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Effects of drought and fire on seedling survival and growth under contrasting light conditions in a seasonal tropical forest

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Abstract

Question: How do tree seedlings differ in their responses to drought and fire under contrasting light conditions in a tropical seasonal forest?

Location: Mae Klong Watershed Research Station, 100-900 m a.s.l, Kanchanaburi Province, western Thailand.

Method: Seedlings of six trees, *Dipterocarpus alatus*, *D. turbinatus*, *Shorea siamensis*, *Pterocarpus macrocarpus*, *Xylia xylocarpa* var. *kerrii* and *Sterculia macrophylla*, were planted in a gap and under the closed canopy. For each light condition, we applied (1) continuous watering during the dry season (W); (2) ground fire during the dry season (F); (3) no watering/no fire (intact, I). Seedling survival and growth were followed.

Results: Survival and growth rate were greater in the gap than under the closed canopy for all species, most dramatically for *S. siamensis* and *P. macrocarpus*. *Dipterocarpus alatus* and *D. turbinatus* had relatively high survival under the closed canopy, and watering during the dry season resulted in significantly higher survival rates for these two species. Watering during the dry season resulted in higher growth rates for five species. All seedlings of *D. alatus* and *D. turbinatus* failed to re-sprout and died after fire. The survival rates during the dry season and after the fire treatment were higher for the seedlings grown in the canopy gap than in the shade for *S. siamensis*, *P. macrocarpus*, *X. xylocarpa* var. *kerrii* and *S. macrophylla*. The seedlings of these species in the canopy gap had higher allocation to below-ground parts than those under the closed canopy, which may support the ability to sprout after fire.

Conclusions: The light conditions during the rainy season greatly affect seedling survival and resistance to fire during the subsequent dry season. Our results suggest differentiation among species in terms of seedling adaptations to shade, drought and fire.

Keywords: Canopy gap; Forest regeneration; Mixed deciduous forest; Thailand; Water condition.

Nomenclature: Smitinand (1980).

Abbreviations: C = Closed canopy; DDF = Deciduous dipterocarp forest; DEF = Dry evergreen forest; Fi = Fire; Ga = Gap; In = Intact; MDF = Mixed deciduous forest; SOC = Standard overcast sky distribution; S:R = Shoot-root ratio; Wa = Watering.

Introduction

Variation in available light plays an important role in the germination, growth and survival of tree seedlings in tropical and temperate forests (Denslow 1987; Brokaw 1985; Nakashizuka et al. 1992). Canopy gaps provide essential regeneration sites for many tree species, especially pioneer and light demanding species (Whitmore 1989). In tropical seasonal (dry) forests, soil water conditions may also be critical and may vary between gaps and shaded areas (Veenendaal et al. 1996). Plants growing in shade are likely to show an increased shoot:root (S:R) ratio response to low irradiance, possibly reducing rooting depth, which may be critical for the survival of understorey seedlings during the dry season (Mulkey et al. 1991). Frequent dry season fires are another factor affecting seedling survival (Marod et al. 2002; Stott et al. 1990; Murphy & Lugo 1986). In seasonal tropical forests, it is essential to understand the interacting effects of drought and fire with light as they affect regeneration.

Experimental manipulation of water availability in a tropical seasonal forest have proved that wetting after drought can cue anthesis in a gregariously flowering shrub and tree (Augspurger 1981; Reich & Borchert 1984) or can advance leaf emergence of several shrubs (Wright 1991). However, fewer experimental studies have been conducted to evaluate the interaction between light availability, water availability and fire occurrence for tree seedlings (but see Poorter & Hayashida-Oliver 2000). We used manipulated light, water and fire occurrence to address the following questions: 1. How do seedlings respond to different light conditions? 2. How do the responses of seedlings to drought and fire differ among species under contrasting light conditions ?

Study site

The study was conducted in a mixed deciduous forest at Mae Klong Watershed Research Station, Thong Pha Phoom District (14°30' - 14°45' N, 98°45' - 99° E), Kanchanaburi Province, western Thailand. The watershed covers 108.9 km^2 and ranges from 100 to 900 m a.s.l. The climate is sub-tropical with a long wet season (April to October) alternating with a short cool dry season and subsequent hot dry season. Mean, minimum and maximum annual rainfall during the last decade (1989-1998) were 1546 mm, 1243 mm and 1897 mm, respectively. Mean monthly temperature is 27.5 °C with a maximum of 39.1 °C in April and a minimum of 14.6 °C in December. The soil water content is almost saturated from May to September and the soil water tension value reaches 10 kPa. The soil is very dry during the dry season and the tension was too high for measurement by the porous cup method (Marod et al. 2002). The parent materials are granite, limestone and shale. Phyllite and quartzite are also found in small patches of the watershed area (Suksawang 1995).

