2 THE IMPORTANCE OF SEED MASS FOR EARLY REGENERATION IN TROPICAL FOREST: A REVIEW

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Abstract

Seed mass is an important component of the shade tolerance of rain forest tree species. Using a meta-analysis we evaluate till what extent seed mass affects the survival, initial size, and growth of seedlings in light environments that are typical of forest gaps and understorey.

Early seedling survival in low light was positively correlated with seed mass, and about two-fold larger for large-seeded species (>0.1 g) compared to small-seeded species (<0.1 g). Survival of the two seed size groups was comparable in high light. Initial size (height, leaf area, biomass) was positively correlated with seed mass. The relationship was stronger when seedlings were compared shortly after emergence and when seedlings were grown at low irradiance. Height ranged from 1-68 cm, leaf area from 1-1500 cm^2, and biomass from 0.007-28g for the smallest-seeded species compared to the largest seeded species. A large initial size enables the seedling to penetrate the leaf litter layer, to escape size-dependent mortality, to be more resilient after disturbance, and to get a better access to resources. Seed mass is a good predictor of plant traits under high-light conditions. At high irradiance seed mass is negatively correlated with the Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Leaf Area Ratio (LAR), Specific Leaf Area (SLA) and Leaf Mass Fraction (LMF), with average coefficients of determination ranging from 0.19 to 0.52. At low irradiance seed mass is only negatively correlated with LAR and SLA For all growth parameters but LMF, the small-seeded species show a more plastic response to an increase in irradiance than the large seeded species.

Small-seeded species have a similar RGR at low irradiance compared to large-seeded species, whereas at high irradiance they realise a higher RGR. The RGR of small-seeded species tends to cross-over with the RGR of large-seeded at irradiance levels below 5%. Large-seeded species have a large initial size but an inherently low RGR. Under high light conditions as found in forest gaps, it would take small-seeded species such as *Cecropia* 6 months to overtake the large-seeded species in size. Small-seeded species need therefore a small time-window of opportunity to attain a dominant position in the regrowing vegetation before the gap is closed.

Introduction

Seed mass varies over 10 orders of magnitude in weight amongst species, from 10^{-6}g in orchids to more than 10^4g for the double coconut *Lodoicea seychellarum* (Harper 1977). Even within plant communities, the seed mass may span a range of 10^5 (Westoby *et al*. 1992). In a Guyanan rain forest, for example, the dry seed mass of woody species ranges from 0.1 mg to 82 g (Figure 2.1, Hammond & Brown. 1995).

Seed mass is considered an important ecological attribute of plants, reflecting interactions between past environment pressures and the evolutionary history of taxa (Westoby *et al*. 1992, Westoby 1998). It has been shown that seed mass plays an important role in seed dispersal (Augspurger 1984b, Westoby *et al*. 1996), seedling establishment (Grime & Jeffrey 1965, Gross 1984, Leishman & Westoby 1994, Lusk 1995, Kidson & Westoby 2000), initial seedling size (Boot 1993 1996), early seedling growth, and competitive ability (Westoby *et al*. 1992, Grubb 1996, Kidson & Westoby 2000).
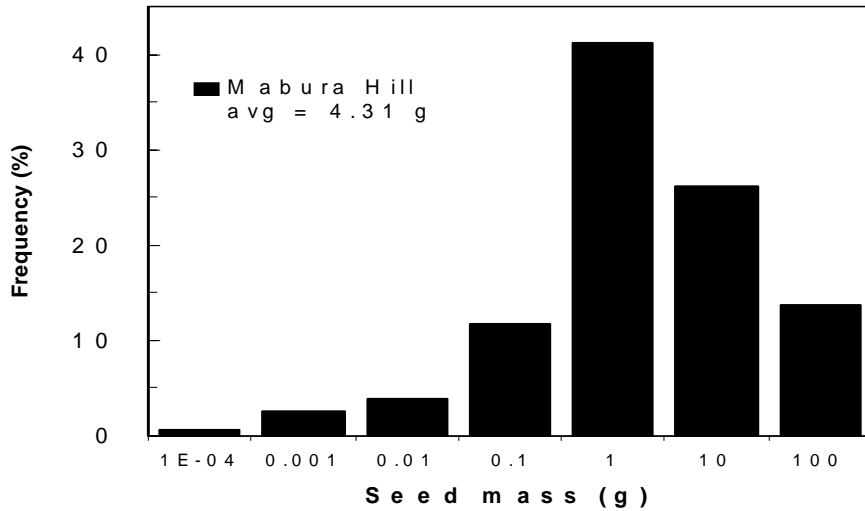
Figure 2.1   Frequency distribution of dry seed mass of 153 woody species in Mabura Hill, Guyana. The average dry seed mass is 4.31 g. Labels: 100 refers to the size class 10 – 100g. Data from Hammond & Brown (1995).

Seed mass is especially seen as an important component of shade tolerance (Leishman & Westoby 1994). Shade tolerance here is defined as the ability of a species to establish, persist, and grow in the shade. A large seed may enable a seedling to survive for a longer period while the seedling is in net carbon deficit (Grime & Jeffrey 1965, Saverimuttu & Westoby 1996), allowing the seedling to survive in the understorey until the formation of a canopy gap. A large seed produces also a larger seedling and thus results in an initial size advantage. The duration of this size advantage, however, depends on the light environment: in large gaps the initially large seedlings of large-seeded species may soon be overtaken by seedlings of small seeded species with higher growth rates (Boot 1993, Rose 2000).

Rain forest trees have been divided into shade-tolerant and shade-intolerant species according to their responses to light. The first group tends to have large seeds that can germinate and persist in the shaded forest understorey, while the second typically has small, widely dispersed seeds from which seedlings establish mainly in gaps (Swaine & Whitmore 1988). In the Guyanan forest of Mabura Hill, for example, shade-tolerant species have about four times the average seed mass of pioneers (Hammond & Brown 1995). Both groups, however, show widely overlapping ranges in seed mass (Figure 2.2). Indeed, in many tropical rain forest floras, there are shade-tolerant understorey species that have minute seeds (< 50 mg) (Grubb 1996).

