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SEEDLING ESTABLISHMENT AND GROWTH ACROSS FOREST TYPES IN AN EVERGREEN/DECIDUOUS FOREST MOSAIC IN WESTERN THAILAND

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ABSTRACT

Mixed deciduous forest and seasonal evergreen forest exist in a patchwork pattern at the landscape level in the Huai Kha Khaeng (HKK) river valley and adjacent areas of western Thailand. To better understand the processes that established this pattern, the survival and growth of seedlings from two seasonal evergreen forest tree species, *Hopea odorata* Roxb. (Dipterocarpaceae), *Litsea cubeba* (Lour.) Pers. (Lauraceae), and two mixed deciduous forest species, *Holarrhena pubescens* (Buch.-Ham.) Wall. ex G. Don. (Apocynaceae) and *Terminalia mucronata* Craib et Hutch. (Combretaceae), were studied in HKK Wildlife Sanctuary, Uthai Thani Province. Seedlings from all four species were planted at sites in mixed deciduous forest and evergreen forest. Mortality was greater in the deciduous forest than in the evergreen forest for all species, although seedlings of all four species survived in both forest types. Growth in height and root-collar diameter, and change in leaf number, varied by forest type and species. Deciduous forest species grew significantly more in evergreen forest sites, while growth of evergreen forest species was not clearly correlated to forest type. Shade-house studies of seedling performance along a drought gradient did not generate clear responses by forest type affiliation of the species. These results suggest that either 1) growth and survival dynamics are affecting community-level patterns at a different life-history stage than the seedlings establishment phase (e.g., germination or seed dispersal stages), or 2) factors excluded from the experiment such as fire and mammalian herbivory are generating the patterns of forest type distribution across the landscape of HKK.

INTRODUCTION

Due to their susceptibility to fire, forests in the dry tropical zone are particularly prone to large-scale disturbance. Droughts and subsequent fires across millions of hectares of Borneo in the early 1980s suggest that fires may not be uncommon in even the moist tropics (GOLDAMMER & SIEBERT, 1989). In areas where the dry tropical forests and moist tropical forests adjoin, fires originating in the dry forests may spread across the landscape, burning even the wettest sites in the moist forests (KELLMAN & TACKABERRY, 1993). The ecological role of fire in these areas is largely unknown. KELLMAN & TACKABERRY (1993) suggested that fire may limit the establishment of dominant species, allowing a greater diversity of species to establish in the understory of the wet forests. Fire exclusion studies have demonstrated the ability of wet forest species to colonize the dry forest in the

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absence of fires [see SWAINE (1992) for Africa, BOWMAN & FENSHAM (1991) for Australia, and JOSHI (1980) for India], although the mechanisms for establishment are unclear (BOWMAN & FENSHAM, 1991).

If disturbance is responsible for creating and maintaining differences between wet and dry forest types, then in the absence of disturbance, patterns of tree growth will not necessarily parallel the current distribution of forest types. In this paper I show that 1) physical factors do not limit the establishment of evergreen (wet) forest species in deciduous (dry) forest and vice versa in an evergreen/deciduous forest mosaic in western Thailand, and 2) growth patterns of experimentally planted seedlings would not explain the current patterns of forest type distribution at HKK. This study focused primarily on the effects of soil moisture on the establishment, survival, and growth of seedlings *from* both forest types *in* both forest types. In particular, it tested the hypothesis that survival and growth of seedlings of species from an evergreen forest and a deciduous forest are not affected by forest type.

MATERIALS AND METHODS

Study Area

The study sites were situated between the Kapook Kapiang Ranger Station (KK) and the Khlong Phuu Research Station (KP) (15° 40' N, 99° 15' E) in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai Thani Province, west-central Thailand, approximately 60 km east of the Burmese border.

Three km to the east of KP lies the Huai Kha Khaeng River which bisects the sanctuary from north to south. The Huai Thap Salao River flows east past the northern edge of KK. Average elevation of all sites is between 500 and 600 m above sea level. Mean annual rainfall is approximately 1480 mm (based on an average from 1983-1993) (Fig. 1a); however, this average may be misleading due to 2 years of exceptionally high rainfall: 1983 (2000 mm) and 1988 (2300 mm). Excluding these 2 years, the average annual rainfall is closer to 1330 mm. Mean July temperature is 27° Celsius; mean January temperature is 19° C. Minimum recorded temperatures have been as low as 12°C and maximum temperatures as high as 38° C. Maximum daily relative humidity drops below 98% only during March and April, i.e. the height of the dry season. Minimum daily relative humidity varies between 40% and 60% except during the dry season, when it is frequently less than 20%.

The year is divided into three seasons: the rainy season (May-October), the cool season (November-January) and the hot or dry season (February-April). The rainy season is divided into two parts (Fig. 1b)—the early rains which fall heavily in May and June, and the late rains which are strongest in September and October. The late rains are typically heavier. The extent and severity of the dry season is variable. Some years have sporadic rainfall during the dry season, others have little or no rain for the entire dry season.

The sanctuary contains four distinct forest types: dry evergreen forest (seasonal rain forest *sensu* SANTISUK, 1988), mixed deciduous forest (tropical mixed deciduous forest *sensu* SANTISUK, 1988), dry dipterocarp forest (deciduous dipterocarp forest *sensu* SANTISUK,

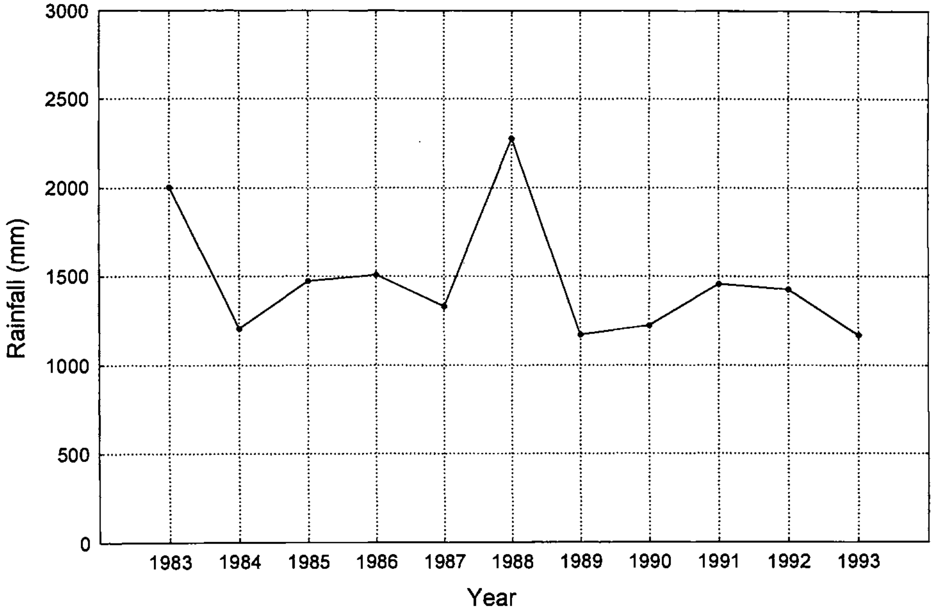


Figure 1a. Total annual rainfall (mm) at the Huai Kha Khaeng Wildlife Sanctuary (1983-1993).