The prevailing forest type in this area is a mixed deciduous forest (MDF) (Ogawa et al. 1961; Rundel & Boonpragob 1995; Marod et al. 1999), with small areas of dry dipterocarp forest (DDF) on the mountain ridges and dry evergreen forest (DEF) along the riparian areas (Kutintara et al. 1995). The experimental plots were set within a natural stand of mixed deciduous forest with a dense understorey of bamboo. The dominant tree species were *Shorea siamensis*, *Dillenia parviflora*, *Xylia xylocarpa* var. *kerrii*, *Pterocarpus macrocarpus* and *Lagerstroemia* spp. Tree density and basal area of the forest were 171 $ind.ha^{-1}$ and 17.25 $m^2.ha^{-1}$, respectively (Marod et al. 1999). Four bamboo species, *Gigantochloa albociliata*, *G. hasskarliana*, *Bambusa tulda* and *Cephalostachyum pergracile*, were dominant in the understorey. There were no evident records of past logging within the forest. However, the activities of local people such as selective felling of particular species or fire setting may have affected the forests surrounding the plots. Within the area, forest fires have occurred during the last decade (D. Marod unpubl. data), and probably occurred repeatedly over the past several hundred years (Rundel & Boonpragob 1995; Ruangpanit 1995).

Methods

Six tree species with high dominance (Marod et al. 1999) were selected for this experiment. These were: a pioneer species, *Sterculia macrophylla*, and five late successional tree species: *Dipterocarpus alatus*, *D. turbinatus*, *Shorea siamensis*, *Pterocarpus macrocarpus* and *Xylia xylocarpa* var. *kerrii* (Smitinand et al. 1980). *D. alatus* and *D. turbinatus* are mainly distributed along moist riparian fringes and lower parts of the slope. *S. siamensis*, which is typically a component species of DDF, is mainly distributed on the dry ridge in this area. Wind is the most important factor in seed dispersal of these species. The remaining species are common component species in MDF (Smitinand et al. 1980; Marod et al. 1999).

Leaf phenology of the seedlings is different among the selected species. *D. alatus* and *D. turbinatus* are only leafless for a brief period in December during which time the old leaves fall and new ones emerge. The other species have seasonal leafless periods. *P. macrocarpus*, *S. siamensis* and *X. xylocarpa* var. *kerrii* shed leaves in late February and new leaves emerge during late March. *S. macrophylla* sheds leaves in late November and new leaves emerge in May (H. Tanaka unpubl.).

Mature seeds of the six species were collected from 15 to 20 fruiting trees within and around the watershed area from March to April 1999. The seeds were sown in a partially shaded garden (40% relative light intensity). Germinated seedlings were moved to black plastic bags (8 cm diameter, 20 cm high) filled with soil taken from the natural MDF for a week, after which they were transplanted into the experimental plots.

The experiment was designed to be a combination of the two light conditions, gap (G) and closed canopy (C), and three treatments (watering during the dry season every two days (W), fire treatment during the dry season (F) and intact (I; this treatment had neither watering nor fire)). To analyse the interactions between light and watering, the experimental sets of (G/C) × (W/I) were used. For the analysis of the interactions between light and fire, we used the sets of (G/C) × (F/I). The plots under the closed canopy were placed in a site with canopy height of 15-25 m and understorey bamboos ca. 12 m high. For the gap site we cleared vegetation (including dense bamboos) in a pre-existing large canopy (tree) gap. Six 4 m × 5 m quadrats were established in the gap site and under the closed canopy site; 15 even-sized seedlings of each species were transplanted from the nursery into random positions within the quadrats. As a result, the seedling density in each quadrat was 4.5 individuals per m^2, which was low enough to avoid direct interactions between the seedlings. One of the three treatments was applied to each of the quadrats randomly with two replications. These quadrats were separated by a 2 m buffer zone.

Transplanting was carried out on 6 May 1999. Seedling survival was checked every 15 days thereafter. The height to the top of the lead shoot and the basal stem diameter of the seedlings were measured three months and nine months after the initiation of the experiment (at the end of the rainy season; October 1999 and at the end of the dry season; April 2000). The fire treatment was conducted in late February during the dry season (two months before the end of the dry season). Litter was manipulated so that it was equivalent to that of natural forests (80 $g.m^{-2}$ dry weight; D. Marod pers. obs.), the litter was then burned. At the end of the experiment, whole plants were carefully excavated and the dry mass of stems, leaves, tap and lateral roots with fine roots were weighed after washing and drying at 70 °C for 48 hr. S:R ratio was calculated by dividing the dry weight of above-ground biomass by that of below-ground biomass for each individual.

To estimate the light conditions in the gap and under the closed canopy, we took five hemispherical canopy photographs in each 4 m × 5 m quadrat at a height of 10 cm above the ground with a fish-eye camera (Nikon, F8 mm) (pictures were taken at the four corners and the centre in each quadrat). The hemispherical photographs were taken during the rainy season (June) and the dry season (February). The relative light intensity was calculated as the percentage of standard overcast sky distribution (SOC, %) by the FEW52b program for Windows '95 (Ishizuka & Kanazawa 1991). The light condition in each quadrat was calculated as the mean of the five values.

For statistical analyses of the effect of two factors, light conditions (C/G) and watering during the dry season (W/I), on seedling size (height and basal diameter) we used ANOVA. Multi-dimensional contingency table analysis (log linear model; Sokal & Rohlf 1995) was conducted to analyse the relationship of the light conditions (C/G), watering (W/I) and fire (F/I) to seedling survival. Log linear models are the counterpart for attribute data to the linear model for continuous variables in ANOVA and multiple regressions. Differences of S:R ratio among species were tested by ANCOVA. The computer software STATISTICA version 5.1 (Anon. 1995) and JMP 5.0.1 (Anon. 2002) were used for these statistical analyses.

