Journal of Tropical Forest Science 24(1): 54–63 (2012)

EFFECTS OF LIGHT AND SOIL FLOODING ON THE GROWTH AND PHOTOSYNTHESIS OF RAMIN (*GONYSTYLUS BANCANUS*) SEEDLINGS IN MALAYSIA

WWP Jans[1, *], L Dibor[2], C Verwer[1], B Kruijt[1], S Tan[2] & PJ van der Meer[1]

[1]*Alterra, Wageningen University and Research, PO Box 47, 6700 AA, Wageningen, The Netherlands*
[2]*Forest Research Centre, Forest Department Sarawak, Kuching, Sarawak, Malaysia*

Received February 2011

JANS WWP, DIBOR L, VERWER C, KRUIJT B, TAN S & VAN DER MEER PJ. 2012. Effects of light and soil flooding on the growth and photosynthesis of ramin (*Gonystylus bancanus*) seedlings in Malaysia. We studied the ecophysiology of ramin (*Gonystylus bancanus*) seedlings in an experimental set up at the Forest Research Centre in Kuching, Sarawak, Malaysia. Ramin seedlings were grown on flooded and drained peat soil under 100, 76, 46 and 23% sunlight, thus simulating effects of different light conditions (canopy gap size) and drainage that occur in natural ramin populations. Seedling growth was highest in partial sunlight (76%) and reduced with reducing light levels. Aboveground productivity and fine root development were significantly higher in seedlings grown on flooded soil compared with those on drained soil. In contrast, investment in coarse root biomass was significantly higher in seedlings grown on drained soil. It appeared that the aboveground growth benefits in flooded conditions were the result of more advantageous conditions for allocation of carbon to leaves, thus enhancing overall relative growth rates through higher light interception rates despite lower photosynthetic capacity. The results of this experiment suggested that drainage of peat swamp forests would seriously hamper natural regeneration of ramin by limiting the growth of seedlings. It is also suggested that selective logging operations which produce medium-size canopy gaps improve ramin regeneration in hydrologically undisturbed mixed swamp forests.

Keywords: Natural regeneration, peat swamp forest, drainage

JANS WWP, DIBOR L, VERWER C, KRUIJT B, TAN S & VAN DER MEER PJ. 2012. Kesan cahaya dan tanah banjir terhadap pertumbuhan serta fotosintesis anak benih ramin (*Gonystylus bancanus*) di Malaysia. Kami mengkaji ekofisiologi anak benih ramin (*Gonystylus bancanus*) di tapak eksperimen Pusat Penyelidikan Perhutanan, Kuching, Sarawak, Malaysia. Anak benih ramin ditanam di atas tanah gambut yang dibanjiri serta disalirkan di bawah sinaran cahaya matahari sebanyak 100%, 76%, 46% dan 23%. Keadaan ini menyerupai keadaan cahaya yang berbeza (saiz ruang kanopi) serta saliran di populasi ramin asli. Pertumbuhan anak benih paling tinggi dalam cahaya matahari separa (76%) dan menurun apabila kadar cahaya berkurangan. Produktiviti atas tanah serta pembentukan akar halus lebih tinggi secara signifikan dalam anak benih yang tumbuh di tanah yang dibanjiri berbanding tanah tersalir. Sebaliknya pelaburan karbon dalam biojisim akar kasar lebih tinggi dalam anak benih yang ditanam di tanah tersalir. Nampaknya faedah pertumbuhan atas tanah yang diperoleh dalam keadaan banjir merupakan hasil keadaan yang lebih baik bagi peruntukan karbon kepada daun. Justeru, kadar pertumbuhan relatif keseluruhan ditingkatkan melalui kadar tampanan cahaya yang lebih tinggi walaupun kapasiti fotosintesis lebih rendah. Keputusan eksperimen mencadangkan bahawa saliran hutan paya gambut akan menghalang pemulihan ramin secara semula jadi dengan mengehadkan pertumbuhan anak benih ramin. Keputusan juga menunjukkan bahawa pembalakan berpilih yang mengakibatkan ruang kanopi bersaiz sederhana menambah baik pemulihan ramin di hutan paya bercampur yang tidak terganggu fungsi hidrologinya.

INTRODUCTION

Gonystylus bancanus (Thymelaeaceae), commonly known as ramin, is a shade tolerant, slow growing tree species endemic to the peat swamp forests of Brunei, Indonesia (Kalimantan, Sumatra) and Malaysia (Peninsular Malaysia, Sabah, Sarawak). Ramin is the dominant tree species in undisturbed mixed swamp forest communities (*Gonystylus–Dactylocladus–Neoscortechinia* association) (Anderson 1961). The species has long been exploited for its valuable timber. Commercial logging of ramin started in the 1950s and has resulted

---

**E-mail: wilma.jans@wur.nl*

in a dramatic population decline of ramin across its geographic range (Soehartono & Mardiastuti 2002). The major causes for the ongoing decrease in ramin populations are forest degradation due to logging and extensive habitat loss due to forest conversion to oil palm plantations (Lee & Chai 1996). In addition, ramin has been observed to regenerate poorly in logged-over peat swamp forests (Lee et al. 1996, Lee 2004). Global concerns on the status of natural ramin populations have led to the listing of ramin in Appendix II of the Convention on International Trade of Endangered Species of Wild Flora and Fauna (CITES) in 2005 (Keong 2007). Considering its dominance in mixed peat swamp forests, ramin is a crucial species for the rehabilitation of degraded peat swamp forests.