In this review, we evaluate the importance of seed mass for tropical forest regeneration by examining the relationship of seed mass with early seedling growth, morphology and physiology.
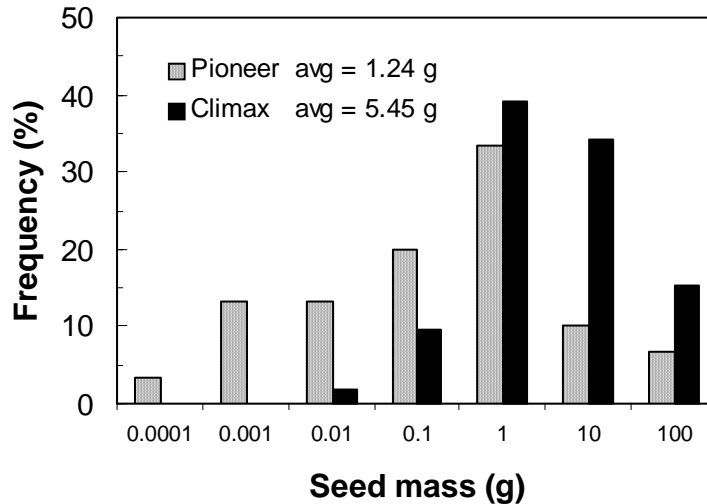
Figure 2.2 Frequency distribution of dry seed mass of woody pioneer species (n=30, grey bars) and climax species (n=105, filled bars) in Mabura Hill, Guyana. The average dry seed mass of pioneer and climax species is respectively 1.24 and 5.45 g. Labels: 100 refers to the size class 10 – 100g. Data from Hammond & Brown (1995).

We address the following questions:

1.   Does seed mass increase seedling survival in low light?
2.   Do large seeds give rise to large seedlings?
3a.   Is seed mass a good predictor of the inherent growth rate of species, and plant traits related to growth?
3b.   Are small seeded species more plastic in properties underlying RGR and hence better capable of adjusting RGR to an increase in light?
4.   At what level of irradiance and after how much time does the initial size advantage of large-seeded species disappear, and are they overtaken by small-seeded species with high RGRs?

We selected 14 published studies, in which seedling germination, recruitment, survival and growth of a wide range of species with varying seed masses was studied in different light environments (Table 2.1). Subsets of these studies were used for the different aspects reported on in this paper because they met the specific criteria required for the questions posed. The assessment of seedling survival required that studies included at least six species with 1000-fold difference in seed mass (< 0.1 g were considered small seeds, > 0.1 g were considered large seeds), grown in at least two different light environments. To address the influence of seed mass on initial seedling size, studies in which seeds of at least 5 species were germinated at low irradiance and/or high irradiance. The evaluation of the seed mass – seedling growth relationship required that a growth analysis had been carried out,

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Table 2.1   Studies reviewed in this paper. The table shows the number of species included in each study, the light levels (as % of full light, with the exception of the study of Peña-Claros and Rose, for which respectively successional age and gap size are given), and for which type of analysis the study has been used. In bold it is indicated which light levels of each study are selected as being representative of low and high irradiance.

Reference	Nr. species	Light levels (%)	Survival	Initial size	Growth	Cross-over
Agyeman *et al.* (1999)	16	**1.9**, 6, 10, **28**, 44, 66			x	x
Augspurger (1984a)	18	**1, 20**	x			
Barigah *et al.* (1998)	10	**4**, 10, **25**, 45, 65			x	
Boot (1996)	6	**2.2**, 9, **30**			x	x
Boot (1993)	6	0.9, **1.8**, 4.3			x	
Huante & Rincon (1998)	10	**20**, 70		x	x	
Kitajima (1994)	13	**1.9**, **23**		x	x	
Osunkoya *et al.* (1994)	12	**2.5**, 10, **37**		x	x	x
Peña-Claros (2001)	6	**1**, 10, **20** year old secondary forest	x		x	
Poorter (1999)	15	**3**, 6, 12, **25**, 50, 100			x	x
Popma & Bongers (1988)	10	**1.6**, 4, **46**		x	x	
Rose (2000)	8	**understorey**, 50, 100, 200, 400, 800, 1600, **3200** m^2 gap	x	x	x	x
Swaine *et al.* (1997)	6	**5**, 8, 16, **27**, 60	x		x	x
Veenendaal *et al.* (1996)	8	**4**, 8, 16, **27**, 60/ 100			x	

at low irradiance (<5%), and/or high irradiance (20-40%) using seedlings of at least 6 species ranging from small seeded to large seeded.

Does seed mass increase seedling survival in low light?

Early survivorship of seedlings in low light varies widely and continuously among tropical tree species (Augspurger 1984a, b, Brokaw 1985, Li *et al.* 1996). In the past few years it has been found that small-seeded light-demanding species are able to germinate and establish in the shaded forest understorey or small gap environments (Raich & Gong 1990, Kyereh, *et al.* 1999, Peña-Claros 2001). These species, however, lack the ability to survive for long periods under these conditions (Li *et al.* 1996, Peña-Claros 2001). If low irradiance is a key factor determining seedling mortality in the shaded understorey, then survival of seedlings in shade will depend on, among other things, the total amount of reserves in the seed and the rate of carbon fixation and respiration of the seedlings under the prevailing light conditions. It follows therefore that seedling survival should be positively related to seed mass

in low light with this relation becoming obscure as irradiance increases. To answer this question a meta-analysis of early survival was carried out for four greenhouse and field studies in which species were grown at two light levels (Table 2.1).

From this analysis is becomes clear that seed mass is positively related to survival in low light, whilst both groups of species survived equally well in high light conditions (Figure 2.3). Small seeded species showed on average 34 % survival in low light when compared with 79 % in high light. Large seeded species on the other hand, recorded 75 % survival in low light and 84 % in high light. Many other studies have also found that large-seeded species persisted longer in shaded conditions and survival chances of small-seeded species increased with an increase in irradiance (Denslow *et al*. 1990, Alvarez-Buylla & Martinez-Ramos 1992, Boot 1996). For the species included here, larger seed size resulted in a two-fold increase in survival in the shade. Such an increase in survival enhances the chance of large-seeded species to survive until a canopy gap is formed, and profit from the increased light availability.