Results

Light conditions under the closed canopy and in the gap

The mean SOC (%) of the quadrat under the closed canopy and in the gap were 2.1 ± 0.9 and 21.2 ± 5.1 during the rainy season and 9.6 ± 1.8 and 25.9 ± 4.1 during the dry season, respectively. The light conditions were significantly different between in the gap and under the closed canopy during both seasons (df = 5, t = 8.24; $p < 0.001$ and t = 7.42; $p < 0.001$, respectively). Light conditions were poor during the rainy season and much better during the dry season under the closed canopy (df = 5; t = 7.86; $p < 0.001$).

Seedling survival

Under the closed canopy, four species other than *Dipterocarpus alatus* and *D. turbinatus* had significantly higher mortality during the rainy season than during the dry season (Fig. 1). The magnitude of the influence of light on seedling mortality during the rainy season varied among species. In particular, *S. siamensis* and *P. macrocarpus* had nearly 100% seedling mortality under the closed canopy during the rainy season. In contrast, *D. alatus* and *D. turbinatus* showed small differences in mortality between the gap and closed canopy, suggesting higher shade tolerance. In contrast to the other species, the seedlings of *D. alatus* and *D. turbinatus* in the gap had higher mortality during the dry season than during the rainy season.

For most of the species, the seedlings in the gap also had higher survival rates than those under the closed canopy during the dry season. The differences in light conditions during the dry season seem to have little effect on the photosynthetic activity of the seedlings which shed their leaves. This suggests that the light conditions during the rainy season and early in the dry season may have a delayed effect on survival during the dry season (Table 1).

The effect of watering during the dry season on seedling survival was significant only for *D. alatus* and *D. turbinatus* (df = 1; $\chi^2 = 4.02$; $p < 0.05$ and $\chi^2 = 7.07$; $p < 0.01$, respectively), suggesting that the other species are less susceptible to drought than these two species.

Fire significantly increased the mortality for all the species, except *Sterculia macrophylla* (Table 1). All of the seedlings of *D. alatus* and *D. turbinatus* died without re-sprouting after the fire. However, a high percentage of the seedlings of the other species in the gap survived by sprouting after the fire (Table 1; Fig. 1).