In undisturbed peat swamp forests, water is hardly ever a limiting factor. However, the conversion of peat swamp areas in oil palm plantations will undoubtedly affect the hydrology of peat swamp forest remnants because the artificial drainage required to grow oil palms often extends further into the peat dome, hence leading to the drying out of peat (Page et al. 2009). So far, the consequences of such hydrological disturbance for seedling and sapling growth of peat swamp forest trees remain unknown. Species occurring in both peat swamp and heath forests more often suffer drought in the latter, indicating that water stress does occur under dry soil conditions (Nishimura & Suzuki 2001). It has been reported that height growth and biomass increase of four dipterocarp seedlings growing in a wet rainforest in Sri Lanka were greater on ever-moist soils compared with periodically dry soils (Ashton et al. 2006). Nevertheless, the effect of drought on seedling survival in tropical moist forest is very much species-dependent (Engelbrecht et al. 2005). In addition to water availability, light is an important limiting resource for tree seedling establishment, growth and survival in tropical rainforests (Chazdon et al. 1996, Agyeman 1999, Balderrama & Chazdon 2005). The growth and survival of ramin may be influenced by increased light levels in logged-over peat swamp forests. Selective logging practices create large gaps within the forest, hence changing the amount of light entering the understorey and forest floor. The increased growth rates and survival of dipterocarp tree seedlings observed in south and south-east Asian rainforests appeared to be associated with more light penetration and larger canopy gaps (Brown & Whitmore 1992, Ashton 1995, Whitmore & Brown 1996). Light and water can also have an interactive effect on plant growth because they both influence allocation patterns of dry matter (Poorter & Hayashida-Oliver 2000, Delissio & Primack 2003, Ashton et al. 2006).

Seedling growth and survival are crucial factors that determine whether ramin can regenerate and regain or maintain its status as one of the dominant species in peat swamp forests. Therefore, it is important to understand how environmental factors control the growth of ramin seedlings and how growth limiting factors can be minimised. To date, very little information is available on the ecophysiology of ramin seedlings and on the growth performance of mature trees. Some emphasis has been given to the role of light in ramin seedling growth (Lee et al. 1996, Shamsudin 1996, Zakaria et al. 1998) but to our knowledge no attention has been given to the role of water in ramin seedling growth in peat swamp forests. This study analysed the effects of light and water availability on photosynthetic rates and carbon allocation of ramin seedlings. We measured net and maximum photosynthetic rates associated with growth under different light levels and different water availability in a shade-house experiment in order to determine the effects of light and drainage on growth strategy and survival of ramin in peat swamp forests in Sarawak, Malaysia.

MATERIALS AND METHODS

Experimental design

The experiment was carried out at the Forest Research Centre in Kuching, Sarawak, Malaysia. Ramin seedlings were grown in 12 growth cabinets, each consisting of two wooden boxes (2 × 1 × 1.6 m) filled with local peat soil. Nine ramin seedlings were randomly selected from a germination experiment and planted in each box.

To create four different levels of light availability, the cabinets were either not covered or covered at the top and sides with two, three or four layers of shade mesh. We measured the photosynthetically active radiation (PAR) availability in the different cabinets using a PAR sensor. The PAR levels achieved were 100, 76, 46 and 23% of full sunlight. Additionally, two water treatments were applied across the two boxes within each cabinet, namely, a drained (D) treatment in boxes where water was allowed to drain to reach field capacity, and a flooded (F) treatment in boxes lined with plastic to retain the water. Water was supplied twice a day for 15 min by a sprinkler irrigation system. However, once a week all the boxes were filled completely with water using a hose, allowing the water to run out of the drained boxes to reach field capacity. The combinations of eight treatments (two water × four light) were each replicated three times.

Biomass and growth

Diameter at root collar and seedling height were measured for all seedlings at the beginning of the experiment. Both these parameters were remeasured three months after planting and thereafter monthly for seven months (i.e. nine months after planting). Based on these measurements, the daily relative growth rates for diameter (RGR_d) and height (RGR_h) were calculated following Hunt (1991):

$$RGR_x = \frac{\ln x(f) - \ln x(i)}{T}$$

where x = either the height or the diameter, f = final and i = initial height or diameter, and T = time interval in days. Assuming that RGR_x remained constant during the year, the potential height and diameter increments for the first year were estimated starting with the average height and diameter of the seedlings at the beginning of the experiment. To see whether treatment significantly affected the RGR_x an analysis of covariance (ANCOVA) was applied, with treatment as factor and initial height or diameter as covariate. When significant interactions between light and water treatments were observed, comparison of light effects within flood treatments, and of flood effects within light treatments were analysed using one-way analysis of variance (ANOVA).

The average relative chlorophyll content per seedling was determined by measuring the chlorophyll content of all leaves on a seedling with a SPAD chlorophyll meter and immediately calculating the average per seedling. Mean and standard error were calculated per treatment and two-way ANOVA was applied to detect significant differences between treatments. At the end of the experiment, three seedlings were harvested from each box. The fresh and dry weights of the coarse roots, fine roots, stems, branches (including petioles) and leaves were determined. Mean and standard error were calculated per treatment and significant differences between treatments were detected using two-way ANOVA. Interactive effects of light and water treatments were analysed as described for the RGR data.

