Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest

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ABSTRACT. In tropical moist forests, length of the dry period may have a profound influence on leaf dynamics, plant growth and survival. To evaluate the role of light and water availability on seedling performance, a 1-y experiment was carried out in a tropical moist forest in the Bolivian Amazon in which seedlings of three tree species (*Brosimum lactescens*, *Cedrela odorata* and *Schizolobium amazonicum*) were planted in gaps and the understorey. Variation in length of the dry period was simulated by subjecting part of the seedlings to a water treatment at the end of the dry period. Gaps and understorey had a similar soil moisture content, which varied between 39% in the wet season and 16% in the dry season. Height and leaf growth rates were higher in gap compared to understorey plants, and in the wet compared to the dry season. A high growth during the wet season provided gap plants with a decisive size advantage over understorey plants during the dry season. Their larger root system allowed gap plants to explore a larger surface area and deeper soil layers for water. Consequently, gap plants of *Cedrela* experienced a shorter deciduous period (22 d) compared to understorey plants (61 d). Watering at the end of the dry season cued the flushing of new leaves by *Cedrela*, although it did not lead to a higher plant growth.

KEY WORDS: Bolivia, deciduousness, gap, seasonal drought, soil moisture content, tree seedlings, tropical moist forest

INTRODUCTION

Rainfall gradients in the tropics give rise to a variety of forest formations (Beard 1955; Hall & Swaine 1976, 1981; van Rompaey 1993). Species distributions vary along this rainfall gradient, with some species being restricted by

the amount of rainfall, and others by the length and intensity of the dry period (Bongers *et al.* 1999). At a given site, the length of the dry period varies from year to year (Veenendaal *et al.* 1996a), which may provide a bottleneck for the successful regeneration of certain tree species in dry years, especially at the seedling stage (Condit *et al.* 1995, Davis & Richards 1933). Species which can be deciduous in the seedling stage have a higher chance of surviving the dry period than evergreen species. Yet, this higher survival is at the expense of a reduced growth (Poorter 1998).

To date, much emphasis has been given to the role of light availability in seedling performance, but less attention has been paid to the role of water availability, let alone the interaction between the two (but see Burslem 1996, Fisher *et al.* 1991, Veenendaal *et al.* 1996b). The water balance of the plant gives a first indication how seedlings respond to seasonal drought in a gap and an understorey environment. Apart from species-specific characteristics, it depends on the water availability in the soil and the vapour pressure deficit in the environment. Despite the increased insolation, the water availability is thought to be higher in gaps due to a lower rainfall interception by the vegetation and less water uptake due to a lower root density (Becker *et al.* 1988). Yet, experimental evidence is not conclusive as sometimes higher (e.g. Becker *et al.* 1988, Veenendaal *et al.* 1996b) and sometimes lower (e.g. Ashton 1992, Turner *et al.* 1992) soil moisture values are reported for gaps compared to the understorey. It is even less clear whether potential differences in soil water availability can be translated into differences in plant water stress. The actual water stress experienced by the plant depends on physiological and morphological plant characteristics.

Understorey plants have a morphology which is characterized by a high biomass fraction in leaves, a high specific leaf area and a high leaf area ratio (Osunkoya *et al.* 1993). Such plant traits confer an advantage during the wet season as they enhance light interception in a light-limited environment. The same traits may be detrimental during the dry season as they imply a limited capacity for water uptake (due to a low biomass fraction in roots), and an increased water loss through transpiration. Gap plants have a more beneficial morphology to withstand dry-season drought than understorey plants, but at the same time they have to cope with considerably higher radiation loads.

To evaluate the role of light and water availability in seedling performance, an experiment was carried out in which seedlings of three tree species were planted in gaps and the understorey of a tropical moist forest. Seedling performance was compared between the wet and dry season. The effect of variation in length of the dry period was simulated by subjecting part of the seedlings to a water treatment. The following questions were addressed: (1) What is the seasonal variation in soil moisture availability, and how does it vary between gap and understorey sites? (2) How do plants respond to light and water availability in terms of survival, leaf dynamics, growth and biomass allocation?
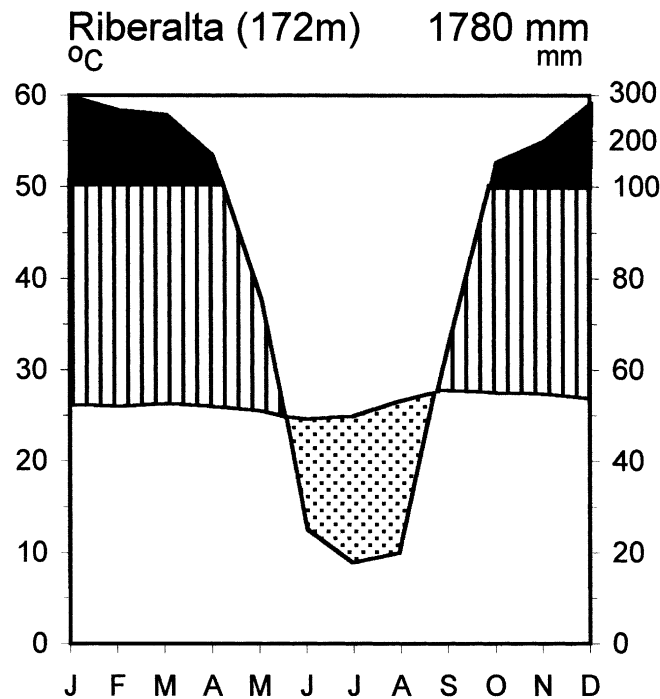
Figure 1. Climate diagram of Riberalta with annual course of rainfall and temperature, based on a 25-y average. The perhumid period (>100 mm mo^{-1}, black), relative humid period (<100 mm mo^{-1}, hatched) and drought period (when potential evapotranspiration exceeds rainfall; dotted) are indicated (data from AASANA, in Beekma *et al.* 1996).

