

# **Comparative growth analysis of seedlings of 13 wet and dry tropical forest tree species: the relative importance of physiological and morphological traits in deep shade and moderate light**

*(Data from this thesis can not be used without consent of the author ([mslot@ufl.edu](mailto:mslot@ufl.edu)) or supervisor ([lourens.poorter@wur.nl](mailto:lourens.poorter@wur.nl)))*

M. SLOT\*

Department of Biology, University of York, UK

Instituto Boliviano de Investigación Forestal, Santa Cruz, Bolivia

---

\* [ms237@york.ac.uk](mailto:ms237@york.ac.uk)



## Summary

1. The effect of irradiance on seedling Relative Growth Rate ( $RGR_M$ : Relative mass Growth Rate;  $RGR_H$ : Relative height Growth Rate), physiology and morphology of tropical wet and dry forest tree species was tested in a shade house experiment and the determinant underlying factor of growth at low (1% of full sunlight; LL) and intermediate (10% of full sunlight; IL) irradiance was identified. Inherent differences between wet forest and dry forest species in IL were analysed.
2. All species had a higher  $RGR_M$  and  $RGR_H$  at IL than at LL and associated higher rates of biomass increase per unit leaf area (ULR: Unit Leaf Rate), photosynthesis ( $A_{MAX}$ ) and dark respiration ( $R_{DARK}$ ). More biomass was allocated to roots (higher RMF: Root Mass Fraction) in IL, whereas in LL plants invested in a larger leaf area as a proportion of total plant mass (LAR: Leaf Area Ratio).
3. In LL ULR was the determinant factor of  $RGR_M$ , whereas in IL LAR and SLA were more important.
4. No inherent growth differences between wet and dry forest species were found under optimum conditions, but the RMF of dry forest species was lower, and the Water Use Efficiency (WUE) was higher than for wet forest species.
5. It was concluded that moderate irradiance has a strong positive growth effect and that the irradiance level determines which underlying factor is most important in determining growth. The dominance of ULR at low irradiance could not be explained but is hypothesised to result from an increased importance of  $R_{DARK}$  at low irradiance. The importance of LAR (and SLA) at intermediate irradiance suggests that 10% of sunlight is suboptimal and that plants therefore try to maximise light interception.
6. Dry forest species appeared to possess high plasticity and a reduced RMF was compensated by a higher WUE to yield equal growth rates to those of wet forest species.
7. The supposed high plasticity of dry forest species and the RGRs equal to wet forest species suggests that growth may not explain the absence of dry forest species in wet forests. The low RMF under optimum conditions as found without competition, may pose problems when competing with species with a high RMF in the field.

## Introduction

Gradients of distribution and diversity of tropical forests species are strongly correlated with a gradient of soil moisture availability and annual rainfall (e.g. Gentry 1988; Swaine 1996; Bongers *et al.* 1999). Species at the dry end of the continuum need to be drought tolerant or resistant to stress associated with drought (Richards 1952; Mulkey & Wright 1996), whereas in wet forests shade tolerance is of greater importance for seedling survival and growth (Khurana & Singh 2001).

Acquisition and use of water and light require different physiological and morphological traits and resource acquisition capacities belowground and aboveground are commonly considered to constrain each other (Bazzaz & Grace 1997). The distribution of species over the rainfall gradient is determined by a trade-off between traits favouring drought tolerance (for which belowground resource acquisition is most important) and traits favouring shade tolerance (aboveground resource acquisition more important). Drought tolerant species that allocate more biomass to roots can not invest much biomass in stem and leaf material, resulting in a reduction in light capture, and hence, shade tolerance (Smith & Huston 1989).

Most tropical forests experience seasonal dry periods (Richards 1952; Becker *et al.* 1988; Windsor 1990; Meinzer *et al.* 1995) and during a prolonged dry season plants may be deprived of rainfall for up to three months after reaching their permanent wilting point (Veenendaal *et al.* 1996). Seedlings should be especially prone to dry season stress as young plants have had little time to develop extensive root systems (Poorter & Hayashida-Oliver 2000). Indeed, drought has been associated with increased mortality and decreased growth rates in seedlings of tropical plants (e.g. Turner 1990; Veenendaal *et al.* 1996; Mulkey & Wright 1996; Cao 2000; Engelbrecht & Kursar 2003). Thus drought resistance is a major factor influencing species distribution in the tropics (Mulkey & Wright 1996).

Within a tropical forest the irradiance can vary from 1-2% in the understory and from 5-30% in gaps (Chazdon 1988; Clark *et al.* 1996). Many species form seedling banks with advanced regeneration in the understory, but most species still depend on the formation of gaps for successful onward growth and without the higher irradiance in gaps they are not able to reach the canopy. Size differences at the time of gap formation may determine to a large extent the success of an individual afterwards. The larger this head start, the more likely it is that the individual will eventually reach the canopy and reproduce (Tilman 1988; Brown & Whitmore 1992; Boot 1996; Zagt & Werger 1998; Westoby 1998; Grime 2001). Thus both survival and growth are crucial for successful regeneration in the forest understory and the ability of species to persist in the dark understory and to make use of increases in light level in gaps is of paramount importance for the future species composition of the forest canopy.

Because plant size, and thus growth, is an important determinant of survival and reproduction in nature, interspecific differences in Relative Growth Rate (RGR)<sup>1</sup> are of fundamental importance in plant ecology (Tilman 1988; Westoby 1998; Grime 2001). RGR depends on environmental conditions and on the physiology and morphology of the plants. This means that when the external environment is constant, interspecific differences in RGR must be due to interspecific differences in plant physiology and morphology. It is therefore important to know how physiological and morphological differences contribute to variation in RGR (Shipley 2002).

Little is known about interspecific variation in traits of seedling growth in relation to light availability among species from different forest types (but see Hoffmann & Franco 2003; Wright & Westoby 2003). To my knowledge no study to date has experimentally tested for differences between wet forest species and dry forest species in their physiological and morphological responses to contrasting levels of irradiance under optimal hydrological conditions. A better understanding of the inherent differences between wet forest and dry forest species in the regulation of growth and their ability to persist in simulated understory and gap light conditions, could help to unravel the complexity of niche differentiation in tropical forests.

In this study I compare the growth, physiology and morphology of wet and dry forest species growing at low (1% of full light) and intermediate (10% of full light) irradiance. Such an experiment under optimal water supply may explain why dry forest species do not grow in wet forests. A follow-up experiment under dry conditions could then provide an explanation for the absence of wet forest species in dry forests. Four questions were addressed in this study:

First, does irradiance have an effect on growth, physiology and morphology of seedlings from wet and dry tropical forest tree species? I hypothesised a strong, positive effect of irradiance on growth and gas exchange while biomass allocation was expected to show a contrasting pattern with increased investment in belowground resource acquisition at the higher light level at the cost of aboveground resource acquisition, and more allocation to aboveground organs at low irradiance.

