of the relationship

Table 1 Studies of the relationship between intraspecific variation in seed size and latitude. In these cases, the proportion of the species' range sampled is recorded in brackets. Seed mass A is the mean seed mass of the population closest to the equator; seed mass B is the mean seed mass of the population closest to the pole. For species marked with an asterisk, the latitudinal range presented represents the range of the species rather than the range of the study.

Species	Family	Latitudinal range of study	Seed mass A (mg)	Seed mass B (mg)	Location	Reference
Significant negative relationship (P < 0.05)						
Arabidopsis thaliana	Brassicaceae	16°N to 63°N	0.03	0.018	Europe	Li et al. (1998)
Glycine argyrea	Fabaceae	25°54' S to 30°55' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. canescens	Fabaceae	18°42' S to 43°04' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. clandestina	Fabaceae	20°10' S to 42°09' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. cyrtoloba	Fabaceae	17°03' S to 30°40' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. latrobeana	Fabaceae	34°42' S to 42°26' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. sp. aff. latifolia B	Fabaceae	20°16' S to 30°05' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tomentella group D5A	Fabaceae	14°06' S to 25°10' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tomentella group T1	Fabaceae	15°28' S to 31°46' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
Lens culinaris ssp. orientalis	Fabaceae	30°19' N to 40°59' N	–	–	Middle East	Fergusson & Robertson (1999)
Pinus contorta ssp. latifolia	Pinaceae	44°32' N to 63°16' N	5.3	2.4	North America	Birot (1978)
P. contorta ssp. contorta	Pinaceae	39°04' N to 59°30' N	5.6	3.8	North America	Birot (1978)
P. contorta ssp. murrayana	Pinaceae	34°10' N to 45°25' N	8.24	4.65	North America	Birot (1978)
P. halapensis	Pinaceae	31°07' N to 35°14' N	28.42	22.33	Morocco	Boulli et al. (2001)
P. sylvestris	Pinaceae	40°00' N to 60°15' N	9.0	5.1	Europe	Reich et al. (1994)
Pseudotsuga menziesii	Pinaceae	31°54' N to 53°37' N	16.73	8.75	North America	Birot (1972)
Quercus alba	Fagaceae	30°N to 45°N	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. bicolor*	Fagaceae	35°N to 45°N (75)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. coccinea	Fagaceae	32°N to 44°N	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. ellipsoidalis*	Fagaceae	40°N to 48°N (60)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. falcata*	Fagaceae	29°N to 40°N (91)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. incana*	Fagaceae	27°N to 36°N (94)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. laevis*	Fagaceae	27°N to 37°N (98)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. laurifolia*	Fagaceae	26°N to 37°N (86)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. macrocarpa*	Fagaceae	28°N to 51°N (83)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. michauxii*	Fagaceae	30°N to 41°N (93)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. palustris*	Fagaceae	35°N to 43°N (88)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. prinoides*	Fagaceae	32°N to 44°N (96)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. prinus	Fagaceae	31°N to 44°N	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. rubra*	Fagaceae	31°N to 48°N (87)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. stellata*	Fagaceae	28°N to 41°N (96)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. velutina*	Fagaceae	30°N to 48°N (75)	–	–	Eastern North America	Aizen & Woodcock (1992)
Rubus chamaemorus	Rosaceae	60°30' N to 69°30' N	9.31	6.48	Finland	Johansson et al. (1997)
Schoenus nigricans	Cyperaceae	39°48' N to 58°34' N	0.39	0.2	Europe	Ernst & Piccoli (1995)
Tsuga mertensiana	Pinaceae	48°33' N to 56°18' N	2.2	2.0	North America	Edwards & El-Kassaby (1996)
Vaccinium corymbosum	Ericaceae	27°N to 44°N	0.47	0.33	North America	Crouch & Vander Kloet (1980)
Significant positive relationship (P > 0.05)						
Amaranthus retroflexus	Amaranthaceae	35°N to 52°N	0.3	0.455	North America and Europe	McWilliams et al. (1968)
Glycine tomentella group T2	Fabaceae	17°00' S to 23°05' S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)

Table 1 *continued*

No significant relationship (*P* > 0.05)

Species	Family	Latitudinal range of study	Seed mass A (mg)	Seed mass B (mg)	Location	Reference
Dendromecon rigida	Papaveraceae	32°44′ N to 40°41′ N	14.3	11.2	California	Bullock (1989)
Empetrum nigrum	Ericaceae	60°30′ N to 69°30′ N	1.26	0.88	Finland	Johansson et al. (1997)
Glycine falcata	Fabaceae	19°20′ S to 28°07′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. latifolia	Fabaceae	22°50′ S to 31°02′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. microphylla	Fabaceae	17°13′ S to 42°02′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. rubiginosa	Fabaceae	30°08′ S to 35°08′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. sp. aff. latifolia A	Fabaceae	24°40′ S to 34°08′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. stenophita	Fabaceae	20°10′ S to 33°20′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tabacina (nonstoloniferous)	Fabaceae	11°42′ S to 33°34′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tabacina (stoloniferous)	Fabaceae	13°14′ S to 37°59′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tomentella group D1	Fabaceae	23°33′ S to 28°51′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tomentella group D3	Fabaceae	10°42′ S to 20°37′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tomentella group D4	Fabaceae	18°02′ S to 23°39′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tomentella group D5B	Fabaceae	14°49′ S to 17°58′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tomentella group T3	Fabaceae	12°41′ S to 17°20′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
G. tomentella group T4	Fabaceae	11°39′ S to 19°03′ S	–	–	Australia	B.R. Murray, A.D.H. Brown and J.P. Grace (unpubl. data)
Nothofagus truncata	Fagaceae	38°00′ S to 42°23′ S	7.9	7.6	New Zealand	Ledgard & Cath (1983)
N. fusca	Fagaceae	37°32′ S to 45°33′ S	6.3	6.3	New Zealand	Ledgard & Cath (1983)
N. menziesii	Fagaceae	38°01′ S to 46°26′ S	3.0	3.5	New Zealand	Ledgard & Cath (1983)
N. solandri var solandri	Fagaceae	38°50′ S to 43°16′ S	3.5	4.8	New Zealand	Ledgard & Cath (1983)
N. solandri var cliffortioides	Fagaceae	39°10′ S to 46°05′ S	3.4	3.5	New Zealand	Ledgard & Cath (1983)
Podocarpus falcatus	Podocarpaceae	24°02′ S to 34°00′ S	1322	344	South Africa	Geldenhuys & Von Dem Bussche (1997)
Prunella vulgaris	Lamiaceae	45°25′ N to 32°08′ N	0.48	0.53	Eastern United States	Winn & Gross (1993)
Quercus austrina*	Fagaceae	29°N to 35°N (83)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. chapmanii*	Fagaceae	26°N to 34°N (50)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. durandii*	Fagaceae	28°N to 35°N (68)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. georgiana*	Fagaceae	33°N to 35°N (75)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. ilicifolia*	Fagaceae	36°N to 44°N (63)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. imbricaria*	Fagaceae	31°N to 44°N (77)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. lyrata*	Fagaceae	30°N to 40°N (80)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. marilandica	Fagaceae	30°N to 41°N	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. muehlenbergii*	Fagaceae	30°N to 44°N (96)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. myrtifolia*	Fagaceae	26°N to 33°N (86)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. nigra	Fagaceae	28°N to 39°N	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. pagodaefolia*	Fagaceae	29°N to 38°N (95)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. phellos*	Fagaceae	32°N to 45°N (65)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. pumila	Fagaceae	28°N to 35°N	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. shumardii*	Fagaceae	28°N to 42°N (80)	–	–	Eastern North America	Aizen & Woodcock (1992)
Q. virginiana*	Fagaceae	25°N to 37°N (83)	–	–	Eastern North America	Aizen & Woodcock (1992)
Sarracenia purpurea	Sarraceniaceae	39°42′ N to 46°36′ N	–	–	Eastern United States	Ellison (2001)

between seed mass and development time, across ten species from Ku-ring-gai Chase National Park in Sydney.

In summary, the questions addressed in this paper are:

1. Is there a relationship between predispersal seed predation and latitude?
2. Is there a relationship between postdispersal seed predation and latitude?
3. What is the magnitude of the cross-species relationship between seed size and latitude?
4. What is the nature of the interaction between seed mass, seed predation and latitude?
5. Is the relationship between seed mass and latitude within species similar in magnitude to the relationship across species?
6. Do large seeds take longer to complete development than small seeds?

METHODS

Pre-dispersal seed predation and post-dispersal seed removal

We compiled results from all the papers cited in reviews by Crawley (1992) and S. Cunningham (unpubl. data). These sources provided a relatively complete search of the pre- and postdispersal seed predation literature up to 1992 (Crawley) and 1994 (Cunningham). We also searched Current Contents (1993–2000), for articles in English containing the words 'seed' and 'predation' in the title or abstract. Papers were excluded if they did not quantify seed predation or removal, were from highly artificial situations such as laboratories or plantations, or were about introduced species. However, studies of predation on the seeds of weeds of arable land were included, as it was considered that the short-lived species resident in these communities might have had sufficient time to adapt to their new environment. In short, we aimed to include only those species that had evolved in, or adapted to the study environment. This gave postdispersal seed removal data for 205 species and predispersal seed predation data for 138 species.