STUDY SITE AND SPECIES

Research was carried out in the reserve 'El Tigre', field site of Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB), located 40 km east of Riberalta in the northern Bolivian Amazon (10°59′S, 65°43′W). Annual rainfall in the region is *c.* 1780 mm, with a distinct low-rainfall period (< 100 mm mo^{-1}) between May and September (Figure 1). A dry period can be defined as those months where the potential evapotranspiration exceeds the precipitation. In northern Bolivia, timing, length and intensity of the dry period vary from year to year. The length of the dry period ranges from 2 to 5 mo per year, and it may even take a longer time period before the soil water level is replenished to field capacity. The forest in the region can be classified as a tropical lowland moist forest with a canopy of 25–35 m high. Some of the canopy trees are deciduous during the dry season (Poorter 2000).

Three tree species were included in the study, differing in shade tolerance and deciduousness. *Schizolobium amazonicum* Huber ex Ducke (Fabaceae) is an evergreen pioneer species. *Cedrela odorata* Blanco (Meliaceae) is a non-pioneer light demanding species. Seedlings of *Cedrela* are facultatively deciduous, depending on the length and the intensity of the dry season and the local site

conditions. *Brosimum lactescens* (S. Moore) C. C. Berg (Moraceae) is a shade-tolerant evergreen tree species. Hereafter the species are referred to by their generic name only.

<div align="center">METHODS</div>

Experimental design

An experiment was set up in which seedlings of the three species were exposed to differences in canopy openness and length of the dry period. In December 1996 two naturally created single treefall gaps were selected. The gaps were spaced 300 m apart. The gaps were cleared by removing the vegetation and woody debris and had sizes (sensu Brokaw 1982) of 160 and 270 m^2 respectively. The removal of the gap vegetation was done to prevent root competition of the gap vegetation with the experimental plants. Within each gap three blocks were established perpendicular to the daily track of the sun at the eastern, middle and western side of the gap. In addition, three understorey locations were selected in the vicinity of each gap at which the understorey vegetation was removed. At the end of the experiment the canopy openness was estimated in each of the 12 blocks with a spherical densiometer (Forest Densiometers Inc., Bartlesville). Average canopy openness of gaps was $32 \pm 6\%$ (mean $\pm$ SD) and of the understorey $5 \pm 1\%$. The gaps showed little lateral canopy closure during the experiment. Hereafter, the two different gaps with accompanying understorey locations will be referred to as sites.

Seedlings of *Schizolobium* and *Cedrela* were germinated from seed under moderate light conditions in a shade house. For *Brosimum* recently germinated wildings were collected from a seedling bank in the understorey. Seedlings were transplanted to the field on 20 December 1996, in the first half of the rainy season. Seedlings were 10–25 cm high at time of transplanting, which corresponds to the size they attain by this time of the year when germinating under natural conditions. For each species nine seedlings were planted randomly per block. The interplant distance was 1 m. Dead seedlings were replaced until 1 mo after initiation of the experiment. Per species, 108 seedlings (two sites × two canopy conditions × three blocks × nine plants) were planted.

At the end of the dry season a water treatment was imposed upon a number of the surviving seedlings, in this way simulating the effect of early rains and a shortening of the dry season. A quantity of 100 mm rainfall a month was taken as typical for the onset of the wet season (Figure 1), and is generally regarded as a threshold value to distinguish between rain forest and more seasonal forest (Whitmore 1990). For seedlings of this size it was assumed that most of the water uptake occurred within a range of 20 cm from the stem base of the plant. Seedlings were subjected to a watering treatment every 10 d, thus mimicking the rainfall pattern at the onset of the wet season: single rainfall events interspersed by prolonged dry periods. Hence, every time each selected seedling received 4.2 l of water ($\pi \times 20^2$ cm$^2 \times 10$ cm mo^{-1} / three times mo^{-1}).

As the water percolation rate of the forest soil in the dry period was very low, a metal frame was placed around the seedling at time of watering, thus preventing lateral runoff. The plants were watered seven times, the first time 15 August at the end of the dry season, and the last time 14 October when the rainy season had started. The water treatment was only imposed on gap plants of *Schizolobium*, and gap and understorey plants of *Cedrela*, as not sufficient individuals were available for understorey plants of *Schizolobium* and gap and understorey plants of *Brosimum*. Watered plants were selected at random, and did not differ significantly in height and size from control plants of the same species exposed to the same canopy conditions.

Plant measurements

Plants were measured seven times at the following dates; 30 January, 29 April, 8 August, 1 and 24 September, 16 October; final measurement and harvest took place at 17 and 20 November. At each census plant survival, height and leaf number were recorded. At final harvest the stem diameter at 5 cm from the stem base, maximal rooting depth and length of the longest root were measured in addition. For each seedling one to three leaves were selected at different height positions in the crown and their leaf area was determined with a portable CI-202 leaf area meter (CID Inc., USA). Plants were divided into leaves, stem plus petioles, and roots, and together with the leaf area sample oven-dried for 48 h at 65 °C and weighed.