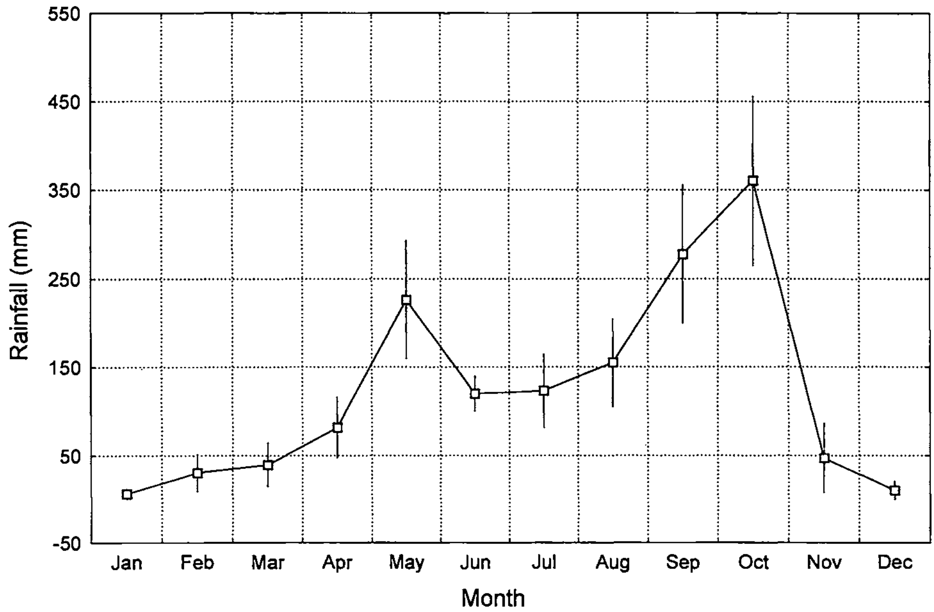


Figure 1b. Average monthly rainfall (mm) at the Huai Kha Khaeng Wildlife Sanctuary (1983-1993). Vertical bars represent 95% confidence intervals.

1988) and hill evergreen forest (lower montane rain forest *sensu* SANTISUK, 1988). Of these forest types, all but hill evergreen forest occur in the area between KP and KK. For the purpose of this study, dry deciduous forest and mixed deciduous forest are together considered "deciduous forest," while the dry evergreen forest is labeled "evergreen forest."

Study Species

The four species selected for the experiment were *Hopea odorata* Roxb. (Dipterocarpaceae), *Litsea cubeba* (Lour.) Pers. (Lauraceae), *Terminalia mucronata* Craib et Hutch. (Combretaceae) and *Holarrhena pubescens* (Buch.-Ham.) Wall. ex G. Don (Apocynaceae).

Hopea odorata and *Litsea cubeba* are restricted to evergreen forest. Although both species can be found in riparian galleries in mixed deciduous/evergreen forest, the current study focused on mid-slope sites to avoid the confounding soil moisture issues of riparian zones. Neither *Hopea odorata* nor *Litsea cubeba* are known from mid-slope sites in either mixed deciduous forest or dry dipterocarp forests between KK and KP.

Terminalia mucronata and *Holarrhena pubescens* are both found in mixed deciduous forest and dry dipterocarp forest at HKK; neither is known from evergreen forest. A 50 ha permanent forest dynamics plot is located in evergreen forest adjacent to the evergreen forest sites established for this study. All individuals of tree species greater than 1 cm diameter at breast height (dbh) have been mapped, measured and identified to species. Neither *Terminalia mucronata* nor *Holarrhena pubescens* were amongst the 110,000+ individuals included in the first census (BUNYAVEJCHEWIN & LAFRANKIE, *unpublished data*).

Hopea odorata and *Terminalia mucronata* are dominant canopy species. *Litsea cubeba* and *Holarrhena pubescens* are midstory or subcanopy species. All four species have wind- or gravity-dispersed seed.

Several species were not included in the field transplant experiments due to insufficient numbers of seedlings but were used in the shade-house experiments. The additional species were: *Afzelia xylocarpa* Craib (Leguminosae), *Saccopetalum lineatum* Craib (Annonaceae), and *Pterocarpus macrocarpus* Kurz. (Leguminosae). All 3 are canopy species; *Saccopetalum lineatum* is restricted to the evergreen forest; *Afzelia xylocarpa* is found in dry sites in the evergreen forest as well as in mixed deciduous forest; *Pterocarpus macrocarpus* is found in both the evergreen and deciduous forests.

Voucher specimens (Appendix) with fruiting material and seedling specimens from all species have been deposited at the Forest Herbarium (BKF), Royal Forest Department, Bangkok, as part of the 50 ha permanent plot voucher collection. In addition, voucher specimens will be deposited at the University of Washington Herbarium, Seattle, WA, USA.

Study Design

The study had two separate, complimentary components: a field study on nursery-raised seedlings transplanted into forest and experiments in a shade-house on relative tolerance to drought.

The field plots for the transplant experiment were established in gap sites in the evergreen and deciduous forests along a 5 km stretch of road between KK and KP. Five "sites" were chosen in each forest type to represent as much variation in the structure and species composition of the forest type as possible. At each site 2 gaps were chosen. Gap diameter was approximately 150% of the height of the surrounding canopy. All vegetation was cleared from the gap in order to exclude fire from the experiment. The sites were protected from mammalian herbivores by wire mesh fencing. In the gap center a 5 x 5 m plot was demarcated. Each plot was then split into four blocks. Groups of 5 seedlings from each species were planted in each block (with the exception of *Terminalia mucronata* in which n=3 seedlings) with 25 cm between individuals. Therefore, each species had 5 seedlings/block, 20 seedlings/gap, 40 seedlings/site, and 200 seedlings/forest type.

The seedlings used in the field study were germinated in a shade house at KK. Flowering and fruiting of mother trees from approximately 35 species were monitored throughout the duration of the experiment. Fallen seeds were collected from the mother trees during the rainy season and placed in germination trays in the shade-house. The trays were watered to prevent desiccation. When the first true leaf of the new germinants had emerged, the seedlings were transplanted to polyethylene seed bags (8 cm in diameter, 15 cm tall). The sole exception was *T. mucronata.* In order to ensure germination, the hard woody seeds were cut. The exposed embryos attracted a swarm of ants (*Pheidologeton* sp.) and within 24 hours all seeds had been removed or sufficiently destroyed to prevent germination. Subsequently, recent *T. mucronata* germinants were collected from the field. They were then planted directly into the seed bags. HKK sanctuary policy does not allow large quantities of soil from the forest to be collected and used for experiments, nor can soil from outside the sanctuary be brought in. As a result the seed bags were filled with sand from a nearby dry stream bed.

The seedlings were planted in September 1994. Seedlings that did not survive transplantation were replaced in October. The first measurements were made in November and repeated every 2 months (November, January, March, and May). Thus, seedling measurements began at the end of the 1994 rainy season, went through a full dry season and into the beginning of the next rainy season (1995). Height, root collar diameter, and leaf number were measured for all seedlings. Seedlings that had died since the previous measurement were exhumed. Rooting depth was measured, after which the dead seedlings were taken to Royal Forest Department (RFD) labs in Bangkok to be oven-dried and measured for root, shoot and leaf dry weight.