Second, is interspecific variation in RGR primarily determined by physiology or by morphology and how does this differ between growth in low irradiance and in intermediate irradiance? Growth at low irradiance was expected to be determined by morphology and in particular by the Leaf Area Ratio (LAR). A high LAR allows plants to maximise the interception of sunlight, the most limiting resource at low irradiance. Where light is sufficiently available for plants to obtain high rates of photosynthesis the efficiency with which light can be used for assimilation and thus growth becomes more important (Grubb *et al.* 1996; Veneklaas & Poorter 1998).

---

<sup>1</sup> See Table 2 for definitions and units of the parameters used in this paper

Interspecific variation in growth at higher irradiance was therefore expected, in accordance with Veneklaas & Poorter (1998), to be determined by the biomass increase per unit leaf area (ULR: Unit Leaf Rate).

Third, do species from wet and dry forests show inherent differences in growth, physiology, and morphology at a given irradiance? Inherent physiological and morphological adaptations that allow dry forest species to survive and grow under sub-optimal water availability were expected to result in lower growth and gas exchange rates than for wet forest species.

Finally, till what extent can the results from the shade house be extrapolated to the field? Here I compare the Specific Leaf Area (SLA) of seedlings grown under controlled environmental conditions in shade houses to the SLA of similarly sized seedlings grown under natural conditions in wet forest and in dry forest and expected in accordance with Poorter & Garnier (1998) that SLA would be reduced in the field.

## Materials and Methods

### PLANT MATERIAL

Thirteen tree species were selected from two forest types (Table 1). Included were species from wet forest types and species from dry forests as well as three species occurring in both, but being far more common in either wet forest (*Cariniana ianeirensis* R. Knuth and *Triplaris Americana* L.) or dry forest (*Sweetia fruticosa* Spreng.). Henceforth the species will be referred to by their genus name only.

Seeds were collected from a semi-deciduous rain forest and from a dry forest. La Chonta, henceforth referred to as a 'wet forest', has an annual rainfall of 1560 mm with a distinct dry period ( $<100$  mm month<sup>-1</sup>) from May to October. Inpa, a 'dry forest', has an annual rainfall of 1100 mm with a distinct dry period ( $<100$  mm month<sup>-1</sup>) from April to October. The seeds were germinated in a nursery shade house in Santa Cruz, Bolivia (16°S, 61°W) at *ca.* 15% of full sunlight in trays with a 50:50 mixture of river sand and organic soil. The recently germinated seedlings were transplanted to individual 200 ml pots filled with  $\frac{1}{2}$  river sand,  $\frac{1}{4}$  soil from the top layer of the wet forest and  $\frac{1}{4}$  soil from the top layer of the dry forest. A dissolvable N, P, K fertiliser tablet was added to avoid nutrient limitations.

**Table 1** Species included in this study and the forest type in which they predominantly occur (Wet is semi-deciduous rainforest, Dry is tropical dry forest).

Species	Family	Origin
<i>Cedrela f issilis</i> Vell.	Meliaceae	Wet
<i>Swietenia macrophylla</i> King	Meliaceae	Wet
<i>Batocarpus amazonicus</i> (Ducke) Fosberg	Moraceae	Wet
<i>Ocotea sp.</i>	Lauraceae	Wet
<i>Triplaris amaricana</i> L.	Polygonaceae	Wet
<i>Cariniana ianeirensis</i> R. Knuth	Lecythidaceae	Wet
<i>Pterogyne nitens</i> Tul.	Leguminosae	Dry
<i>Astronium urundeuva</i> (allemao) Engl.	Anacardiaceae	Dry
<i>Anadenanthera colubrina</i> (Vell. Conc.) Benth.	Leguminosae	Dry
<i>Sweetia f ruticosa</i> Spreng.	Leguminosae	Dry
<i>Ceiba speciosa</i> (A. St-Hil)	Bombacaceae	Dry
<i>Hymenaeae courbaril</i> L.	Leguminosae	Dry
<i>Eriotheca roseorum</i> Cuatrec.	Bombacaceae	Dry

From each species about twenty individuals were grown in each of four replicate neutral-density shade houses either at 1% of full sunlight (LL: low light) or at 10% of full sunlight (IL: intermediate light). The shade houses, two providing LL (Nos. 1 and 3) and two IL (Nos. 2 and 4), were established on a row on a south-north line on the terrain of the Instituto Boliviano de Investigación Forestal. As no significant differences in growth, physiology and morphology between the shade houses with the same light level were found (data not shown) the data were pooled per light level in the analyses.

## GROWTH EXPERIMENT

When the first or second leaf pair had developed a first harvest of five individuals per shade house took place. The moment of harvest differed among the species as the rates of development of the species with different life history traits varied. The harvest was meant to take place in the period in which the seedling has used up the reserves provided by the seeds or the storage cotyledons (Kitajima & Fenner 2000). After six weeks another five plants per shade house were harvested, the remaining plants being left for measurements of gas exchange parameters (see below).

**Table 2** Parameters used, their meaning, the formulas of how they were derived and their units.  $M_1$  and  $M_2$  are dry mass at  $t_1$ (initial harvest) and  $t_2$  (final harvest) respectively, H is plant height and LA is leaf area.

Parameter	Meaning	Formula	Units
$RGR_M$	Relative mass growth rate *	$\frac{\overline{\ln(M_2)} - \overline{\ln(M_1)}}{t_2 - t_1}$	mg increase $g^{-1}$ plant $d^{-1}$
$RGR_H$	Relative height growth rate	$\frac{\overline{\ln(H_2)} - \overline{\ln(H_1)}}{t_2 - t_1}$	mm increase $m^{-1} d^{-1}$
ULR	Unit leaf rate	$\frac{\overline{M_2} - \overline{M_1}}{t_2 - t_1} \times \frac{2}{(\overline{LA_1} + \overline{LA_2})}$	g increase $m^{-2} d^{-1}$
$A_{MAX,M}$	Maximum photosynthetic rate (per unit leaf mass)	$\frac{CO_2 \text{ uptake at saturating light}}{M \text{ exposed leaf}}$	nmol $CO_2 g^{-1}$ leaf $s^{-1}$
$R_{DARK,M}$	Leaf dark respiration (per unit leaf mass)	$\frac{CO_2 \text{ released in darkness}}{M \text{ exposed leaf}}$	nmol $CO_2 g^{-1}$ leaf $s^{-1}$
WUE	Water use efficiency	$A_{MAX} / \text{stomatal conductance}$	$\mu\text{mol } \mu\text{mol}^{-1}$
SLA	Specific leaf area	leaf area / leaf mass	$m^2 kg^{-1}$
LAR	Leaf area ratio	leaf area / plant mass	$m^2 kg^{-1}$
LMF	Leaf mass fraction	leaf mass / plant mass	$g g^{-1}$
SMF	Stem mass fraction	stem+petiole mass / plant mass	$g g^{-1}$
RMF	Root mass fraction	root mass / plant mass	$g g^{-1}$

\* All mass-based parameters are expressed per unit dry mass

At harvesting each plant was separated into roots, leaf blades and stems plus petioles and stem length was measured. Leaves were scanned (Canon portable laserjet 2000, Canon Inc. Tokyo, Japan) and leaf areas determined using Pixels! Version 1.3 (R. van Berloo, Wageningen University & Research Centre, The Netherlands). After at least 48 hours oven drying at 70°C dry mass of the plant parts was measured with a microbalance.