Abiotic measurements

Daily rainfall was measured with a rain-gauge in a large clearing, within 1 km from the research plots. The annual course of volumetric soil moisture content was monitored using time-domain reflectory (TDR) (Trime FM-2, Eijkelkamp Agrisearch equipment, Giesbeek, The Netherlands). Nineteen times during the year, measurements of soil moisture content were taken in each of the 12 blocks. As the measurement alters soil structure, each time the soil moisture content was determined in the vicinity of another, randomly selected, plant in the same block. Local soil conditions can be highly variable, and therefore three measurements were made around the plant and averaged. Whether watering treatment had an effect on soil moisture content was checked by evaluating soil moisture content for a watered and a control plant. This was done in each of the 12 blocks at respectively 5 h and 2, 5 and 7 d after watering. The TDR gives an estimate of the soil moisture content, over the first 20 cm of the soil. To evaluate whether soil moisture content varied with soil depth, at three dates (24 September, 10 October, 4 November) additional measurements were made at the same spots in the gaps and understorey at 20–40 cm of soil depth.

Analysis

From the primary data the following variables were derived; the root mass ratio (RMR, root mass per unit plant mass, in g g^{-1}), stem mass ratio (SMR, stem

and petiole mass per unit plant mass, in g g^{-1}), leaf mass ratio (LMR, leaf mass per unit plant mass, in g g^{-1}), specific leaf area (SLA, leaf area per unit leaf mass, in m^2 kg^{-1}) and the leaf area ratio (LAR, leaf area per unit plant mass, in m^2 kg^{-1}). The leafless period was defined as the time between the first census when a plant became leafless and the first census when it flushed again.

Statistical analysis

In one of the gaps *Schizolobium* plants suffered a high mortality rate at the onset of the experiment due to the activity of leaf-cutter ants. To make straightforward comparisons between species and environments the *Schizolobium* plants from this gap were excluded from the survival analysis. Differences in seedling survival between species and canopy conditions were analysed with log-linear analysis.

For the growth and morphological variables a separate analysis of variance (ANOVA) was carried out per species, with canopy condition and water treatment as fixed effects, site as a fixed block effect, and plant size as a covariate. In block designs it is assumed that there is no interaction between the main effect and the block effect, and therefore such an interaction was not included as a term in the analysis. The effect of the 12 blocks was not analysed; due to a highly variable mortality between blocks, such an analysis would result in a very unbalanced design. Only plants which survived till the end of the experiment were included in the analysis. For *Cedrela* a three-way ANOVA was used, with canopy openness, site and water treatment as main factors. For *Schizolobium* only the gap plants were analysed, using a two-way ANOVA with water treatment and site as main factors. Lastly, for *Brosimum* a two-way ANOVA was used, with canopy openness and site as factors. To account for size differences between different treatments, the ln-transformed plant biomass was included as a covariate in the statistical analysis, assuming similar allometric slopes for gap and understorey plants. Dependent variables were ln-transformed prior to analysis, to increase homoscedasticity.

Differences in annual course in soil moisture content between gap and understorey were analysed with a repeated-measures ANOVA. The data of the 19 measurements made over time in each of the 12 blocks were used. The temporal measurements were taken as the within-subjects factor, and canopy condition as the between-subjects factor. Variation in soil moisture content with soil depth, and between watered and control plants was evaluated with a paired t-test. All statistical analyses were carried out using SPSS (1997).

RESULTS

Water availability

Annual rainfall was 1708 mm, with a distinct dry period from May to mid September (Figure 2). The soil moisture content tracked the rainfall pattern closely and ranged from 39% in the wet season to 16% in the dry season. At
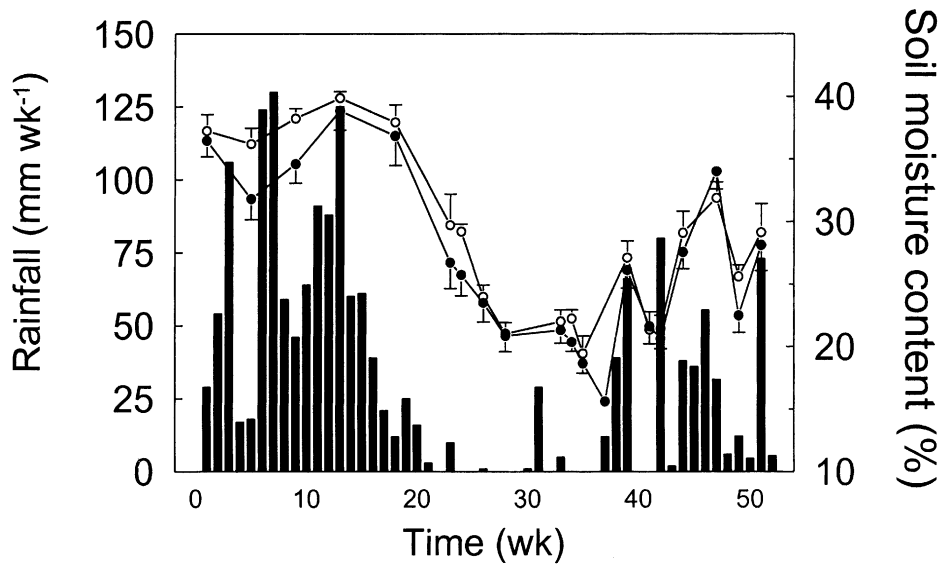
Figure 2. Annual course of rainfall (filled bars) and soil moisture content for gap (open circles) and understorey (filled circles) sites in 'El Tigre'. One-sided error bars represent 1 SE. Data are for 1997.