Measurement of soil moisture was by standard gravimetric procedure. Samples were collected from all field plots included in the study. Soil samples were taken from 2 depths in the soil column (5–15 cm and 40–55 cm). Four samples per site were taken and combined for each depth. The samples were placed in air-tight bags, and weighed, oven-dried and re-weighed at RFD labs in Bangkok.

The shade house experiments included a variable watering regime experiment and a pressure bomb experiment. They were performed under a shade structure (~ 60% sunlight intercepted) established behind KK adjacent to Huai Thap Salao, a perennial stream. Seedlings from all species had been transplanted from the 8 cm diameter seed bags into 20 cm diameter seed bags at the end of the 1994 rainy season to avoid pot-bound roots.

Both of the shade-house experiments were conducted during the 1995 dry season (February-May, 1995).

The variable watering regime experiment in the shade-house used three watering regimes: high (250 ml/seedling every week), medium (250 ml/seedling every 2 weeks) and low (250 ml/seedling every 3 weeks). Seedlings from 7 species were exposed to each treatment in a randomized block design. The experiment contained 9 blocks with 16 seedlings/species/ treatment. The experiment began in February at the height of the dry season. In early May, as the rainy season began, the polyethylene sheeting that protected the seedlings was removed, exposing the seedlings to the natural watering regime. Height, leaf number and root collar diameter were measured every 2.5 months (February, April, and July 1995).

For the pressure bomb experiment in the shade house, seedlings of 6 species (*Hopea odorata*, *Litsea cubeba*, *Saccopetalum lineatum*, *Terminalia mucronata*, *Holarrhena pubescens* and *Pterocarpus macrocarpus*) were exposed to a drought gradient ranging from 2 to 14 days without water. On the final day of the treatment, seedling xylem pressure potential (XPP) was measured twice, once in the predawn and once in the early afternoon (7AM and 1PM). For each drought treatment (i.e. 2 days, 4 days, etc.), 3 seedlings were used per measurement (3 in the morning and 3 in the afternoon) per species.

Analytical Methods

Analysis of variance (ANOVA) was used to test differences in soil moisture content and relative growth rate (RGR) between forest types. By using RGR it is possible to make comparisons between seedlings with different initial sizes and leaf numbers. RGR was calculated as:

$$\mathrm{RGR} = \frac{\ln(G_2) - \ln(G_1)}{t_2 - t_1}$$

where G is a growth metric (height, etc.) and t is time in days. The final measurements (May 1995) were used as G_2. ANOVA was also used to analyze the final height measurements from the variable watering regime experiment. (Only the results for height growth in the variable watering regime experiment are presented here as they are representative of the results of the other growth metrics.) The Chi-square statistic was used to analyze 2x2 contingency tables for differences in mortality between forest types (ZAR, 1984). Student's t-test was used to determine the effect of initial seedling size and leaf number on seedling survival. Linear regression was used to compare patterns of final seedling size and leaf number to soil moisture content in individual gaps. Spearman's Rank Correlation Test was used to compare patterns of seedling survival to patterns of soil moisture content in individual gaps as both variates were non-normally distributed (ZAR, 1984).

Due to the effects of mortality, it was not possible to maintain a uniform sample size for analyses. To address this problem growth analyses were done only on seedlings that had survived all four measurement periods. Differences in seedling growth patterns for

Litsea cubeba were clouded by the particularly high levels of mortality. As a result it has been excluded from the seedling growth analyses.

The replication of the field experiment yielded several possible levels of variation. At the subplot level (i.e. between two gaps at the same site), there were occasional significant differences in growth although none were consistent. The sole exception was the pair of gaps at site 5 in the evergreen forest in which growth differences were routinely higher for all species at site B. At the block level there were no consistent trends, suggesting that gap edge effects based on orientation relative to the incident angle of sunlight were unimportant to the seedlings. As the subplot effects were minor and inconsistent and the block effects nonsignificant, they have not been included in the following results. Where ANOVA is used, Forest Type (deciduous vs. evergreen) is the main effect unless stated otherwise.

RESULTS

Soil Moisture

Differences in the soil moisture content (% dry weight of soil) of the upper horizon between the evergreen and deciduous forest were not significantly different during any measurement period (Fig. 2). In the lower horizon there were significant differences for November, January and March, but not May (November, $p<0.017$; January, $p<0.004$; March, $p<0.025$; May, $p<0.178$; ANOVA with forest type as main effect). Most of the soil water loss from the lower layer in the deciduous forest occurred between November and January. In the evergreen forest the lower horizon dried more slowly, reaching its lowest levels in March.

Soil moisture content declined from approximately 10% in both forest types and in both layers during November 1994 to <5% in March. The advent of the rainy season in late April and May re-moistened the soil to levels greater than or equal to November 1994 levels.

Seedling Mortality

By the end of the study (May 1995), approximately 30% of the *Terminalia mucronata* seedlings had died (Figure 3). The trend was constant for the 3 measurement periods.

By the end of the study, 10% of the *Holarrhena pubescens* seedlings in the evergreen forest and 27% of the seedlings in the deciduous forest had died. Mortality in the evergreen forest was constant across all measurement periods. The majority of the mortality in the deciduous forest occurred between January and March. Seedlings that had died back to the root-collar sprouted vigorously with the advent of the rainy season.

Over the course of the study, nearly 40% of the *Hopea odorata* seedlings in the evergreen forest and 60% of the seedlings in the deciduous forest died. In the evergreen forest, mortality was constant between January and May. In the deciduous forest the majority of the mortality occurred between January and March.