The thus obtained data allowed the calculation of parameters of leaf display: Leaf Area Ratio (LAR) and Specific Leaf Area (SLA) (see Table 2), and of biomass allocation: Leaf Mass Fraction (LMF), Stem Mass Fraction (SMF), Root Mass Fraction (RMF). Relative biomass Growth Rate was calculated according to Hunt (1982) (see Table 2). Relative height Growth Rate ( $RGR_H$ ) was calculated similarly, using the natural logarithm of plant height instead of plant mass.

The productive efficiency of plants was expressed as the Unit Leaf Rate (ULR) according to Hunt (1982). The  $RGR_M$  is affected by ontogenetic drift as growth proceeds because the proportion of structural compounds of plants increases as they grow. This would affect the comparisons between growth of different sized seedlings and saplings for the mere fact that change in biomass forms the basis of the calculation (Gregory 1918, quoted in

Hunt (1982)). ULR is less affected by ontogenetic drift as it is based on biomass changes expressed on a mean leaf area basis, a factor that is less size dependent as plant mass. A precondition to the use of the ULR calculation by Hunt (1982) is that total leaf area is linearly related to plant dry mass. For all species-light level combinations this condition was met (all  $r^2 > 0.43$  at LL and  $r^2 > 0.57$  at IL;  $P < 0.05$  in all cases).

In addition to the measurement of plants grown in the shade house seedlings were collected from a wet forest (June 2004) and from dry forest (August 2004) for comparison of SLA between plants grown under controlled conditions and in the field. Small gaps and the understory were used to collect plants for the comparison with the IL and the LL shade houses respectively. Per species five seedlings were collected per light level. The leaves were scanned and the leaf area determined, the plants were dried for > 48 hour at 70°C and weighed and SLA was calculated.

#### GAS EXCHANGE MEASUREMENTS

The plants that remained after the final harvest were used for gas exchange measurements. This was done for eight plants per IL shade house for most species. In the LL shade houses survival rates were reduced (L. Poorter, unpublished results) and not all species had plants remaining after the final harvest, others had fewer than eight. The measurements were made on attached, fully expanded leaves using a CIRAS-1 portable infrared gas analyser (PP-Systems, Amesbury, MA, USA) operating in open flow mode and fitted with a Parkinson leaf cuvette which allowed for measurements on 2.5 cm<sup>2</sup> leaf area. The CO<sub>2</sub> concentration of the reference air was kept between 360 and 380 ppm by a CO<sub>2</sub> control module and all measurements were performed at a relative humidity of 75%, typical conditions for shade houses the plants were grown in.

Preceding the measurements of photosynthesis at saturating light ( $P_{MAX}$ ) several photosynthesis light response curves were measured for each species from which the photosynthetic photon flux density (PPFD:  $\mu\text{mol}$  photosynthetic active radiation in  $\text{m}^{-2} \text{s}^{-1}$ ) at light saturation was determined. Based on these measurements the saturating light intensity for further measurements was set at 850  $\mu\text{mol PAR m}^{-2}\text{s}^{-1}$  for most species and at 750  $\mu\text{mol PAR m}^{-2}\text{s}^{-1}$  for some species grown at LL.

The Water Use Efficiency (WUE) was indirectly assessed using  $A_{MAX}$  / stomatal conductance as an indicator (Osmond, Björkman & Anderson 1980; Farquhar, O'Leary & Berry 1982).

Dark respiration was measured on leaves that were pre-darkened with dark cloth for at least 30 minutes. As the leaf cuvette could not be temperature regulated the measurements were performed at different temperatures. To correct for this the temperature sensitivity of respiration ( $Q_{10}$ : the proportional increase in  $R_{DARK}$  with a 10°C increase in temperature) was assumed to be 2.0 and based on this assumption all  $R_{DARK}$  values were standardised to a temperature of 25°C. The  $Q_{10}$  is not 2.0 for all species under all conditions (Atkin & Tjoelker 2003) and particularly the  $Q_{10}$  of plants under stress may deviate from 2.0 (M. Slot, unpublished). For this study it was

however considered sufficiently accurate, as the majority of the  $R_{\text{DARK}}$  measurements could be made within a small ( $<5^{\circ}\text{C}$ ) temperature range and consequently the error resulting from an erroneous assumption about the  $Q_{10}$  would be small (e.g. an overestimation by 10% of the  $Q_{10}$  of a species measured at  $5^{\circ}\text{C}$  below the standard temperature of  $25^{\circ}\text{C}$  would result in an overestimation of  $R_{\text{DARK}}$  of only 2.5%).

All measured leaves were collected and their SLA was calculated following above mentioned procedure. This allowed the gas exchange parameters to be expressed on leaf mass basis.

## STATISTICAL ANALYSES

All variables were transformed to their natural logarithms to approximate to the normal distribution and to obtain equality of variances.

Because no significant differences were found between the two LL shade houses and the IL shade houses (Paired t-tests,  $P>0.1$  in all cases) the data were pooled per light level. This was preferred over using mean values per shade house as replicates in the analyses, as the procedure of nesting 'shade house' in 'light level' would reduce the degrees of freedom of the error term in the analysis.

The effect of irradiance on growth ( $RGR_M$ ,  $RGR_H$ ) and on ULR was analysed with two-way ANOVAs with light and forest type as independent factors using species as unit of replication; the effect on physiology ( $A_{\text{MAX}}$ ,  $R_{\text{DARK}}$ , WUE) and morphology (LAR, SLA, LMF, SMF, RMF) was analysed per species with 'measured plant' as unit of replication.

Species means of growth parameters and parameters of physiology and morphology were used as units for the correlation analysis. Spearman's rank correlation coefficients were used as a conservative test of correlation that is robust to problems with sample distribution. For significant relationships a parametric test of correlation (Pearson's correlation coefficient) was also performed.

To analyse inherent differences in growth, physiology and morphology between species from wet and from dry forest independent t-tests with species means were used for the parameters of interest with species as unit of replication.

Differences in SLA between shade house grown and field grown seedlings were explored using a Spearman's rank correlation analyses using mean SLA values per species (shade house  $n=10-16$ , field  $n=5$ ) both at low and at intermediate light.