the end of the rainy season the soil dried out with an approximate time-lag of 1 mo, whereas at the onset of the rainy season rewetting of the soil occurred very quickly. Gap sites had a little higher soil moisture content than understorey sites (28.6 vs. 27.2 %), but this difference was not significant (repeated measures ANOVA, $F = 1.24$, df = 1, 10; $P > 0.05$). Gap and understorey sites had a similar seasonal course of soil moisture content (i.e. there is no interaction between canopy openness and time; $F = 0.95$, df = 18, 180; $P > 0.05$). Gap and understorey sites had a similar increase in soil moisture content with soil depth (21.5% at 10 cm depth compared to 24.9% at 30 cm depth, paired t-test, $t = -3.55$, df = 11, $P < 0.01$) if a prolonged dry period (10 d) preceded the measurements. However, the soil moisture content was not significantly different between the two depths ($P > 0.05$), if substantial rain fell within a few days before measurement. Watering of plants had a transient effect on the soil moisture content; after 5 h the effect of watering could still be detected (8.3% higher than control, $t = -7.3$, df = 11, $P < 0.001$), but after 2 d watered and control plants experienced a similar soil moisture content ($t = -2.1$, $P > 0.05$, in all cases).

Survival

There was a striking difference in survivorship of the three tree species, and this varied with light conditions (log-linear analysis, partial χ^2 for species–light interaction = 23.7, df = 2; $P < 0.001$) (Figure 3). By the end of the experiment, *Cedrela* had on average the highest survival rate (95%) and *Brosimum* the lowest (25%). *Cedrela* survived equally well in both environments. *Schizolobium* had a
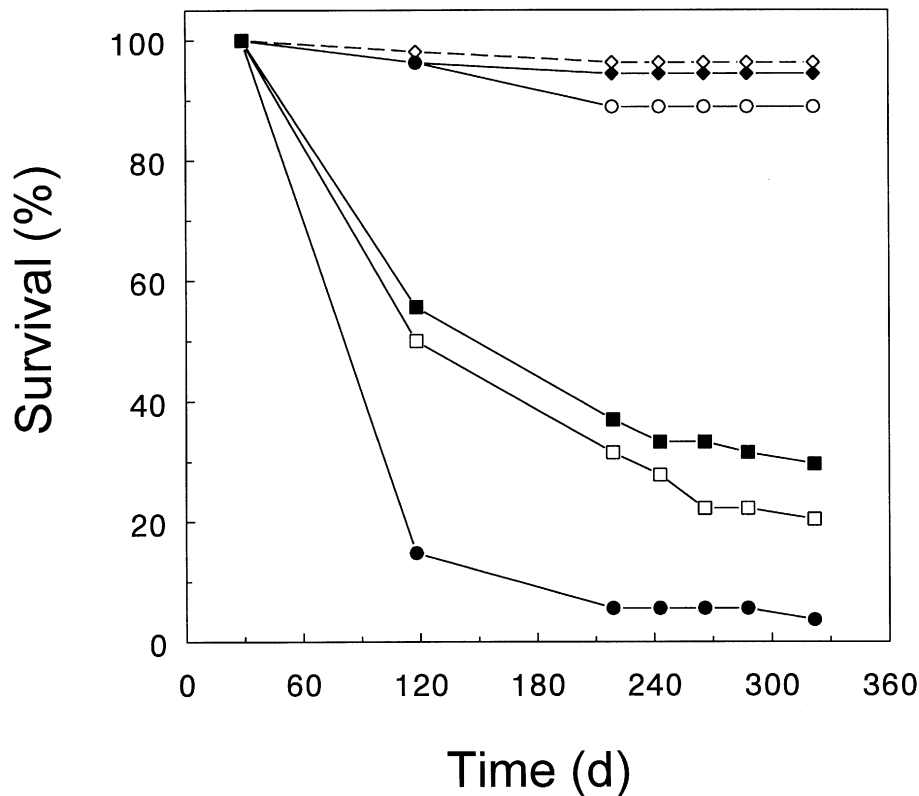
Figure 3. Survivorship of *Cedrela odorata* (diamonds), *Schizolobium amazonicum* (circles) and *Brosimum lactescens* (squares) in gap (open symbols) and understorey (filled symbols) sites. Means are calculated on the basis of all plants in each environment, with the exception of the gap plants of *Schizolobium*, for which only one gap is used (see Methods).

high initial mortality rate, and survived better in the gap environment. In contrast, *Brosimum* showed a constant mortality rate, and survived (non-significantly) better in the understorey than in gaps. Logistic regression shows that for each of the three species, survival at the end of the experiment was positively correlated with leaf number in January, at the onset of the experiment ($P < 0.07$ for *Brosimum*; $P < 0.05$ for the other two species). Watering of the plants did not affect survival (data not shown).