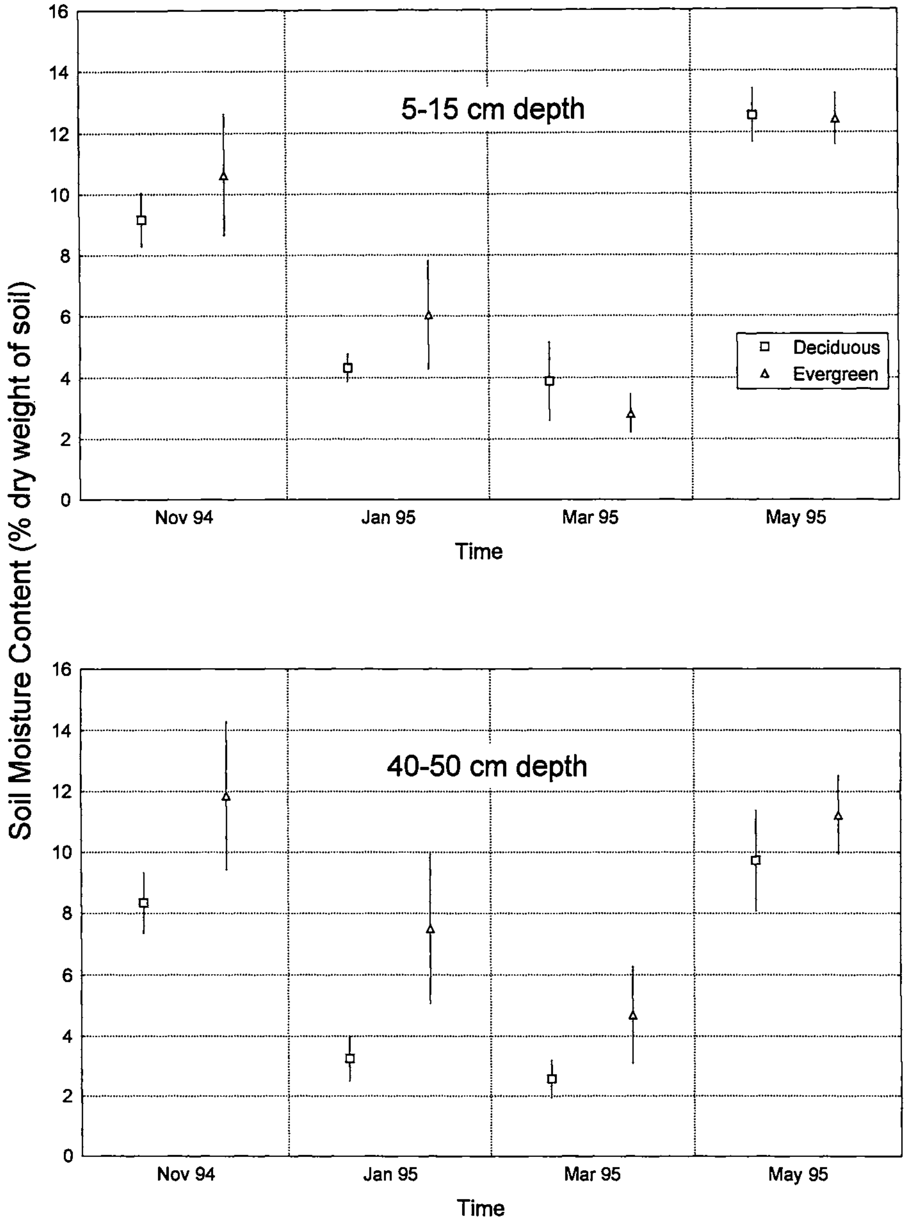


Figure 2. Mean soil moisture content (% dry weight of soil) at two horizons (5-15 cm, 40-50 cm) in the evergreen and deciduous forests at Huai Kha Khaeng Wildlife Sanctuary. Vertical bars represent 95% confidence intervals.

Litsea cubeba experienced the greatest mortality of the species in the study. By January 10% of the seedlings had died in both forest types. By March 60% had died in the evergreen forest and 80+% had died in the deciduous forest. By the last measurement period in May, only 15% of the seedlings in the evergreen forest and 4% in the deciduous forest remained alive. The few seedlings that had survived in the deciduous forest had all died back to the root collar.

Seedling survival was significantly different between forest types for all species except *Terminalia mucronata* (Table 1). In each case the proportion of seedlings surviving was higher in the evergreen forest than in the deciduous forest. *Terminalia mucronata* had slightly better survival rates in the deciduous forest during the first 3 measurement periods; however, by the end of the experiment the values for survival of *Terminalia mucronata* seedlings were almost identical between forest types.

Effect of Initial Size on Seedling Mortality

Initial seedling height (measured in November 1994) was related to survival over the subsequent 6 months in the 2 deciduous forest species (Table 2). For *Terminalia mucronata* and *Holarrhena pubescens* seedlings, both in the evergreen and deciduous forests, greater initial height was negatively correlated to survival. The correlation between initial height and subsequent mortality was stronger for *Holarrhena pubescens*, although the absolute differences in the mean initial heights between those surviving and those dying was greater for *Terminalia mucronata*. Neither of the evergreen forest species, *Hopea odorata* and *Litsea cubeba*, appeared to have a significant correlation between initial height and later mortality.

Initial root collar diameter was correlated to survival for *Holarrhena pubescens* (Table 3). The correlation was negative and almost identical between seedlings planted in the evergreen forest and those planted in the deciduous forest. The other 3 species showed no significant relationship between root collar diameter and survival.

Initial leaf number was positively correlated to survival for *Hopea odorata* and *Litsea cubeba* (Table 4). The relationship was not significant for *Litsea cubeba* seedlings in the deciduous forest due to the low number of surviving seedlings, but the trend was similar. Neither of the deciduous forest species, *Terminalia mucronata* and *Holarrhena pubescens*, showed a correlation between initial leaf number and subsequent mortality.

Seedling Growth

Terminalia mucronata and *Holarrhena pubescens* had similar patterns of growth for absolute height between forest types until the last measurement period when the seedlings in the evergreen forest outgrew those in the deciduous forest (Figure 4). Differences in RGR were highly significant for both deciduous forest species, the greater growth occurring in the evergreen forest sites (Table 5). *Hopea odorata* and *Litsea cubeba* had similar absolute height growth in both forest types throughout the experiment (Figure 4). *Hopea odorata* did not have significant differences between forest type in RGR for height (Table 5).

Table 1. 2 x 2 Contingency Tables ($\chi 2$) for differences in mortality associated with forest type (*P<0.1, **0.05, *** P<0.01).

Species	Deciduous Dead	Deciduous Alive	Evergreen Dead	Evergreen Alive	P	Sign.
Terminalia mucronata	41	79	39	81	0.082	ns
Holarrhena pubescens	58	142	21	179	0.039	**
Hopea odorata	116	84	77	123	<0.001	***
Litsea cubeba	192	8	169	31	<0.001	***

Table 2. Effect of initial seedling height on survival to final measurement (May 1995) using Student's t-test (* P<0.1, ** P<0.05, *** P<0.01).

Species	Forest Type	Mean ht. (cm) dead	Mean ht. (cm) alive	d.f.	t	P	Sign.
Terminalia mucronata	Deciduous	13.60	12.05	118	1.75	0.084	*
	Evergreen	14.32	12.72	118	1.92	0.057	*
Holarrhena pubescens	Deciduous	11.02	9.94	198	2.51	0.013	**
	Evergreen	12.35	10.91	198	2.66	0.008	***
Hopea odorata	Deciduous	14.06	14.11	198	–0.95	0.924	ns
	Evergreen	14.01	14.23	198	–0.39	0.696	ns
Litsea cubeba	Deciduous	7.57	7.88	198	–0.38	0.703	ns
	Evergreen	7.74	7.73	198	0.02	0.985	ns