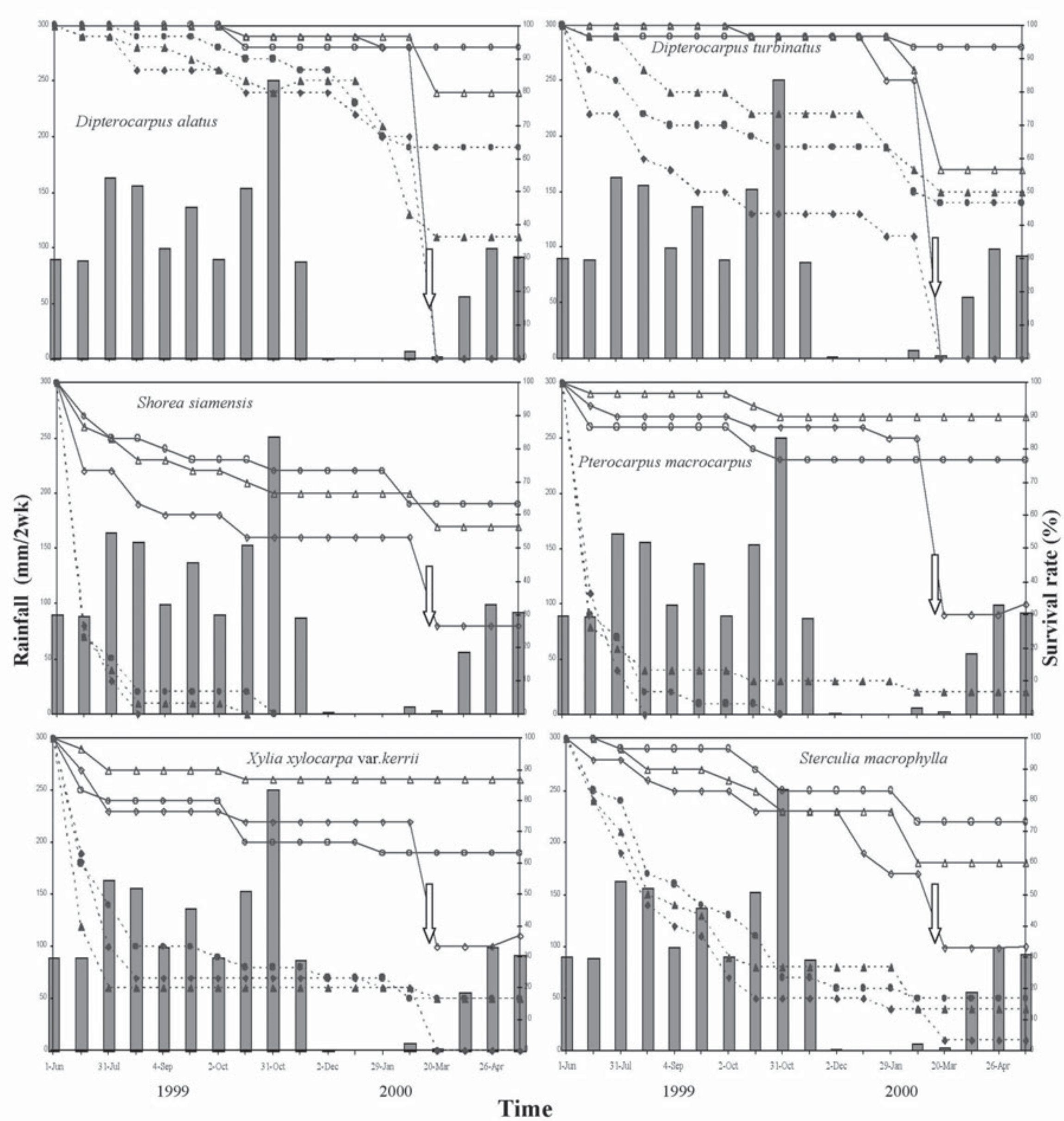

Fig. 1. Seasonal patterns of seedling survival for the six species. ° = watering treatment during the dry season; △ = control, ◇ = fire treatment. Closed and open symbols indicate the seedlings under closed canopy and in gap, respectively. The shaded column shows the amount of rainfall (mm per 2 wk), the arrow indicates the time of the fire treatment during the dry season.

Seedling growth

During the rainy season, all of the species had significantly higher seedling growth rates in the canopy gap than under the closed canopy (Table 2, Figs. 2 and 3). Seedlings of *D. alatus* and *D. turbinatus* had particularly large growth improvement in the gap compared with the other species.

Effect of watering during the dry season on seedling growth rates under both of the light conditions was significant only for diameter growth of *D. turbinatus* (df = 1; $F = 5.34$; $p < 0.05$; see Table 2). Since all seedlings of *S. siamensis* and *P. macrocarpus* under the closed canopy died before the dry season started, the effect of watering and fire were analysed only for the seedlings in the gap. Watering resulted in greater height and basal diameter for *S. siamensis* seedlings compared to the controls (df = 1; $F = 5.72$; $p < 0.05$ and $F = 17.84$; $p < 0.001$, respectively), while those of *P. macrocarpus* were significantly greater only in basal diameter (df = 1; $F = 14.90$; $p < 0.001$, Table 2, Figs. 1 and 2).

Table 1. Effects of the treatment on the seedling survival (Log-linear model).

	D. alatus			*D. turbinatus*			*S. siamensis*			*P. macrocarpus*			*X. xylocarpa* var. *kerrii*			*S. macrophylla*		
	df	χ^2	*p*	df	χ^2	*p*	df	χ^2	*p*	df	χ^2	*p*	df	F	*p*	df	χ^2	*p*
SR1 Ga/Ca	1	4.18	*	1	6.85	**	1	77.52	***	1	94.04	***	1	44.81	***	1	42.70	***
SR2 Ga/Ca	1	20.67	***	1	7.64	**	1	54.25	***	1	84.33	***	1	45.15	***	1	38.64	***
Wa/In	1	11.43	**	1	2.65	NS	1	0.00	NS	1	0.82	NS	1	2.09	NS	1	0.83	NS
Ga/Ca × Fi/In	1	0.00	NS	1	0.00	NS	1	0.00	NS	1	0.00	NS	1	0.00	NS	1	0.00	NS
G/C	1	5.01	**	1	7.05	**		-	-	-	-	-	1	5.01	**	1	5.89	**
SR3 Wa/In	1	4.02	*	1	7.07	**	1	0.23	NS	1	1.29	NS	1	2.27	NS	1	1.28	NS
Ga/Ca × Fi/In	1	0.7	NS	1	0.22	NS	-	-	-	-	-	-	1	0.07	NS	1	0.37	NS
Ga/Ca	1	8.15	**	1	11.03	**	1	33.51	***	1	48.30	***	1	50.57	***	1	21.19	***
SR4 Fi/In	1	43.34	***	1	40.53	***	1	4.97	*	1	10.97	**	1	8.36	**	1	3.53	NS
Ga/Ca × Fi/In	1	0.00	NS	1	25.27	**	1	0.00	NS	1	0.00	NS	1	0.00	NS	1	0.13	NS
Ga/Ca	1	7.45	**	1	4.85	*	-	-	-	-	-	-	1	11.47	***	1	3.43	NS
SR5 Fi/In	1	13.28	***	1	33.62	***	1	3.97	*	1	12.97	**	1	7.69	**	1	3.82	NS
Ga/Ca × Fi/In	1	0.00	NS	1	13.09	***	-	-	-	-	-	-	1	0.07	NS	1	0.03	NS

Ga/Ca : Gap and Canopy
Wa/In : Watering and Intact
Fi/In : Fire and Intact
- : No analyses

SR1 : Survival from the start of the experiment to the end of the rainy season
SR2 : Survival from the start of the experiment to the end of the dry season
SR3 : Survival from the start to the end of the dry season (during the dry season)
SR4 : Survival from the start of the experiment to the time after fire treatment
SR5 : Survival from the start of the dry season to the time after fire treatment

