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SEED SIZE, GERMINATION AND SEEDLING RELATIVE GROWTH RATES IN THREE TROPICAL TREE SPECIES

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BURSLEM, D. F. R. P. & MILLER, J. 2001. Seed size, germination and seedling relative growth rates in three tropical tree species. The rates of germination and seedling relative growth rates (under laboratory conditions) were related to seed size within and between species for three light-demanding tree species from dry semi-deciduous and/or dry forest in Ghana (*Afzelia africana, Milicia excelsa* and *Pericopsis elata*). The three species illustrated three potential mechanisms for early colonisation and dominance of canopy gap sites: rapid germination (*Pericopsis*), fast relative growth rates (*Milicia*) or relatively large seed size (*Afzelia*). The high relative growth rates of *Milicia* seedlings resulted from their high specific leaf area and leaf mass ratio rather than rapid rates of net assimilation per unit leaf area, but the differences between the two other species were determined by differences in unit leaf rate. Within *Afzelia*, larger seeds germinated less quickly but seedlings from larger seeds had higher relative growth rates; within *Pericopsis*, larger seeds possessed a higher N concentration in the embryo-cum-endosperm fraction but did not germinate or grow faster than small seeds. We conclude that differential seed size, germination and seedling relative growth rates must all be considered among the mechanisms determining colonisation of regeneration sites by different species. Differences in trends of germination and seedling relative growth rates with seed size may stabilise seed size variation within a species.

Key words: *Afzelia africana* - *Milicia excelsa* - *Pericopsis elata* - germination - Ghana - relative growth rate analysis - tree seedlings - tropical forest

BURSLEM, D. R. F. P. & MILLER, J. 2001. Saiz biji benih, kadar percambahan dan kadar pertumbuhan relatif anak benih di dalam tiga spesies pokok tropika. Kadar percambahan dan kadar pertumbuhan relatif anak benih (di bawah keadaan makmal) adalah berkaitan dengan saiz biji benih di dalam dan antara spesies bagi tiga spesies pokok yang memerlukan cahaya daripada hutan kering separa daun luruh dan/atau hutan kering di Ghana (*Afzelia africana, Milicia excelsa* dan *Pericopsis elata*). Ketiga-tiga spesies menggambarkan tiga mekanisme yang berpotensi untuk pengkolonian awal dan dominans tapak ruang sudur: percambahan yang pantas (*Pericopsis*), kadar pertumbuhan relatif yang cepat (*Milicia*) atau saiz biji benih yang besar secara relatif (*Afzelia*). Kadar pertumbuhan relatif yang tinggi bagi anak benih *Milicia* berpunca daripada luas daun spesifik dan nisbah jisim daun yang tinggi berbanding dengan kadar asimilasi bersih bagi satu unit luas daun, tetapi perbezaan antara dua spesies yang lain ditentukan oleh perbezaan dalam kadar daun unit. Dalam *Afzelia*, biji benih yang lebih besar bercambah lebih perlahan tetapi anak benih daripada biji benih mempunyai kadar pertumbuhan relatif yang lebih tinggi; dalam *Pericopsis*, biji benih yang lebih besar mempunyai kepekatan N yang lebih tinggi di dalam bahagian embrio dan

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endosperma tetapi tidak bercambah atau tumbuh lebih cepat berbanding dengan biji benih kecil. Kami membuat kesimpulan bahawa perbezaan saiz biji benih, kadar percambahan dan kadar pertumbuhan relatif anak benih mestilah dipertimbangkan antara mekanisme yang menentukan pengkolonian tapak pemulihan oleh spesies yang berbeza. Perbezaan dalam trend kadar percambahan dan kadar pertumbuhan relatif anak benih dengan saiz biji benih dapat menstabilkan perubahan saiz biji benih di dalam sesuatu spesies.