For each species in each study, seed predation rates were averaged over all sites, times and densities in order to produce one mean predation rate. Averaging was weighted according to the number of seeds in each category where this information was available. Where a species occurred in more than one study an average seed mass and predation rate were calculated. As seed fate has rarely been measured in studies of postdispersal seed 'predation', we have been forced to review rates of postdispersal seed removal rather than rates of postdispersal seed predation *per se*. Implications of this limitation are fully discussed in A.T. Moles and M. Westoby (unpubl. data).

Pre-dispersal seed predation data quantify the proportion of seeds destroyed between seed initiation and seed dispersal. Post-dispersal seed removal rates are given for 24-h periods. Results from studies that quantified removal over longer time periods were converted to 24-h basis assuming exponential removal (equation 1).

Proportion of seeds removed in 1 day

$$= 1 - [\text{Proportion of seeds remaining after n days}^{(1/n)}]$$

This conversion assumes that proportion of seeds removed per 24 h was independent of the duration of study. This was the simplest assumption we could make, and the only one possible with much of the data. Exponential decline has commonly been observed (Boman & Casper, 1995; Hammond & Brown, 1995; Holl & Lulow, 1997; Kollmann et al., 1998; Hulme & Hunt, 1999). Studies over more than 60 days were excluded.

Seed mass

The relationship between latitude and seed mass was investigated, first, for species included in the seed predation studies, and secondly across a broad range of species from the literature. For species included in the predation paper, seed mass data were gathered from the same sources as the predation data wherever possible, or from other published sources (details in A.T. Moles and M. Westoby, unpubl. data). For seed mass in relation to latitude, we were able to gather a larger data set including 2706 species from 193 families (Appendix 1). While probably not a comprehensive collection of all data that might be available, this does represent a significant advance on the number of species previously considered for the relationship between latitude and seed mass.

Latitude

Latitude data were taken from the site descriptions in the source papers wherever possible. Where necessary, latitudes from nearby locations were used in place of exact readings for the field sites. Where more than one site was used for a species, an average latitude was calculated for each species, unless the range of latitudes used was >5°, in which case the species were excluded from this compilation.

Relationships between seed mass and latitude within species

In order to assess whether the magnitude of the intraspecific relationship between seed mass and latitude was similar to that observed at the interspecific level, we compiled available data regarding the mean seed mass of the populations at highest and lowest latitudes for each species, and compared the within-species change in mean seed mass per degree of latitude to the slope of the between-species relationship.

Seed development

In order to investigate the hypothesis that large seeds take longer to complete development than small seeds, we carried out a small study in Ku-ring-gai Chase National Park, a temperate coastal environment near Sydney that supports fire-prone forest and heath. Three senescing flowers on each of five individuals of ten species were tagged in June and July

2000. The ten species used were the only species found at two sites in Ku-ring-gai Chase that had a large enough number of senescing flowers at this time. Tagged plants were monitored at least once a week until the seeds had completed development. Seed development was considered to have begun when the flower showed visible signs of senescence. Seed development was considered complete when the seed or fruit exterior became hard and assumed the coloration associated with ripeness in that species. The date of completion of development was estimated as half way between the last date the seed/fruit was seen in an unripe state and the first date the seed/fruit was seen in a ripe state. Where plants produced fruit or inflorescences with multiple closely packed seeds with significantly different ripening times we calculated development as beginning when the first flower showed signs of senescence and finishing when the first seed reached maturity. For these species, seed mass was determined by weighing twenty seeds on a Cahn microbalance after they had been oven-dried at 60 °C for at least 3 days.

Statistics

Seed mass, the proportion of seeds surviving predispersal seed predation and the proportion of diaspores remaining after 24 h of exposure to postdispersal seed predators were $\log_{10}$-transformed before all calculations. In the two cases in which all seeds were removed within 24 h, we added 0.01 to the proportion of seeds remaining before performing the log transformation. The relationships between latitude and predispersal seed predation, postdispersal seed removal and seed mass were analysed across species using standard linear regressions (Sokal & Rohlf, 1995). Phylogenetic regressions (Grafen, 1989) were performed on the relationships between latitude and $\log_{10}$ seed mass and $\log_{10}$ seed predation rates. The phylogenetic tree used follows APG (1998) to order level, with updates from Kuzoff & Gasser (2000) on the position of basal angiosperm groups. Within families, we followed Douglas (1995) for Proteaceae, Crisp & Doyle (1995) for Fabaceae, Simon (1993) for Poaceae and Wilson (1984) for Chenopodiaceae. We performed phylogenetic regressions using a generalized linear interactive modelling program (Phylo.glm version 1.03; Grafen, 1989). Path segment lengths for the phylogenetic trees were calculated by assigning a height to each node that was one less than the number of species below or at that node in the tree (Grafen, 1989).

RESULTS

Predispersal seed predation and latitude

The proportion of seeds surviving predispersal seed predation ranged from 2 to 98.5% across the 122 species included in this study. Contrary to our expectations, there was no significant relationship between latitude and the proportion of individuals surviving predispersal seed predation (cross-species regression, $P = 0.63$; $R^2 = 0.02$; phylogenetic regression, $P = 0.60$; $R^2 = 0.006$; Fig. 1).

Postdispersal seed removal and latitude

The proportion of diaspores remaining after 24 h of exposure to postdispersal seed predators ranged from 0 to 100% across 205 species. There was no significant relationship between latitude and the proportion of diaspores remaining after 24 h (cross-species regression $P = 0.54$; $R^2 = 0.02$; phylogenetic regression $P = 0.57$; $R^2 = 0.003$; Fig. 2).

Relationships between seed mass and latitude across species

Seed mass ranged from 0.01 mg (*Hypericum gramineum*; Hypericaceae, from Australia) up to 816,000 mg (*Bertholletia excelsa*; Lecythidaceae, from Brazil) across the 309
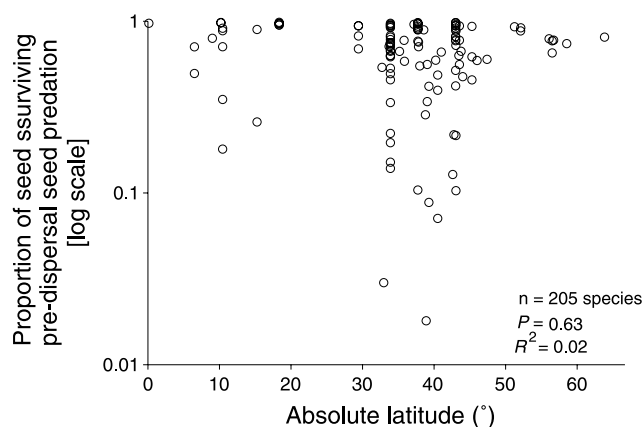

Figure 1 The relationship between the proportion of individuals surviving predispersal seed predation and latitude. Latitude is expressed as an absolute number of degrees away from the equator. Each point represents the mean value for one species.
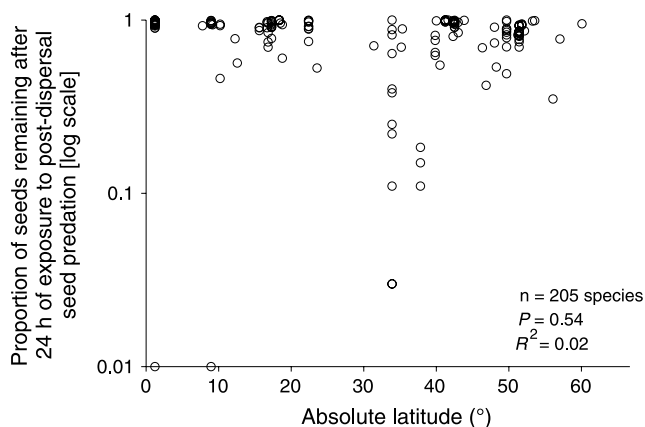

Figure 2 The relationship between latitude and the proportion of diaspores remaining after 24 h of exposure to postdispersal seed predators. Latitude is expressed as an absolute number of degrees away from the equator. Each point represents the mean value for one species.
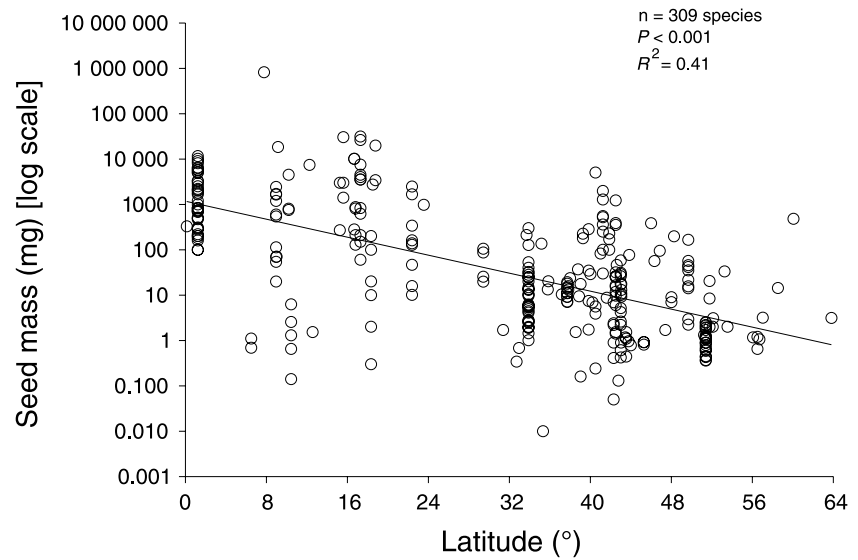
Figure 3 The relationship between seed mass and latitude for species for which seed predation data were available. Latitude is expressed as an absolute number of degrees away from the equator. Each point represents the mean value for one species.