Leaf gas exchange

Net photosynthesis rate (A_n) was measured with a portable infrared gas analysis system. From the third till the ninth month after planting, monthly leaf gas exchange measurements were taken for all treatments under ambient condition between 5 a.m. (before sunrise) and 2 p.m. Only the first fully grown top leaf each of three seedlings per treatment were measured.

At the end of the experiment, CO_2 response curves and subsequently light response curves were drawn using an LED light unit connected to the gas analysis system. For the CO_2 response curves, phothosynthetically active radiation (PAR) was fixed at 1000 µmol m^{-2} s^{-1} and the CO_2 level was increased steadily from 0 to 25, 50, 100, 150, 250, 500, 750, 1000, 1500 and finally 2000 ppm. The A_n was in a steady state for approximately 30 s when measurements were taken. For light response curves, the CO_2 concentration was fixed at 1000 ppm; this was the maximum level of A_n response as defined by the CO_2 response curves. Light was decreased steadily from 2000 to 0 µmol m^{-2} s^{-1} in the following light steps, namely, 2000, 1500, 1000, 750, 600, 450, 300, 200, 100, 50 and 0 µmol m^{-2} s^{-1}. Based on results of the CO_2 response curves, the maximum rate of carboxylation (Vc_{max}) and maximum electron transport rate (J_{max}) were estimated with the model described by Farquhar et al. (1980). From the results of the light response curves, the initial light-use efficiency (α) and the maximum net photosynthetic rate (A_{max}) were estimated using a rectangular hyperbola (Prioul & Chartier 1977). Mean and standard error were calculated per treatment, month and hour. Due to missing values and errors in the response curves we performed one-way ANOVA.

RESULTS

Biomass and growth

At the start of the experiment the average diameter (mean ± SE) at root collar was 3.3 ± 0.3 mm and the average seedling height was 20.2 ± 2.7 cm. RGR_d and RGR_h were influenced significantly by light and water treatments ($F_{8,\,207} = 21.1$, $p < 0.001$ and $F_{8,\,207} = 31.0$, $p < 0.001$ respectively). RGR_d and RGR_h were significantly higher under flooded conditions, except for the lowest light level (Figure 1). Relative growth rates under flooded as well as drained conditions decreased with decreasing light levels but the difference was only significant ($p < 0.05$) at 23% light treatment. A significant interaction was found between the light and water treatments for RGR_h ($F_{1,\,207} = 81.96$, $p < 0.01$) but not for RGR_d. Under flooded conditions, RGR_h differed significantly between light levels ($F_{3,\,103} = 8.65$, $p < 0.001$). Under drained conditions, this effect was not significant. Flood effects within light treatments were only significant for the 100 and 76% light treatments ($F_{1,\,51}=15.54$, $p < 0.001$ and $F_{1,\,51} = 14.99$, $p < 0.001$ respectively).

The annual potential growth was highest under flooded conditions exposed to high light levels (≥ 46% sunlight), ranging from 55.7 to 70.9 cm height growth year^{-1} and 9.02 to 11.81 mm diameter growth year^{-1} at 46 and 100% sunlight respectively (Figure 2). In drained conditions, the estimated annual growth ranged between 31.9 and 39.3 cm year^{-1} for height growth and between 5.74 and 7.87 mm year^{-1} for diameter growth.

At all light levels except for 23%, the dry weights of leaves, stems and fine roots in the flooded boxes were significantly ($p < 0.05$) higher compared with the drained boxes (Table 1). In both flooded and drained conditions, biomass increased with increasing light levels and reached its maximum at 76% sunlight. Seedlings exposed to the lowest light level (23%) had the lowest biomass dry weights of leaves, stem, coarse and fine roots in both watering treatments. Average dry weight of coarse roots did not differ significantly ($p > 0.05$) between treatments (except between the flooded boxes with 23% sunlight and the drained boxes with 76% sunlight). Overall the total dry weight of seedlings in the flooded treatment was significantly ($p < 0.05$) higher compared with that in the drained boxes. No differences were found in the fresh/dry ratio of seedlings. No significant interaction ($p > 0.05$) was found between the light and water treatments for dry weights of leaves, stems, coarse roots, fine roots and branches.

In all light treatments, the fraction of dry weight allocated in the coarse roots was higher in the drained treatment compared with the flooded treatment (Figure 3). On the other hand, the fractions of dry weight allocated in the fine roots and stems were higher in the flooded treatment compared with the drained treatment. The average root/shoot ratio was 0.25 in flooded boxes and 0.36 in drained boxes, which indicated that seedlings in drained boxes had relatively more root biomass than seedlings exposed to flooding. However, this difference was not significant ($p < 0.05$) in the 23% sunlight treatment.