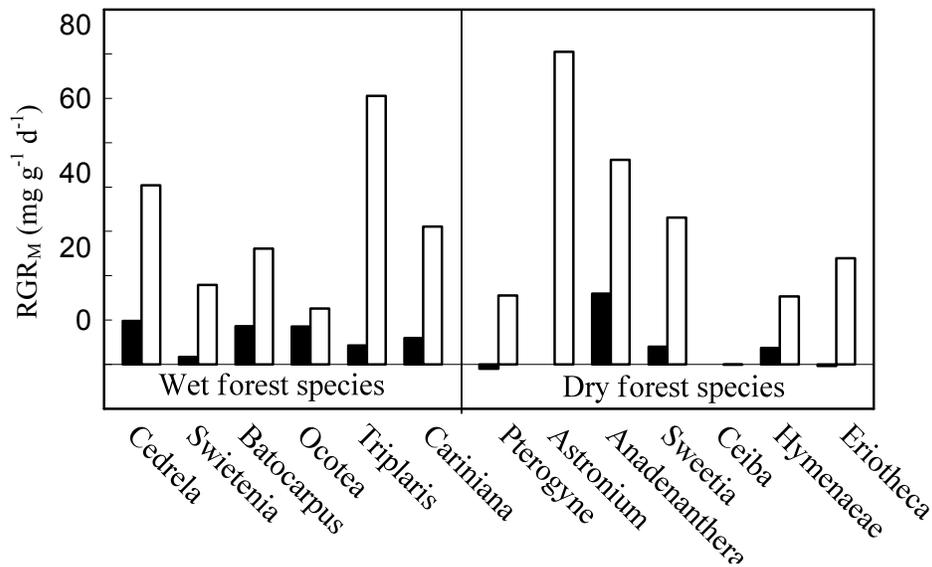
All statistical analyses were performed using SPSS 11.01 (SPSS inc. Chicago, Ill., USA).

## Results

### EFFECT OF IRRADIANCE ON PLANT GROWTH

Irradiance had a strong effect on growth of all species in this study (Fig. 1; Table 3). At intermediate irradiance (IL) both  $RGR_M$  and  $RGR_H$  were significantly higher than at low irradiance (LL) ( $F=18.3$ ,  $P<0.001$  and  $F=10.1$ ,  $P<0.01$  respectively). Figure 1 shows that there was large interspecific variation in  $RGR_M$  both at IL and at LL, but that without exception growth was higher at IL for wet forest species as well as for dry forest species.

Negative growth rates were recorded for some species. This means that leaves and/or small twigs were shed with the result that the total plant biomass at the final harvest was lower than at the initial harvest. Such negative growth was only recorded for species growing in LL, and interestingly, only for dry forest species.



**Fig. 1** Effect of low light (closed bars) and intermediate light (open bars) on  $RGR_M$  of thirteen tropical tree species from wet and dry forest.  $RGR_M$  values were calculated per species using the data from all individuals ( $n=10-16$ ) and consequently no measure of spread could be calculated. *Astronium* and *Ceiba* plants did not survive at low irradiance; hence the species have no  $RGR_M$  value for the low light treatment.

Physiology and morphology were also strongly affected by irradiance (Table. 3). At the higher irradiance level (*i.e.* IL) the  $ULR$ ,  $A_{MAX, M}$  and  $R_{DARK, M}$  were for almost all species significantly higher than in LL and also the WUE was for most species significantly higher in IL. The parameters of leaf display (*i.e.* LAR and SLA) were significantly lower in IL while the LMF and RMF revealed an increase in biomass allocation to roots at the cost of allocation to leaves in IL. The SMF appeared to be little and in an inconsistent way affected by irradiance.

(Data from table 3 are excluded from this document pending publication)

**Table 3** Parameters of growth ( $RGR_M$ ,  $RGR_H$ ), gas exchange ( $U_L$ ,  $P_{MAXM}$ ,  $R_{DARKM}$ ,  $WUE$ ), leaf display ( $LAR$ ,  $SLA$ ) and biomass allocation ( $LMF$ ,  $SMF$ ,  $RMF$ ) at low irradiance (LL, 1% of full sunlight) and at intermediate irradiance (IL, 10% of full sunlight). Significance of LL vs. IL differences is indicated for the parameters that could be calculated per individual plant. For some species not all parameters could be calculated as height, weight or leaf area data were occasionally not available. From *Anadenanthera* and LL *Ceiba* and *Astronium* no plants were available for measurements of gas exchange.

## FACTORS DETERMINING GROWTH RESPONSE TO LIGHT

Correlation analysis was performed to identify which of the underlying factors of growth was of greatest importance in determining interspecific variation in biomass growth ( $RGR_M$ ) and height growth ( $RGR_H$ ) at low and intermediate irradiance (Table 4).

In low irradiance  $RGR_M$  correlated significantly ( $P < 0.05$ ) with physiology (ULR,  $R_{DARK}$ ) but not with leaf display (LAR, SLA) or biomass allocation (LMF, SMF, RMF). In intermediate light on the other hand, the physiological factors correlated weakly with  $RGR_M$ , but there was a significant correlation between  $RGR_M$  and both LAR and SLA ( $P < 0.05$ ). Similar to the situation at low light the  $RGR_M$  was not correlated with any of the biomass allocation parameters. This means that in LL physiology and in IL leaf display primarily determine biomass growth of the plants in this study (Fig. 2).

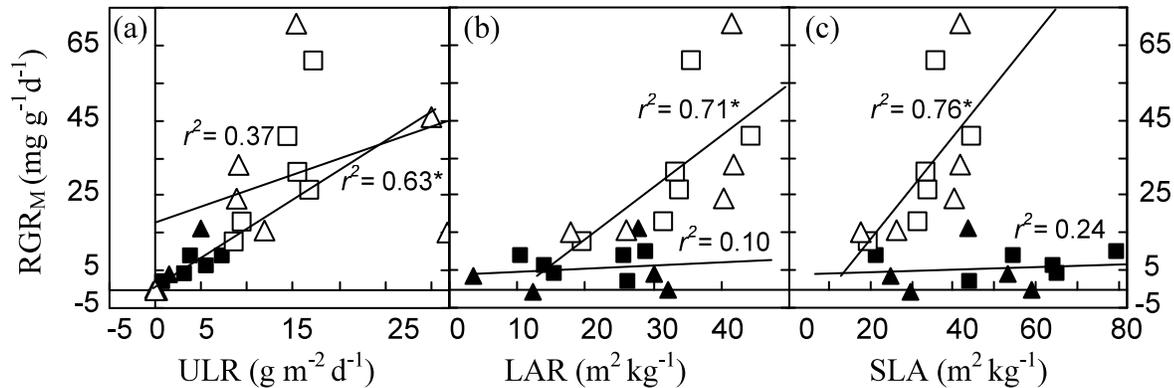
**Table 4** Correlation matrix of seedling traits of species grown in low light (LL, 1% of full sunlight) or intermediate light (IL, 10% of full sunlight). The values in the table are Pearson's correlation coefficients. Correlation coefficients shown in bold font are significant at a level indicated by the number of astrices: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