Introduction

The wide variation in seed size within functional groups of tropical forest trees has been emphasised recently by Grubb (1996). Research on the factors maintaining this diversity has mostly highlighted the comparative advantages of large seeds. It has been shown that large seeds give rise to large seedlings which are more effective at competing for scarce resources (Howe & Richter 1982), resisting and recovering from herbivory (Harms & Dalling 1997) or overcoming the constraints of establishment through deep layers of soil or litter (Molofsky & Augspurger 1992). The corollary of these findings is that seedlings derived from small seeds must either arrive earlier, or germinate or grow faster in relative terms, than individuals with larger seeds if they are to overcome their initial size disadvantage and compete effectively with their neighbours. Some of these trends have received empirical support. For example, in temperate herbs germination rate has sometimes been found to increase with a decrease in seed size (e.g. Cideciyan & Malloch 1982), while a negative relationship between seed size and seedling relative growth rates (RGR) has been found for groups of coexisting tropical trees (Osunkoya *et al.* 1994, Huante *et al.* 1995), as well as other taxa (Fenner 1983, Gross 1984, Shipley & Peters 1990, Marañón & Grubb 1993). For tropical tree seedlings grown at relatively high irradiance, interspecific differences in RGR are determined more by differences in leaf area ratio than unit leaf rate (Osunkoya *et al.* 1994, Huante *et al.* 1995). To our knowledge, germination and seedling relative growth rates have not been considered together in comparative studies of tropical trees.

In tropical forests, early colonisation and fast growth rates are particularly important for species which establish and grow to maturity in canopy gaps. This species group has been characterised as possessing relatively small seeds (Swaine & Whitmore 1988), although Metcalfe and Grubb (1995) and Grubb (1996) have recently highlighted the wide range in seed size for gap-demanding species of tropical lowland rain forests in Southeast Asia and Australia respectively. In tropical forests, dense carpets of seedlings are usually present soon after canopy gap creation, and rapid growth combined with asymmetric competition for light places a premium on early colonisation for species with a high light-demand as seedlings. Either these seedlings are present prior to gap formation or they germinate after gap creation, but our focus here is on the latter group and processes occurring in large gaps. In these sites competition for light and space between conspecifics will place the same set of constraints on small-seeded individuals within a cohort as on small-seeded species within the community. This is an unexplored area of tropical forest ecology.

The suggested link between seed size and seedling competitive ability requires that resource availability increases as a direct function of seed size, which is reasonable only if the internal supply rates of critical limiting resources do not change with seed size. Studies of nutrient concentrations in the seeds of tropical trees do not support this assumption, i.e. a negative correlation between N concentrations in the embryo-cum-endosperm (EE) fraction and EE dry mass was found by Grubb (1996) comparing species of Australian tropical Lauraceae, and by Grubb and Coomes (1997) for species of tropical heath and palm forests in Venezuela. Similar negative correlations between the EE concentrations of some nutrients and EE dry mass have been found in intraspecific comparisons of tropical trees from Africa and Southeast Asia (Oladokun 1989, Grubb & Burslem 1998). Under conditions of external limiting nutrient supply, the greater supply of nutrients from internal reserves might allow seedlings from small-seeded plants to reduce their dry mass allocation to roots or increase their net assimilation rates per unit leaf area compared to seedlings from larger seeds. Either of these processes would tend to increase RGR and generate the negative relationship with seed size observed in numerous studies. In this paper we report N concentrations in seed fractions within and between three tropical tree species, and compare their germination rates and seedling RGRs using classical growth analysis. We test the hypotheses that (1) small-seeded species and individuals germinate faster and possess a higher RGR than the large-seeded species or individuals, (2) differences in RGR will be determined more by differences in leaf area ratio than unit leaf rate (ULR), and (3) in cases where differences in RGR are determined by differences in ULR, the higher RGRs will be associated with species or individuals with higher N concentrations in the embryo-cum-endosperm (EE) fraction.