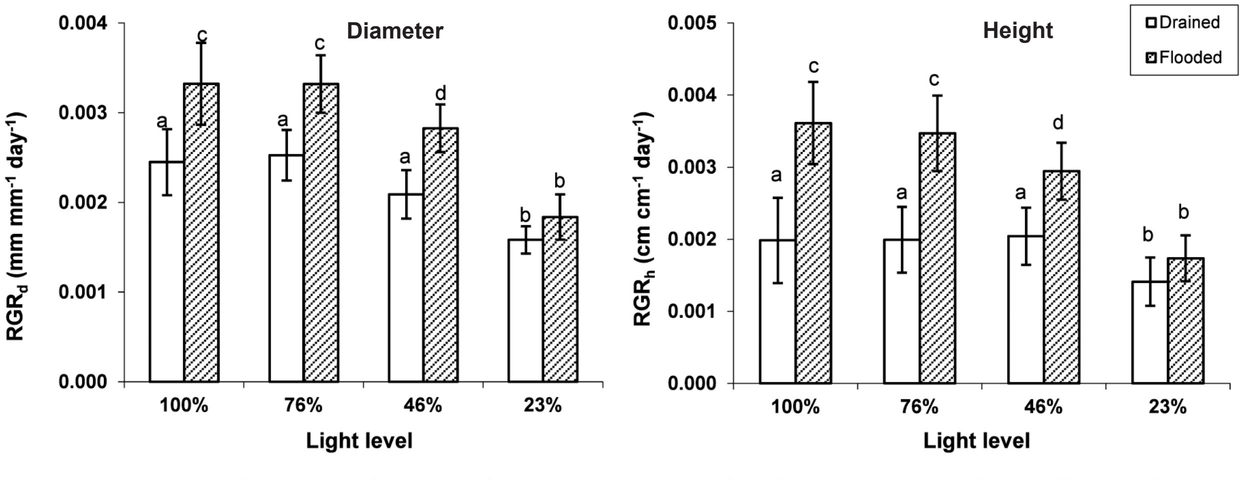


Figure 1 Average relative growth rate for diameter (RGR_d) and height (RGR_h) of seedlings following different light and water treatments; bars not sharing a common letter differ at $p < 0.05$ level

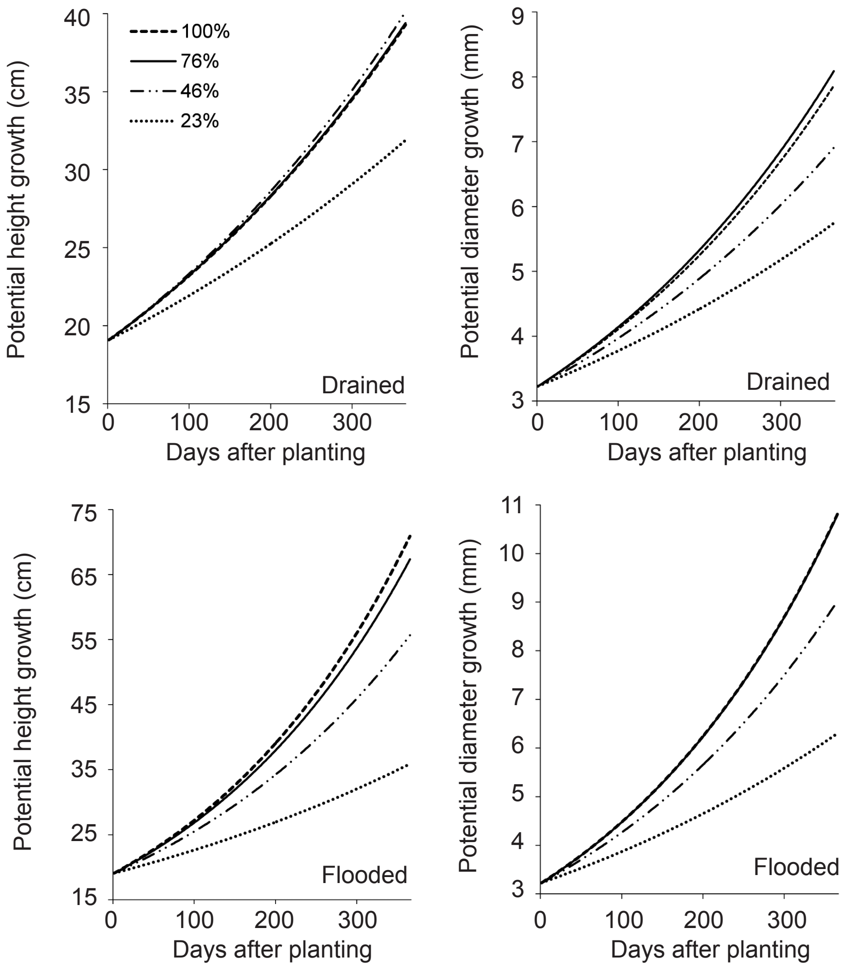


Figure 2 Potential annual height growth and diameter growth of seedlings at the different light and water treatments

Table 1 Mean dry weight (g ± SE) of stem, leaf, coarse root, fine root, plant total and the fresh/dry ratio of seedlings at different light and water treatments measured nine months after planting