Why is the influence of seed mass on survival restricted to low light environments? Boot (1996) has argued that seed mass is only influential on seedling survival at irradiance levels below the whole-plant light compensation point. At such low irradiance, species with a low metabolic activity (expressed by a low inherent RGR) have an increased longevity (Saverimuttu & Westoby 1996), but at higher irradiance
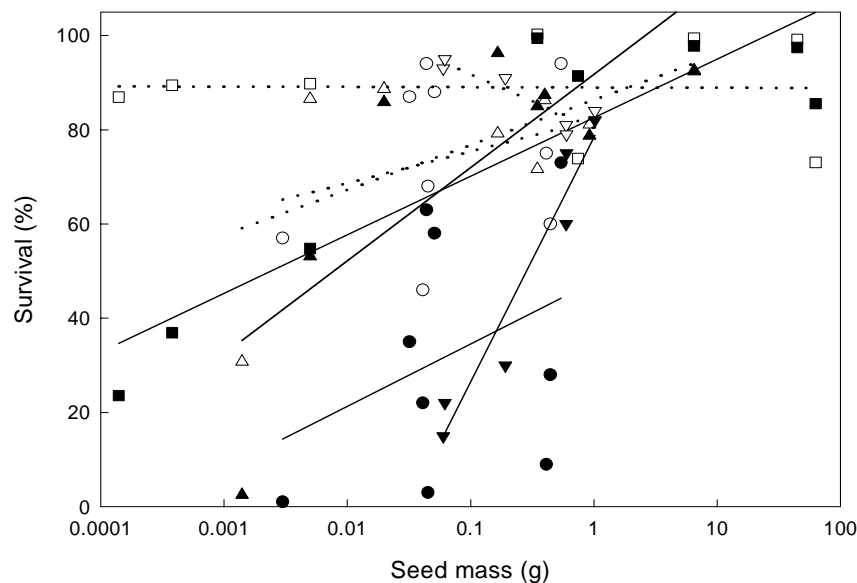

Figure 2.3   Survival rates after approximately two months for tropical rain forest species growing at high irradiance (open symbols, broken regression line) and low irradiance (filled symbols, continuous regression line). Data are from Augspurger 1984 (circle), Swaine *et al*. 1997 (downward triangle), Rose 2000 (square), Peña-Claros 2001 (upward triangle).

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levels the amount of stored reserves and the rate at which these are reallocated to stem, roots and leaves are less important for survival, since light is not limiting. Another reason may be that small-seeded species are prone to herbivory (Kitajima 1996). With so little reserves available, they are not able to recover in the understorey, as a large seeded species with abundant resources may be able to do (Harms & Dalling 1997).

Do large seeds give rise to large seedlings?

To address the question if large seeds result in large seedlings, we evaluated three size-related traits (height, leaf area, and whole-plant biomass) that are crucial for plant performance in a forest environment. Plant height after emergence determines whether seedlings are able to emerge from the litter layer, and whether they are able to overtop neighbouring understorey plants and get access to light. The leaf area determines the ability to capture light. The total biomass is closely associated with the size of the foraging organs, and the resistance to falling debris and herbivores.

We selected five greenhouse and field studies (Table 2.1) in which seeds of different species were germinated at the same time and in which seedlings were compared within 2 months of germinating. These studies were carried out at low irradiance (<5%) and/or a high irradiance (20-40% of full light).

Correlations with seed mass
All three size variables showed a close, positive, correlation with seed mass (Figure 2.4). The strength of the correlations changed with the duration and irradiance level of the study. Responses were greater when seedlings were compared shortly after emergence (e.g., the study of Kitajima (1994), in which seedlings were evaluated after 8 weeks), and when seedlings were grown at low irradiance (Figure 2.4).

Height was positively correlated with seed mass for three out of four comparisons, with the slopes being almost identical (Figure 2.4a). Height ranged from 1 cm for small-seeded species to 68 cm for large seeded species. A similar positive relationship with seed mass has been found amongst 50 temperate species (Ganade & Westoby 1999). The greater height of large-seeded species is both the result of a greater biomass and a stronger etiolation response (Leishman & Westoby 1994, ter Steege *et al.* 1994).

Figure 2.4 (Opposite page) The relationship between seed mass and a) seedling height, b) leaf area, and c) total biomass. Data are based on a literature compilation. Species were grown at low irradiance (0-5%, filled symbols) or high irradiance (20-40%, open symbols). Each data point represents a different species. Regression lines are shown for each study separately (significant regressions as continuous lines, insignificant regressions as broken lines). Data are from Popma & Bongers 1988 (circles), Osunkoya *et al.* 1994 (diamonds), Kitajima 1994 (triangles), Huante & Rincon 1998 (hexagonals), Rose 2000 (squares).
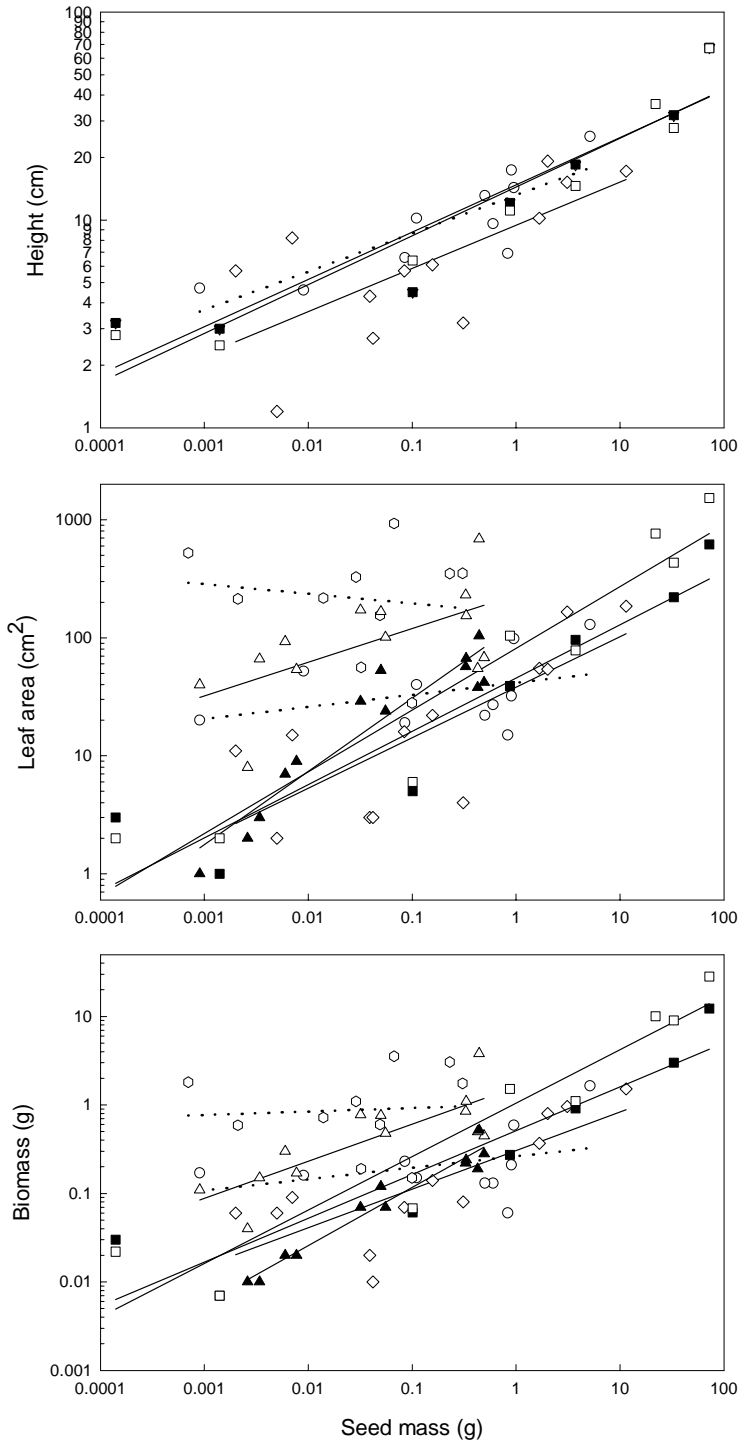
Total leaf area was positively correlated with seed mass for 5 out of 7 studies. Leaf area ranged from 1 cm^2 in the smallest seeded species, to 1500 cm^2 in the largest seeded species (Figure 2.4b). The total leaf area is a function of the leaf mass, and the amount of leaf area species can deploy with a given leaf mass (the Specific Leaf Area; SLA). The total leaf mass is tightly correlated with the seed mass, but the SLA tends to be larger for small-seeded species compared to large-seeded species (see the section on growth analysis). As a consequence, the relationship between total leaf area and seed mass is less tight than first expected. There was considerable variation in leaf area at a given seed mass between studies. This is probably caused by differences in length of the growing period and environmental conditions between studies. As noted above, the total leaf area is strongly affected by SLA, which varies substantially with ontogeny and irradiance (see the section on growth analysis, Veneklaas & Poorter 1998, and Poorter 1999).