Materials and methods

Test species

The test species used were *Afzelia africana* Sm. (Caesalpinaceae), *Milicia excelsa* (Welw.) C.C. Berg (Moraceae) and *Pericopsis elata* (Harms) Van Meeuwen (Papilionaceae). From hereon they will be referred to by their genus names only. All three species are native to Ghana where they occur in dry forest (*Afzelia*), throughout the forest zone (*Milicia*) and dry semi-deciduous forest (*Pericopsis*) respectively (Hawthorne 1995). The three species have overlapping distributions in dry semi-deciduous forest where annual rainfall is about 1200 mm and the mean total length of the two dry seasons (mean monthly rainfall < 100 mm) is about five months (Swaine *et al.* 1997). All three species possess light-demanding seedlings, and *Milicia* is a strict pioneer (Hawthorne 1995). These species were selected because they possess an appropriate ecology and contrasting seed mass values, and because of the availability of seeds for our study. Seeds were collected in Ghana during January 1994 (*Pericopsis*) and during 1995 (*Afzelia, Milicia*), transferred to Aberdeen and then stored at room temperature until use in our experiments.

Seed viability determination

Seed viability was determined using the tetrazolium assay (International Seed Testing Association 1993) in the case of *Afzelia* and *Pericopsis* and by germination trials in all three species. For the tetrazolium assay the embryo-cum-endosperm (EE) fractions of 12 or 18 seeds per species were extracted from all associated fruit and seed structures, and placed in a 1% aqueous solution of 2,3,5-triphenyltetrazolium chloride for 48 h at 25 °C (i.e. room temperature). Embryos were scored as viable if stained red (endosperm red) and dead if stained pink (endosperm colourless). Germination trials were conducted using samples of six whole seeds per species placed in seed-trays of Fisons Levingtons potting compost on a glasshouse bench (maximum temperature 25 °C; minimum temperature 15 °C; irradiance approximately 400 μmol m^{-2} s^{-1} over a 12 h day). Germination was recorded daily for 14 days.

Germination tests

In *Afzelia* and *Pericopsis* the range of variation in seed mass and the number of seeds available allowed us to distinguish seed size classes within each species, but the seeds of *Milicia* were too small to classify individually. For *Afzelia* the fresh mass of the whole seed (including aril) was classified as either small (0.5 –1.9 g; n = 60) or large (2.0–4.0 g; n = 52). Regression analysis indicated that there is a strong positive relationship between the fresh mass of the whole seed including aril and the dry mass of the embryo-plus-endosperm (EE) fraction in this species. The EE fractions of *Pericopsis* seeds could be extracted easily without damaging them and were classified on the basis of fresh mass into small (0.176–0.225 g; n = 97) or large (0.226–0.296 g; n = 137) size classes. For all three species intact seeds were sown at a depth of 5 mm in a 50/50 mixture of sand and Fisons Levingtons compost in sufficient numbers to guarantee a minimum of about 20 germinants per species/ seed size class on the basis of the seed viability determination. This number ranged from 54 seeds for the large size class of *Afzelia* to 300 seeds of *Milicia.* Seed-trays were kept on a glasshouse bench (environmental conditions as above), watered daily with 15 ml of tap-water and monitored for seed germination (extension of radical 1 mm beyond the seed coat) daily for 32 days.

Seedling growth conditions

Germinants from the seed germination trials, with cotyledons but no true leaves, were transplanted singly into pots (10 cm height x 10 cm top diameter) containing a 3:1 mixture of sand and Fisons Levingtons potting compost. They were then placed in each of two identical phytotrons at 35/30 °C (12/12 hours day/night) and 80% relative humidity and arranged within them in a completely randomised design with respect to other species/seed-size class plants. Irradiance at pot level was about 400 μmol m^{-2} s^{-1} during simulated daylight conditions. At the same time, additional random samples of 9 germinants of *Afzelia* (small seed size class), 17 germinants of *Afzelia* (large seed size class) and *Pericopsis* (small seed size class), 20 germinants of *Milicia* and 21 germinants of *Pericopsis* (large seed size class) were removed from the seed-trays and dried to constant mass at 80 °C to obtain a value for initial dry mass. An additional harvest was carried out after 8 days (*Milicia,* 20 plants), 10 days (*Pericopsis,* 20 and 22 plants from the small and large seed size classes respectively) or 11 days (*Afzelia,* 12 and 15 plants from the small and large seed size classes respectively), at which times seedlings were removed and dried as above. A third harvest was made for two species after an additional seven days (*Milicia,* 20 plants) or eight days (*Pericopsis,* 18 and 19 plants from the small and large seed size classes respectively), and the dry mass values obtained separately as above. At all harvests, plants were separated into stems, leaves and roots, and leaf areas were determined using a meter (Delta-T Devices, Cambridge, UK) or graph paper before drying, except that for *Pericopsis* dry mass fractions were obtained only at the third harvest. Although the seedling growth experiments were not running concurrently for different species (because of variation between species in time to germination), the conditions in the phytotrons did not change and we are confident that comparisons between species are meaningful (see below).