Leaf dynamics

All three species showed an increase in leaf number through the rainy season. Leaf numbers declined (*Cedrela*, *Schizolobium*) or remained constant (*Brosimum*) over the dry season, and increased again at the onset of the wet season (Figure 4). Gap plants had a larger number of leaves than understorey plants. For *Cedrela* all the understorey plants were leafless in the middle of the dry season, whereas gap plants still maintained some leaves. Accordingly, the leafless period was on average longer for understorey plants (at least 61 d)
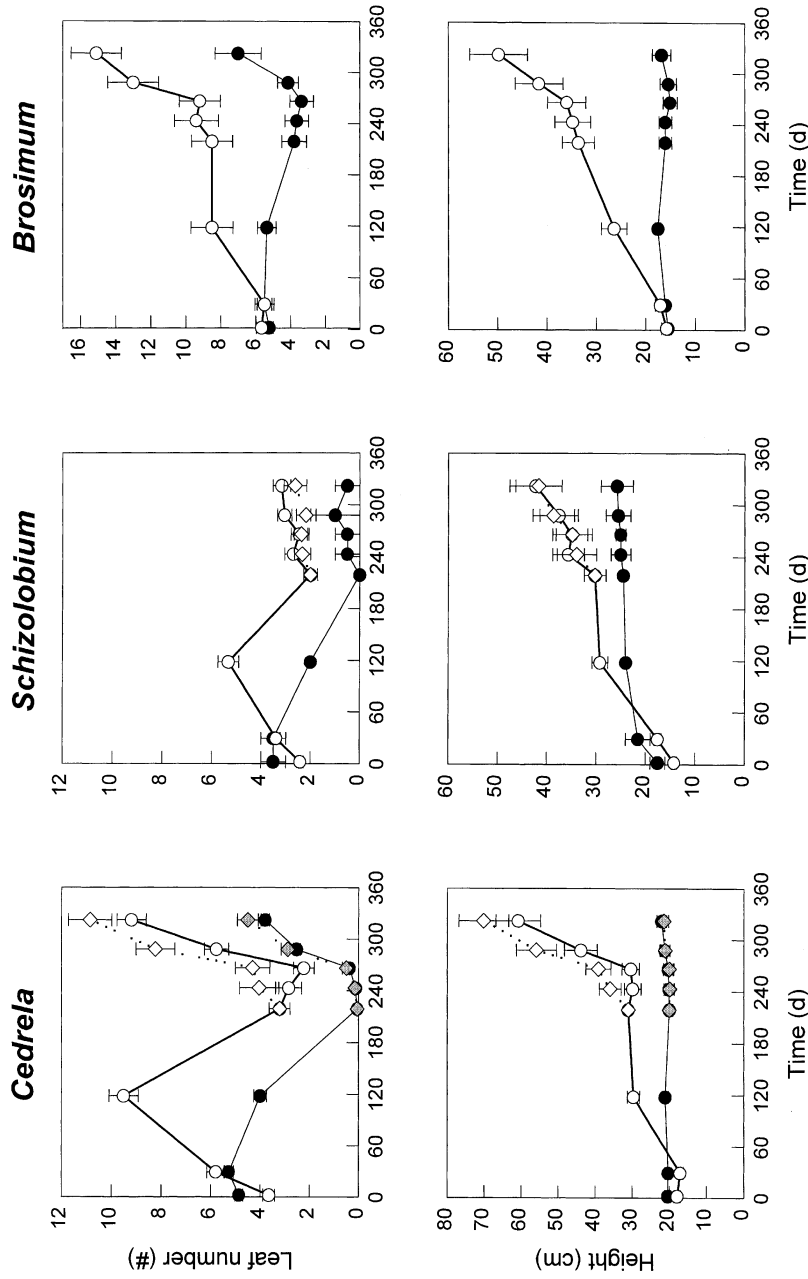
Figure 4. Leaf number (top row) and plant height (lower row) of gap (open symbols) and understorey (filled symbols) seedlings of three tree species *Cedrela odorata*, *Schizolobium amazonicum* and *Brosimum lactescens*. The time is indicated in Julian days. The water treatment started on day 226, and the first significant rains after the dry period fell on day 263. Watered plants are represented by diamonds and broken lines, and control plants by circles and continuous lines. Arithmetic means and SEs are based on all plants which survived till the end of the experiment in each environment. The number of watered and control plants in gap (underlined) and understorey (bold) were respectively: *Cedrela* 26/26/**26**/**25**; *Schizolobium* 16/17/**0**/**2**; *Brosimum* 0/11/**0**/**16**.

compared to gap plants (at least 22 d) (t-test for non-watered gap and understorey plants, t = 6.23, df = 43.1, P < 0.001). Watering cued the flushing of leaves, while the control plants still shed their leaves in response to the dry season drought. Watering led to an increased leaf number for gap and understorey plants of *Cedrela* (Table 1) but did not have any effect on leaf phenology of *Schizolobium*.

Height growth

All three species showed the same pattern in which understorey plants showed little or no growth (Figure 4). For gap plants of *Cedrela* and *Schizolobium*, height growth was high during the rainy season, came to a virtual standstill during the dry season and accelerated again with the first rains. In contrast, *Brosimum* showed continuous growth during the dry season with a slight increase in height growth with the first rains. Watering had a transient effect on height growth of *Cedrela* (Figure 4, Table 1). Height growth started as soon as plants were subjected to the water treatment, more rapidly for gap plants compared to understorey plants (i.e. there is an interaction between light and water). However, when the rainy season started the control plants flushed as well, and plant height was similar for watered and control plants by the end of the experiment (Table 1).

Biomass and allocation

Gap plants had a much larger biomass than understorey plants by the end of the experiment whereas watering did not have an effect (Table 2). Both the maximal root length and the rooting depth were larger for gap plants than for understorey plants (Figure 5a,b). Rooting depth did not surpass 10 cm for understorey plants and was about twice as deep for gap plants. Many plant traits change as plants increase in size. To account for this ontogenetic drift, biomass was included in the statistical analysis as a covariate. Gap and understorey plants of *Brosimum* only differed in their SLA when compared at a similar

Table 1. Effect of light (L), water (W), site (S) and their interactions on leaf number and plant height of *Cedrela odorata*, *Schizolobium amazonicum*, and *Brosimum lactescens*. For each species a separate analysis of variance was carried out. Numbers indicate the order of the census since start of the water treatment (see text). Leaf number and plant height at the onset of the water treatment were included in the analysis as a covariate (Cov) in turn. Significance levels and coefficients of determination are shown.