NS : Not significant
* : $p < 0.05$
** : $p < 0.01$
*** : $p < 0.001$

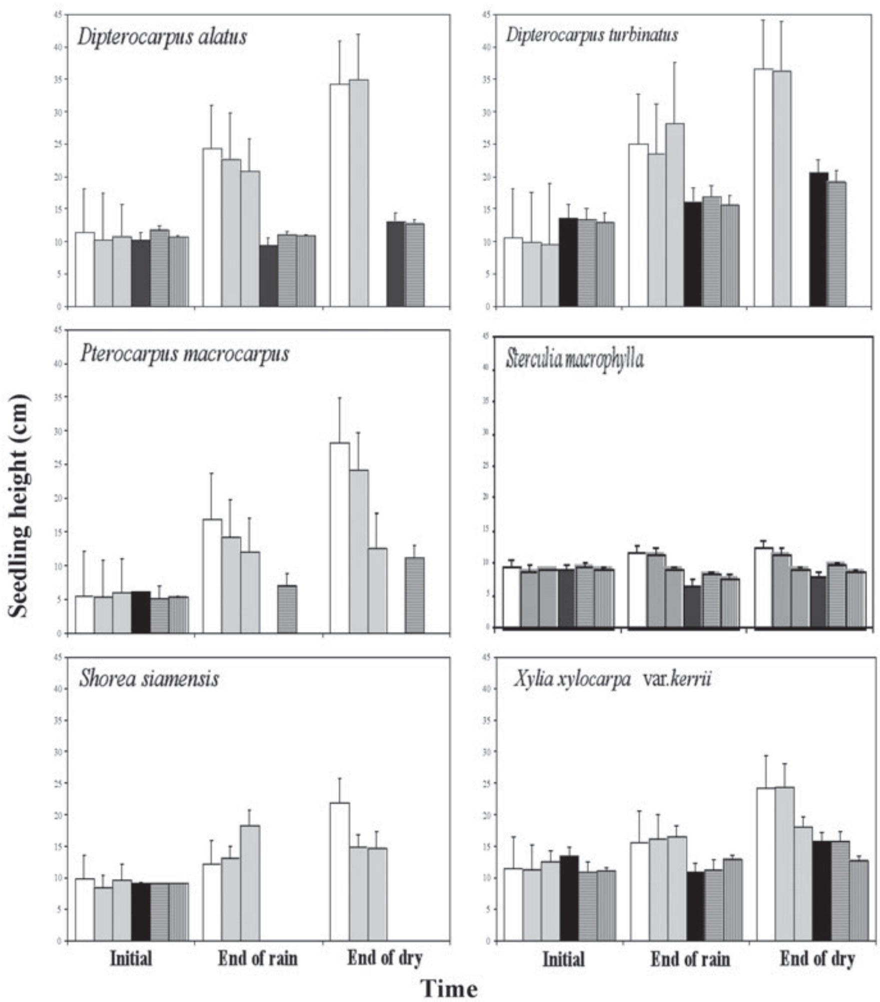

Fig. 2. Height of the seedlings at the start of the experiment, at the end of the rainy season and at the end of the dry season. The first three columns indicate the seedlings in gap: watering treatment; ▭, control; ▧, fire treatment; ▨.

The next three columns indicate the seedlings under the closed canopy: watering; ■, control; ▤, fire; ▥.
Means and SE are shown.

Table 2. Effects of the treatment on the seedling growth (ANOVA).

		D. alatus			*D. turbinatus*			*S. siamensis*			*P. macrocarpus*			*X. xylocarpa* var. *kerrii*			*S. macro-phylla*		
		df	χ^2	*p*	df	χ^2	*p*	df	χ^2	*p*	df	χ^2	*p*	df	F	*p*	df	χ^2	*p*
Ht1	Ga/Ca	1	160.08	***	1	30.19	***	-	-	-	-	-	-	1	15.10	***	1	12.04	***
	Ga/Ca	1	11.04	***	1	53.44	***	-	-	-	-	-	-	1	11.05	**	1	4.93	*
Ht2	W/I	1	0.04	NS	1	0.14	NS	1	5.72	*	1	2.69	NS	1	0.03	NS	1	0.06	NS
	Ga/Ca × Wa/In	1	0.05	NS	1	0.06	NS	-	-	-	-	-	-	1	0.04	NS	1	0.95	NS
	Ga/Ca	-	-	-	-	-	-	-	-	-	-	-	-	1	4.72	*	1	4.22	*
Ht3	Fi/In	-	-	-	-	-	-	1	24.79	***	1	31.25	***	1	55.82	***	1	43.25	***
	Ga/Ca × Fi/In	-	-	-	-	-	-	-	-	-	-	-	-	1	0.95	NS	1	0.55	NS
Do1	Ga/Ca	1	149.44	***	1	82.28	***	-	-	-	-	-	-	1	10.29	**	1	8.64	**
	Ga/Ca	1	11.47	***	1	102.86	***	-	-	-	-	-	-	1	11.47	**	1	12.91	***
Do2	W/I	1	1.16	NS	1	5.34	*	1	17.84	***	1	14.90	***	1	1.16	NS	1	0.76	NS
	Ga/Ca × Wa/In	1	0.09	NS	1	4.73	*	-	-	-	-	-	-	1	0.42	NS	1	0.76	NS
	Ga/Ca	-	-	-	-	-	-	-	-	-	-	-	-	1	1.12	NS	1	0.68	NS
Do3	Fi/In	-	-	-	-	-	-	1	0.11	NS	1	3.89	*	1	0.73	NS	1	1.22	NS
	Ga/Ca × Fi/In	-	-	-	-	-	-	-	-	-	-	-	-	1	0.94	NS	1	0.72	NS