Nitrogen determinations

The concentration of N in the EE fraction was determined for ten seeds of each of the size classes identified above for *Afzelia* and *Pericopsis* and for three pooled samples of 100 whole seeds of *Milicia.* For *Afzelia* and *Pericopsis* individual seeds were weighed fresh, the EE fraction was extracted, then dried and milled. For *Milicia,* the pooled samples of 100 whole seeds were dried and milled. A sample of the milled fractions was digested in a mixture of hydrogen peroxide and concentrated sulphuric acid and analysed for total N by the indophenol-blue method (Allen 1989).

Growth rates and statistical analyses

Seedlings were ranked by dry mass at successive harvests and paired by rank for derivation of mean and variance of plant growth and dry mass allocation measures (Hunt 1978). Seedling relative growth rates (RGR) and unit leaf rates (ULR) were calculated according to the following formulae (Evans 1972):

$$\mathrm{RGR} = (\ln W_2 - \ln W_1)/(T_2 - T_1)$$
$$\mathrm{ULR} = (W_2 - W_1)/(T_2 - T_1).(\ln L_2 - \ln L_1)/(L_2 - L_1)$$

where W_2 and W_1 are the dry mass values and L_2 and L_1 the leaf areas of seedlings at times T_2 and T_1 respectively. Mass ratios of leaves (LMR), stems (SMR) and roots (RMR), leaf area ratio (LAR) and specific leaf area (SLA) were calculated according to Evans (1972). For *Afzelia* and *Milicia* the values of all dry mass allocation variables presented were averaged across the two harvests, but for *Pericopsis* the data for LMR, SMR, RMR and SLA were available from the final harvest only.

Germination rates were analysed using the chi-squared test, RGR and other variates by analysis of variance or standard least-squares regression following angular transformation for percentage data (untransformed data are presented in the figure and tables). In analyses of seedling performance the two phytotrons were initially treated as a block factor in the model.

Results

Seed mass and N concentration

The mean dry mass of 'seeds' varied across three orders of magnitude between species, but their mean N concentration was much less variable (Table 1). The difference in mean dry mass of the EE fraction between size classes was much greater in absolute and relative terms for *Afzelia* than *Pericopsis*. For both species there was a tendency for the N concentration in the EE fraction to increase with EE dry mass (Table 1, Figure 1), although the regression was non-significant in the case of *Afzelia* ($p = 0.093$).

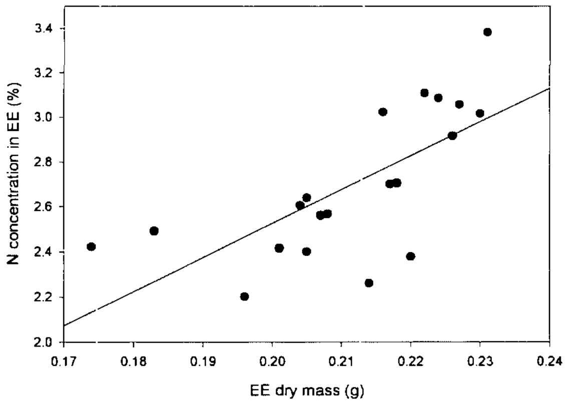
Table 1. (a) Mean ± standard error of the mean dry mass (mg) and N concentration (%) of the embryo-cum-endosperm (EE) fraction for *Afzelia africana, Milicia excelsa* and *Pericopsis elata* with sample sizes (n_1) and variance ratio comparing N concentrations (means not sharing the same superscript letter are significantly different at $p < 0.05$), and (b) range of whole seed fresh mass (g) and mean ± standard error of the mean dry mass (mg) and N concentration of the EE fraction for the two size classes of seeds within *Afzelia* and *Pericopsis* with sample sizes (n_2) and variance ratios comparing N concentrations between size classes