		Cedrela odorata						*Schizolobium amazonicum*				*Brosimum lactescens*			
		Cov	L	W	S	L*W	r^2	Cov	W	S	r^2	Cov	L	S	r^2
Leaf number	1	***	—	—	—	—	0.91	***	—	**	0.43	***	—	—	0.89
	2	***	*	*	—	—	0.55	**	—	—	0.32	***	*	—	0.79
	3	***	***	**	—	—	0.63	*	—	—	0.25	***	—	*	0.60
	4	***	***	*	—	—	0.67	*	—	—	0.23	—	*	—	0.39
Height	1	***	***	*	—	—	0.97	**	—	—	0.91	***	—	—	0.86
	2	***	***	*	—	*	0.94	***	—	—	0.89	**	—	—	0.56
	3	***	***	—	—	—	0.92	***	—	—	0.86	***	—	—	0.80
	4	***	***	—	—	—	0.90	***	—	—	0.81	***	—	—	0.79

—, P > 0.05; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

Table 2. Effect of light (L), water (W), site (S) and their interactions on plant size (biomass, diameter) and morphology of *Cedrela odorata*, *Schizolobium amazonicum*, and *Brosimum lactescens*. For each species a separate analysis of variance was carried out. Plant size was evaluated without a covariate. For the morphological variables, ln-transformed biomass at final harvest was included in the analysis as a covariate (Cov). Significance levels, coefficients of determination, and means of contrasts (U = understorey, G = gap, C = control, W = watered) are shown.

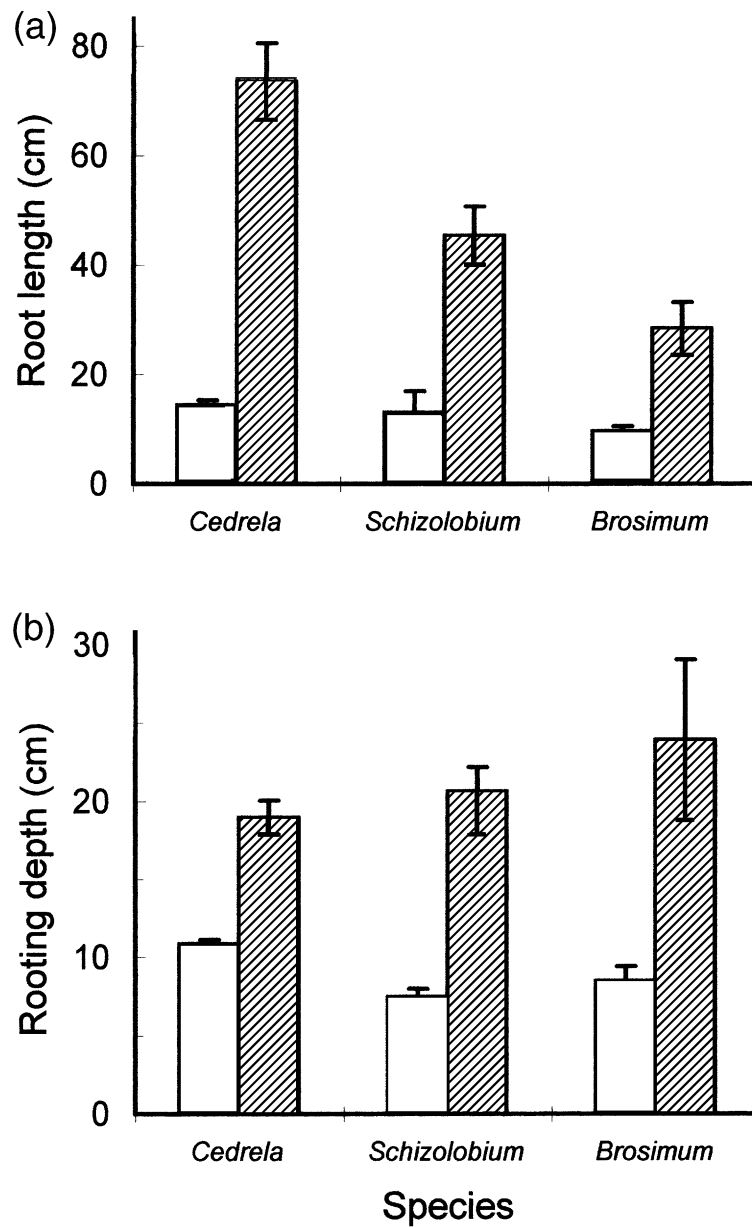|	*Cedrela odorata*								*Schizolobium amazonicum*						*Brosimum lactescens*					
	Cov	L	W	S	L*W	r^2	U	G	Cov	W	S	r^2	C	W	Cov	L	S	r^2	U	G
Biomass (g)	—	***	—	*	—	0.79	0.6	21.6	—	—	—	0.08	6.0	9.0	—	***	—	0.73	0.3	2.8
Diameter (mm)	—	***	—	*	—	0.73	2.9	10.6	—	—	—	0.10	6.3	7.4	—	***	—	0.69	1.5	3.8
Root length (cm)	***	—	—	—	—	0.83	29.5	27.2	***	—	—	0.40	35.8	31.2	***	—	—	0.73	15.3	11.3
Rooting depth (cm)	***	*	—	—	—	0.57	15.7	12.0	**	—	—	0.27	18.4	16.9	***	*	—	0.68	15.1	7.1
RMR (g g⁻¹)	***	**	—	—	—	0.14	0.44	0.33	***	—	***	0.49	0.18	0.22	—	—	—	0.13	0.28	0.30
SMR (g g⁻¹)	*	—	—	—	—	0.45	0.34	0.28	—	—	—	0.05	0.53	0.49	—	—	—	0.17	0.41	0.48
LMR (g g⁻¹)	—	***	—	—	—	0.37	0.21	0.36	**	—	*	0.34	0.26	0.22	—	—	—	0.11	0.28	0.22
SLA (m² kg⁻¹)	***	***	—	—	—	0.91	69.5	43.0	**	—	—	0.31	21.3	19.5	*	*	*	0.85	39.6	31.9
LAR (m² kg⁻¹)	***	—	—	—	—	0.47	14.4	15.4	—	—	*	0.25	5.7	3.8	—	—	—	0.11	11.0	5.5