species included in seed predation studies, and from 0.0007 mg (two species in the Orchidaceae from Australia) to 816,000 mg (*Bertholletia excelsa*) across the broader 2706 species data set. Seeds were significantly larger towards the tropics in both the cross-species regression ($P < 0.001$; $R^2 = 0.41$; Fig. 3), and the phylogenetic regression ($P < 0.001$; $R^2 = 0.43$) across the species included in the seed predation studies. Similarly, seeds were significantly larger towards the tropics across the full 2706 species ($P < 0.001$; $R^2 = 0.21$; Fig. 4). Although there was a wide range of seed mass at any given latitude, the trend with latitude was highly significant. Slope was −0.85 (95% CIs: −0.79 to −0.91) log units per 20° latitude, that is a sevenfold reduction in mean seed mass for every 20° moved towards the poles, a 1000-fold reduction across 70.5° of latitude.

Both the upper and lower limits of the seed mass range seemed to decrease towards the poles (Fig. 4), and there was no significant relationship between the variance in seed mass and latitude (all sites represented by at least eight species included in analysis; $P = 0.23$, $R^2 = 0.046$; $n = 33$). Thus, it appears that the change in seed mass with increasing latitude is caused by a simple downward shift in the lognormal distribution of seed mass. However, sampling biases might have affected this result – particularly at the smaller end of the seed mass spectrum. For instance, although few very small-seeded species were included in the tropical data sets, many small-seeded taxa (e.g. Orchidaceae) are present in tropical ecosystems. Similar bias might also be present in the data from seed predation studies, as seed predation may be easier to study in large-seeded species.
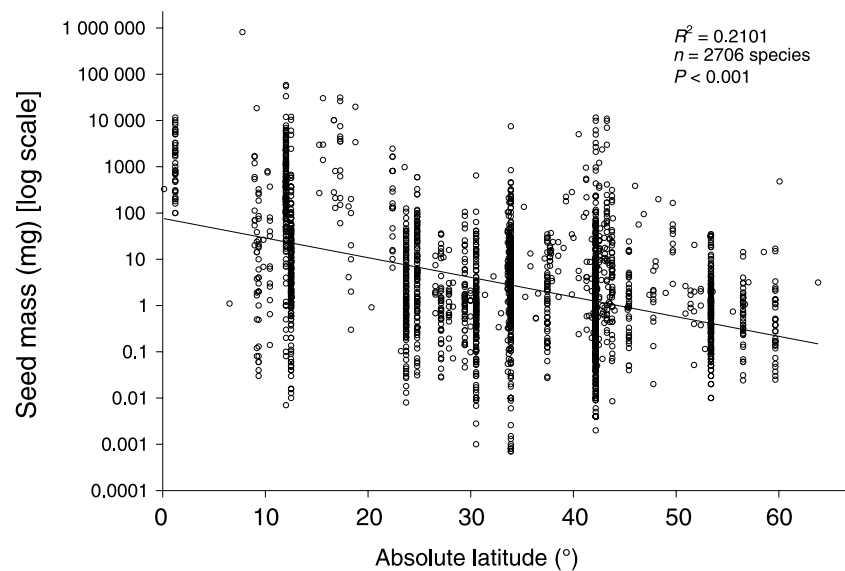

Figure 4 The relationship between seed mass and latitude across the global database. Latitude is expressed as an absolute number of degrees away from the equator. Each point represents the mean value for one species.
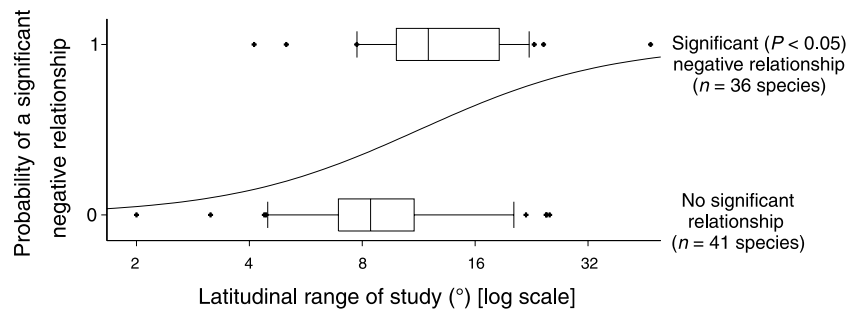
Figure 5 The relationship between the latitudinal range encompassed by intraspecific studies of the relationship between seed mass and latitude, and the probability of finding a significant negative relationship. Box plots show the distribution of latitudinal ranges for studies showing significant vs. nonsignificant relationships. The boxes encompass the 25th percentile to the 75th percentile. The line inside the box represents the median. Whiskers indicate the 10th and 90th percentiles. Outliers are shown as dots. The curve was fitted using logistic regression ($P < 0.001$), and shows the probability of a study with a given latitudinal range finding a significant negative relationship between seed mass and latitude.

Interactions between seed mass, latitude and seed predation

The relationship between latitude and seed mass was still significant after controlling for variation in either predispersal seed predation ($P = 0.007$), or post-dispersal seed removal ($P < 0.001$). The proportion of individuals surviving predispersal seed predation, and the proportion of individuals remaining after 24 h of exposure to postdispersal seed predators, remained unrelated to latitude after variation in seed mass was accounted for ($P = 0.586$ and 0.189, respectively).

Phylogenetic considerations

The results of the phylogenetic regressions and the cross-species regressions were very similar. Conceivably, there might have been positive relationships between seed mass, seed predation and latitude within genera or families, that is across distal branch-points in the phylogenetic tree, and these might have been overridden in the cross-species regression by large differences in basic natural history between families or other major clades, producing an overall negative relationship. The fact that phylogenetic regressions were similar to cross-species regression eliminates this possibility from consideration.

Relationships between seed mass and latitude within species

Species with wider latitudinal range were more likely to show a significant decline in seed mass with latitude (logistic regression, $P < 0.001$; Fig. 5). Studies spanning less than *c.* 11° latitude had less than a 50% chance of finding a significant negative relationship. There was no significant difference in the mean slope between species showing significantly larger seeds towards the tropics, and those showing no significant relationship ($P = 0.99$). Evidently the major reason for the lack of a significant intraspecific relationship between seed mass and latitude in some studies is that over a small latitudinal range, the shift in seed mass is
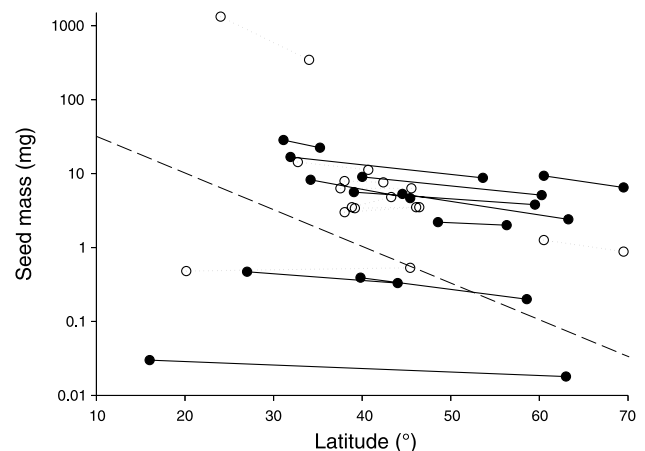
Figure 6 Intraspecific relationships between seed mass and latitude. Filled circles and solid lines represent species in which there was a significant relationship between seed mass and latitude; unfilled circles and dotted lines represent species with no significant relationship between seed mass and latitude. The two points shown for each species are the upper and lower latitudes encompassed within the study, and the mean seed mass of populations found at that latitude. Note that this information was not available for all species. Raw data are presented in Table 1. The dashed line represents the slope of the relationship between seed mass and latitude from the global cross-species relationship (Fig. 4).

small enough that it cannot be detected against the background of other sources of variation.

The mean decrease in seed mass within species was -0.29 log units, or *c.* 1.9-fold, per 20° of latitude. This was 3.6-fold less than the slope of the relationship across species (Fig. 6).