Ga/Ca : Gap and Canopy
Wa/In : Watering and Intact
Fi/In : Fire and Intact
- : No analyses

Ht1 : Height at the end of the rainy season
Ht2 : Height at the end of the dry season
Ht3 : Height at the time after fire treatment

Do1 : Basal diameter at the end of the rainy season
Do2 : Basal diameter at the end of the dry season
Do3 : Basal diameter at the time after fire treatment

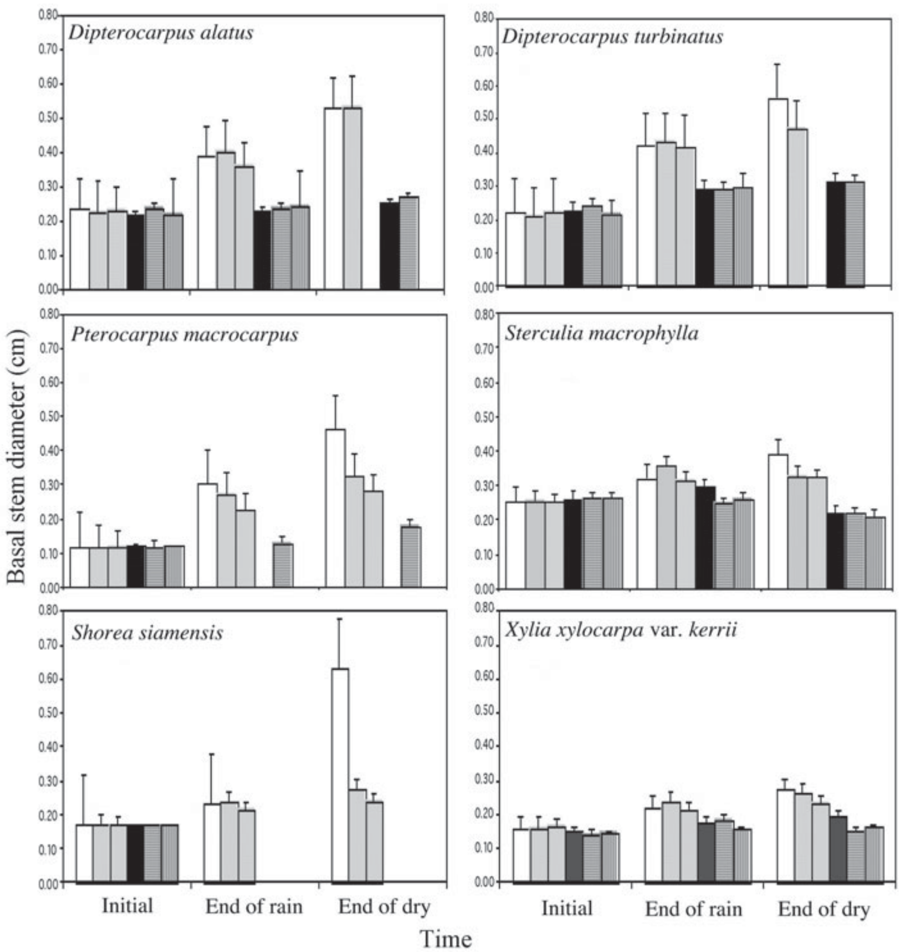

Fig. 3. Basal diameter of the seedlings at the start of the experiment, at the end of the rainy season and at the end of the dry season. The column symbols are as in Fig. 2. Means and SE are shown.

The effects of fire on seedling growth rates were highly significant for height (Table 2). Re-sprouted stems did not reach the height of the undamaged stems. In contrast, the effect of fire on the basal diameter was not significant, except for the seedlings of *P. macrocarpus* (df = 1; $\chi^2 = 3.89$; $p < 0.05$).

Shoot-root allocation

There were significant differences in S:R ratio among species for individuals grown in the gap (Fig. 4, ANCOVA, $p < 0.01$). S:R ratios of *D. alatus* and *D. turbinatus* were significantly higher than those of the other species, and those of *S. macrophylla* and *P. macrocarpus* were significantly lower than those of the other species (*t*-test; $\alpha = 0.05$; $t = 1.96954$). S:R ratios of *X. xylocarpa* and *S. siamensis* were midway between them. According to Tukey's HSD test, the difference between *S. siamensis* and *D. turbinatus* was marginal. The differences of S:R ratios among the species were not significant for the seedlings under the closed canopy.