—, P > 0.05; *, P < 0.05; **, P < 0.01; ***, P < 0.001

Figure 5. Root length (a) and rooting depth (b) of understorey (open bars) and gap (hatched bars) and plants of *Cedrela odorata*, *Schizolobium amazonicum*, and *Brosimum lactescens*. Error bars represent 1 SE. For plant numbers see the legend to Figure 4.

biomass. Understorey plants of *Cedrela* had deeper roots, a higher RMR and SLA, and a lower LMR compared to gap plants (Table 2). In some cases, the different sites led to a different plant morphology. Watering on the other hand did not affect biomass allocation and plant morphology.

<center>DISCUSSION</center>

Water availability

In tropical forest, most of the length and mass of tree roots is concentrated in the upper 20 cm of the soil (Jetten 1994, Odum 1970). Similar patterns have been found for the seedling roots in this study (Figure 5b). The soil moisture content was measured over the same soil range, and therefore it gives a fairly good indication of the soil humidity in the root zone of the plant.

The dry season had a profound influence on soil moisture content (Figure 2). Dry season soil moisture content fell to values as low as 16%. No soil water retention curves are available for the soils in 'El Tigre', but based on the pF curves made for sandy clay loam soils (Jetten 1994) the corresponding soil water potential is below -1.5 MPA which is generally considered to be the permanent wilting point for plants. This suggests that water availability can be a limiting factor for plant performance during the dry season.

Soil moisture values were similar for gap and understorey sites (Figure 2) despite large differences in vegetation structure and incident radiation between these two habitats (Schulz 1960). Yet, the consequences for the soil water balance are equivocal. Soil moisture contents can be higher in gaps due to the combined effects of (a) an increased input of rain through a higher throughfall (Jetten 1994) and water drip from gap bordering tree crowns (Geiger 1965), and (b) a slower depletion of soil water reserves through a reduced root density (Ostertag 1998, Sanford 1990) and a reduced leaf area index (Jetten 1994). However, soil moisture contents can also be lower in gaps due to higher radiation loads, which lead to desiccation of the top soil through evaporation (Brouwer 1996) and higher transpiration rates of gap plants (Meinzer *et al.* 1995) or gap bordering trees which have their roots extended into the gap. Both higher (Becker *et al.* 1988, Jetten 1994, Ostertag 1998, Veenendaal *et al.* 1996b), similar (Howe 1990, Orwig & Abrams 1995, Veenendaal *et al.* 1996b, Vitousek & Denslow 1986), and lower (Ashton 1992, Parker 1985, Turner *et al.* 1992) soil moisture values have been reported for gaps compared to understorey sites. Comparable soil moisture contents in gap and understorey might have been due to the opposite effects of processes that increase and decrease the soil water availability. One might expect the topsoil to be drier and the subsoil to be wetter in gaps compared to the understorey. Integration of the soil moisture over both layers can lead to similar soil moisture values as in the understorey. Other factors which contribute to an apparent lack of differences are a low number of replicates, a small gap size, and a high spatial variation in soil texture. In our study site, spatial variation in gravel content may lead to a 10% variation in soil moisture content over a distance of only a few decimetres (Schmidtkunz 1997; L. Poorter, *pers. obs.*). If soil conditions are sufficiently homogeneous, then even within large gaps a spatial gradient in soil water availability can be found, with a lower soil moisture content in the more exposed sites (Poorter 1998).

Survival

Differences in survival patterns in gap and understorey reflect the differences in shade-tolerance of the species (Figure 3). *Schizolobium* is a typical pioneer species which only survives in a high light environment. *Brosimum*, the shade-tolerant species, showed a slightly higher survival in the shaded understorey than in gaps. *Cedrela* is intermediate in this respect, and can survive both in a gap and an understorey environment.

Cedrela had a high survival rate (cf. Poorter 1998). By shedding its leaves it reduced water loss in a period of low water availability. Seedling mortality of *Schizolobium* peaked in the rainy season, shortly after planting. For understorey plants this was probably due to a negative carbon balance and depletion of seed reserves. From other field studies in tropical forests it is known that mortality rates can peak during the dry season (Garwood 1982, Gerhardt 1996, Howe 1990, Veenendaal *et al.* 1996b).

The probability of survival was positively related to leaf number at the onset of the experiment. A high leaf number indicates that plants were well established, and implies as well a large, photosynthetically active leaf area.

Leaf phenology

In *Schizolobium* and *Cedrela* leaf loss rates increased, and leaf production rates decreased during the dry season leading to lower standing leaf numbers during the dry season compared to the rainy season (Figure 4). Comparable patterns in leaf phenology have been reported for other species (Poorter 1998). A decline in water availability over the season requires whole-plant adjustments in the ratio between transpiring leaf area and water-acquiring roots. Shedding of leaves allows for a rapid adjustment of leaf area to root surface ratio to drought.