(a) Between species	*Afzelia*	*Milicia*	*Pericopsis*	F
EE dry mass (mg)¶	1256 ± 113	2.4 ± 0.05	211 ± 3	
EE N conc. (%)¶	3.0 ± 0.09^{a}	2.5 ± 0.03^{ab}	2.7 ± 0.07^{b}	4.9*
n_1	19	300†	20	

(b) Within species	*Afzelia*		F	*Pericopsis*		F
Size class	I	II		I	II	
Whole seed fresh mass (g)	0.5–1.9	2.0–4.0		0.176–0.225	0.226–0.296	
EE dry mass (mg)	872 ± 97	1681 ± 76		200 ± 4	223 ± 2	
EE N conc. (%)	2.8 ± 0.04	3.2 ± 0.04	3.9	2.5 ± 0.02	2.9 ± 0.02	23.4***
n_2	10	9		10	10	

¶Whole seeds of *Milicia*.
†Means are for three batches of 100 seeds.
*p<0.05, ***p<0.001.

(a) *Pericopsis elata*



(b) *Afzelia africana*

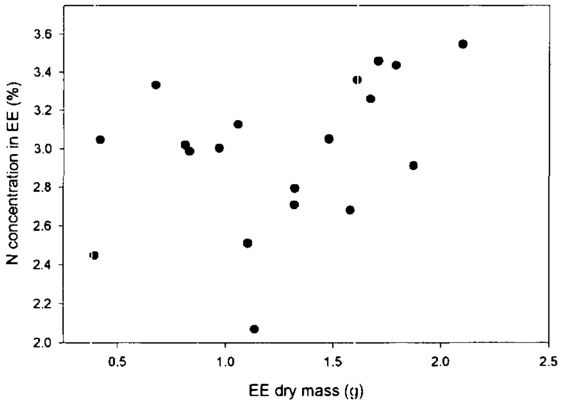


Figure 1. Relationship between dry mass (g) of the embryo-cum-endosperm fraction and the N concentration (%) in that fraction for seeds of (a) *Pericopsis elata* and (b) *Afzelia africana*. The equation for the regression line plotted for *Pericopsis* is as follows: $y = -0.5 + 15.1\ x$ ($p < 0.001$).

Germination

The three species varied in their mean time to germination and the extent of germination after 32 days (Table 2). Germination of *Pericopsis* seeds occurred sooner than for the other two species and was complete within 14 days of sowing, while germination of *Afzelia* seeds would have probably continued beyond the 32-day monitoring period. *Milicia* showed an intermediate mean time to germination but a lower final germination percentage than the other two species.

Table 2. Mean and standard error time to germination (days) among the n_1 germinants and final germination percentage out of the n_2 seeds sown for *Afzelia, Milicia* and *Pericopsis* after 32 days

	Afzelia	*Milicia*	*Pericopsis*	
Mean time to germination (days)	25.8 ± 0.4^c	22.2 ± 0.3^b	12.4 ± 0.1^a	F = 745 ***
n_1	52	70	106	
Final germination (%)	45.2	23.3	45.3	X^2 = 34.1***
n_2	115	300	234	

Larger seeds showed a significantly higher final germination percentage in *Pericopsis*, but a lower final germination percentage in *Afzelia* (Table 3). *Afzelia* seeds in the smaller size class germinated almost two days earlier on average than those in the larger size class, whilst size class did not influence mean time to germination in *Pericopsis* (Table 3).