Watering did not have significant effect on the S:R ratios for any species (ANCOVA, $p > 0.05$). S:R ratio of the seedlings in the gap was significantly lower than that of the seedlings in the shade when all the species were pooled, but specifically it was significant only for *S. macrophylla* and *D. alatus* (ANCOVA, $p < 0.05$). Re-sprouting after the fire did not result in smaller S:R ratios than the intact for the survived species except for *X. xylocarpa* var. *kerrii*. Re-sprouting of *S. macrophylla* after the fire occurred later than the other species.

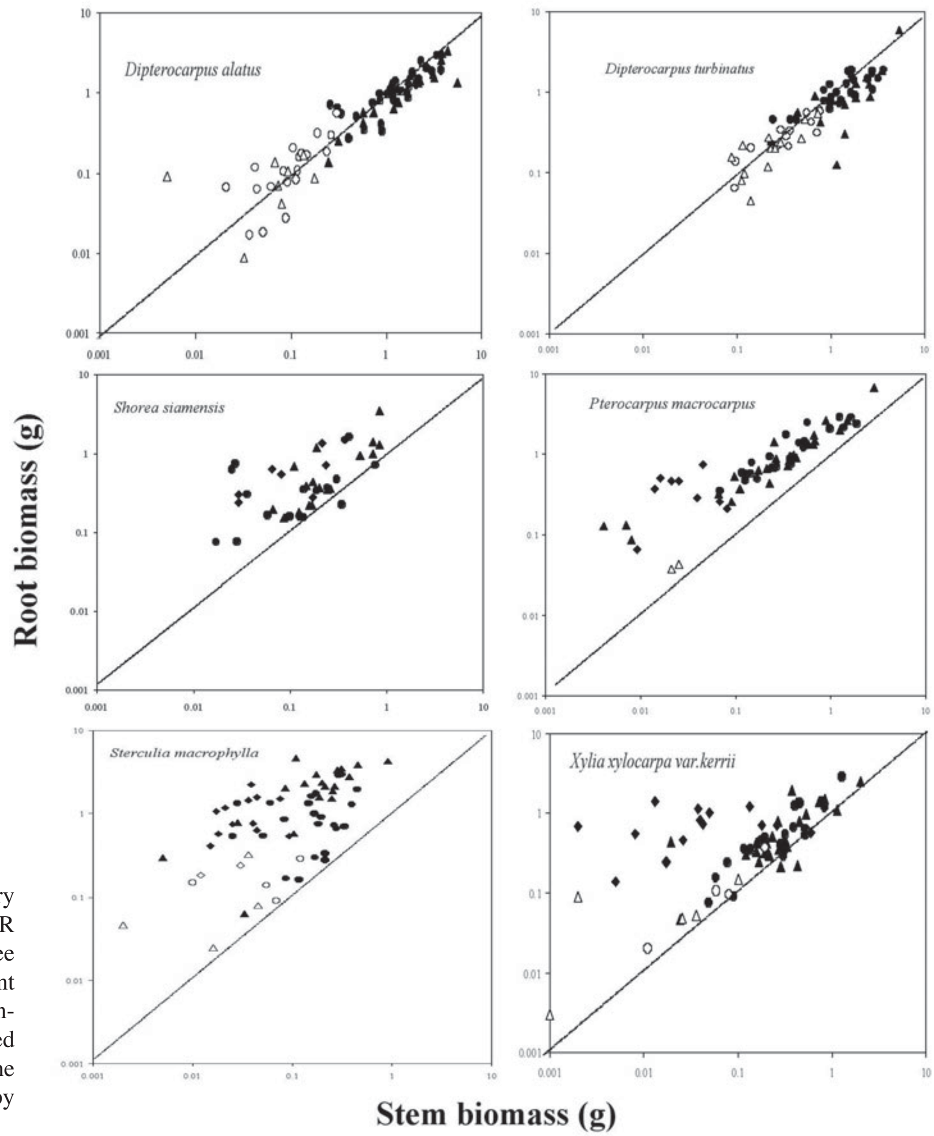

Fig. 4. Log-log plot of root dry mass against stem dry mass (S:R ratio) for seedlings of six tree species. ○ = watering treatment during the dry season, △ = control, ◇ = fire treatment. Closed and open symbols indicate the seedlings under closed canopy and in gap, respectively.

Table 3. Summary of species characteristics. 1 = low; 2 = medium; 3 = high; 4 = very high

Factors/Species	Da	Dt	Xx	Sm	Pm	Ss
Shade tolerance	3	3	2	2	1	1
Drought tolerance	1	1	3	3	3	3
Irrigation effect	3	3	1	1	2*	2*
Fire resistance	1	1	3	4	3	4
Allocation to root	1	1	3	4	4	3

*: Effect was detected only for growth. Da = *Dipterocarpus alatus*; Dt = *Dipterocarpus turbinatus*; Xx = *Xylia xylocarpa* var. *kerrii*; Sm = *Sterculia macrocarpus*; Pm = *Pterocarpus macrocarpus*; Ss = *Shorea siamensis*.