Light	Water	Stem	Leaf	Coarse Root	Fine root	Branch	Plant total	Fresh/dry
100%	D	1.81 ± 0.36 a	2.00 ± 0.42 a	0.97 ± 0.22 ab	0.16 ± 0.06 a	0.07 ± 0.02 a	5.01 ± 0.97 a	2.18
	F	3.77 ± 0.68 bc	3.97 ± 0.79 bc	1.08 ± 0.28 ab	0.79 ± 0.20 bc	0.19 ± 0.06 b	9.80 ± 1.86 b	2.36
76%	D	2.90 ± 0.68 a	3.15 ± 0.78 a	2.28 ± 0.54 a	0.33 ± 0.12 a	0.13 ± 0.03 b	8.79 ± 1.74 b	2.37
	F	5.26 ± 0.62 b	5.24 ± 0.96 b	1.42 ± 0.19 ab	1.31 ± 0.15 b	0.29 ± 0.08 bc	13.50 ± 1.75 c	2.54
46%	D	1.98 ± 0.49 a	1.88 ± 0.35 a	1.18 ± 0.30 ab	0.19 ± 0.06 a	0.07 ± 0.01 a	5.29 ± 1.06 a	2.37
	F	4.17 ± 0.74 b	4.09 ± 0.60 b	1.31 ± 0.23 ab	0.58 ± 0.15 c	0.17 ± 0.03 b	10.32 ± 1.78 b	2.23
23%	D	1.42 ± 0.30 a	1.75 ± 0.44 a	0.90 ± 0.19 ab	0.06 ± 0.02 a	0.06 ± 0.01 a	4.19 ± 0.95 a	2.10
	F	2.15 ± 0.45 ca	2.25 ± 0.50 ca	0.76 ± 0.11 b	0.35 ± 0.16 c	0.08 ± 0.02 a	5.58 ± 1.15 ab	2.10

D = drained, F = flooded; values not sharing a common letter within a column differ at $p < 0.05$

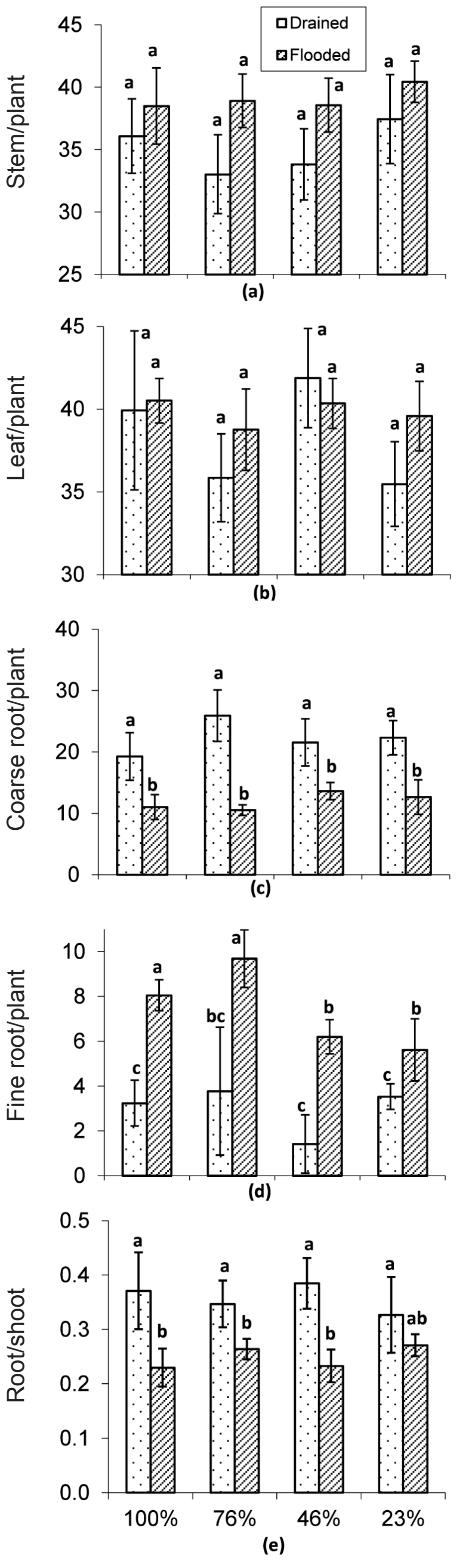


Figure 3 (a–d) The fractions of stem, leaf, coarse root and fine root of the total plant dry weight and (e) root/shoot ratio of seedlings at different light and water treatments nine months after planting; bars not sharing a common letter differ at $p < 0.05$

Leaf gas exchange

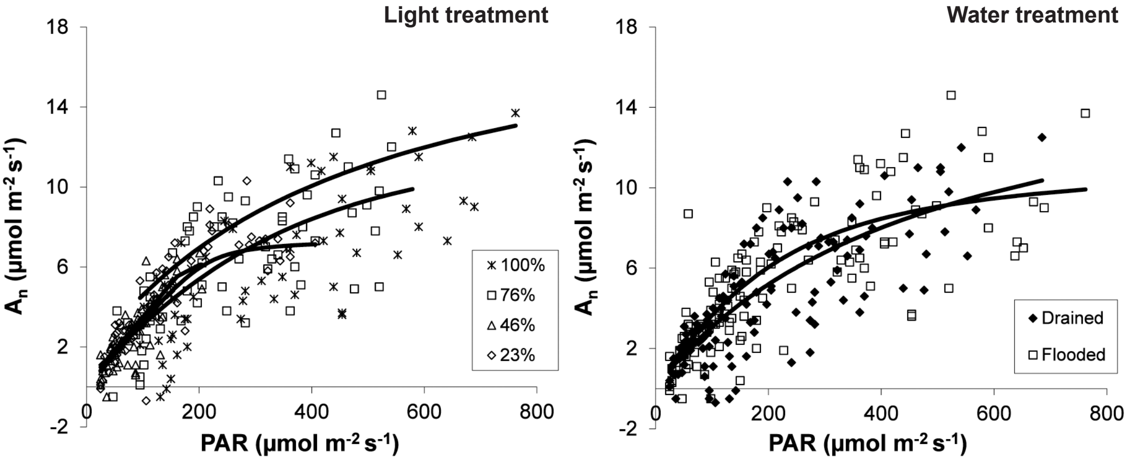
No significant difference ($p > 0.05$) was found in the relationship between PAR and A_n (derived from the monthly measurements) between seedlings in the different light and water treatments (Figure 4).