Table 3. Mean and standard error time to germination (days) among the n_1 germinants and final germination percentage out of the n_2 seeds sown for small (I) and large (II) seeds of *Afzelia* and *Pericopsis* as defined in Table 1

	Afzelia			*Pericopsis*		
	I	II		I	II	
Mean time to germination (days)	25.1 ± 0.4	26.9 ± 0.8	F = 4.5*	12.6 ± 0.2	12.4 ± 0.2	F = 0.5
n_1	34	18		34	72	
Final germination (%)	55.7	33.3	X^2 = 5.8*	35.1	52.6	X^2 = 7.0**
n_2	61	54		97	137	

Interspecific differences in seedling growth and form

Milicia had the smallest seeds (two and three orders of magnitude lower than *Pericopsis* and *Afzelia* respectively) and seedlings with the highest relative growth rates (RGR) among the three species (Table 4). The high RGR of *Milicia* seedlings was associated with a high allocation of dry mass to leaves with a high specific leaf area, combined with intermediate values of net assimilation rate per unit leaf area (unit leaf rate). Allocation of dry mass to stems was correspondingly low in *Milicia*.

The species with larger seeds also differed significantly in their relative growth rates, although the mechanism differed from the comparison of these two species with *Milicia* (Table 4). *Afzelia* seedlings had greater RGRs than those of *Pericopsis* and maintained much higher unit leaf rates (Table 4). The higher ULR of *Afzelia* was sufficient to more than offset its lower allocation of mass to leaf and lower SLA. Root mass ratio and SMR were consistently greater for *Afzelia* than the other two species. *Pericopsis* seedlings possessed the lowest RGRs and ULRs by a wide margin and intermediate values for all measures of plant form.

Table 4. Mean ± standard error of the mean seedling relative growth rate (RGR, mg g^{-1} day^{-1}), unit leaf rate (ULR, mg cm^{-2} day^{-1}), leaf area ratio (LAR, cm^{2} g^{-1}), specific leaf area (SLA, cm^{2} g^{-1}), leaf mass ratio (LMR), root mass ratio (RMR) and stem mass ratio (SMR) for *Afzelia, Milicia* and *Pericopsis*

	Afzelia	*Milicia*	*Pericopsis*	F
RGR (mg g^{-1} day^{-1})	60.8 ± 3.9^{b}	136 ± 3.2^{a}	15.8 ± 1.3^{c}	530***
ULR (mg cm^{-2} day^{-1})	0.424 ± 0.041^{a}	0.274 ± 0.008^{b}	0.056 ± 0.004^{c}	75.7***
LAR (cm^{2} g^{-1})	151 ± 29.7^{c}	491 ± 14.6^{a}	269 ± 8.6^{b}	202***
SLA (cm^{2} g^{-1})	422 ± 21.3^{c}	703 ± 31.4^{a}	586 ± 14.1^{b}	39.4***
LMR	0.36 ± 0.018^{c}	0.66 ± 0.020^{a}	0.52 ± 0.010^{b}	83.7***
RMR	0.27 ± 0.019^{a}	0.21 ± 0.019^{b}	0.19 ± 0.005^{b}	11.3***
SMR	0.37 ± 0.014^{a}	0.13 ± 0.010^{b}	0.29 ± 0.011^{c}	79.8***
n	25/26	20	36/37	
Harvest interval (days)	11	15	8	

Intraspecific differences in seedling growth and form

For *Afzelia*, but not *Pericopsis*, relative growth rates were significantly greater for seedlings derived from larger seeds, and in *Afzelia* there were corresponding, non-significant, trends for seedlings derived from larger seeds to possess a greater unit leaf rate and higher allocation to leaf area and leaf dry mass (Table 5).

Table 5. Mean ± standard error of the mean seedling relative growth rate (RGR, mg g^{-1} day^{-1}), unit leaf rate (ULR, mg cm^{-2} day^{-1}), leaf area ratio (LAR, cm^{2} g^{-1}), specific leaf area (SLA, cm^{2} g^{-1}), leaf mass ratio (LMR), root mass ratio (RMR) and stem mass ratio (SMR) for seedlings derived from small (I) and large (II) seeds for *Afzelia* and *Pericopsis* as defined in Table 1.