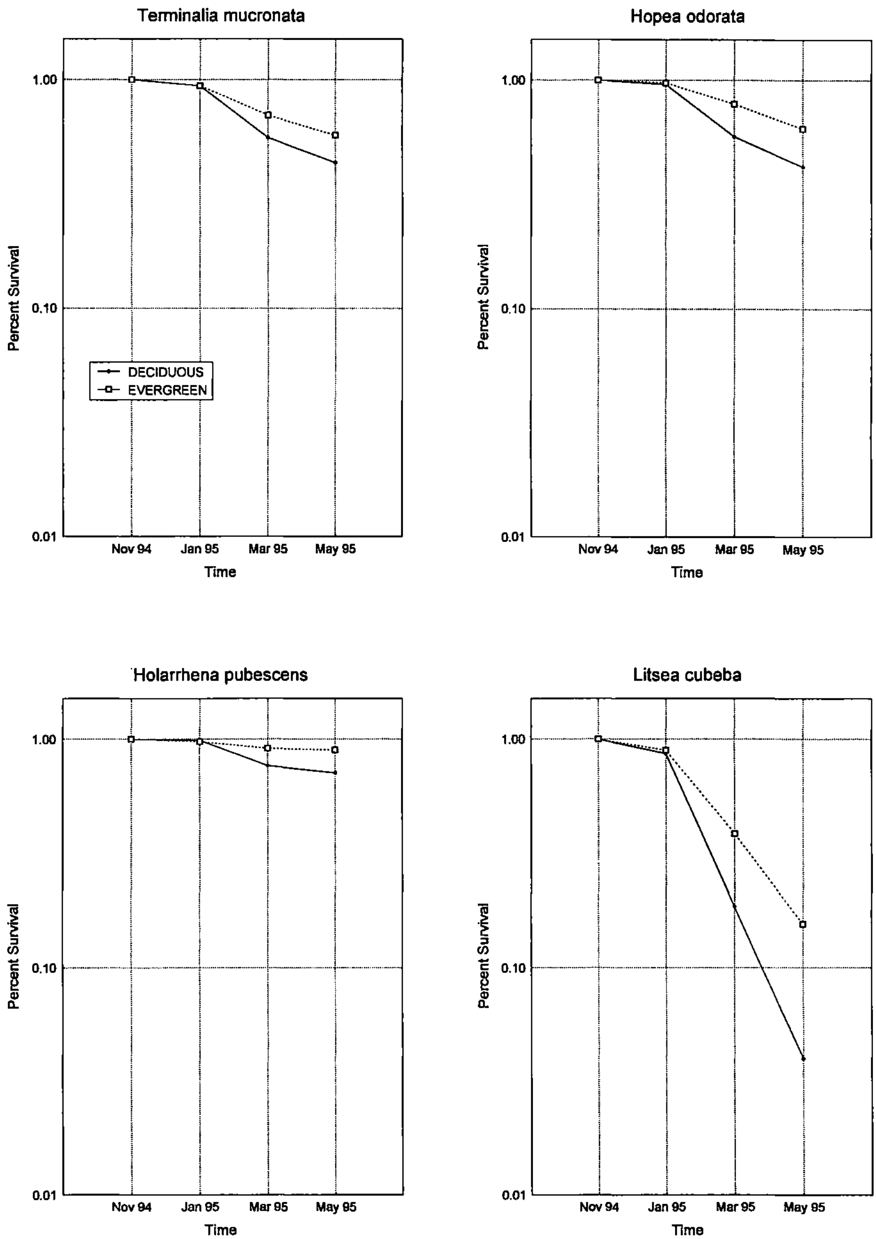


Figure 3. Percent survival of seedlings from 4 species at Huai Kha Khaeng Wildlife Sanctuary. *Holarrhena pubescens* and *Terminalia mucronata* are both associated with the mixed deciduous forest. *Hopea odorata* and *Litsea cubeba* are both associated with the seasonal evergreen forest.

The absolute measure of root collar diameter was not particularly different by forest type in either *Terminalia mucronata* or *Hopea odorata* (Figure 5), but the differences in RGR were significant (Table 5). This difference can be attributed to the different mean root collar diameter at the initial measurement period. Initial mean root collar diameter was smaller in the evergreen forest than in the deciduous forest, while the final differences in mean root collar diameter were negligible. *Holarrhena pubescens* showed a clear trend in both absolute and relative root collar diameter growth (Figure 5 and Table 5). Seedlings planted in the evergreen forest were larger at every measurement period (Figure 5). Root collar diameter decreased during the height of the dry season for all species (Figure 5). Whether this shrinkage is attributable to changes in the phloem, xylem or both is unknown. Similar results have been observed in trees and planted seedlings in seasonal tropical forests in central America (BORCHERT, 1994, GERHARDT, 1996).

Both of the deciduous forest species had dropped most of their leaves by March 1995 (Figure 6). Seedlings of *Terminalia mucronata* and *Holarrhena pubescens* planted in the deciduous forest lost their leaves more rapidly than those planted in the evergreen forest. With the new leaf flush at the onset of the rainy season (May 1995), absolute numbers of leaves were nearly identical (Figure 6). Relative production of leaves was significantly higher for *Holarrhena pubescens* in the evergreen forest (Table 5). *Terminalia mucronata* showed no significant differences between forest types in relative leaf production (Table 5). *Hopea odorata* had consistently higher numbers of leaves in the evergreen forest (Figure 6); however, this is attributable to initial conditions as the relative amount of leaf production was not significantly different (Table 5).

While absolute differences in height, root collar diameter and leaf number between forest types are typically small, there are significant differences in RGR for these metrics between forest types. All of the significant differences in RGR, with one exception (*Hopea odorata*, root collar diameter), occur in the deciduous forest species, *Terminalia mucronata* and *Holarrhena pubescens.* In every instance, the greater growth occurred in the evergreen forest (Table 5).

Growth and Survival versus Soil Moisture Content

Soil moisture content was not correlated to seedling survival for any species during any measurement period (Spearman Rank Correlation procedure, Table 6). The sole exception was *Litsea cubeba* in which the percent seedling survival was correlated with March 1995 soil moisture content ($p=0.0278$, $n=20$, Table 6).

In general, seedling size and leaf number at the last measurement period (May 1995) were not significantly correlated to soil moisture content; however, there were several exceptions (Table 7). Of those instances in which a significant correlation between final seedling size and soil moisture conditions occurred, all were positively correlated except leaf number in *Hopea odorata* when compared to May 1995 soil moisture content. The most significant correlation was between final height of *Terminalia mucronata* and soil moisture content at all 4 measurement periods; especially high correlations occurred for November 1994 and January 1995 soil moisture content ($p<0.0001$ and $p<0.0002$, respectively, Table 7). Neither final root collar diameter nor final leaf number of *Terminalia mucronata* were correlated to soil moisture content in any measurement period. For

Table 3. Effect of initial seedling root collar diameter on survival to final measurement (May 1995) using Student's t-test (* P<0.1, ** P<0.05, *** P<0.01).

Species	Forest Type	Mean RCD (cm) dead	Mean RCD (cm) alive	d.f.	t	P	Sign.
Terminalia mucronata	Deciduous	0.194	0.200	118	–0.78	0.439	ns
	Evergreen	0.176	0.182	118	–0.64	0.521	ns
Holarrhena pubescens	Deciduous	0.163	0.151	198	2.77	0.006	***
	Evergreen	0.160	0.151	198	1.68	0.095	*
Hopea odorata	Deciduous	0.212	0.215	198	–0.58	0.569	ns
	Evergreen	0.195	0.197	198	–0.45	0.652	ns
Litsea cubeba	Deciduous	0.136	0.139	198	–0.30	0.763	ns
	Evergreen	0.127	0.134	198	–1.40	0.164	ns

Table 4. Effect of initial seedling leaf number on survival to final measurement (May 1995) using Student's t-test (* P<0.1, ** P<0.05, *** P<0.01).