Seed development time

Seed development time was confirmed as positively correlated with seed mass across ten species from Ku-ring-gai Chase National Park (Fig. 7; $P < 0.001$, $R^2 = 0.77$; Appendix 2). The standardized major axis slope of this relationship was 0.14, that is, a tenfold increase in seed mass corresponded to

Figure 7 Median development time vs. seed mass for ten species from Ku-ring-gai Chase National Park in Sydney.

c. 40% increase in development time. These data lend support to the hypothesis that maximum attainable seed mass might be constrained by the length of the growing season in a given habitat (Stebbins, 1974).
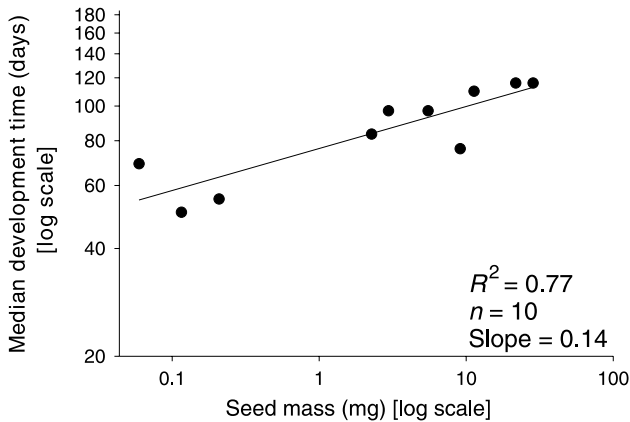
DISCUSSION

Why was seed predation not higher towards the tropics?

The lack of a relationship between seed size and latitude was contrary to expectations based on predator diversity and abundance (see Introduction). One possible explanation for the absence of this relationship is that there might have been selection for increased seed defences in areas near the equator where seeds were exposed to a higher risk of predation (perhaps as a result of greater diversity and abundance of seed predators at low latitudes). If increased defence reduced seed predation, the net outcome might be no particular relationship between seed predation and latitude.

If the mechanism described above were in operation, one might expect to see higher levels of seed defences towards the tropics. We are only aware of one study investigating this relationship: Crouch & Vander Kloet (1980) showed that seed coats were thicker at lower latitude across four species of *Vaccinium*. However, it is clear that many important leaf defences (including high concentrations of alkaloids, leaf toughness and high tannin concentration) are greater towards the tropics (reviewed in Coley & Aide, 1991). Similarly, tropical birds have been shown to have higher investment in immune system function than temperate birds (Møller, 1998). These observations are sufficiently consistent with our interpretation to suggest further investigation could be worthwhile.

A second explanation for the lack of a relationship between seed predation and latitude could be that increases in seed predator diversity and density towards the equator are no more than proportional to increases in seed produc-

tion and diversity. It is well known that plant diversity is particularly high in tropical forests. It might also be the case that the total production of seed is higher at lower latitudes, as net primary productivity is generally higher towards the equator (Bondeau *et al.*, 1999; Schloss *et al.*, 1999).

Implications of the lack of a relationship between seed predation and latitude

Janzen (1970) and Connell (1971) suggested that density-dependent mortality might increase plant diversity by reducing the probability of successful seedling establishment near conspecific adults. These authors also suggested that the greater climatic fluctuations in temperate ecosystems might reduce the efficacy of predators in maintaining this diversity. These ideas have been widely taken up, and today the Janzen–Connell hypothesis is one of the major explanations cited to explain the high levels of diversity in tropical forests (Wright, 2002). Our results are clearly of importance to this body of literature. As rates of seed predation are not higher in the tropics, it seems unlikely that the strength of the density-dependent mortality would be stronger in the tropics. If density-dependent mortality is just as strong at high latitudes as at low latitudes, the Janzen–Connell hypothesis does not predict higher diversity in the tropics than in the temperate zone. Clearly, investigations of the Janzen–Connell hypothesis that compare density-dependent mortality at tropical and temperate sites will be necessary to determine whether this mechanism can contribute to greater diversity in tropical regions.

Why is there a relationship between seed size and latitude?

Several hypotheses have previously been put forward to explain why there is a relationship between seed size and latitude, including (1) differences in the light availability in different habitats, (2) differences in the seed disperser assemblages, and (3) differences in the predominance of plant growth forms (reviewed in Lord *et al.*, 1997). The evidence to date shows that although these factors do influence seed mass, gradients in seed mass with latitude exist even after these variables are accounted for. For instance, Levin (1974) found an increase in mean seed mass from herbs to shrubs to shrubby trees to trees, but also a greater mean seed mass in tropical species than in temperate species within herbs (802 species), shrubs (204 species), vines (sixty-two species), shrubby trees (eighty-eight species) and trees (280 species). Similarly, Lord *et al.* (1997) found that tropical floras did have relatively higher proportions of woody and vertebrate-dispersed species, but also that seed mass decreased from the tropics to the subtropics to the temperate zone within ten of eleven growth-form dispersal-mode combinations. Thus, while growth form, disperser assemblage and habitat type may contribute to the observed relationship between seed mass and latitude, other mechanism(s) must also be operating. The following paragraphs outline two further factors that might be significant contributors.

Development time

It has been suggested that the length of the growth period of a habitat might constrain the upper bound of seed mass by constraining the amount of time available for seed provisioning (Baker, 1972; Stebbins, 1974). This mechanism could potentially disadvantage large seeds at higher latitudes, as there is some evidence that small seeds can complete development in a shorter time than large seeds (Fig. 7).

Total seed production

The smaller number of seeds produced by large-seeded species (Jakobsson & Eriksson, 2000; Henery & Westoby, 2001) is thought to be compensated for mainly during seedling establishment. Seedlings from large-seeded species have been shown to be stronger competitors than seedlings from small-seeded species (Leishman, 2001), and are better at tolerating a wide range of environmental stresses, such as prolonged periods in deep shade, herbivory and nutrient deprivation (reviewed in Leishman et al., 2000). Under theory about coexistence of seed size strategies (Geritz, 1995; Fagerstrom & Westoby, 1997), large-seeded species secure patches by outcompeting small-seeded species, while small-seeded species rely on establishing in sites that are not reached by the less abundant propagules of large-seeded species. This theory can combine with a latitudinal trend in net primary productivity (NPP) to offer a new hypothesis for the observed trend for larger seeds towards the tropics. The NPP is generally thought to be higher towards the tropics (Bondeau et al., 1999; Schloss et al., 1999). It seems reasonable to expect that higher NPP translates into higher biomass of seeds produced per unit area. If average seed size did not shift, then the total seedfall density would be greater at higher NPP latitudes. This would decrease the probability of a small seed reaching an otherwise unoccupied site. In this way, selection would favour larger seeds in high productivity environments such as the tropics. Note that a critical assumption in this theory – that of greater total reproductive output in vegetation towards the tropics – has not yet been tested.

In summary, many potential explanations for the greater size of seeds in the tropics have been offered, involving habitat type, plant growth form, seed disperser assemblage, the length of the growing period and NPP. These mechanisms are not mutually exclusive, and it is most likely that some combination of these factors generates the pattern observed in nature.

ACKNOWLEDGMENTS

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BIOSKETCHES

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Appendix I Table of raw data. Pre-remain data are the proportion of seeds surviving predispersal seed predation, and postremain data are the proportion of seeds remaining after 24 h of exposure to postdispersal seed predators. Latitude data are presented as degrees and minutes