Biomass was significantly correlated with seed mass for 5 out of 7 studies. Biomass ranged from 7 mg in the smallest seeded species, to 28 g in the largest seeded species (Figure 2.4c). A similar positive relationship with seed mass was found between 80 temperate woody species (Cornelissen *et al.* 1998). The larger amount of energy and nutrients stored in the endosperm allows large-seeded species to produce bigger seedlings (Kitajima 1996).

Penetration of the litter layer
What is the functional significance of having a large initial size? In a Bolivian moist forest, most species start to germinate at the onset of the rainy season. Similar patterns have been found in Panama and Guyana (Garwood 1983, ter Steege *et al.* 1994). At this moment the leaf litter layer is on average 3.6 cm thick (measured as the distance between the soil and the upper leaf of the loose litter layer). Only 5% of the forest floor consists of bare soil, while 23% has a litter thickness of more than 5 cm (L. Poorter, unpublished data). The presence of a litter layer may hamper the germination and establishment of plants (Molofsky & Augspurger 1992, Peña-Claros 2001) and reduce their photosynthesis (Facali & Pickett 1991). The establishment of tiny-seeded species (with a seed mass < 50 mg) is therefore confined to litter-free places, rocky microsites (Grubb 1996) or logs (Lusk 1995, Van der Meer *et al.* 1998). While small seed reserves may not permit seedling radicles to penetrate the thick litter layer (Putz 1983), large-seeded species do form a longer radicle or hypocotyl, which allows them to penetrate the litter layer successfully (Kidson & Westoby 2000). Also, for seeds that germinate under the litter layer a large initial seedling size allows them to pass through it. Indeed, Molofsky and Augspurger (1992) found that large seeded species had a larger establishment success in a litter treatment compared to small seeded species.

Escape from size-dependent mortality
Large seedlings have a considerably higher survival rate compared to small seedlings (section 1 and references therein). For example, survival rates of the understorey tree *Duguetia neglecta* increase rapidly with size, from 75% y^{-1} for seedlings < 15 cm height, via 94% y^{-1} for seedlings between 15-30 cm, to 100% y^{-1} for seedlings between 30-65 cm (Zagt 1997). It is likely that size drives differences

in survival, rather than age; larger seedlings have a higher survival rate because they can explore a larger air and soil volume to capture resources, and because they are more resistant to damage. Probably the same mechanism operates between species, if their seedlings are dissimilar in size.

Access to resources
Vertical expansion is especially important when resource gradients are unidirectional, as is the case for light, or for soil water in the dry season. Tall seedlings may overtop neighbouring plants and herbs and get access to light, especially in dense seedling banks. However, the vertical light gradient in the understorey is not very steep (Yoda 1974, Zagt 1997, Arets 1998), and therefore it is not likely that a 40 cm tall plant receives considerably higher light levels than a 10 cm tall plant, which may have its leaves at the same height or above the carpet of seedlings and herbs at the forest floor. The greater height may confer an advantage, once a gap is opened up in the canopy and there is a strong competition between the plants during gap-phase regeneration (Zagt & Werger 1998).

A larger leaf area allows seedlings to intercept more light. Whether such a large leaf area also implies a more positive carbon balance, depends on the ratio between leaf area and plant respiring tissue (the Leaf area Ratio; LAR) (Boot 1996).

Tall seedlings take advantage from a better access to soil water. Poorter and Hayashida-Oliver (2000) studied the performance of *Cedrela odorata* seedlings during the dry season, and found that large plants had a deeper root system, and disproportionally better access to soil water compared to small plants (cf. Veenendaal *et al.* 1996a, b). As a consequence, large seedlings experience less drought stress, and a shorter leafless period (Poorter & Hayashida-Oliver 2000).

Susceptibility to, and resilience after disturbance
Large seedlings suffer less from disturbance than do small seedlings. Falling debris, and herbivory are important disturbance agents in tropical forests. Twenty five percent of the understorey seedlings are exposed annually to falling debris (Clark & Clark 1989), and on average 10% of the leaf area is removed annually by herbivores (Coley & Barone 1996). Litterfall-induced stem damage is larger than 20% y^{-1} for small seedlings, whereas this declines to 7% y^{-1} for plants > 50 cm tall (Clark & Clark 1991). Large seedlings are, in addition to that, more resilient after biomass loss due to disturbance. The larger pool of non-structural carbohydrate reserves stored in the stem and roots enables them to recuperate from biomass loss due to herbivory or falling debris, and produce new sprouts and leaves (Armstrong & Westoby 1993, Harms & Dalling 1997).

Is seed mass a good predictor of the inherent growth rate of tree species and their plasticity?