Species	Forest Type	Mean leaf # dead	Mean leaf # alive	d.f.	t	P	Sign.
Terminalia mucronata	Deciduous	6.60	6.50	118	0.16	0.870	ns
	Evergreen	6.44	7.01	118	–0.97	0.334	ns
Holarrhena pubescens	Deciduous	6.41	6.06	198	1.42	0.157	ns
	Evergreen	5.33	5.54	198	–0.72	0.469	ns
Hopea odorata	Deciduous	7.94	8.59	198	–2.09	0.038	**
	Evergreen	7.06	7.66	198	–2.18	0.030	**
Litsea cubeba	Deciduous	6.37	7.50	198	–1.54	0.125	ns
	Evergreen	5.26	6.43	198	–3.15	0.002	***

Table 5. One-factor (Forest Type) ANOVA on RGR for each species for each growth metric. The E/D column indicates in which forest type superior growth occurred in cases of significant differences (* P<0.1, ** P<0.05, *** P<0.01).

Species	(d.f.)	Metric	F-value	P	Sign.	E/D
Terminalia mucronata	(1, 151)	Height	11.51	<0.001	***	E
		RCD	24.55	<0.001	***	E
		Leaf #	1.45	0.230	ns	
Holarrhena pubescens	(1, 273)	Height	18.87	<0.001	***	E
		RCD	26.32	<0.001	***	E
		Leaf #	14.72	0.000	***	E
Hopea odorata	(1, 192)	Height	0.31	0.580	ns	
		RCD	3.11	0.079	*	E
		Leaf #	0.05	0.831	ns	

Table 6. Spearman Rank Correlation Coefficients for comparisons between seedling survival to final measurement (May 1995) and soil moisture content for each measurement period (n=20 for all species)(* P<0.1, ** P<0.05, *** P<0.01).

Species	Measurement date	r_s	P	Sign.
Terminalia mucronata	Nov-94	0.08	0.75	ns
	Jan-95	0.18	0.44	ns
	Mar-95	0.19	0.41	ns
	May-95	–0.06	0.82	ns
Holarrhena pubescens	Nov-94	–0.02	0.94	ns
	Jan-95	0.05	0.83	ns
	Mar-95	0.18	0.45	ns
	May-95	–0.12	0.61	ns
Hopea odorata	Nov-94	0.07	0.77	ns
	Jan-95	0.15	0.53	ns
	Mar-95	0.21	0.36	ns
	May-95	–0.08	0.73	ns
Litsea cubeba	Nov-94	0.28	0.23	ns
	Jan-95	0.27	0.25	ns
	Mar-95	0.49	0.03	**
	May-95	0.19	0.43	ns

Table 7. Regression coefficients for growth metrics on soil moisture content from each measurement period (* P<0.1, ** P<0.05, *** P<0.01). The +/- column indicates, in the case of significant associations, whether the correlation is positive or negative.

Species	Metric date	Measurement	r^2	F	P	Sign.	+/-
Terminalia mucronata	Height	Nov-94	0.611	25.18	<0.001	***	+
		Jan-95	0.596	23.57	<0.001	***	+
		Mar-95	0.172	3.33	0.087	*	+
		May-95	0.256	5.52	0.032	**	+
	RCD	Nov-94	0.046	0.78	0.391	ns	
		Jan-95	0.032	0.53	0.479	ns	
		Mar-95	0.005	0.08	0.784	ns	
		May-95	0.004	0.06	0.807	ns	
	Leaf #	Nov-94	0.074	1.29	0.274	ns	
		Jan-95	0.078	1.35	0.263	ns	
		Mar-95	0.003	0.04	0.840	ns	
		May-95	0.000	0.00	0.980	ns	
Holarrhena pubescens	Height	Nov-94	0.203	4.58	0.046	ns	
		Jan-95	0.115	2.33	0.144	ns	
		Mar-95	0.163	3.49	0.078	*	+
		May-95	0.026	0.45	0.509	ns	
	RCD:	Nov-94	0.128	2.64	0.122	ns	
		Jan-95	0.046	0.87	0.365	ns	
		Mar-95	0.075	1.45	0.244	ns	
		May-95	0.215	4.92	0.040	**	+
	Leaf #	Nov-94	0.119	2.43	0.136	ns	
		Jan-95	0.179	3.93	0.063	*	+
		Mar-95	0.147	3.11	0.095	*	+
		May-95	0.009	0.17	0.686	ns	
Hopea odorata	Height	Nov-94	0.045	0.71	0.411	ns	
		Jan-95	0.054	0.86	0.368	ns	
		Mar-95	0.032	0.50	0.489	ns	
		May-95	0.065	1.06	0.320	ns	
	RCD:	Nov-94	0.010	0.16	0.698	ns	
		Jan-95	0.020	0.30	0.592	ns	
		Mar-95	0.016	0.24	0.629	ns	
		May-95	0.070	1.12	0.306	ns	
	Leaf #	Nov-94	0.001	0.02	0.886	ns	
		Jan-95	0.001	0.02	0.891	ns	
		Mar-95	0.043	0.68	0.423	ns	
		May-95	0.200	3.75	0.072	*	-

Holarrhena pubescens final height and final leaf number were correlated to soil moisture content in March 1995 and final root collar diameter and leaf number were correlated to soil moisture content in January 1995. *Hopea odorata* showed no significant correlation, except as previously mentioned, for leaf number versus May 1995 soil moisture content.

With the exception of the high correlations of height of *Terminalia mucronata* to soil moisture content, the majority of correlations were only significant at the 10% level. The lack of a consistent pattern between any growth metric and soil moisture content at any given time, particularly during the dry season, suggests that soil moisture conditions are not directly responsible for seedling growth in the species studied.

Shade-House Experiments

Variable watering regime

Final seedling height was poorly correlated to intensity of watering regime for most species studied. *Holarrhena pubescens, Litsea cubeba, Saccopetalum lineatum, Afzelia xylocarpa* and *Hopea odorata* showed no significant response in total height to decreasing frequency of watering (Table 8). *Pterocarpus macrocarpus* exhibited significant differences between treatments (Table 8) with the tallest seedlings occurring in the moderate watering treatment (Figure 7). Final seedling height of *Terminalia mucronata* was highly positively correlated to watering intensity (p=0.0193, Table 8 and Figure 7). The close relationship between water availability and height growth for *Terminalia mucronata* in this experiment parallels the results in the previous section in which final seedling height (May 1995) has a positive and highly significant correlation to soil moisture content in individual gaps.

Pressure bomb

The pressure bomb experiment was performed on seedlings of 6 species in the shade house (Fig. 8). During the dry season seedlings were exposed to droughts varying from 2 to 14 days. The seedlings were then sampled and the XPP was measured by a pressure bomb. Measurements were made in the early morning before sunrise and at mid-day. For the morning measurements, the seedlings of evergreen forest species showed varied results. *Hopea odorata* seedlings had much higher XPP for the 12 and 14 day droughts. *Litsea cubeba* and *Saccopetalum lineatum* showed no consistent trends. The XPP of the deciduous forest species did not change with respect to the duration of the drought. The results from the afternoon measurements were consistent by forest type. The seedlings of the evergreen forest all had increasing XPP values for the 10, 12 and 14 day droughts. The seedlings from the deciduous forest showed no changes.