	Afzelia africana			*Pericopsis elata*		
	I	II	F	I	II	F
RGR (mg g^{-1} day^{-1})	49.1 ± 2.8	71.6 ± 7.1	6.1*	16.0 ± 2.9	14.9 ± 1.3	0.1
ULR (mg cm^{-2} day^{-1})	0.414 ± 0.059	0.447 ± 0.079	0.1	0.065 ± 0.016	0.057 ± 0.005	0.4
LAR (cm^{2} g^{-1})	131 ± 15.7	168 ± 16.1	2.5	273 ± 14.9	267 ± 9.3	0.1
SLA (cm^{2} g^{-1})	406 ± 33.8	455 ± 31.2	1.1	611 ± 23.8	563 ± 14.1	3.2
LMR	0.34 ± 0.021	0.38 ± 0.027	1.2	0.52 ± 0.017	0.53 ± 0.011	0.2
RMR	0.26 ± 0.022	0.26 ± 0.019	0.0	0.19 ± 0.009	0.19 ± 0.007	0.4
SMR	0.40 ± 0.020	0.36 ± 0.021	1.8	0.30 ± 0.020	0.28 ± 0.010	0.6
n	9	14		18	19	
Harvest interval (days)	11	11		8	8	

Discussion

We hypothesised that the small-seeded species, and small-seeded individuals within a species, would germinate faster and possess a higher relative growth rate (RGR) than the large-seeded species or individuals, and that these differences in RGR would be determined more by differences in leaf area ratio (LAR) than unit leaf rate (ULR). In cases where differences in RGR were determined by differences in ULR we predicted that the higher RGRs would be associated with species or individuals with higher N concentrations in the embryo-cum-endosperm (EE) fraction. We will evaluate these hypotheses separately for the two types of comparisons made in this study.

Differences between species

The three species differed in most germination and seedling growth characteristics, although not all of these differences could be related to seed size (Tables 2 and 4). For example, although the largest-seeded species (*Afzelia*) showed the lowest germination rate, the hypothesis was not supported for the comparison between *Milicia* and *Pericopsis.* Similarly, although *Milicia* was the smallest-seeded species and had the highest seedling relative growth rates, it had a relatively slow rate of germination. *Pericopsis,* with seeds of intermediate size, germinated much earlier than those of the two other species, and this behaviour would partially offset the much lower RGRs of its seedlings if similar behaviours occurred in the field. Thus the three species illustrate three different potential mechanisms for gaining early dominance of a new canopy gap: early germination (*Pericopsis*), fast growth (*Milicia*) or relatively large seed size (*Afzelia*). The ecological significance of the potential for early germination tends to have been ignored relative to seed size and seedling relative growth rate in comparative studies of light-demanding tropical tree species, and our study suggests that it might be an important factor for some species.

The species with the smallest seeds, *Milicia excelsa,* showed the highest relative growth rates and maintained the highest photosynthetic area per unit plant dry mass (Table 4). The high leaf area ratio of *Milicia* seedlings resulted from a high allocation of seedling dry mass to leaves with a large specific leaf area, as found for other tropical tree species (Osunkoya *et al.* 1994, Huante *et al.* 1995).

The direction of difference in RGR between *Afzelia* and *Pericopsis* was contrary to expectation based on the conventional seed size vs RGR trend, and the mechanism determining the difference was the greater ULR of the larger-seeded *Afzelia* seedlings (Table 2). Although *Afzelia* also possessed higher concentrations of N in the EE fraction than *Pericopsis,* it remains to be determined whether that factor contributed to their differential rates of net assimilation per unit leaf area. It is possible that these differences would become exaggerated for plants growing in competition or under limiting nutrient supply. For example, in the temperate annual herb *Abutilon theophrasti,* seedlings derived from seeds containing higher N concentrations are more successful in pairwise intraspecific competition experiments (Parrish & Bazzaz 1985). New experiments are needed to investigate whether the outcome of interspecific competition between tropical tree seedlings may be determined by a similar mechanism. Contrary to Grubb (1996), and Grubb and Coomes (1997), we found no trend of increasing N concentrations in the EE fractions of smaller seeds. Indeed for our smaller sample the opposite trend was suggested, although much more sampling would be required to determine the significance of this trend.