In addressing this question we specifically sought to determine whether this relationship varied with irradiance, and what were the underlying mechanisms. To

evaluate this, one should compare the growth of different species. The absolute growth rate of seedlings is strongly size dependent. Comparisons between species and individuals differing in size are therefore most straightforward using the Relative Growth Rate (RGR, biomass growth per unit plant biomass, in mg g^{-1} d^{-1}). To analyse what underlying plant traits give rise to interspecific differences in RGR, we analysed the RGR as the product of a "physiological" plant trait, the Net Assimilation Rate (NAR; biomass growth per unit leaf area, in g m^{-2} d^{-1}), and a morphological plant trait, the Leaf Area Ratio (LAR; leaf area per total plant mass, in m^2 kg^{-1}). LAR can be factored into the biomass allocated to the leaves, the Leaf Mass Fraction (LMF; leaf mass per unit plant mass, in kg kg^{-1}), and the leaf area constructed with this leaf biomass, the Specific Leaf Area (SLA; leaf area per unit leaf mass, in m^2 kg^{-1}).

We selected 13 published studies, in which: a) a growth analysis was carried out, b) at least 6 species were compared, and c) seedlings were grown at low irradiance (<5%), and/or high irradiance (20-40%) under greenhouse conditions or in the field. The low irradiance is typical for the light levels encountered in the forest understorey, whereas the high irradiance is typical for large treefall gaps and logging gaps. In most studies the first harvest was carried out after the cotyledons were exhausted, or had been abscised. The seed mass was therefore not included in the calculation of the RGR (but see Kitajima 1994, Rose 2000). If data on NAR were not available (e.g., Kitajima 1994), we calculated NAR as the ratio of RGR over LAR.

For each combination of study and light level, we regressed RGR and its components on log-transformed seed mass (in g), using species as data points (Figure 2.5 a-e). If a regression slope differed significantly from zero, then seed mass is correlated with growth-related species traits. To evaluate whether all studies show a similar trend with seed mass, we used a t-test to determine whether the mean slope differed from zero, using independent studies as data points. It is often hypothesised that small-seeded species have a more plastic response to increased irradiance than do large-seeded species. If this is true, then the regression slope at high irradiance should be steeper than the slope at low irradiance. Therefore, we compared the regression slopes for each study at both high and low irradiance, using a paired t-test.

Relative Growth Rate
At high irradiance the RGR decreased with the seed mass of the species (Figure 2.5a, Table 2.2, t-test, P<0.01) (cf. Swanborough & Westoby 1996). A similar, negative relationship was found in an experiment with 80 temperate woody species (Cornelissen *et al.* 1996). Small-seeded pioneer species are able to profit from high irradiance, and realise a higher growth rate than the large seeded species. At low irradiance the relationship between growth and seed mass can be negative, absent, or positive, dependent on whether the light levels are well above (3%, Poorter 1999), around (2.5%, Osunkoya *et al.* 1994) or below (1.9%, Popma & Bongers 1988) the light compensation point of the pioneer species. As a consequence, the overall relationship between RGR and seed mass is not significant at low irradiance (t-test,
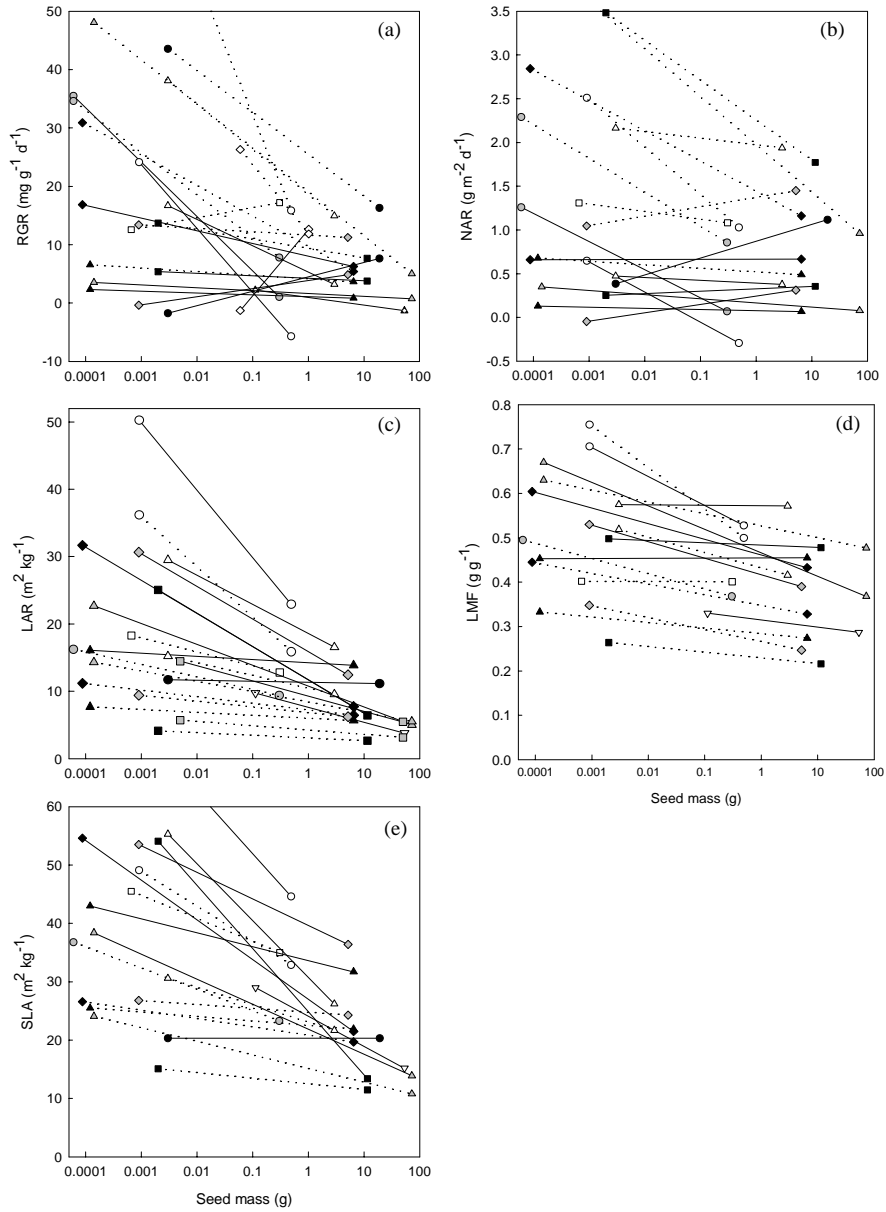
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Figure 2.5 Regression lines of growth analysis parameters regressed on log(seed mass), for low light (continuous lines) and high light (broken lines) grown plants. Regression lines connect the lowest and highest seed mass included in each study. The different symbols at the extremes of the regression lines indicate the different studies. Data are from Agyeman *et al*. 1998 (black circles), Boot 1993 (open downward triangles), Boot 1995 (grey circles), Huante & Rincón 1998 (open squares), Kitajima 1994 (open circles), Osunkoya *et al*. 1994 (black squares), Peña-Claros 2001 (black triangles), Poorter 1999 (black diamonds), Popma & Bongers (grey diamonds), Swaine *et al*. 1997 (open diamonds), Veenendaal *et al*. 1996 (open triangles), Rose 2000 (grey triangles).