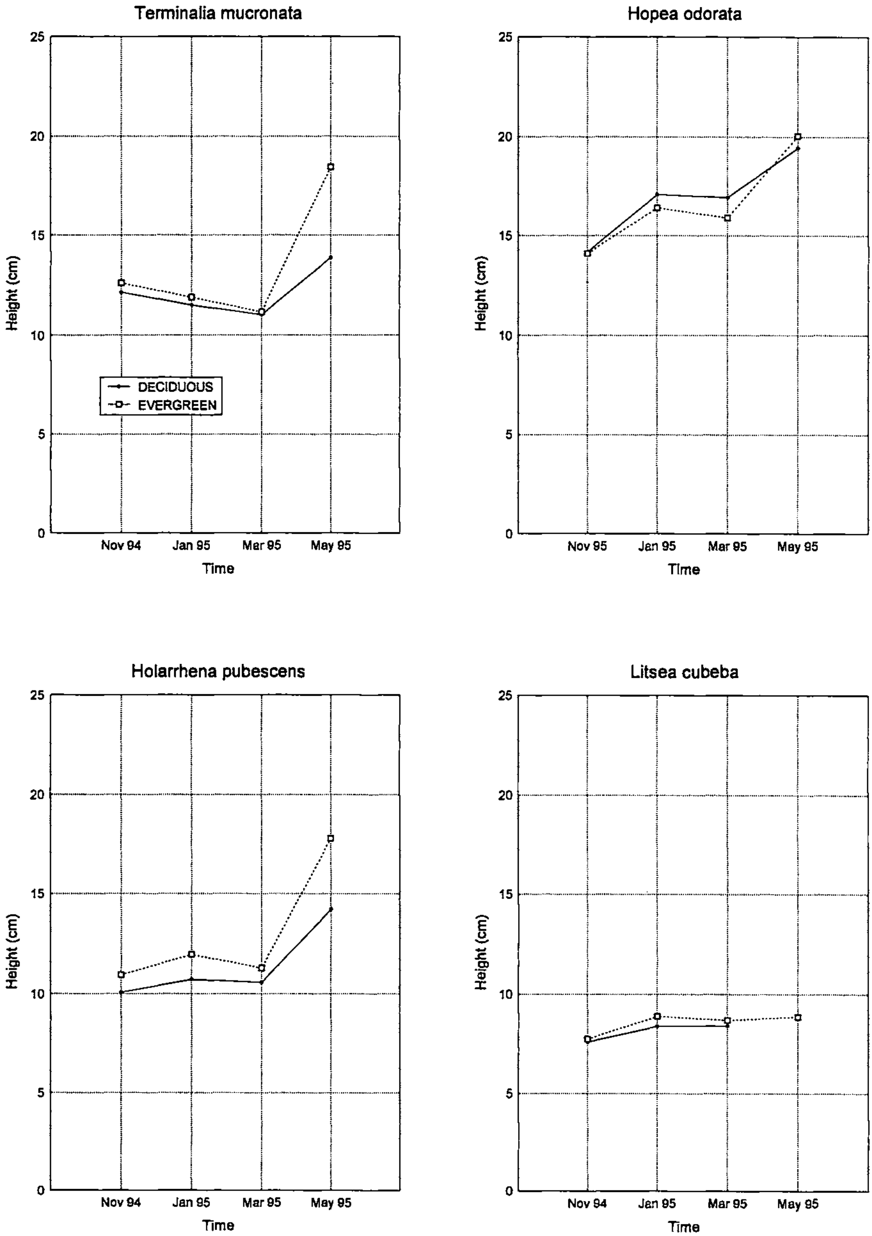


Figure 4. Mean height of seedlings, by species, in deciduous and evergreen sites measured at 2 month intervals. Measurements are not complete for *Litsea cubeba* as survival was so low that there were insufficient seedlings (<5) for a representative sample.

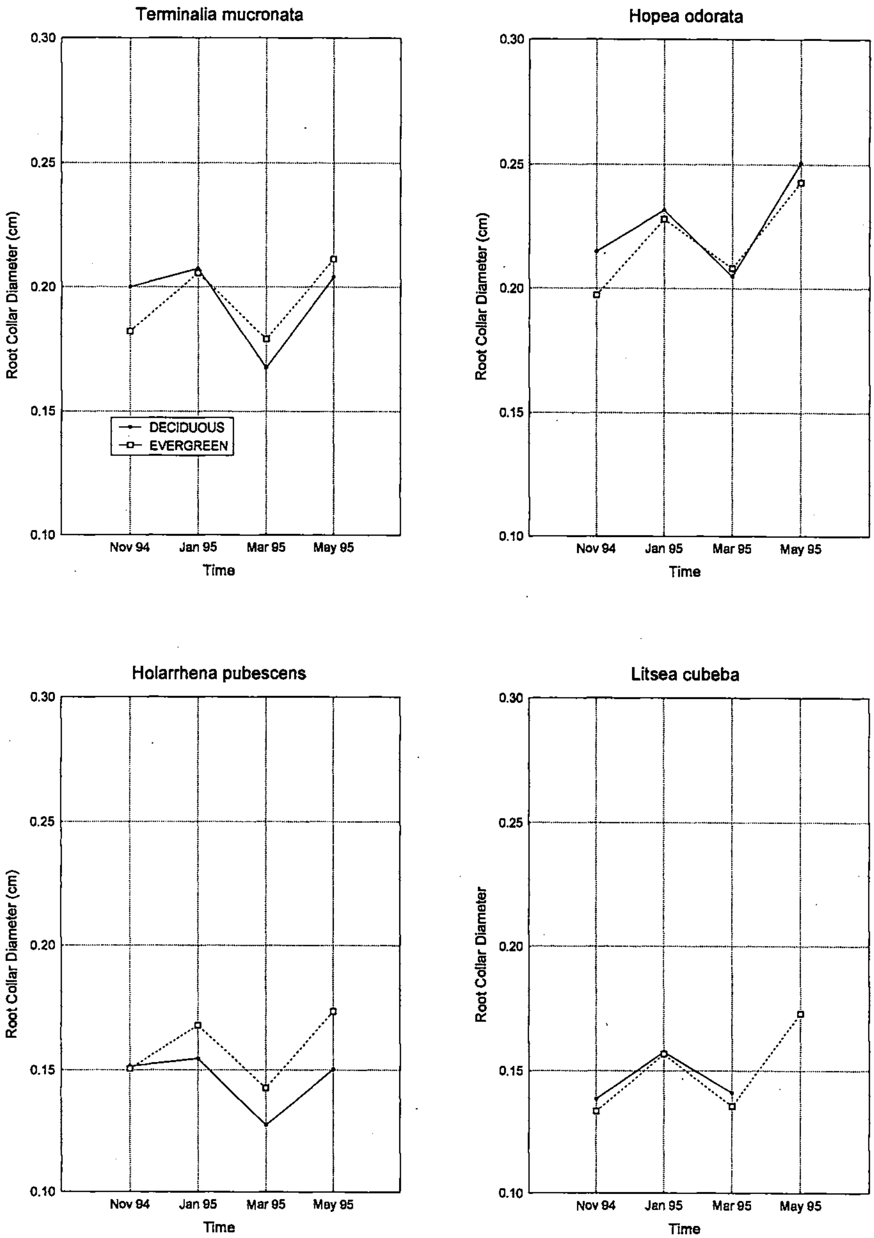


Figure 5. Mean root collar diameter of seedlings, by species, in deciduous and evergreen sites measured at 2 month intervals. Measurements are not complete for *Litsea cubeba* as survival was so low that there were insufficient seedlings (<5) for a representative sample.