Relative chlorophyll content of leaves decreased with increasing light levels (Table 2). The values were higher in the flooded boxes compared with the seedlings in the drained boxes, except for 23% sunlight. An interactive effect was found between the water and light treatments for the chlorophyll content of the leaves.

There was no significant difference in Vc_{max} between light treatments (Table 2). However, Vc_{max} for flooded boxes was significantly lower than the drained boxes except for the 23% light level. Generally, J_{max} for drained boxes increased with increased light levels. In contrast, the J_{max} for the flooded boxes increased with decreasing light levels. The J_{max} for the flooded boxes was significantly lower compared with seedlings in the drained boxes except for seedlings in the 23% sunlight where J_{max} was significantly higher in the flooded boxes. At 76% light, A_{max} was significantly ($p < 0.05$) higher for seedlings in the drained than flooded boxes. Generally, α values were similar for all treatments except for 76% sunlight. No interactive effect was found between the water and light treatments for the different photosynthetic parameters.

DISCUSSION

The amounts of PAR in the 23 and 46% light levels of this study fell within the range reported for an understorey and canopy gap situation in logged-over peat swamp forest in Sarawak (Jans et al. 2004). The 23% light for an understorey is high compared with 2 to 45% light for understorey and gap situations respectively in a Costa Rican rainforest (Chazdon 1992). Reducing light to 2% of ambient under experimental conditions is extremely difficult. Similarly, the soil moisture content of 75% in the flooded boxes of our experiment is comparable with that measured in the field (79% in canopy gaps and 71% in the understorey) by Jans et al. (2004) in logged-over peat swamp forest in Sarawak. These numbers



(a) (b)

Figure 4 Relationship between photosynthetically active radiation (PAR) and net photosynthesis rate (A_n) for the different (a) light and (b) water treatments

Table 2 Mean values of maximum rate of carboxylation (Vc_{max}), maximum electron transport rate (J_{max}), maximum net photosynthetic rate (A_{max}), initial light-use efficiency (α) and relative chlorophyll content (fraction) for different light and water treatments measured nine months after planting

Light	Water	Vc_{max} (µmol m^{-2} s^{-1})	J_{max} (µmol m^{-2} s^{-1})	A_{max} (µmol m^{-2} s^{-1})	α (µmol CO_2 µmol E^{-1})	Relative chlorophyll content (fraction)
100%	D	60.4 ± 0.1 a	257 ± 1 a	22.8 ± 0.3 a	0.065 ± 0.003 a	42.5 ± 2.3 a
	F	44.1 ± 0.1 d	66 ± 7 e	na	na	49.7 ± 1.3 b
76%	D	77.9 ± 10.8 b	169 ± 14 b	23.0 ± 0.4 a	0.068 ± 0.003 a	49.5 ± 1.5 b
	F	32.7 ± 5.5 e	68 ± 4 e	10.6 ± 0.3 b	0.049 ± 0.004 b	55.3 ± 1.4 c
46%	D	74.2 ± 0.1 b	127 ± 0 c	11.3 ± 0.3 b	0.070 ± 0.006 a	56.2 ± 1.2 c
	F	45.0 ± 4.5 ad	88 ± 4 d	15.0 ± 0.9 c	0.070 ± 0.010 a	64.7 ± 1.1 e
23%	D	54.3 ± 5.2 c	96 ± 4 d	15.6 ± 0.4 c	0.067 ± 0.007 a	61.1 ± 1.4 d
	F	60.7 ± 3.6 c	160 ± 6 b	25.3 ± 0.7 d	0.054 ± 0.003 a	60.8 ± 0.8 d

D = drained, F = flooded; values are means ± SE; na = not available; values in a column not sharing a common letter differ at $p < 0.05$

illustrated to what extent we were able to match naturally occurring conditions, which was clearly easier for soil moisture than for understorey light.

The growth of ramin seedlings increased with increasing light levels, up to 76% sunlight. Exposure to full sunlight, however, seemed to level off or even decrease the growth again (Figure 1). Seedlings at the 76% light level showed the highest RGR and height, diameter and dry weight increments. In line with our results, Lee et al. (1996) reported the highest growth rates for ramin seedlings at ≥ 40% sunlight. In another study, 15 tropical tree species had the highest growth rates between 50 and 75% sunlight, above which growth rates declined (Poorter 1999). *Quercus pagoda* seedlings had lower leaf mass when grown under 27% sunlight compared with full sunlight (Gardiner & Krauss 2001). Higher height and diameter growth rates of ramin seedlings were observed in a canopy gap compared with seedlings in the understorey of a logged-over peat swamp forest (Jans et al. 2004). Shade-acclimated leaves function at a similar or higher photosynthetic rate due to morphological and physiological acclimation to lower irradiance resulting in a higher growth rate and dry weight production.