Brosimum is a drought-tolerant species, as it maintained a constant leaf number over the dry season. *Cedrela* followed a drought-avoiding strategy by shedding its leaves (Figure 4). The leafless period was three times longer for understorey plants compared to gap plants, which suggests that they experience a substantially longer dry period. A higher drought stress in understorey plants is the result of a smaller root system (Figure 5), rather than a lower soil moisture content (Figure 2). Both longer and deeper roots facilitate the exploration of a larger soil volume, and the access to deeper soil layers where water availability is higher. Illustrative in this respect is that large-sized gap plants have higher dry season pre-dawn leaf water potentials (i.e. they experience less drought stress) than small-sized understorey plants of the same age cohort (Veenendaal *et al.* 1996b). Similarly, gap plants which can sustain the highest transpiration rates during the dry season are also the ones who obtain their water from deeper soil layers (Jackson *et al.* 1995).

Watering cued the leaf flushing of *Cedrela* seedlings, but did not affect leaf phenology of *Schizolobium* (Figure 4). Leaf flushing in the dry season depends on the water status of the tree. In tropical dry forests, it has been shown that

leaf abscission leads to rehydration of the stem and the flushing of new leaves (Borchert 1994, Reich & Borchert 1984). For *Cedrela*, the deciduous species, not much water is lost through transpiration. Watering might have had a positive influence on the water status of the plant leading to the flushing of new leaves. Conversely, in *Schizolobium* watering might have had little effect on the water status of the plant, as most of the extra available water is transpired via old leaves. Thus, differences in the water balance of the species, may explain their different phenological responses to watering. In a moist forest in Panama, a field experiment was set up in which tracts of forest were irrigated for a 5-y period (Wright 1991). Dry season irrigation advanced leaf flushing of several *Piper* and *Psychotria* species, although some species only responded in some years, whereas others species did not respond at all (Wright 1991). An increase in plant water potential (Reich & Borchert 1984), change in photoperiod (Longman & Jeník 1987) and high temperature (Longman & Jeník 1987) may trigger leaf flushing in a tropical environment. In our experiment, watering of plants had a transient effect on the soil moisture content. Therefore it is more likely that watering acted as a cue for leaf flushing, than that it had a lasting effect on the water status of the plants (cf. Wright 1991).

Biomass and height

The three species differed greatly in size, with the light-demanding species realising the largest biomass and the shade-tolerant species the smallest. Gap plants attained a biomass which was on average 10 (*Brosimum*) to 33 (*Cedrela*) times higher than understorey plants (Table 2).

Watering had only a transient effect on height growth of *Cedrela*, and no effect on final biomass of *Cedrela* and *Schizolobium*. It is striking that the advantage of an earlier leaf flushing could not be translated into a higher biomass growth. It might be that the water treatment was imposed too late into the dry season to have a significant effect on plant growth. However, even if plants are irrigated continuously during the dry season, the same patterns emerge; irrigation leads to earlier leaf flushing and a larger leaf area but it does not lead to an increased basal area (Wright 1991) or whole plant biomass (Fisher *et al.* 1991). In controlled experiments, it is found that seedlings show little (two species) or no (nine species) response in height or biomass growth when exposed to different frequencies of watering (Burslem 1996, Burslem *et al.* 1996, Hayashida-Oliver 1997, Okali & Dodoo 1973). In such pot experiments, regular rewatering may allow the plants to recuperate from water stress. Only after a prolonged period of drought are marked responses in survival and growth found (Veenendaal & Swaine 1998).

Allocation

At a given biomass, understorey plants of *Cedrela* had a lower LMR and larger SLA, leading to a similar LAR compared to gap plants (Table 2). It is not clear whether the low LMR of understorey seedlings is a reflection of a functional

response to the (light) environment, or whether it is because the understorey seedlings flushed later than the gap seedlings. Final harvest occurred 2 mo after the first rains, and although all understorey seedlings had flushed by that time it might be that allocation patterns are different further into the rainy season. An increased SLA and LAR in the shade enhance light interception in a light-limited environment, and is often found in controlled seedling experiments (Osunkoya *et al.* 1994, Veneklaas & Poorter 1998, Poorter 1999).

Understorey plants of *Cedrela*, had deeper roots and a higher RMR than gap plants when corrected for biomass differences. At first sight these responses in allocation suggest that during the dry season water is a more limiting resource for understorey plants than for gap plants. However, the observed responses can entirely be attributed to the later flushing of the understorey seedlings; if the leaf component is neglected and gap and understorey seedlings are compared at a similar woody biomass, then they have a similar rooting depth and root to stem mass ratio.

Adjustments in the root–shoot ratio in drought stressed plants can be done by shedding of leaves or an increased biomass partitioning to root growth. Rather than increased biomass partitioning to roots, the efficient placement of roots in deeper, wetter soil layers will increase water uptake by the plant. Indeed, such patterns have been observed for herbaceous species growing in drying soils (Reader *et al.* 1992, Sharp & Davies 1985).

Concluding remarks

There was a marked spatial and temporal variation in height growth and leaf phenology. Height and leaf growth rates were higher in gap compared to understorey plants, and in the wet compared to the dry season. There was an interaction between light environment and dry season drought; high growth during the wet season provides gap plants with a decisive size advantage over understorey plants during the dry season. Their larger root system allows the gap plants to explore a larger surface area and deeper soil layers for water, and as a consequence they experience a shorter dry season than the superficially rooted understorey plants. Watering at the end of the dry season cued the flushing of new leaves by *Cedrela*, although it did not lead to a higher plant growth.

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