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Table 2.2   Regression coefficients of growth analysis parameters (RGR, NAR, LAR, SLA and LMF) regressed on log(seed mass), for low light (LL, <5% irradiance) and high light (HL, between 20 and 40% irradiance) grown plants respectively. The regression slope (b), coefficients of determination (r^2), and significance level (P) are shown for each study separately, and for all studies combined (Overall). N indicates the number of species in LL and HL respectively.

REF	N	RGR						NAR					
		LL			HL			LL			HL		
		b	r2	p	b	r2	p	b	r2	p	b	r2	p
Agyeman et al. (1999)	17/17	2.46	0.11	ns	-7.17	0.38	ns	0.193	0.03	ns			
Barigah et al. (1998)	9/9												
Boot (1993)	6/0	-1.32	0.59	ns									
Boot RGA (1995)	4/6	-5.57	0.08	ns	-7.24	0.84	*	-0.095	0.11	ns	-0.367	0.66	ns
Huante & Rincon (1998)	0/10				-3.52	0.13	ns				-0.086	0.04	ns
Kitajima (1994)	13/13	-10.91	0.73	***	-23.66	0.78	***	-0.344	0.59	**	-0.541	0.38	*
Osunkoya et al (1994)	12/12	-0.42	0.10	ns	-1.61	0.57	**	0.028	0.09	ns	-0.455	0.19	ns
Pena-Claros (2001)	5/7	-0.31	0.67	ns	-0.62	0.45	ns	-0.013	0.56	ns	-0.040	0.40	ns
Poorter (1999)	15/15	-2.17	0.38	*	-5.23	0.65	***	0.001	0.00	ns	-0.345	0.28	*
Popma & Bongers (1988)	10/10	1.40	0.34	**	-0.57	0.04	ns	0.095	0.36	ns	0.107	0.10	ns
Rose et al. (2000)	7/8	-0.49	0.17	ns	-7.54	0.93	***	-0.048	0.10	ns	-0.545	0.55	*
Swaine et al. (1997)	6/6	11.29	0.60	ns	-11.75	0.43	ns						
Veenendaal et al. (1996)	8/8	-4.51	0.77	**	-7.74	0.49	ns	-0.032	0.04	ns	-0.075	0.01	ns
Overall		-0.96	0.41	ns	-6.97	0.52	**	-0.02	0.21	ns	-0.26	0.29	*

 P>0.05). The small-seeded species, however, show a stronger increase in growth with an increase in irradiance (paired t-test, n=10, P<0.05) (cf. Leishman & Westoby 1994). An opening in the canopy due to natural treefall or to logging favours small-seeded species therefore more strongly than the less plastic large-seeded species.

There are two reasons why small seeded species have a high inherent RGR. First, RGR declines with the size of plants. When plants grow taller, they have a larger part of their biomass in stem and a smaller part of their biomass in leaves, leading to a low LAR and thus a low RGR. Since large seeds give rise to large seedlings, it is likely that part of the association of RGR and seed mass is caused by this decreasing RGR (ter Steege 1990, Walters *et al.* 1993). Second, small-seeded species are characterised by a high NAR and LAR, which allows them to realise a high growth rate, as discussed below.

Net Assimilation Rate
Light-dependent changes in RGR are paralleled by the changes in NAR. NAR decreases with the seed mass at high irradiance (Figure 2.5b, Table 2.2, t-test, P<0.05), while this relationship breaks down at low irradiance (t-test, P>0.05). As a consequence, small-seeded species show a stronger increase in NAR with an increase in irradiance (paired t-test, n=8, P<0.05). The NAR is closely related to the whole-plant rate of photosynthesis (Poorter & van der Werf 1998). In general, plants adjust their photosynthetic capacity to the light environment (Rijkers 2000). There is little scope for a high photosynthetic capacity in the understorey, as the maintenance costs are high, and the probability of high irradiance during sunflecks is low. Large-seeded climax species that are adapted to the forest understorey have therefore a low inherent photosynthetic capacity. Small-seeded pioneer species are adapted to the high irradiance of gaps. In such an environment it is advantageous to have a high light-saturated photosynthetic rate. However, such a high photosynthetic capacity cannot be maintained in the understorey. As a result, small-seeded pioneer species

Table 2.2   Continued.

| LAR | | | | | | SLA | | | | | | LMF | | | | | |
| LL | | | HL | | | LL | | | HL | | | LL | | | HL | | |
b	r2	p	b	r2	p	b	r2	p	b	r2	p	b	r2	p	b	r2	p
-0.15	0.00	ns				0.01	0	ns									
-2.25	0.35	ns	-0.64	0.27	ns												
-2.21	0.49	ns				-5.17	0.62	ns				-0.016	0.08	ns			
-17.02	0.79	ns	-2.10	0.81	*	-29.39	0.34	ns	-3.99	0.5	ns	-0.239	0.73	ns	-0.038	0.84	*
			-2.06	0.18	ns				-3.95	0.08	ns				0.000	0.00	ns
-10.01	0.69	***	-7.43	0.59	**	-10.63	0.47	*	-5.92	0.24	ns	-0.065	0.30	ns	-0.093	0.73	***
-4.95	0.56	**	-0.39	0.12	ns	-10.82	0.41	*	-0.95	0.16	ns	-0.005	0.01	ns	-0.013	0.02	ns
-0.46	0.04	ns	-0.43	0.08	ns	-2.37	0.07	ns	-0.76	0.09	ns	0.000	0.00	ns	-0.012	0.02	ns
-4.91	0.71	***	-0.97	0.14	ns	-6.80	0.43	**	-1.42	0.1	ns	-0.035	0.14	ns	-0.024	0.06	ns
-4.84	0.12	**	-0.85	0.92	ns	-4.55	0.15	ns	-0.65	0.02	ns	-0.037	0.29	ns	-0.027	0.19	ns
-3.09	0.92	**	-1.54	0.48	ns	-4.27	0.87	*	-2.31	0.36	ns	-0.053	0.98	***	-0.027	0.27	ns
-4.32	0.35	ns	-1.89	0.15	ns	-9.73	0.57	*	-2.98	0.14	ns	-0.001	0.00	ns	-0.034	0.13	ns
-4.93	0.46	**	-1.83	0.37	*	-8.37	0.39	**	-2.55	0.19	**	-0.05	0.28	0.078	-0.03	0.25	**

have a high plasticity in both their photosynthetic capacity and their NAR (Raaimakers *et al*. 1995, Strauss-Debenedetti & Bazzaz 1996).