Seedling growth rates and consequently total plant biomass were significantly higher in flooded boxes compared with seedlings in drained boxes. The difference in biomass between flooded and drained boxes increased with increasing light levels. An increase in leaf mass after a short period of flooding was reported for *Q. pagoda* seedlings (Gardiner & Krauss 2001). Seedlings in the flooded boxes allocated more dry mass to fine roots and stems while seedlings in drained boxes allocated more dry mass to coarse roots. A decrease in root dry weight is a common response to flooding in trees (Kozlowski 1997). Comparable results were found by Ashton et al. (2006) for dipterocarp seedlings. In this study, interactive effects of light and water were observed for RGR; this is unlike studies by Poorter and Hayashida-Oliver (2000), Delissio and Primack (2003) and Ashton et al. (2006) which reported no interactive effects of light and water on the performance of seedlings in tropical forests.

The higher root/shoot ratio found in seedlings grown in drained boxes was probably an adaptation to low water availability. The seedlings in the flooded boxes invest more in aboveground biomass and fine roots, resulting in a lower root/shoot ratio. This is in agreement with Burslem (1996) who also observed a higher proportion of roots in seedlings in a tropical forest in Singapore when the water availability reduced, which led to a higher ability to establish in drier habitats. Ramin seedlings in peat swamp forests are most competitive and successful under flooded conditions with a fairly open canopy (Lee et al. 1996). We conclude that ramin seedlings in flooded conditions invest less in belowground biomass, and because the roots can still function under this flooding, this makes ramin more competitive above ground.

A higher chlorophyll content of leaves in 25–30% sunlight was also found by Mielke and Schaffer (2010) and Gardiner and Krauss (2001). In contrast with our results, flooding usually causes a reduction in leaf chlorophyll content as a stress symptom observed in tropical tree species (Gardiner and Krauss 2001). As ramin roots are not affected by flooding, stress is not a factor here while low light conditions enhance the chlorophyll content as is to be expected for understorey plants.

While an effect of light on values of photosynthetic capacity, i.e. Vc_{max} could not be demonstrated, this parameter was found to be lower in flooded conditions, contradicting observations of higher growth rates under flooding. Mielke and Schaffer (2010) reported no significant difference between light treatments on A_{max} of *Eugenia uniflora* seedlings, even after a period of flooding. The trend for J_{max} was not clear and significant. Photosynthetic capacity is probably only weakly related to growth as strategies of carbon allocation and water-use efficiency may be as important as photosynthetic efficiency at leaf level. It appeared that the aboveground growth benefits in flooded conditions were the result of more advantageous conditions for allocation of carbon to leaves, thus, enhancing overall relative growth rates through higher light interception rates despite lower photosynthetic capacity.

From the present study, it was concluded that ramin seedlings were shade tolerant, and had higher photosynthesis and more rapid growth in partial sunlight. Shade-tolerant seedlings optimise their light interception by making larger and darker leaves but, ultimately, it is the higher photosynthesis rate under high light conditions that results in faster seedling growth (Poorter 2001). However, this does not necessarily mean that ramin will grow best under higher light levels in natural conditions, as competition with other species may make it perform relatively better at low light (Lee et al. 1996). Moreover, and more clearly, ramin seedlings had the highest aboveground productivity (both photosynthesis and growth) in flooded or very moist soils. Drainage led to less aboveground growth, which was partly compensated for by more investment in coarse root biomass. This might be a result of soil nutrients becoming available due to peat oxidation, which would reduce the need for nutrient foraging and fine root production. However, this explanation does not support the lower total plant biomass and growth rates found in drained soil. Alternatively, effects of root herbivory may explain differences in coarse and fine root biomass. Additional research would be required to explain the allocation patterns found in our experiment.

Compared with other peat swamp forest species ramin is a slow grower (Sukardi & Sutiyono 1994). This suggests that seedlings of ramin are not competitive in most forest conditions but more successful under inundated conditions in swamp forests where more rapidly growing generalists cannot establish (Lee et al. 1996). It may well be that the highest success rate for ramin occurs under moderate light conditions and high water tables, i.e. in swamps (Lee et al. 1996). Drainage leads to lower growth rates and perhaps to denser wood which may, under some conditions, be beneficial as well. In terms of management, this study suggested that ramin culture would benefit from prevention of drainage and from selective logging operations that resulted in medium-size canopy gaps. Peat swamp forests are among the most threatened forest types in the world. The extent of drained peat swamp forest areas as a result of agricultural development is still increasing. Thus, there is an urgent need for more observational and experimental studies of the effects of drainage on the growth and survival of ramin seedlings and peat swamp forest tree species in general.

ACKNOWLEDGEMENTS

We wish to thank the Sarawak Forest Department for facilities and research materials. We greatly acknowledge the assistance of the staff from the Sarawak Forestry Corporation. This work was part of the Ramin Project, funded under the Joint Working Group Malaysia–The Netherlands. Additional support was received from the Dutch Ministry of Agriculture, Nature and Food Quality.

REFERENCES

Agyeman VK, Swaine MD & Thompson J. 1999. Responses of tropical tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology* 87: 815–827.

Anderson JAR. 1961. The ecology and forest types of the peat swamp forests of Sarawak and Brunei in relation to their silviculture. PhD thesis, University of Edinburgh, Edinburgh.

Ashton PMS. 1995. Seedling growth of co-occurring *Shorea* species in the simulated light environments of a rain forest. *Forest Ecology and Management* 72: 1–12.

Ashton MS, Singhakumara BMP & Gamage HK. 2006. Interaction between light and drought affect performance of Asian tropical tree species that have different topographic affinities. *Forest Ecology and Management* 221: 42–51.