Species	Family	Location	Seed mass (mg)	Pre remain	Post remain	Reference	Latitude	N/S
Taxus baccata	Taxaceae	England,Spain	56.3		0.691	Hulme (1996, 1997)	46 20	N
Juniperus virginiana	Cupressaceae	Virginia	10.4	0.959		Holthuijzen *et al.* (1987)	37 11	N
Podocarpus nubigena	Podocarpaceae	Chile	352.14		0.985	Diaz *et al.* (1999)	42 30	S
Prumnopitys ferruginea	Podocarpaceae	New Zealand	520		0.989	Moles & Drake (1999)	41 14	S
Prumnopitys taxifolia	Podocarpaceae	New Zealand	100	0.812	0.995	Sullivan *et al.* (1995), Moles & Drake (1999)	41 52	S
Gnetum cf. microcarpa	Gnetaceae	Indonesia	830		0.983	Blate *et al.* (1998)	1 13	S
Abies alba	Pinaceae	Germany	9		0.909	Schreiner *et al.* (2000)	48 0	N
Picea abies	Pinaceae	Germany	7		0.737	Schreiner *et al.* (2000)	48 0	N
Picea glauca	Pinaceae	Alberta	2		0.992	Radvanyi (1970)	53 33	N
Pinus flexilis	Pinaceae	Arizona	179.1	0.088		Benkman (1995)	39 16	N
Pinus strobiformis	Pinaceae	Arizona	225	0.418		Benkman (1995)	39 16	N
Thysanotus multiflorus	Liliaceae	Sydney	4.1		0.11	Rodgerson (1998)	33 53	S
Ripogonum scandens	Smilacaceae	New Zealand	250		0.996	Moles & Drake (1999)	41 14	S
Astrocaryum murumuru	Arecaceae	Peru	7400		0.78	Cintra (1997)	12 15	S
Chaemaedorea allenii	Arecaceae	Costa Rica	69.25		0.976	Holl & Lulow (1997)	8 57	N
Rhopalostylis sapida	Arecaceae	New Zealand	228.38	0.77	0.975	Sullivan *et al.* (1995), Moles & Drake (1999)	41 52	S
Alopecurus myosuroides	Poaceae	England	1.99	0.933	0.949	Povey *et al.* (1993)	51 46	N
Alopecurus pratensis	Poaceae	England	1.21	0.475	0.749	Hulme (1998)	51 24	N
Arrhenatherum elatius	Poaceae	UK	2.19	0.455	0.923	Edwards & Crawley (1999)	51 24	N
Avena fatua	Poaceae	England	20.37	0.62	0.929	Povey *et al.* (1993)	51 46	N
Bromus sterilis	Poaceae	England	8.4		0.941	Povey *et al.* (1993)	51 46	N
Chionochloa crassicula	Poaceae	New Zealand	0.96	0.668		Kelly *et al.* (1992, 2000)	43 46	S
Chionochloa flavescens	Poaceae	New Zealand	1.09	0.775		Kelly *et al.* (1992)	43 32	S
Chionochloa macra	Poaceae	New Zealand	1.53	0.559		Kelly *et al.* (1992)	43 32	S
Chionochloa oreophila	Poaceae	New Zealand	0.44	0.939		Kelly *et al.* (1992)	43 32	S
Chionochloa pallens	Poaceae	New Zealand	1.17	0.631		Kelly *et al.* (1992, 2000), Kelly & Sullivan (1997)	43 27	S
Chionochloa rigida	Poaceae	New Zealand	0.92		0.843	Kelly *et al.* (2000)	45 17	S
Chionochloa rubra	Poaceae	New Zealand	0.78		0.843	Kelly *et al.* (2000)	44 0	S
Chionochloa spiralis	Poaceae	New Zealand	0.81		0.843	Kelly *et al.* (2000)	45 17	S
Chionochloa teretifolia	Poaceae	New Zealand	0.91		0.927	Kelly *et al.* (2000)	45 17	S
Dactylis glomerata	Poaceae	England	1.08		0.814	Hulme (1998)	51 24	N
Festuca novae-zelandiae	Poaceae	New Zealand	0.9	0.723	0.843	Lord & Kelly (1999)	43 2	S
Festuca ovina	Poaceae	England	0.89		0.843	Hulme (1998)	51 24	N
Festuca pratensis	Poaceae	England	2.52		0.843	Hulme (1998)	51 24	N
Festuca rubra	Poaceae	UK	0.69		0.927	Edwards & Crawley (1999)	51 24	N
Festuca rubra commutata	Poaceae	England	0.89		0.814	Hulme (1998)	51 24	N
Festuca rubra litoralis	Poaceae	England	1.08		0.853	Hulme (1998)	51 24	N
Festuca rubra rubra	Poaceae	England	1.2		0.698	Hulme (1998)	51 24	N

Appendix 1 *continued*

Species	Family	Location	Seed mass	Pre	Post	Reference	Latitude	
Holcus lanatus	Poaceae	England	0.43		0.804	Hulme (1998)	51	24 N
Lolium pratense	Poaceae	England	2.11		0.843	Hulme (1998)	51	24 N
Oryza meridionalis	Poaceae	Queensland	1.53		0.565	Wurm (1998)	12	34 S
Phleum pratense	Poaceae	England	0.45		0.853	Hulme (1998)	51	24 N
Poa annua	Poaceae	England	0.36		0.862	Hulme (1998)	51	24 N
Poa pratensis	Poaceae	England	0.37		0.862	Hulme (1998)	51	24 N
Carex pilulifera	Cyperaceae	Denmark	1.17	0.79	0.35	Kjellsson (1985)	56	4 N
Heliconia tortuosa	Musaceae	Costa Rica	112.68		0.968	Holl & Lulow (1997)	8	57 N
Fissistigma sp.	Annonaceae	Indonesia	310		0.973	Blate *et al.* (1998)	1	13 S
Friesodelsia sp. 1	Annonaceae	Indonesia	160		0.944	Blate *et al.* (1998)	1	13 S
Friesodelsia sp. 2	Annonaceae	Indonesia	220		0.948	Blate *et al.* (1998)	1	13 S
Orophea sp.	Annonaceae	Indonesia	700		0.99	Blate *et al.* (1998)	1	13 S
Polyalthia sumatrana	Annonaceae	Indonesia	820		0.986	Blate *et al.* (1998)	1	13 S
Xylopia sp.	Annonaceae	Indonesia	740		0.975	Blate *et al.* (1998)	1	13 S
Gymnacranthera eugeniifolia	Myristicaceae	Indonesia	200		0.972	Blate *et al.* (1998)	1	13 S
Knema latericia	Myristicaceae	Indonesia	1670		0.992	Blate *et al.* (1998)	1	13 S
Beilschmiedia bancroftii	Lauraceae	Queensland	3520		0.909	Osunkoya (1994)	17	17 S
Beilschmiedia sp.	Lauraceae	Indonesia	5600		0.991	Blate *et al.* (1998)	1	13 S
Beilschmiedia tawa	Lauraceae	New Zealand	1280		0.987	Moles & Drake (1999)	41	14 S
Cryptocarya sp. 1	Lauraceae	Indonesia	2100		0.992	Blate *et al.* (1998)	1	13 S
Cryptocarya sp. 2	Lauraceae	Indonesia	5800		0.987	Blate *et al.* (1998)	1	13 S
Endiandra palmerstonii	Lauraceae	Queensland	31310		0.906	Osunkoya (1994)	17	17 S
Machilus breviflora	Lauraceae	Hong Kong	339		0.994	Hau (1997)	22	23 N
Ocotea endresiana	Lauraceae	Costa Rica	750		0.46	Wenny (2000)	10	12 N
Ocotea floribunda	Lauraceae	Costa Rica	1643.32		0.993	Holl &Lulow (1997)	8	57 N
Ocotea leucoxylon	Lauraceae	Costa Rica	100	0.97	0.999	Myster (1997)	18	20 N
Phoebe cinnamomifolia	Lauraceae	Costa Rica	597.46		0.955	Holl & Lulow (1997)	8	57 N
Hedycarya arborea	Monimiaceae	New Zealand	360			Moles & Drake (1999)	41	14 S
Laureliopsis philippiana	Monimiaceae	Chile	1.53		0.976	Diaz *et al.* (1999)	42	30 S
Drimys winteri	Winteraceae	Chile	5.99		0.906	Diaz *et al.* (1999)	42	30 S
Piper arieianum	Piperaceae	Costa Rica	1.3	0.71		Greig (1993)	10	26 N
Piper culebranum	Piperaceae	Costa Rica	0.65	0.88		Greig (1993)	10	26 N
Piper phytolaccaefolium	Piperaceae	Costa Rica	6.23	0.18		Greig (1993)	10	26 N
Piper sancti-felicis	Piperaceae	Costa Rica	0.14	0.91		Greig (1993)	10	26 N
Piper urostachyum	Piperaceae	Costa Rica	2.56	0.35		Greig (1993)	10	26 N
Aextoxicon punctatum	Aextoxicaceae	Chile	387.35		0.947	Diaz *et al.* (1999)	42	30 S
Berberis buxifolia	Berberidaceae	Chile	9.74		0.948	Diaz *et al.* (1999)	42	30 S
Berberis darwinii	Berberidaceae	Chile	11.74		0.971	Diaz *et al.* (1999)	42	30 S