Discussion

The effects of light

All seedlings had higher mortality under the closed canopy than in the gap during both rainy and dry seasons. The mortality during the dry season was also greater than that during the rainy season for the seedlings grown under the closed canopy for the shade tolerant evergreen species, *D. alatus* and *D. turbinatus*. Shady conditions greatly increase the first year seedling mortality, not only through higher mortality during the growing season but also through higher mortality during the subsequent dry deciduous season. Stored carbon through accumulation during the rainy season may affect the survival during the dry season for these evergreen species. In addition, the importance of early dry season photosynthesis before canopy leaf shedding has been identified by ecophysiological studies on adult trees in a tropical seasonal forest (Kitajima et al. 1997; Newell et al. 2002).

S. siamensis and *P. macrocarpus* had particularly high mortality during the rainy season under the closed canopy. All the *S. siamensis* seedlings and > 95% of *P. macrocarpus* seedlings died before the end of the rainy season. For these two species, light is more critical for establishment than for the other species. Damping off disease is the main cause of mortality for *P. macrocarpus* seedlings under the shade during the rainy season in the natural forests (Marod et al. 2002).

The effects of drought

Water stress limits tree growth during the dry season (Reich & Borchert 1984). Even when water stress does not act as a critical limiting factor, changes in moisture availability will act as a controlling factor for growth (Alvim & Alvim 1978). In tropical seasonal forests, drought is known as an important mortality factor for tree seedlings (Lieberman & Li 1992; Gerhardt & Hytteborn 1992; Goldammer 1990; Lloret 1998). However, experimentally increasing water supply during the dry season did not cause significant differences in seedling survival for many of the species in this forest. Only *D. alatus* and *D. turbinatus* had significantly higher survival rates when they were watered during the dry season. For these two species, soil water content during the dry season may be a limiting factor for establishment. Their distribution bias to relatively wet sites such as stream galleries (Smitinand et al. 1980; Marod et al. 1999) could be largely explained by this regeneration habit. The other species had low mortality during the dry season and there were no significant differences in survival after watering. This may suggest a high adaptation of the seedlings of these species to drought in the dry season.

Water supply during the dry season brought significantly increased growth only for *D. turbinatus* seedlings, and for the seedlings of the two highly drought adapted species *P. macrocarpus* and *S. siamensis*. Increased growth of the latter two deciduous species may be caused by their plasticity via increased leaf longevity. The leaves of these species were shed later in the watering than control treatment (Marod pers. obs.).

Fire effects

Ground fires are frequent events in DDF at intervals of 1-3 yr (Rundel & Boonpragob 1995). All of the dominant dipterocarp species in DDF are known to exhibit adaptations to fire such as thick bark and re-sprouting ability from the root collar. In MDFs ground fire is also a common, but less frequent disturbance (Marod et al. 1999). Because of temporal and spatial variation in fire occurrences, there should be a variable level of adaptation to the fire among the component species in this type of forests. This is precisely what we found: *D. alatus* and *D. turbinatus* were severely damaged by fire as well as by drought. *P. macrocarpus* and *X. xylocarpa* var. *kerrii* seedlings were moderately affected by fire, while *S. siamensis* was not affected at all. Seedlings of *S. macrophylla* also survived well, but its re-sprouting responses were late after the fire.

Re-sprouting is one of the important adaptive traits to fires which usually completely kill the above-ground parts of the shrubs, tree seedlings and saplings (Bond & Midgley 2001). The ability of seedling to re-sprout after fire disturbance is related to root carbohydrate reserves, which are reflected in the high root biomass and low S:R ratio. High root biomass may be important both in improving access to soil moisture and the storage of resources for vigorous re-sprouting. S:R ratios of seedlings also seem to be related to the habitats of the species (Garwood 1996; Baker 1972). Seedlings of *S. siamensis*, *P. macrophylla*, *X. xylocarpa* var. *kerrii* and *S. macrophylla*, which are distributed on dry to medium soil moisture conditions, increased their resistance to fire by developing great root biomass. *S. macrophylla* and *S. siamensis* both had high re-sprouting rates, but delayed re-sprouting of *S. macrophylla* until the rainy season suggests some kind of physiological constraints. By contrast, *D. alatus* and *D. turbinatus* had higher S:R ratios. These species were vulnerable to fire, dying without re-sprouting after fire.

Species co-existence

Our results suggest differentiation among species in terms of seedling adaptations to shade, drought and fire (Table 3). The tree species examined can be classified into three groups based on their requirement for light. 1. *D. alatus* and *D. turbinatus* are well adapted to the shade conditions, but have little adaptation to drought and fire. These seedling characteristics allow them to establish under the small scale gap disturbance regime, but restrict their distribution to moist sites along the stream or lower part of the slopes. 2. *P. macrocarpus* and *S. siamensis* are highly light demanding, but have adapted to both drought and fire. Establishment of these species may be highly resistant to fire and drought, but require much light which partly results from fire disturbance, and thus they are distributed on fire prone xeric sites. 3. *X. xylocarpa* var. *kerrii* and *S. macrophylla* have intermediate light demands and are more or less adapted to drought and fire. These species may establish utilizing both gap and fire disturbances, and can be distributed over a wide range of topographic conditions.

The same kind of diversification of the adaptation to light, drought and fire may occur among the other co-existing species in mixed deciduous forests. Further studies on the seedling adaptation to these factors for other species involved are needed to understand the maintenance mechanisms of species co-existence in this type of forests (Grubb 1977).

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