Leaf Area Ratio and its components

The Leaf Area Ratio (LAR) indicates the "leafiness" of the plant. LAR is negatively correlated with the seed mass in both light environments (Figure 2.5c). This relationship is more pronounced at low irradiance than at high irradiance (paired t-test, $P < 0.05$ in both cases). A high LAR in the understorey allows plants to enhance their light interception in a light-limited environment. Surprisingly, the large-seeded climax species, which are supposedly adapted to the understorey, are characterised by a low LAR (cf. Veneklaas & Poorter 1998)! The higher LAR of small seeded species is mainly caused by a high Specific Leaf Area (SLA, Figure 2.5e) and, to a lesser extent, by a high Leaf Mass Fraction (LMF). The SLA indicates how efficient leaf area is deployed per unit leaf biomass invested. The LMF is negatively correlated to seed mass at high irradiance (t-test, $P<0.01$), but this relationship disappears at low irradiance (t-test, $P>0.05$) (Figure 2.5d). The high LAR helps small-seeded pioneer species to grow faster than shade-tolerant species at moderate shade. This rapid growth, however, is at the expense of an increased risk of mortality. Kitajima (1994) found a positive relationship between the LAR of species, and their mortality rate in the shade. This is most probably caused by the high SLA, which is characteristic of species with a high LAR. A high SLA is associated with thin, watery leaves, thin cell walls, low lignin content and low leaf toughness (Coley 1983, van Arendonk & Poorter 1994, Cornelissen *et al*. 1999).

Such leaves are more susceptible to fungal pathogens (Augspurger 1984b), and more attractive to herbivores (Coley 1983, Cornelissen *et al*. 1998). A loss of biomass, due to wilting or herbivory, is especially deleterious in the shade, as carbon gain is

low and lost biomass is not easily replaced. As a consequence, the small-seeded species trade high growth for high survival.

Is seed mass a good predictor of plant traits related to growth?

Seed mass appears to be a good predictor of plant traits under high-light conditions. At high irradiance seed mass is negatively correlated with RGR, NAR, LAR, SLA and LMF, with average coefficients of determination ranging from 0.19 to 0.52 (Table 2.2). At low irradiance seed mass is only negatively correlated with LAR and SLA, with corresponding mean coefficients of determination ranging from 0.39 to 0.46. For all growth parameters but LMF, the small-seeded species show a more plastic response to an increase in irradiance than the large seeded species.

Differences between small and large seeded species in inherent growth rate and morphological and physiological traits closely parallel the observed differences between pioneer and shade tolerant species (Veneklaas & Poorter 1998, Walters & Reich 1999). There are also important exceptions: *Carapa guianensis*, one of the large-seeded species in this study, has an RGR comparable to small seeded species and the high RGR of *Cecropia obtusa* in the study of Rose (2000) was not based on a high SLA but a high NAR (thick leaves with a high photosynthetic capacity) (Pons *et al.*, in press). Classifying species into functional groups, based on their seed mass is, however, still far less arbitrary, than classifying species into pioneers and shade tolerant species, based upon observed habitat preferences in the field. Such a seed mass based classification may provide in addition a powerful tool to predict species responses to (changes in) the light environment (cf. Westoby 1998).

When do small and large seeded species cross-over?

At what irradiance level do small and large seeded species cross-over?
Small-seeded species have a lower, similar, or higher RGR at low irradiance compared to large-seeded species, whereas at high irradiance they realise a higher RGR. It is still unclear at what light levels the RGR of small-seeded species crosses over with the RGR of large-seeded. The light level of this cross-over point may have large implications for the coexistence of tree species (Sack & Grubb 2001), and the changes in species composition after disturbance (see Chapters 3 – 8). We selected 6 published studies that examined RGR of small and large-seeded species (Table 2.3). All had (a) a minimum of 6 species with a range of small to large seeds, (b) a seed mass range large enough to arbitrarily distinguish between large and small-seeded species (species with seed masses < 0.1g were considered to have small seeds, species with seeds > 0.1g to have large seeds, sensu Chapters 1, 8), (c) at least three light levels, the lowest levels being smaller than 4% and the highest light level being between 20 and 60%.

RGR was regressed on log-transformed light values (% of full light). This was done for each study separately, each data point representing one species and the slopes groups of species with similar seed mass. The regression coefficient of small-seeded

Table 2.3   Regression of RGR on log-transformed percentage of full light, for small and large seeded species. For each study, the number of species in each seed mass class (n), the coefficient of determination (r^2); the slope (b), the significance level (P) and the calculated light level at which the regression lines cross over (x, in % of full light) are shown for the group of small seeded species (S) and large seeded species (L).

Study	Seed mass	n	r^2	b	p	x
Boot (1993)	S	3	0.05	6.16	ns	0.4
	L	3	0.35	2.98	ns	
Osunkoya *et al.* (1994)	S	6	0.71	2.82	***	0.7
	L	6	0.63	1.72	***	
Poorter (1999)	S	3	0.01	3.84	ns	0.2
	L	10	0.00	0.99	ns	
Popma & Bongers (1988)	S	3	0.63	2.16	*	$1 * 10^{-8}$
	L	6	0.69	2.25	***	
Rose *et al.* (2000)	S	3	0.29	18.00	ns	3.1
	L	5	0.45	4.48	***	
Swaine *et al.* (1997)	S	3	0.31	14.92	*	11.2
	L	3	0.10	0.06	ns	

species is expected to be larger than that of large-seeded species because they are expected to show a stronger response of RGR to irradiance. We used a paired t-test to test this hypothesis, comparing the slopes of large and small seeded species per study.

The regression slope of the small-seeded species was significantly steeper than large-seeded species in four of the six studies (t-test, p<0.05). Further, in five of the studies the RGR of the small seeded species crossed over with the RGR of the large-seeded species, below 5% full sunlight (Table 2.3). From these comparisons it is evident that although the absolute difference in RGR between large and small-seeded species increases with increasing irradiance, small seeded species have, in general, a higher RGR than large seeded species. This is reflected in their ability to grow much faster than large seeded species at low light levels. They, however, are unable to maintain their high growth rate in the shade (see above). The study of Swaine *et al.* (1997) was the only exception with small-seeded species realising higher RGRs at approximately 11% full sun than their large seeded counterparts. This may be due to the fact that the seed mass range in this study was not as large as in the other studies.