	$RGR_M$	$RGR_H$	ULR	$A_{MAX,M}$	$R_{DARK,M}$	LAR	SLA	LMF	SMF
<b>LL</b>	<b><math>RGR_M</math></b>								
	$RGR_H$	<b>0.66*</b>							
	ULR	<b>0.63*</b>	0.04						
	$A_{MAX,M}$	0.06	-0.18	0.43					
	$R_{DARK,M}$	<b>0.69*</b>	0.03	0.27	<b>0.86**</b>				
	LAR	0.10	0.13	-0.49	-0.61	-0.37			
	SLA	0.24	0.39	-0.31	-0.27	-0.09	<b>0.69*</b>		
	LMF	-0.35	<b>-0.65*</b>	0.03	0.47	0.21	0.24	0.21	
	SMF	-0.34	<b>0.70*</b>	0.02	-0.40	-0.18	-0.20	0.02	<b>-0.88**</b>
	RMF	0.37	0.39	-0.01	-0.27	0.11	0.02	-0.40	<b>-0.61*</b>
									0.21
<b>IL</b>	<b><math>RGR_M</math></b>								
	$RGR_H$	<b>0.69**</b>							
	ULR	0.32	0.48						
	$A_{MAX,M}$	-0.09	-0.02	0.33					
	$R_{DARK,M}$	0.36	-0.23	<b>0.66*</b>	0.49				
	LAR	<b>0.71*</b>	0.28	-0.52	-0.59	<b>-0.75*</b>			
	SLA	<b>0.76*</b>	0.36	-0.29	<b>-0.73*</b>	<b>-0.85**</b>	<b>0.91***</b>		
	LMF	0.35	0.23	-0.26	0.05	0.05	0.53	0.21	
	SMF	-0.36	-0.22	-0.20	-0.14	0.20	-0.50	-0.23	<b>-0.86***</b>
	RMF	-0.33	-0.23	-0.14	0.01	-0.28	-0.42	-0.23	<b>-0.72**</b>
									0.30

$RGR_H$  was correlated ( $P < 0.05$ ) with both LMF and SMF at low, but not in IL. The correlation with LMF in LL was strongly negative, *i.e.* plants that allocated a great proportion of their biomass to leaves had lower height growth than plants with a lower LMF. Not surprisingly this negative correlation between  $RGR_H$  and LMF was

associated with a positive correlation between  $RGR_H$  and SMF. In IL none of the parameters appeared to be dominant in determining height growth.

Worth mentioning is further is the strong, negative correlation of  $A_{MAX, M}$  and  $R_{DARK}$  with SLA at intermediate irradiance. Thus plants with a high SLA and relatively thin leaves have a much lower per-unit-mass  $A_{MAX}$  than plants with smaller, relatively thick leaves.



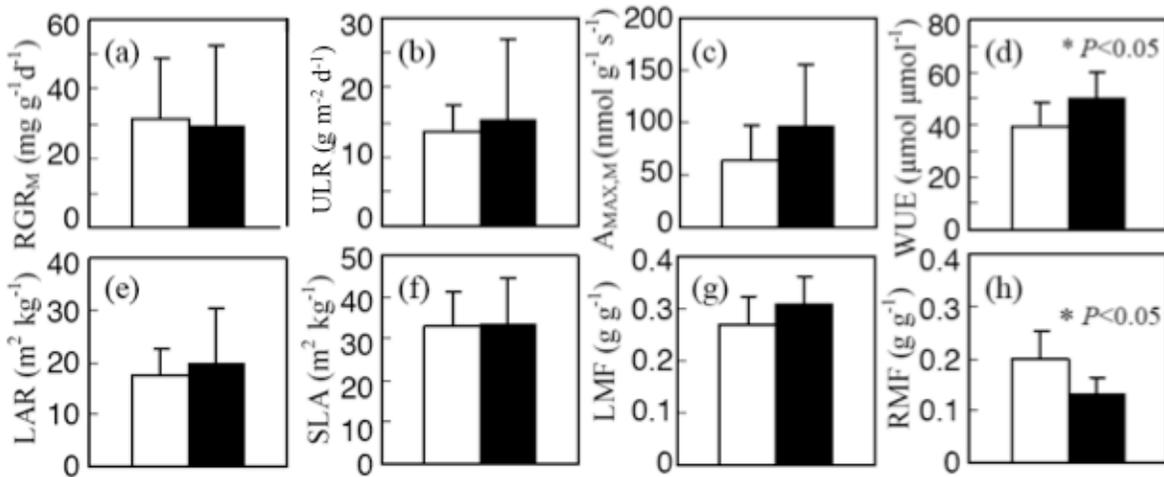
**Fig. 2** Correlation of  $RGR_M$  with ULR (a), LAR (b) and SLA (c) at low light (closed symbols) and at intermediate light (open symbols). Squares represent wet forest species, triangles represent dry forest species. Pearson's correlation coefficient are shown for the correlations for all species pooled per light level.

Figure 2 clearly shows the difference in the most dominant factors underlying growth between the two light levels. The factors with the strongest correlation with  $RGR_M$  were similar for wet forest species and dry forest species so the data shown here present the correlation for all thirteen species pooled per light level.

Strong correlations existed between  $RGR_M$  and ULR in LL (Fig. 2a) and between  $RGR_M$  and LAR (Fig. 2b) and SLA (Fig. 2c) at intermediate light.

#### INHERENT DIFFERENCES BETWEEN WET FOREST SPECIES AND DRY FOREST SPECIES

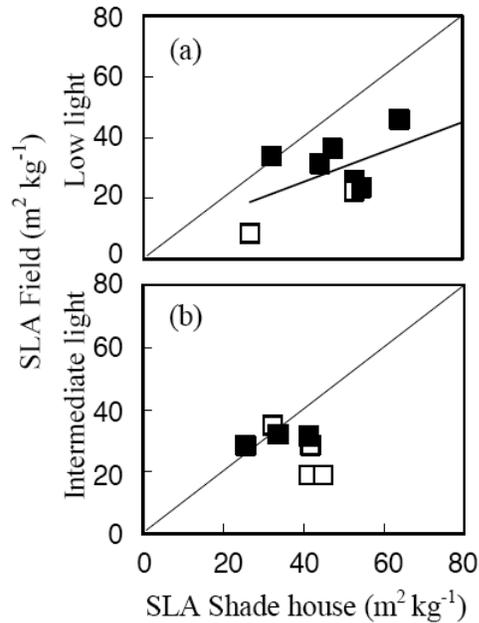
Wet forest species and dry forest species grown in intermediate irradiance with optimal water supply show surprisingly little differences in growth and in the physiological and morphological factors underlying growth (Fig. 3). Only the Water Use Efficiency and the Root Mass Fraction differed significantly ( $P < 0.05$  for both). Dry forest species had greater WUE, but interestingly, wet forest species had a higher RMF than dry forest species.



**Fig. 3** Inherent differences in growth (a), physiology (b-d) and morphology (e-h) between wet forest species (open bars) and dry forest species (closed bars) grown at intermediate light. Error bars represent 1 SD (n=6-7). \* $P < 0.05$  in a one-way ANOVA with (wet of dry) as fixed independent factor.

#### COMPARISON OF SLA BETWEEN FIELD AND SHADE HOUSE CONDITIONS

For few species sufficient plants of equal size to those in the shade houses could be found during the dry season in which the experiment was executed. Consequently no clear trends could be shown with statistical confidence ( $P=0.17$  and  $P=0.34$  for Spearman's rank correlation and Pearson's correlation coefficient). However, the LL shade house vs. forest understory comparison suggests that understory seedlings have an appreciably lower SLA (Fig. 4a). SLA of plants from the IL shade houses did on the other hand not appear to be any higher than that of plants from small gaps and gap edges (Fig. 4b).