Species	Family	Location	Seed mass			Reference			Hemisphere
Berberis hispanica	Berberidaceae	Spain	23.66	0.549		Herrera (1984)	38	0	N
Berberis vulgaris	Berberidaceae	Germany, England	14.09		0.89	Kollmann et al. (1998)	49	40	N
Jeffersonia diphylla	Berberidaceae	Indiana, West Virginia	36.84	0.285	0.15	Heithaus (1981), Smith et al. (1986)	38	47	N
Coscinium fenestratum	Menispermaceae	Indonesia	6500		0.992	Blate et al. (1998)	1	13	S
Sanguinaria canadensis	Papaveraceae	West Virginia	15.69	0.71	0.184	Heithaus (1981)	37	49	N
Trollius europaeus	Ranunculaceae	Sweden & France	1.06	0.776		Hemborg & Despres (1999)	56	42	N
Banksia attenuata	Proteaceae	West Aus	105.2	0.94		Cowling et al. (1987)	29	25	S
Banksia leptophylla	Proteaceae	West Aus	25.4	0.94		Cowling et al. (1987)	29	25	S
Banksia menziesii	Proteaceae	West Aus	86.7	0.69		Cowling et al. (1987)	29	25	S
Banksia prionotes	Proteaceae	West Aus	19.8	0.82		Cowling et al. (1987)	29	25	S
Embothrium coccineum	Proteaceae	Chile	16.43		0.95	Diaz et al. (1999)	42	30	S
Gevuina avellana	Proteaceae	Chile	1220.75		0.978	Diaz et al. (1999)	42	30	S
Grevillea barklyana	Proteaceae	NSW	136	0.667	0.697	Vaughton (1998)	35	10	S
Grevillea buxifolia	Proteaceae	Sydney	53		0.4	Auld & Denham (1999)	33	53	S
Grevillea caleyi	Proteaceae	Sydney	298.3			Auld & Denham (1999)	33	53	S
Grevillea linearifolia	Proteaceae	Sydney	24		0.22	Auld & Denham (1999)	33	53	S
Grevillea longifolia	Proteaceae	Sydney	127.5		0.88	Auld & Denham (1999)	33	53	S
Grevillea shiressii	Proteaceae	Sydney	25		0.64	Auld & Denham (1999)	33	53	S
Grevillea speciosa	Proteaceae	Sydney	28		0.82	Auld & Denham (1999)	33	53	S
Stenocarpus sinuatus	Proteaceae	Queensland	60		0.979	Osunkoya (1994)	17	17	S
Illeostylus micranthus	Loranthaceae	New Zealand	5.16	0.94		Sullivan et al. (1995)	43	0	S
Phytolacca rivinoides	Phytolaccaceae	Costa Rica	10	0.965		Myster (1997)	18	20	N
Phytolacca americana	Phytolaccaceae	Pensylvannia	7.42		0.815	Hyatt (1998), Boman & Casper (1995)	39	50	N
Rumex acetosa	Polygonaceae	UK	0.79		0.928	Edwards & Crawley (1999)	51	24	N
Silene alba	Caryophyllaceae	Netherlands	1.1	0.496		Biere & Honders (1996)	6	30	N
Silene dioica	Caryophyllaceae	Netherlands	0.69	0.709		Biere & Honders (1996)	6	30	N
Silene uniflora	Caryophyllaceae	Sweden	0.65	0.653		Pettersson (1994)	56	30	N
Silene vulgaris	Caryophyllaceae	Baltic	1.2	0.769		Pettersson (1991)	56	30	N
Hamamelis virginiana	Hamamelidaceae	Michigan	46.3	0.128		De Steven (1983)	42	36	N
Euonymus europeaus	Celastraceae	Germany, England	35.1		0.85	Kollmann et al. (1998)	49	40	N
Calophyllum brasiliense	Clusiaceae	Costa Rica	2427.42		0.988	Holl & Lulow (1997)	8	57	N
Calophyllum calaba var. *bracteatum*	Clusiaceae	Indonesia	1000		0.984	Blate et al. (1998)	1	13	S
Hypericum gramineum	Clusiaceae	Canberra	0.01		0.889	Willis et al. (1997)	35	19	S
Aleurites moluccana	Euphorbiaceae	Queensland	7520		0.951	Osunkoya (1994)	17	17	S
Baccaurea stipulata	Euphorbiaceae	Indonesia	100		0	Blate et al. (1998)	1	13	S

Appendix 1 *continued*

Species	Family	Location	Seed mass	Pre	Post	Reference	Latitude		N/S
Bischofia javanica	Euphorbiaceae	Hong Kong	10.1		0.892	Hau (1997)	22	23	N
Hyeronima oblonga	Euphorbiaceae	Costa Rica	19.95		0.961	Holl & Lulow (1997)	8	57	N
Micrantheum ericoides	Euphorbiaceae	Sydney	2.8		0.03	Rodgerson (1998)	33	53	S
Sapium discolor	Euphorbiaceae	Hong Kong	46.6		0.752	Hau (1997)	22	23	N
Bruguiera exaristata	Rhizophoraceae	Queensland	3000		0.901	Smith (1987), McGuinness (1997)	15	36	S
Bruguiera gymnorrhiza	Rhizophoraceae	Queensland	19800		0.94	Smith (1987)	18	46	S
Ceriops tagal	Rhizophoraceae	Queensland	1400		0.869	Smith (1987), (McGuinness (1997)	15	36	S
Rhizophora mangle	Rhizophoraceae	Belize	10100		0.978	McKee (1995)	16	40	N
Rhizophora stylosa	Rhizophoraceae	Queensland	30300		0.906	Smith (1987), McGuinness (1997)	15	36	S
Viola selkirkii	Violaceae	Japan	0.61		0.845	Ohkawara & Higashi (1994)	43	0	N
Viola verecunda	Violaceae	Japan	0.42		0.97	Ohkawara & Higashi (1994)	43	0	N
Elaeocarpus angustifolius	Elaeocarpaceae	Queensland	4510		0.969	Osunkoya (1994)	17	17	S
Elaeocarpus ruminatus	Elaeocarpaceae	Queensland	830		0.936	Osunkoya (1994)	17	17	S
Elaeocarpus stipularis	Elaeocarpaceae	Indonesia	3240		0.996	Blate *et al.* (1998)	1	13	S
Aristotelia chilensis	Elaeocarpaceae	Chile	15.26		0.985	Diaz *et al.* (1999)	42	30	S
Asarum canadense	Aristolochiaceae	West Virginia	13.21	0.756	0.11	Heithaus (1981)	37	49	N
Agalea borneensis	Connaraceae	Indonesia	470		0.924	Blate *et al.* (1998)	1	13	S
Rourea minor	Connaraceae	Indonesia	510		0.958	Blate *et al.* (1998)	1	13	S
Roureopsis acutipetala	Connaraceae	Indonesia	100		0.899	Blate *et al.* (1998)	1	13	S
Cercocarpus ledifolius	Rosaceae	Utah	8.74		0.999	Russell & Schupp (1998)	41	37	N
Crataegus laevigata	Rosaceae	Germany, England	45.54		0.98	Kollmann *et al.* (1998)	49	40	N
Crataegus monogyna	Rosaceae	Spain, Germany	76.53		0.995	Hulme (1997), Kollmann *et al.* (1998)	43	50	N
Prunus annularis	Rosaceae	Costa Rica	191.41		0	Holl & Lulow (1997)	8	57	N
Prunus avium	Rosaceae	Germany, England, Minnesota	198		0.535	Kollmann *et al.* (1998), Webb & Willson (1985)	48	16	N
Prunus spinosa	Rosaceae	Germany, England	165.39		0.49	Kollmann *et al.* (1998)	49	40	N
Prunus turneriana	Rosaceae	Queensland	3990		0.908	Osunkoya (1994)	17	17	S
Prunus virginiana	Rosaceae	Minnesota	94.7		0.42	Webb & Willson (1985)	46	51	N
Rosa canina	Rosaceae	Germany, England	15.61		0.87	Kollmann *et al.* (1998)	49	40	N
Rubus alleghiensis	Rosaceae	Pennsylvania	1.73		0.624	Boman & Casper (1995)	39	50	N
Rubus fruticosus	Rosaceae	Germany, England	2.23			Kollmann *et al.* (1998)	49	40	N
Rubus spectabilis	Rosaceae	Alaska	3.17		0.777	Bermejo *et al.* (1998)	57	2	N
Sorbus aucuparia	Rosaceae	Sweden	3.14	0.807		Sperens (1997)	63	49	N
Artocarpus cf. *nitidus*	Moraceae	Indonesia	200		0.899	Blate *et al.* (1998)	1	13	S
Brosimum alicastrum	Moraceae	Mexico	2721		0.96	Burkey (1994)	18	30	N

Species	Family	Location	Seed mass			Reference			
Cecropia schreibiana	Moraceae	Costa Rica	0.3	0.95	0.997	Myster (1997)	18	20	N
Pseudolmedia spuria	Moraceae	Costa Rica	1700.84		0.945	Holl & Lulow (1997)	8	57	N
Acacia baileyana	Fabaceae	Melbourne	19.2	0.898		New (1983)	37	43	S
Acacia dealbata	Fabaceae	Melbourne	9.1	0.962		New (1983)	37	43	S
Acacia decurrens	Fabaceae	Melbourne	14.8	0.981		New (1983)	37	43	S
Acacia elongata	Fabaceae	Sydney	10.44	0.18		Auld (1983) Auld & O'Connell (1989)	33	53	S
Acacia floribunda	Fabaceae	Melbourne	7.03	0.915		New (1983)	37	43	S
Acacia gerrardii	Fabaceae	Uganda, Saudi Arabia	70.43	0.795		Mucunguzi (1995), Abdullah & Abulfatih (1995)	9	0	N
Acacia linifolia	Fabaceae	Sydney	24.73	0.782		Auld (1983)	33	53	S
Acacia longifolia	Fabaceae	Melbourne, Sydney	13.33	0.774		New (1983), Auld (1983)	35	48	S
Acacia mearnsii	Fabaceae	Melbourne	11.2	0.935		New (1983)	37	43	S
Acacia melanoxylon	Fabaceae	Melbourne	11	0.104		New (1983)	37	43	S
Acacia myrtifolia	Fabaceae	Sydney	9.62	0.917		Auld (1983)	33	53	S
Acacia pravissima	Fabaceae	Melbourne	7.2	0.972		New (1983)	37	43	S
Acacia pycnantha	Fabaceae	Melbourne	17.75	0.889		New (1983)	37	43	S
Acacia saligna	Fabaceae	Melbourne	14.1	0.967		New (1983)	37	43	S
Acacia sclerophylla	Fabaceae	Sydney	4.9		0.25	Rodgerson (1998)	33	53	S
Acacia sieberiana	Fabaceae	Uganda	328.66	0.972		Mucunguzi (1995)	0	8	S
Acacia suaveolens	Fabaceae	Sydney	32.44	0.495		Auld & Myerscough (1986), Auld (1983)	33	53	S
Acacia terminalis	Fabaceae	Sydney	39.94	0.808		Auld (1983)	33	53	S
Acacia ulicifolia	Fabaceae	Sydney	13.55	0.668		Auld (1983)	33	53	S
Acacia verniciflua	Fabaceae	Melbourne	9.2	0.765		New (1983)	37	43	S
Adenanthera sp.	Fabaceae	Indonesia	180		0.996	Blate *et al.* (1998)	1	13	N
Astragalus cibarius	Fabaceae	Utah	5.6	0.071		Green & Palmbald (1975)	40	30	N
Astragalus utahensis	Fabaceae	Utah	3.9	0.396		Green & Palmbald (1975)	40	30	N
Bossiaea heterophylla	Fabaceae	Sydney	12.94	0.336		Auld (1983)	33	53	S
Bossiaea obcordata	Fabaceae	Sydney	2.56	0.628		Auld (1983)	33	53	S
Bossiaea scolopendria	Fabaceae	Sydney	14.85	0.151		Auld (1983)	33	53	S
Cassia marilandica	Fabaceae	Tennessee	20.15	0.584	0.992	Baskin & Baskin (1977)	35	51	N
Castanospermum australe	Fabaceae	Queensland	26220			Osunkoya (1994)	17	17	S
Cercidium floridum	Fabaceae	California	211	0.713		Mitchell (1977)	33	42	N
Daviesia alata	Fabaceae	Sydney	5.59	0.94		Auld (1983)	33	53	S
Dillwynia floribunda var. *tereifolia*	Fabaceae	Sydney	1.44	0.95		Auld (1983)	33	53	S
Dillwynia retorta var. *retorta*	Fabaceae	Sydney	5.98	0.532		Auld (1983)	33	53	S