Differences within species

In *Afzelia,* seeds in the small size class germinated on average two days faster and to a greater extent than larger seeds (Table 3), and the earlier germination of smaller seeds was partially offset by the faster relative growth rates of seedlings from larger seeds (Table 5). All else being equal, these factors would tend to maintain intraspecific variation in seed size in this species. The lower final germination of the larger size class may simply reflect its later germination and the fact that germination was not complete when monitoring stopped. In *Pericopsis,* the variation in mean seed size between size classes was much lower (Table 1) and there was no effect of size class on germination rate or seedling relative growth rate, although larger seeds showed a higher final germination percentage (Tables 3 and 5). These results suggest that seed size variation in *Afzelia* is maintained by the differential germination and seedling growth characteristics of small vs. large seeds, but minimised by the lack of such differences in *Pericopsis.*

Other studies have also found widely varying effects of increasing seed size on germination rates, e.g. a decrease in *Trifolium subterraneum* (Black & Wilkinson 1963) and *Rumex obtusifolius* (Cideciyan & Malloch 1982) and an increase in *Hyptis suaveolens* (Wulff 1973), *Mirabilis hirsuta* (Weis 1982), and two Himalayan *Quercus* spp. (Tripathi & Khan 1990). Different species also vary in the relationship between seed size and RGR (c.f. Choe *et al.* 1988, Zhang & Maun 1990, Hendrix *et al.* 1991). It is possible that differential amounts of seed size variation within species contribute to the diversity of outcomes obtained in experiments of this kind.

In *Pericopsis,* the N concentration of the embryo-cum-endosperm (EE) fraction increased with EE dry mass (Table 4, Figure 1), but there was no difference between size classes in mean relative growth rate. In *Afzelia,* seedlings from the larger size class of seeds possessed a significantly greater RGR, but there was no relationship between EE dry mass and its N concentration. Therefore there is no support for the hypothesis of a mechanistic link between N concentration in the EE and seedling relative growth rates under the experimental conditions we used, although it remains to be determined whether a link would emerge under conditions of limiting N supply.

Some of these results contrast with a number of recent studies of tropical forest trees and other species. For example, a negative, rather than positive, relationship between EE dry mass and its N concentration was found for 10/12 species of Southeast Asian woody plants from relatively aseasonal rain forests on nutrientpoor soil (Grubb & Burslem 1998). The positive correlations between seed size and N concentrations in the EE fraction (Figure 1) may have occurred for a variety of reasons. For example, we cannot discount the possibility that our sample of *Pericopsis* seeds was collected from a range of mother trees which differ in their N status.

The concentrations of N in the EE fraction are also mostly greater in the three African species (means 2.5–3.0 %) than the Southeast Asian species (means 0.4–1.9 %, plus 5.7 % for *Albizia splendens*) studied by Grubb and Burslem (1998). However, the inter-continental comparisons are confounded by phylogenetic differences. A more appropriate comparison is that between the respective papilionoid legumes from Africa, *Pericopsis elata* (EE mean dry mass 211 mg, N concentration 2.7 %), and Southeast Asia, the climber *Derris thyrsiflora* (EE mean dry mass 206 mg, N concentration 2.3 %, P.J. Grubb and D.F.R.P. Burslem, unpublished data). Any difference in N concentrations might reflect the lower nitrification potential of the strongly leached and acidic Southeast Asian soils compared to the soils of much greater pH in the less seasonal African semi-deciduous dry forest (c.f. Grubb *et al.* 1994, Swaine *et al.* 1997), although the edaphic controls on the nutrient concentration of tropical forest tree seeds remain poorly understood.

Conclusion

Small-seeded species within a functional group and small-seeded individuals within a species do not always possess higher RGRs, and do not need to if differential germination rates contribute to the process of early colonisation of newly-created regeneration sites. Similarly, not all differences in seedling RGRs are determined by differences in LAR and SLA, possibly because the higher concentrations of nutrients in the seeds of some species allow them to develop higher rates of assimilation per unit leaf area. Finally, differential germination and seedling growth characteristics of small vs. large seeds within a species may contribute to the maintenance of seed size variation. Field experiments are now required to determine the ecological signficance of these findings.

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