**Fig. 4** Comparison of species-specific SLA of shade house seedlings with the SLA of seedlings grown under natural conditions in wet (open symbols) or dry forest (closed symbols). Low light shade house seedlings ( $n=10-16$ ) were compared with understory seedlings ( $n=5$  per species)(a) and intermediate light shade house seedlings ( $n=16$ ) were compared with plants collected from small canopy gaps ( $n=5$  per species)(b). A 1:1 line is included to facilitate the comparison.

## Discussion

### MODERATE IRRADIANCE ENHANCES GROWTH

Lower growth rates at low irradiance is typical as species growing in high stress, low disturbance habitats grow slower, whereas high irradiance and low stress is associated with a higher RGR (Grime 1979).

All species in the experiment indeed showed a strong positive response to irradiance, with low irradiance  $RGR_M$  even being negative for some species. Negative growth means that leaves or occasionally small twigs were shed presumably because plants could no longer maintain a positive carbon balance because their light compensation point (LCP) exceeded that of the available light. I do not have sufficient light response curves to accurately calculate LCPs per plant, but previous studies have shown that whole plant LCPs may occur at 0.5-2% of full sunlight (Boot 1993; Poorter 1999). The shedding of leaves in the 1% irradiance treatment in the current experiment is thus likely to be related to the exceeding of LCPs. What is apparent though is that only dry forest species showed negative growth and reduced survival in low irradiance. An analysis of growth difference at low irradiance however revealed no significant difference between wet and dry forest species (data not shown), mainly because of the high RGR of *Anadenanthera* and the low number of species due to the absence of RGR

data of non-surviving plants (Table 3). This exposes a possible weakness of the current experiment which stresses the need for careful interpretation of the results: only survivors were included in the final harvest and gas exchange measurements were made on plants that had survived more than 2 months of treatment. Consequently contrasts between species and between forest types may have been reduced as a result of excluding dead or dying plants and the numbers of them for the different species.

#### DETERMINANT FACTORS OF GROWTH: ULR AND LAR

The correlations of physiological and morphological parameters with  $RGR_M$  at low and intermediate irradiance were opposite to what was hypothesised. Not leaf display was the most important factor determining interspecific variation in  $RGR_M$  at low light, but ULR was. At the higher irradiance level it were not the physiological parameters, but LAR that was most closely correlated  $RGR_M$  (LAR can be regarded as the product of SLA and LMF and it is therefore not surprising that with LAR also one of the underlying factors correlated significantly with  $RGR_M$ ). Similar results were found by Bloor & Grubb (2003) who showed that  $RGR_M$  of 15 shade tolerant tropical rain forest tree species correlated strongest with ULR at 0.8% irradiance and with LAR at 10% irradiance.

It appears that unlike what was expected 10% irradiance might still be sub-optimal for most species and that a relatively large area of photosynthesising material (a high LAR (and thus a high SLA and/or LMF)) is still advantageous for optimisation of growth. Poorter (1999) has demonstrated that the relative importance of LAR and ULR for interspecific variation in  $RGR_M$  of tropical tree seedlings changes along a light gradient. He showed that for plants grown in up to 15% of full sunlight LAR was the determinant factor of  $RGR_M$ , while at higher levels of irradiance ULR became the dominant underlying factor of  $RGR_M$ . The 'intermediate light' treatment in the present study was 10% and indeed LAR was the factor most strongly correlated with  $RGR_M$ .

Several authors have shown that in low light where carbon gain is minimal respiration rates become increasingly important for the  $RGR_M$  (Givnish 1988; Boot 1996; Reich 1998) and that is what Bloor & Grubb used to explain the dominance of the physiological factor ULR at low irradiance. This is an understandable suggestion, as ULR has been reported to be closely linked with photosynthesis and respiration (Konings 1989; Poorter & Van der Werf 1998). However, I found no correlation of either  $A_{MAX}$  or  $R_{DARK}$  with ULR in low irradiance, despite the significant correlation of  $R_{DARK}$  with  $RGR_M$ . This correlation was also tested for  $A_{MAX}$  and  $R_{DARK}$  on leaf area basis (data not shown) as the area-based values should be most closely linked to the area-based biomass increase that is represented by ULR. An important factor here may be that photosynthesis was measured at saturating light as a measure of photosynthetic capacity, rather than at growth irradiance, which would be stronger related to ULR.

In addition there may be a ‘sampling effect’ in the gas exchange measurements: these measurements were made after the final harvests and only survivors with presumably higher gas exchange rates were available for measurements. This means that also for plants with limited or even negative growth the measurements of gas exchange were done on relatively vigorous plants. High rates of photosynthesis measured on few surviving plants of a species with a low ULR would for example reduce the predicted positive relationship between  $A_{MAX}$  and ULR. It is therefore suggested that the increased importance of  $R_{DARK}$  may explain the LL correlation between  $RGR_M$  and ULR, but this cannot be evidenced by my data.

In low irradiance there is a trade-off between  $RGR_H$  and biomass allocation to leaves (LMF) that did not exist in intermediate irradiance. While plants in IL show height growth without significant changes in biomass allocation, plants in LL either grow tall (an inherent trait to outcompete neighbouring plants in intercepting irradiance) or they stay little and invest in leaves to increase shade tolerance and light interception in the undergrowth. The experiment included insufficient species per forest type to identify differences in these strategies between them.

The trade-off between  $A_{MAX}$  and  $R_{DARK}$  and SLA (Reich 1998) is only apparent in IL where SLA is lower and gas exchange rates are higher than in LL. This negative correlation between  $A_{MAX}$  and SLA did however not exist when area-based gas exchange rates were used and the correlation between  $A_{MAX, MASS}$  ( $\text{nmol g}^{-1} \text{s}^{-1}$ ) and SLA ( $\text{m}^2 \text{kg}^{-1}$  or  $\text{cm}^2 \text{g}^{-1}$ ) is not surprising in a dataset (of  $A_{MAX}$  at IL) with relatively little variation in  $A_{MAX, AREA}$  between species.