Appendix I *continued*

Species	Family	Location	Seed mass	Pre	Post	Reference	Latitude	
Erythrina goldmanii	Fabaceae	Mexico	210		0.697	Hammond (1995)	16 48	N
Fordia filipes	Fabaceae	Indonesia	500		0.958	Blate et al. (1998)	1 13	S
Glycyrrhiza lepidota	Fabaceae	N & S Dakota	385	0.59		Boe & Wynia (1985)	46 0	N
Gompholobium glabratum	Fabaceae	Sydney	1.99	0.632		Auld (1983)	33 53	S
Gompholobium grandiflorum	Fabaceae	Sydney	2.47	0.712		Auld (1983)	33 53	S
Gompholobium latifolium	Fabaceae	Sydney	4.42	0.196		Auld (1983)	33 53	S
Hovea linearis	Fabaceae	Sydney	20.05	0.456		Auld (1983)	33 53	S
Isoberlinia angolensis	Fabaceae	Zambia	2990	0.259		Chidumayo (1997)	15 15	S
Julbernardia globiflora	Fabaceae	Zambia	270	0.895		Chidumayo (1997)	15 15	S
Kennedia rubicundra	Fabaceae	Sydney	31.5	0.928		Auld (1983)	33 53	S
Lathyrus vernus	Fabaceae	Sweden	14.35	0.74	0.772	Ehrlen (1996) (. Ehrlen (1993))	58 32	N
Lotus corniculatus	Fabaceae	England	1.13		0.834	Hulme (1998)	51 24	N
Medicago lupulina	Fabaceae	England	1.88		0.843	Hulme (1998)	51 24	N
Medicago sativa	Fabaceae	England	1.7		0.843	Hulme (1998)	51 24	N
Phyllota grandiflora	Fabaceae	Sydney	5.85	0.75		Auld (1983)	33 53	S
Phyllota phylicoides	Fabaceae	Sydney	2.73	0.825		Auld (1983)	33 53	S
Pultenaea daphnoides	Fabaceae	Sydney	5.39	0.738		Auld (1983)	33 53	S
Pultenaea elliptica	Fabaceae	Sydney	1.92	0.75		Auld (1983)	33 53	S
Pultenaea ferruginea var. deanei	Fabaceae	Sydney	5.77	0.741		Auld (1983)	33 53	S
Pultenaea flexillis	Fabaceae	Sydney	6.21	0.677		Auld (1983)	33 53	S
Pultenaea retusa	Fabaceae	Sydney	5.9	0.962		Auld (1983)	33 53	S
Pultenaea stipularis	Fabaceae	Sydney	10.25	0.62		Auld (1983)	33 53	S
Sophora microphylla	Fabaceae	New Zealand	58	0.89		Sullivan et al. (1995)	43 0	S
Sphaerolobium vimineum	Fabaceae	Sydney	1.01	0.726		Auld (1983), Auld & O'Connell (1989)	33 53	S
Trifolium dubium	Fabaceae	England	1.92		0.814	Hulme (1998)	51 24	N
Trifolium pratense	Fabaceae	England	0.59		0.843	Hulme (1998)	51 24	N
Trifolium repens	Fabaceae	England	0.63		0.843	Hulme (1998)	51 24	N
Viminaria juncea	Fabaceae	Sydney	5.33	0.973		Auld (1983)	33 53	S
Fagus grandifolia	Fagaceae	Pennsylvania	283.5		0.763	Boman & Casper (1995)	39 50	N
Lithocarpus glaber	Fagaceae	Hong Kong	1662.4		0.972	Hau (1997)	22 23	N
Lithocarpus sp.	Fagaceae	Indonesia	8100		0.993	Blate et al. (1998)	1 13	S
Carya tomentosa	Juglandaceae	New Jersey	5039.9		0.549	McCarthy (1994)	40 30	N
Corynocarpus laevigatus	Corynocarpaceae	New Zealand	1980		0.975	Moles & Drake (1999)	41 14	S
Laguncularia racemosa	Combretaceae	Belize	280		0.964	McKee (1995)	16 40	N
Amomyrtus huma	Myrtaceae	Chile	25.82		0.971	Diaz et al. (1999)	42 30	S

Species	Family	Location				Reference			
Amomyrtus meli	Myrtaceae	Chile	25.82		0.911	Diaz *et al.* (1999)	42	30	S
Eucalyptus baxteri	Myrtaceae	Victoria	17.5	0.34		Andersen (1989)	39	2	S
Eucalyptus salmonphloia	Myrtaceae	Western Australia	1.7		0.71	Yates *et al.* (1995)	31	23	S
Leptospermum juniperinum	Myrtaceae	Victoria	0.16	0.56		Andersen (1989)	39	2	S
Syzygium sp. 1	Myrtaceae	Indonesia	2000		0.947	Blate *et al.* (1998)	1	13	S
Syzygium sp. 2	Myrtaceae	Indonesia	2500		0.932	Blate *et al.* (1998)	1	13	S
Syzygium sp. 3	Myrtaceae	Indonesia	1800		0.986	Blate *et al.* (1998)	1	13	S
Syzygium sp. 4	Myrtaceae	Indonesia	680		0.99	Blate *et al.* (1998)	1	13	S
Syzygium sp. 5	Myrtaceae	Indonesia	2200		0.983	Blate *et al.* (1998)	1	13	S
Miconia racemosa	Melastomataceae	Costa Rica	2	0.97	0.994	Myster (1997)	18	20	N
Oenothera biennis	Onagraceae	Michigan	0.41		0.963	Mittelbach & Gross (1984)	42	18	N
Ovidia pillo-pillo	Thymeleaceae	Chile	24.65		0.971	Diaz *et al.* (1999)	42	30	S
Brassica rapa	Brassicaceae	Washington	1.7	0.6		Nakamura *et al.* (1995)	47	24	N
Codonocarpus cotonifolius	Gyrostemonaceae	Sydney	2.7		0.38	Rodgerson (1998)	33	53	S
Cistus ladanifer	Cistaceae	Spain	0.24		0.486	Acosta *et al.* (1997)	40	30	N
Hibiscus moscheutos	Malvaceae	Maryland	9.41		0.018	Kudoh & Whigham (1998)	38	53	N
Hoheria angustifolia	Malvaceae	New Zealand	2.6		0.517	Sullivan *et al.* (1995)	43	0	S
Lasiopetalum ferrugineum	Malvaceae	Sydney	1.9	0.98	0.03	Rodgerson (1998)	33	53	S
Microcos cf. crassifolia	Malvaceae	Indonesia	280		0.993	Blate *et al.* (1998)	1	13	S
Microcos paniculata	Malvaceae	Hong Kong	127.6		0.886	Hau (1997)	22	23	N
Plagianthus regius	Malvaceae	New Zealand	4.2			Sullivan *et al.* (1995)	43	0	S
Sterculia stipulata	Malvaceae	Indonesia	300		0.941	Blate *et al.* (1998)	1	13	S
Choerospondias axillaris	Anacardiaceae	Hong Kong	2464.8		0.987	Hau (1997)	22	23	N
Rhus glabra	Anacardiaceae	Wisconsin	10.05	0.42		Chung & Waller (1986)	43	0	N
Spondias mombin	Anacardiaceae	Mexico	867		0.846	Hammond (1995)	16	48	N
Bursera simaruba	Burseraceae	Mexico	129		0.962	Hammond (1995)	16	48	N
Canarium cf. apertum	Burseraceae	Indonesia	9000		0.999	Blate *et al.* (1998)	1	13	S
Canarium denticulatum ssp. *denticulatum*	Burseraceae	Indonesia	10100			Blate *et al.* (1998)	1	13	S
Santiria tomentosa	Burseraceae	Indonesia	830		0.983	Blate *et al.* (1998)	1	13	S
Cabralea canjerana	Meliaceae	Brazil	980		0.528	Pizo (1997)	23	33	S
Carapa procera	Meliaceae	French Guiana	18400		0.939	Forget (1996)	9	9	N
Dysoxylum cf. cyrtobotryum	Meliaceae	Indonesia	6300		0.984	Blate *et al.* (1998)	1	13	S
Dysoxylum schiffneri	Meliaceae	Queensland	620		0.991	Osunkoya (1994)	17	17	S
Guarea glabra	Meliaceae	Costa Rica	800	0.978	0.946	Wenny (1999)	10	12	N