Balderrama SIV & Chazdon RL. 2005. Light-dependent seedling survival and growth of four tree species in Costa Rican second-growth rain forests. *Journal of Tropical Ecology* 21: 383–395.

Brown ND & Whitmore TC. 1992. Do dipterocarp seedlings really partition tropical rain forest gaps? *Philosophical Transactions of the Royal Society of London* B335: 369–378.

Burslem D. 1996. Differential response to nutrients, shade and drought among tree seedlings of lowland tropical forest in Singapore. Pp 211–243 in Swaine MD (ed) *The Ecology of Tropical Forest Tree Seedlings*. Volume 17. Parthenon Publishing Ltd, Carnforth.

Chazdon RL. 1992. Photosynthetic plasticity of 2 rain-forest shrubs across natural gap transects. *Oecologia* 92: 586–595.

Chazdon RL, Pearcy R, Lee D & Fetcher N. 1996. Photosynthetic responses of tropical plants to contrasting light environments. Pp 5–55 in Mulkey SS et al. (eds) *Tropical Forest Plant Ecophysiology*. Chapman & Hall, New York.

Delissio LJ & Primack RB. 2003. The impact of drought on the population dynamics of canopy-tree seedlings in a seasonal Malaysian rain forest. *Journal of Tropical Ecology* 19: 489–500.

Engelbrecht MJ, Kursar TA & Tyree MT. 2005. Drought effects on seedling survival in a tropical moist forest. *Trees* 19: 312–321.

Farquhar GD, Caemmerer S Von & Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. *Planta* 149: 78–90.

Gardiner ES & Krauss KW. 2001. Photosynthetic light response of flooded cherrybark oak (*Quercus pagoda*) seedlings grown in two light regimes. *Tree Physiology* 21: 1103–1011.

Hunt R. 1991. *Plant Growth Curves: The Functional Approach to Plant Growth Analysis*. Cambridge University Press, Cambridge.

Jans WWP, Dibor L, Kruijt B, Van Der Meer P & Tan KSS. 2004. *Leaf Properties, Photosynthetic Rates and Growth Strategies of Ramin*. Report No. 16 of the Ramin Project: Sustainable Management of Peat Swamp Forest with Special Reference to Ramin. Forest Department Sarawak, Kuching.

Keong CH. 2007. Implementing ramin's CITES listing. *ITTO Tropical Forest Update* 17: 3–6.

Kozlowski TT. 1997. Responses of woody plants to flooding and salinity. *Tree Physiology Monograph* 1: 1–29.

Lee HS. 2004. *Improving Biodiversity and Sustainability of Peat Swamp Forests of Sarawak*. Report No. 12 of the Ramin Project: Sustainable Management of Peat Swamp Forests of Sarawak with Special Reference to Ramin. Forest department Sarawak, Kuching.

Lee HS & Chai F. 1996. Production functions of peat swamp forests in Sarawak. Pp 129–136 in Maltby E et al. (eds) *Tropical Lowland Peatlands of South East Asia. Proceedings of a Workshop on Integral Planning and Management of Tropical Lowland Peatlands*. 3–8 July 1992, Cisarua.

Lee DW, Krishnapillay B, Haris M, Marzalina M & Yap SK. 1996. Seedling development of *Gonystylus bancanus* (ramin melawis) in response to light intensity and spectral quality. *Journal of Tropical Forest Science* 8: 520–531.

Mielke MS & Schaffer B. 2010. Photosynthetic and growth responses of *Eugenia uniflora* L. seedlings to soil flooding and light intensity. *Environmental and Experimental Botany* 68: 113–121.

Nishimura TB & Suzuki E. 2001. Allometric differentiation among tropical tree seedlings in heath and peat swamp forests. *Journal of Tropical Ecology* 17: 667–681.

Page S, Hoscilo A, Wosten H, Jauhiainen J, Silvius M, Rieley J, Ritzema H, Tansey K, Graham L, Vasander H & Kimin S. 2009. Restoration of lowland tropical peatlands in Southeast Asia: current knowledge and future research directions. *Ecosystems* 12: 888–905.

Poorter L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* 13: 396–410.

Poorter L. 2001. Light-dependent changes in biomass allocation and their importance for growth of rain forest species. *Functional Ecology* 15: 13–123.

Poorter L & Hayashida-Oliver Y. 2000. Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology* 16: 481–498.

Prioul JL & Chartier P. 1977. Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO_2 fixation: a critical analysis of the methods used. *Annals of Botany* 41: 789–800.

Shamsudin I. 1996. *Gonystylus bancanus*: some observation on its flowering, fruiting, seed predation and germination. *Journal of Tropical Forest Science* 8: 242–426.

Soehartono T & Mardiastuti A. 2002. *CITES Implementation in Indonesia*. Nagao International Environmental Foundation, Tokyo.

Sukardi I & Sutiyono I. 1994. The growth of wildings of peat swamp species. *Bulletin Penelitian Hutan* 559: 19–32.

Whitmore TC & Brown ND. 1996. Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Philosophical Transactions of the Royal Society of London* B351: 1195–1203.

Zakaria H, Tan S & Chai FYC. 1998. *Regeneration of Ramin (Gonystylus bancanus) (Miq.) Kurz and Selected Commercial Species in Logged-Over Mixed Swamp Forests, 20 or More Years After Logging*. Report No. 01–04–06–006 of the IRPA Project. Forest Department Sarawak, Kuching.