#### EQUAL RGR OF WET AND DRY FOREST SPECIES: COMPENSATORY DIFFERENCES IN PHYSIOLOGY AND MORPHOLOGY

Contrary to predictions there was no difference in  $RGR_M$  nor in  $RGR_H$  between wet and dry forest species in intermediate irradiance (IL) and favourable water supply. This is not surprising, as the factors earlier shown to determine RGR in IL, LAR and SLA, did not differ significantly between wet and dry forest species. The hypothesis that growth at optimum conditions would differ was based on the assumption that some of the physiological and morphological traits that enable dry forest species to persist and grow under marginal water availability would be inherent. As a consequence a trade-off between the traits required for the acquisition of water and those important for the acquisition of irradiance would be displayed and growth would be impeded in dry forest species compared to that of wet forest species. Under dry conditions more biomass is allocated to roots in order to optimise the acquisition of water (Grime 1979; Gerhardt & Frederiksson 1995; Holbrook, Whitbeck & Mooney 1995; Cao 2000; Engelbrecht & Kursar 2003). The RMF was therefore expected to be higher in dry forest species, but it was higher in wet forest species. This also contradicts results by Hoffmann & Franco (2003) who in an analysis of growth responses of savannah and cerrado woodland species to irradiance, found that

savannah species allocated more biomass to roots and less to aboveground organs than woodland species. The current experiment may be compared with that of Hoffmann & Franco (2003) in that under natural conditions dry forest species, like savannah species, are expected to have a greater investment in belowground resource acquisition while wet forest and woodland species are both expected to display traits for optimal aboveground resource acquisition. Like in the current experiment they found no significant difference in RGR at “low light” (26% of full sunlight, representative for cerrado woodland understory light conditions), but they found that woodland species had a significantly higher LAR of than savannah species, but that their ULR was significantly lower, thus balancing out any growth.

Such relationships were not found in the present study. However, the WUE of dry forest species was significantly higher than that of wet forest species, which feeds the speculation that dry forest species are very plastic: their higher WUE allows them to reduce the investment in belowground biomass in favour of aboveground biomass and thus they attain growth rates similar to those of wet forest species. Wright, Reich & Westoby (2001) also found changes in stomatal conductance over a rainfall gradient, with the result that WUE, if calculated as  $A_{MAX}$  / stomatal conductance, is higher at dry sites. As the present experiment was done under favourable water conditions this suggests that this trait is inherent to dry forest species.

#### CONTROLLED CONDITIONS ALLOW HIGHER SLA IN LOW IRRADIANCE

In low irradiance the SLA of plants grown in the field was - as expected - lower than that of plants grown under controlled conditions, although this was due to a limited number of species included in the comparison not significant. Plants in the field experience more stresses than under controlled conditions, including competition, herbivory and variable availability of water and nutrients. In addition, seedlings in the field tend to be older than shade house plants at a given height (L. Poorter, personal communication). These factors all result in lower SLA as there is a trade-off in protection against and recovering from abovementioned stresses and maintaining a high SLA (Poorter & Garnier 1999). Equally if not more important is that the LL shade house was likely to be darker than the forest understory, especially in the dry season when a some overstory trees had shed their leaves (personal observation).

The difference in water availability between the field and the shade houses was expected to result in a reduced cell expansion in field grown plants and thereby in a lower SLA. This could be particularly important in intermediate light, as gaps tend to be dryer than the understory and consequently the difference in soil moisture availability with that in the shade houses would be larger. As no apparent differences in SLA were found between IL shade house seedlings and gap seedlings, this drought-induced difference in cell expansion may be rejected as an important factor.

## CONCLUSION

The presented results confirm that light is a factor of paramount importance for seedling growth in both wet forest species and dry forest species and that the factors underlying growth are strongly dependent on the growth light level. The results further show that RGR is not different for wet forest and dry forest species when grown in 10% of full sunlight with favourable moisture conditions, but that there is a tendency for reduced survival of dry forest species in low irradiance. This suggests that the hypothesised trade-off between drought tolerance and shade tolerance is at least partly due to inherent adaptations to drought. Although the  $A_{MAX}$  of dry forest species was in low irradiance significantly lower than that of wet forest species no direct explanations were found for the reduced survival, possibly as a result of sampling bias towards more vigorous plants. The results can consequently not provide an explanation for the absence of dry forest species in wet forests. As comparisons of growth under controlled conditions and field conditions have been shown to result in different biomass allocation (this study; Poorter & Garnier 1999) it is suggested that field studies may reveal better explanations.

## Acknowledgements

This study was carried out as an MRes. project for which NERC and NUFFIC provided financial support. I am grateful to Lourens Poorter for his excellent supervision and for the data he readily provided. Victor Hugo Lopez has provided invaluable help with harvesting and weighing plants; Victor Hugo Hurtado has been of great help with his tree spotter skills. Marielos Peña and the IBIF team are thanked for letting me use their facilities, for logistical support, for their hospitality and willingness to help whenever necessary.

## References

- Atkin, O.K. & Tjoelker, M.G. (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, **8**, 343-351.
- Bazzaz, F.A. & Grace, J. (1997) *Plant resource allocation*. Academic Press, San Diego, California.
- Becker, P., Rabenholt, P.E., Idol, J.R. & Smith, A.P. (1988) Water potential gradients for gaps & slopes in a Panamanian tropical moist forest's dry season. *Journal of tropical Ecology*, **4**, 173-184.
- Bloor, J.M.G. & Grubb, P.J. (2003) Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology*, **91**, 77-85.

- Bongers, F., Poorter, L., Van Rompaey, R.S.A.R. & Parren, M.P.E. (1999) Distribution of twelve moist forest canopy species in Liberia and Cote d'Ivoire: response curves to a climatic gradient. *Journal of Vegetation Science*, **10**, 371-382.
- Boot, R.G.A. (1993) *Growth and survival of tropical rainforest tree seedlings in forest understory and canopy openings. Implications for forest management* (Tropenbos documents 6). Tropenbos Foundation, Wageningen.
- Boot, R.G.A. (1996) The significance of seedling size and growth rate of tropical rainforest tree seedlings for regeneration in canopy openings. *Ecology of tropical forest tree seedlings* (ed. M.D. Swaine), pp. 267-284. UNESCO, New York.
- Brown, N.D. & Whitmore, T.C. (1992) Do dipterocarp seedlings really partition tropical rainforest gaps? *Philosophical Transactions of the Royal Society of London-Series B: Biology Sciences*, **335**, 369-378.
- Cao, K-F. (2000) Water relations & gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. *Journal of Tropical Ecology*, **16**, 101-116.
- Clarck, D.B., Clarck, D.A., Reich, P.M., Weiss, S. & Oberbauer, S.F. (1996) Landscape-scale evaluation of understory light & canopy structure: methods & application in a neotropical lowland rain forest. *Canadian Journal of Forest Research*, **26**, 747-757.
- Chazdon, R.L. (1988) Sunflecks in the forest understory. *Advances in Ecological Research*, **18**, 1-63.
- Engelbrecht, B.M.J. & Kursar, T.A. (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia*, **136**, 383-393.
- Farquhar, G.D., O'Leary, M.H. & Berry, J.A. (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, **9**, 121-137.
- Field, C.B. & Mooney, H.A. (1983) Leaf age & seasonal effect on light, water & nutrient use efficiency in a California shrub. *Oecologia*, **56**, 348-355.
- Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, **75**, 1-34.
- Gerhardt, K. & Frederiksson, D. (1995) Biomass allocation by broad-leaved mahogany seedlings in abandoned pastures & secondary dry forest in Guanacaste, Costa Rica. *Biotropica*, **27**(2), 174-182.
- Givnish, T.J. (1988) Adaptation to sun and shade, a whole plant perspective. *Australian Journal of Plant Physiology*, **15**, 63-92.
- Grime, J.P. (1979) *Plant strategies & Vegetation processes*. Chichester, Wiley, New York.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley & Sons, New York.