Sack and Grubb (2001) hypothesised that the irradiance level at which species cross-over increases with the size of the plants. If this is the case, then small seeded pioneer species may grow faster than large-seeded climax species when compared as seedlings, but they may grow slower when compared as saplings.

After how much time does the initial size advantage of large-seeded species dissipate in large gaps, and are they overtaken by the small-seeded species?
To address this question, we carried out a theoretical exercise. Using data from Rose (2000), we compared the growth of 8 species in a large logging gap. We assumed that all species experience similar light conditions, start at 60% of their initial seed mass (thus excluding the seed pericarp which does not provide any carbon to the

developing seedling), and maintain their maximum RGR over time. The increase in log plant mass over time was calculated for each species as seed mass x e$^{(rgrmax \times time)}$).

Assuming constant RGR, it would take *Cecropia obtusa* 174 days to attain the same plant mass as *Mora gongrijpii* that has a 6 orders of magnitude heavier seed. *Hymenaea courbaril* on the other hand would take 786 days respectively to attain equal mass as *Mora* (Figure 2.6). This is a conservative estimate, as the small-seeded species is likely to start from seed, whereas the large-seeded species will be present as advanced regeneration. Nevertheless, if the re-growing gap vegetation is not too dense shortly after a large disturbance, the small seeded pioneers can exploit their inherently higher growth rate to compensate for the small initial plant size and gain advantage over the slow growing climax species. Similar results were found in a growth experiment in French Guiana. *Jacaranda copaia*, a pioneer species with tiny seeds and a low initial biomass, by the end of the experiment attained a larger biomass than two *Carapa* species, which started off with a considerably larger seed mass (Barrigah *et al*. 1998). Fast growth of small seeded pioneers in large gaps was also demonstrated in an experiment where eight species were planted in gaps and allowed to grow for a longer period (Rose 2000). The initially small *Cecropia obtusa, Goupia glabra* and *Sclerolobium guianense* dominated the canopy after one year in the larger gaps (1600 and 3200 m^2). In the small gap, the large-seeded
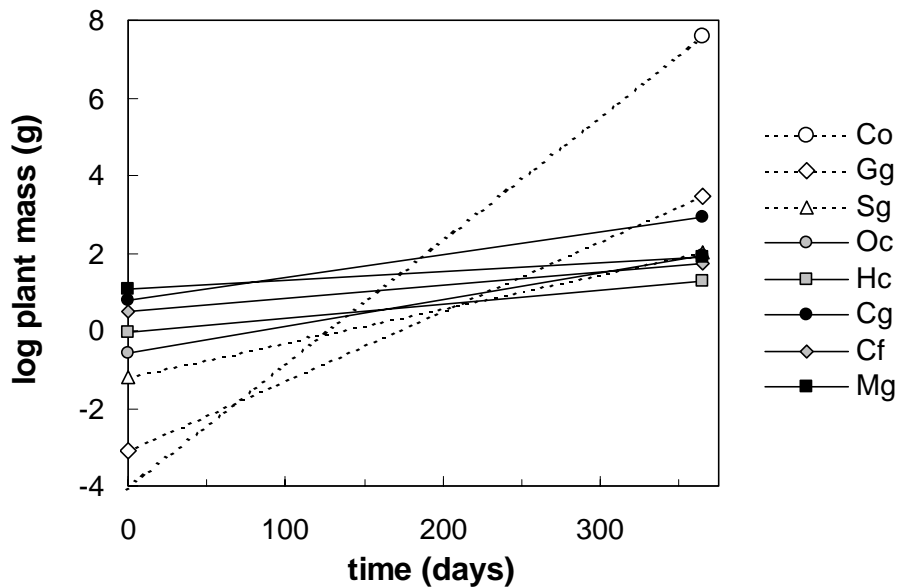

Figure 2.6   Biomass growth of eight species and their cross-over points in time. Log plant mass was calculated on the basis of the seed mass and maximum RGR (log plant mass = seed mass x e$^{(rgrmax \times time)}$) for each species over one year (365 days). The figure is from Pons *et al*. (in press) and based on data from Rose (2000).

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species were amongst the tallest species. *Pentaclethra macroloba*, a species with intermediate seed size, showed the fastest growth in the small gap, and also substantial height growth in the largest gaps. The remarkable combination of tolerance of deep shade and fast growth in gaps was also demonstrated for this species in Costa Rica (Fetcher *et al*. 1994).

Concluding remarks

The general ideas about the role of seed size in establishment (Foster 1986, Leishman *et al*. 2000) have been supported, and expanded by our meta-analysis. One of the advantages of a large seed is associated with survival in shade. If seed reserves are not immediately allocated to the slow growing seedling, then the reserves in the cotyledons can sustain the seedling for a prolonged period until conditions become more favourable. This is particularly evident in the very large seeded *Chlorocardium rodiei* that keeps it reserves for up to a year after germination in the understorey, and even for five years when growing in gaps (Boot 1993, ter Steege *et al*. 1994). In the process, plant mass including cotyledons gradually decreases due to a negative carbon balance in the shaded understorey environment, but survival is high. Another advantage of a large seed is associated with the competitive advantage of the large initial size. Large seeds always come with the disadvantage of the trade-off with small numbers. Large numbers of seeds are essential for species that exploit the unpredictable window for establishment after an occasional heavy disturbance. Small seed size improves dispersal (Hammond *et al*. 1996) and also survival in the soil seed bank (Leishman *et al*. 2000). Chance to be there at the right time and place are thus maximised. A high RGR is however, important to compensate for the low initial plant mass as argued above.

The observed relationship between seed size, initial seedling size and RGR varies with irradiance. In disturbed areas, where the primary competitors for space and resources are other seedlings, species with large seeds may only have a competitive advantage when seedling densities are high (Gross 1984). In that case competition is largely asymmetric, and large seedlings may shade the smaller ones. However if seedling densities are low, then species with small seeds and high RGRs will have a competitive advantage since they are able to quickly overgrow seedlings with lower growth rates. Grime (1979) has suggested that high RGR may be adaptive for small seeded pioneer species as it allows them to monopolise available space rapidly and reproduce before being replaced by slower growing species. Clearly, the importance of seed size in determining seedling establishment success depends on this relationship between seed (or seedling) size and other life history characteristics such as RGR.