Appendix I *continued*

Species	Family	Location	Seed mass	Pre	Post	Reference	Latitude		
Guarea kunthiana	Meliaceae	Costa Rica	4500	0.983	0.928	Wenny (1999)	10	12	N
Lansium sp.	Meliaceae	Indonesia	5100		0.984	Blate et al. (1998)	1	13	S
Swietenia humilis	Meliaceae	Mexico	807		0.747	Hammond (1995)	16	48	N
Acronychia pedunculata	Rutaceae	Hong Kong	161.1		0.917	Hau (1997)	22	23	N
Flindersia brayleyana	Rutaceae	Queensland	150		0.985	Osunkoya (1994)	17	17	S
Alectryon excelsus	Sapindaceae	New Zealand	170	0.913		Sullivan et al. (1995), Moles & Drake (1999)	41	52	S
Castanospora alphandii	Sapindaceae	Queensland	3530		0.918	Osunkoya (1994)	17	17	S
Diploglottis diphyllostegia	Sapindaceae	Queensland	210		0.783	Osunkoya (1994)	17	17	S
Cornus drummondii	Cornaceae	Illinois USA	28.9		0.989	Willson & Whelan (1993)	40	0	N
Cornus sanguinea	Cornaceae	Germany, England	56.46		0.79	Kollmann et al. (1998)	49	40	N
Diospyros morrisiana	Ebenaceae	Hong Kong	138.3		0.996	Hau (1997)	22	23	N
Diospyros sp.	Ebenaceae	Indonesia	3300		0.989	Blate et al. (1998)	1	13	S
Bertholletia excelsa	Lecythidaceae	Brazil	816000		0.927	Peres & Baider (1997)	7	46	S
Ardisia revoluta	Myrsinaceae	Costa Rica	53.99		0.946	Holl & Ludlow (1997)	8	57	N
Myrsine australis	Myrsinaceae	New Zealand	17.41	0.981		Sullivan et al. (1995)	43	0	S
Myrsine salicinia	Myrsinaceae	New Zealand	29	0.814		Sullivan et al. (1995)	43	0	S
Ipomopsis aggregata	Polemoniaceae	Colorado	1.53	0.89		Hainsworth et al. (1984)	38	33	N
Palaquium sp.	Sapotaceae	Indonesia	1200		0.98	Blate et al. (1998)	1	13	S
Sideroxylon portoricense	Sapotaceae	Costa Rica	542.3		0.992	Holl & Ludlow (1997)	8	57	N
Gordonia axillaris	Theaceae	Hong Kong	15.8		0.919	Hau (1997)	22	23	N
Ternstroemia magnificum	Theaceae	Indonesia	11600		0.983	Blate et al. (1998)	1	13	S
Ternstroemia sp.	Theaceae	Indonesia	730		0.945	Blate et al. (1998)	1	13	S
Asclepias syriaca	Apocynaceae	Illinios	6.91	0.593		Franson & Willson (1983)	40	13	N
Centaurea maculosa	Gentianaceae	Michigan	2.19		0.805	Mittelbach & Gross (1984)	42	18	N
Coprosma grandifolia	Rubiaceae	New Zealand	30			Moles & Drake (1999)	41	14	S
Gonzalagunia spicata	Rubiaceae	Costa Rica	20	0.95	0.997	Myster (1997)	18	20	N
Nertera granadensis	Rubiaceae	Chile	1.41		0.983	Diaz et al. (1999)	42	30	S
Palicourea riparia	Rubiaceae	Costa Rica	200	0.985	0.998	Myster (1997)	18	20	N
Avicennia germinans	Avicinniaceae	Belize	10120		0.903	McKee (1995)	16	40	N
Avicennia marina	Avicinniaceae	Queensland	3400		0.602	Smith (1987)	18	46	S
Myoporum laetum	Myoporaceae	New Zealand	100		0.986	Moles & Drake (1999)	41	14	S
Fraxinus excelsior	Oleaceae	England	33.25			Gardner (1977)	53	15	N
Ligustrum vulgare	Oleaceae	Germany, England	21.6		0.89	Kollmann et al	49	40	N
Nestegis cunninghamii	Oleaceae	New Zealand	550		0.992	Moles & Drake (1999)	41	14	S
Plantago lanceolata	Plantaginaceae	England	1.28		0.936	Hulme (1998)	51	24	N

Species	Family	Location				Reference			
Linaria vulgaris	Scrophulariaceae	New York	0.13	0.218		Arnold (1982)	42	46	N
Verbascum thapsus	Scrophulariaceae	Michigan	0.05		0.966	Mittelbach & Gross (1984)	42	18	N
Rhaphithamnus spinosus	Verbenaceae	Chile	31.69		0.995	Diaz *et al.* (1999)	42	30	S
Solanum laciniatum	Solanaceae	New Zealand	2.2	0.78		Sullivan *et al.* (1995)	43	0	S
Stemonurus cf. *malaccensis*	Icacinaceae	Indonesia	5000		0.989	Blate *et al.* (1998)	1	13	S
Stemonurus cf. *umbellatus*	Icacinaceae	Indonesia	2900		0.957	Blate *et al.* (1998)	1	13	S
Daucus carota	Apiaceae	Michigan	0.9		0.985	Mittelbach & Gross (1984)	42	18	N
Griselinia littoralis	Griseliniaceae	New Zealand	26	0.974		Sullivan *et al.* (1995)	43	0	S
Griselinia lucida	Griseliniaceae	New Zealand	31	0.94		Sullivan *et al.* (1995)	43	0	S
Arcticum lappa	Asteraceae	Ontario	13	0.957		Rollo *et al.* (1985)	43	3	N
Arcticum minus	Asteraceae	Ontario	10.7	0.103		Rollo *et al.* (1985)	43	3	N
Arcticum sp. Green	Asteraceae	Ontario	9.24	0.216		Rollo *et al.* (1985)	43	3	N
Arcticum sp. Purple	Asteraceae	Ontario	17.6	0.876		Rollo *et al.* (1985)	43	3	N
Centaurea nigra	Asteraceae	UK	2.46		0.925	Edwards & Crawley (1999)	51	24	N
Cirsium palustre	Asteraceae	Netherlands	2	0.877		van Leeuwen (1983)	52	5	N
Cirsium vulgare	Asteraceae	Netherlands	3.1	0.915	0.866	Klinkhamer *et al*	52	8	N
Haplopappus squarrosus	Asteraceae	California	0.68	0.03		Louda (1982)	32	57	N
Haplopappus venetus	Asteraceae	California	0.34	0.538		Louda (1983)	32	43	N
Tragopogon dubius	Asteraceae	Michigan	6.94		0.962	Mittelbach & Gross (1984)	42	18	N
Xanthium strumarium	Asteraceae	Long island (USA)	82.4	0.661		Hare (1980)	41	0	N
Sambuccus nigra	Caprifoliaceae	Germany, England	2.93		0.82	Kollmann *et al*	49	40	N
Viburnum acerifolium	Caprifoliaceae	Pennsylvania	34.6		0.649	Boman & Casper (1995)	39	50	N
Viburnum lantana	Caprifoliaceae	Germany, England	41.67		0.7	Kollmann *et al.* (1998)	49	40	N
Viburnum opulus	Caprifoliaceae	Sweden	480		0.951	Englund (1993)	60	4	N
Dipsacus sylvestris	Dipsacaceae	Michigan	2.39		0.99	Mittelbach & Gross (1984)	42	18	N
Scabiosa columbaria	Dipsacaceae	Netherlands	1.32	0.928	0.82	Verkaar *et al.* (1986)	51	14	N

Appendix 2 Species list and data for the ten species from Ku-Ring-Gai Chase National Park used to investigate the relationship between seed mass and seed development time.

Species	Family	Median development time (days)	Seed mass (mg)
Acacia myrtifolia	Mimosaceae	110	11.3
Acacia suaveolens	Mimosaceae	116	28.5
Boronia ledifolia	Rutaceae	76	9.1
Conospermum ericifolium	Proteaceae	83.5	2.3
Dilwynia retorta	Fabaceae	97	5.5
Epacris longiflora	Epacridaceae	50.5	0.12
Epacris pulchella	Epacridaceae	69	0.06
Grevillea sericea	Proteaceae	116	21.7
Phyllota phylicoides	Fabaceae	97	2.96
Woollsia pungens	Epacridaceae	55	0.21

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