- Grubb, P.J., Lee, W.G., Kollmann, J. & Bastow Wilson, J. (1996) Interaction of irradiance and soil nutrient supply on growth of seedlings of ten European tall-shrub species and *Fagus sylvatica*. *Journal of Ecology*, **84**, 827–840.
- Holbrook, N.M., Whitbeck, J.L. & Mooney, H.A. (1995) Drought responses of Neotropical deciduous forest trees. *Tropical Deciduous Forest Ecosystems* (eds. S.H. Bullock, S.E. Medina & H.A. Mooney), pp. 243-276. Cambridge University Press, London.
- Hoffmann, W.A. & Franco, A.C. (2003) Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *Journal of Ecology*, **91**, 475-484.
- Huante, P. & Rincon, E. (1998) Responses to light changes in tropical deciduous woody seedlings with contrasting growth rates. *Oecologia*, **113**, 53–66.
- Huante, P., Rincon, E. & Acosta, I. (1995) Nutrient availability and growth rate of 34 species from a tropical deciduous forest in Mexico. *Functional Ecology*, **9**, 849–858.
- Hunt, R. (1982). *Plant Growth Curves. The Functional Approach to Plant Growth Analysis*. Edward Arnold, London.
- Khurana, E. & Singh, J. S. (2001) Ecology of tree seed and seedlings: implications for tropical forest conservation and restoration. *Current Science*, **80**(6), 748-757.
- Kitajima, K. (1994) Relative importance of photosynthetic traits & allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**, 419-428.
- Kitajima, K., Mulkey, S.S. & Wright, S.J. (1997) Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. *American Journal of Botany*, **84**(5), 702-708.
- Kitajima, K. & Fenner, M. (2000) Ecology of seedling regeneration. *Seeds: the ecology of regeneration in plant communities* (Ed. M. Fenner), pp. 331-359. CABI Publishing, Wallingford, UK.
- Kobe, R.K. (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship & growth. *Oikos*, **80**, 226-233.
- Konings, H. (1989) Physiological and morphological differences between plants with a high NAR or a high LAR as related to environmental conditions. *Causes and Consequences of Variation in Growth Rate and Productivity in Higher Plants* (eds. H. Lambers, M.L. Cambridge, H. Konings & T.L. Pons), pp. 101-123. SPB Academic Publishing BV, The Hague.
- Lambers, H. (1985) *Higher Plant Cell Respiration* (eds. R. Douce & D.A. Day), pp. 418-473. Springer Verlag, Berlin.
- Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research*, **23**, 187-261.

- McKenna, M.F. & Shipley, B. (1999) Interacting determinants of interspecific relative growth: empirical patterns and a theoretical explanation. *Ecoscience*, **6**, 286–296.
- Meinzer, F.C., Goldstein, G., Jackson, P., Holbrook, N.M., Gutiérrez, M.V. & Cavelier, J. (1995) Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties. *Oecologia*, **101**, 514–522.
- Meziane, D. & Shipley, B. (1999) Interacting components of interspecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. *Functional Ecology*, **13**, 611–622.
- Mulkey, S.S. & Wright, S.J. (1996) Influence of seasonal drought on the carbon balance on tropical forest plants. *Tropical Forest Plant ecophysiology* (eds. S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 187–216. Chapman & Hall, London.
- Osmond, C.B., Björkman, O. & Anderson, D.J. (1980) *Physiological Processes in Plant Ecology. Towards a Synthesis with Atriplex*. Springer-Verlag, New York.
- Poorter, L. (1999). Growth responses of fifteen rain forest tree species to a light gradient; the relative importance of morphological and physiological traits. *Functional Ecology*, **13**, 396–410.
- Poorter, L. & Hayashida-Oliver, Y. (2000) Effects of seasonal droughts on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology*, **16**, 481–498.
- Poorter, H. & Van der Werf, A.K. (1998) Is inherent variation in RGR determined by LAR at low irradiance and NAR in high irradiance? A review of herbaceous species. *Inherent Variation in Plant Growth, Physiological Mechanisms and Ecological Consequences* (eds. H. Lambers, H. Poorter & M.M.I. Van Vuuren), pp. 309–336. Backhuys, Leiden.
- Poorter, H. & Garnier, E. (1999). Ecological significance of inherent variation in relative growth rate and its components. *Handbook of Functional Plant Ecology* (eds. F.I. Pugnaire & F. Valladore), pp. 81–103. Marcel Dekker Inc., New York.
- Reich, P.B. (1998) Variation among plant species in leaf turnover rates and associated traits, implications for growth at all life stages. *Inherent Variation in Plant Growth, Physiological Mechanisms and Ecological Consequences* (eds. H. Lambers, H. Poorter & M.M.I. Van Vuuren), pp. 467–487. Backhuys, Leiden.
- Richards, W. (1952) *The Tropical Rain Forest*. Cambridge University Press, London.
- Ryser, P. & Wahl, S. (2001) Interspecific variation in RGR and the underlying traits among 24 grass species grown in full daylight. *Plant Biology*, **3**, 426–436.
- Shipley, B. (2002) Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. *Functional Ecology*, **16**, 682–689.

- Smith, T.M. & Huston, M.A. (1989) A theory of the spatial & temporal dynamics of plant communities. *Vegetatio*, **83**, 49-69.
- Swaine, M.D. (1996) Rainfall and soil fertility as factors limiting forest species distributions. *Journal of Ecology*, **84**, 419-428.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- Turner, I.M. (1990) The seedling survivorship and growth of three *Shorea* species in a Malaysian tropical rain forest. *Journal of Tropical Ecology*, **6**, 469-478.
- Van der Werf, A., Visser, A.J., Schieving, F. & Lambers, H. (1993) Evidence for optimal partitioning of biomass and nitrogen availabilities for a fast- and slow-growing species. *Functional Ecology*, **7**, 64-74.
- Veenendaal, E.M. Swaine, M.D., Agyeman, V.K. Abebrese, I.K. & Mullins, C.E. (1996) Differences in plant and soil water relations in and around a forest gap in West Africa may influence seedling establishment and survival. *Journal of Ecology*, **84**, 83-90.
- Veneklaas, E.J. & Poorter, L. (1998) Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. *Inherent Variation in Plant Growth, Physiological Mechanisms and Ecological Consequences* (eds. H. Lambers, H. Poorter & M.M.I. Van Vuuren), pp. 337-361. Backhuys, Leiden.
- Westoby, M. (1998) A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**(2), 213–227.
- Windsor, D.M. (1990) Climate & moisture availability in a tropical forest, long term record for Barro Colorado Island, Panama. *Smithsonian Contributions to Earth Sciences*, **29**, 1-45.
- Wright, I.J., Reich, P.B. & Westoby, M. (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, **15**(4), 423-434.
- Zagt, R.J. & Werger, M.J.A. (1998) Community structure and demography of primary species in tropical rain forest. *Dynamics of tropical communities* (eds. D.M. Newbery, H.H.T. Prins & N. Brown), pp 193-220. Blackwell Scientific Publishers, Cambridge.