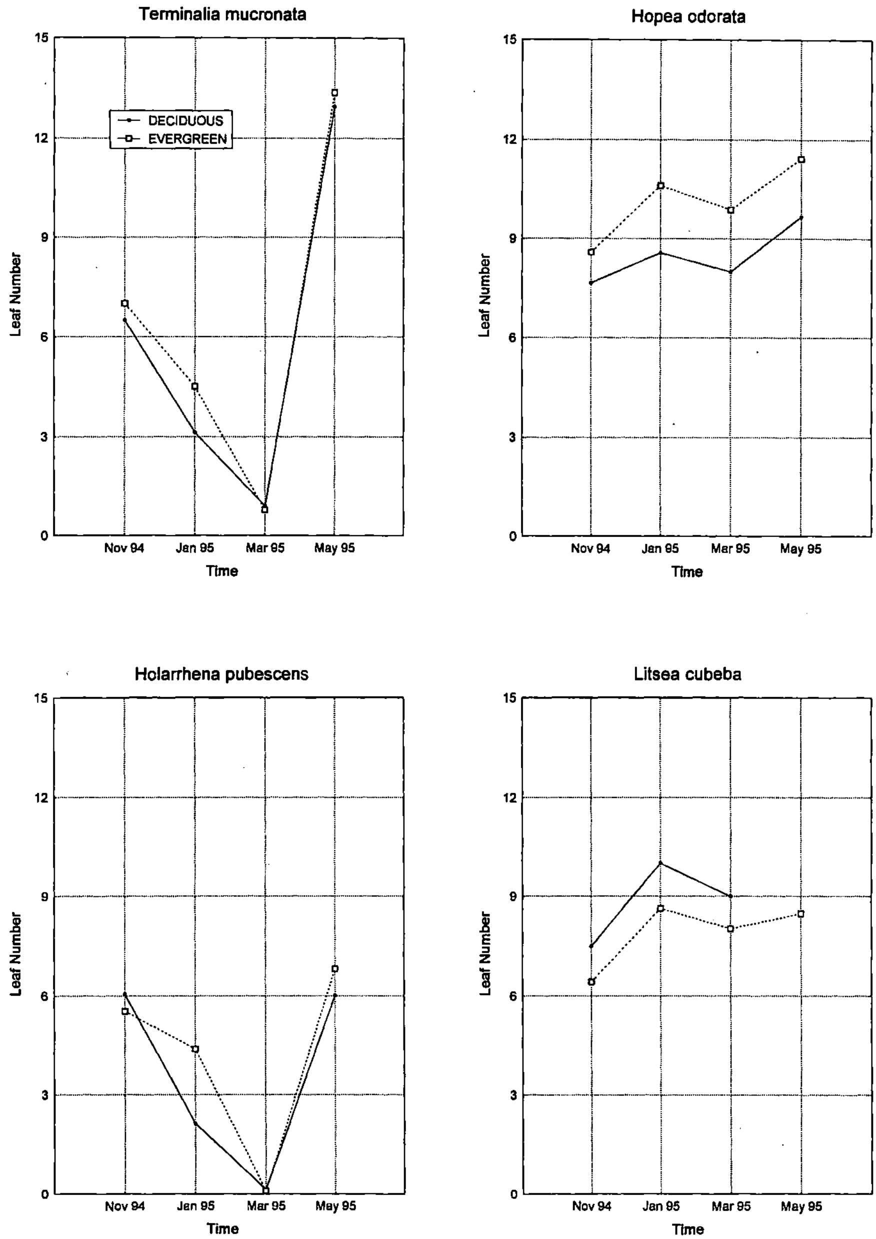
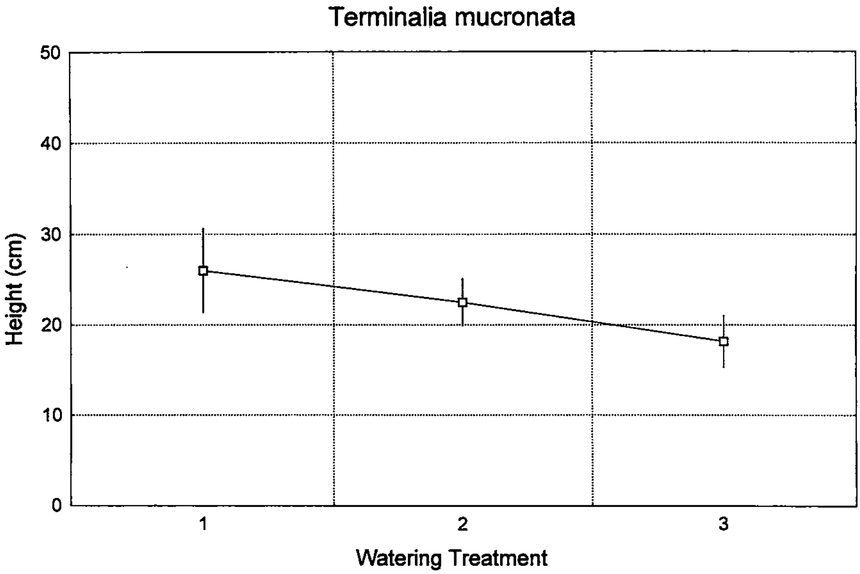


Figure 6. Mean leaf number of seedlings, by species, in deciduous and evergreen sites measured at 2 month intervals. Measurements are not complete for *Litsea cubeba* as survival was so low that there were insufficient seedlings (<5) for a representative sample.



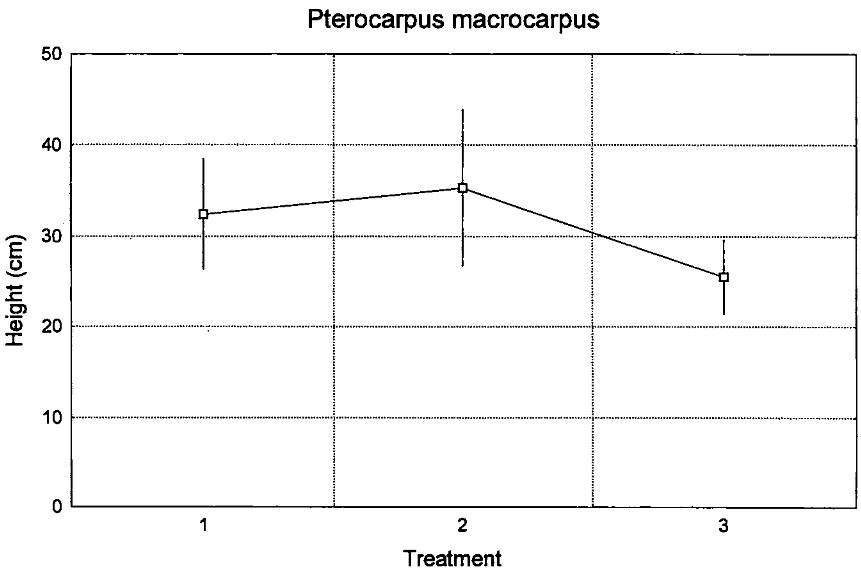


Figure 7. Mean seedling height of seedlings from variable watering regime experiment in which treatment effect was significant (see Table 8). Vertical bars represent the 95% confidence intervals.

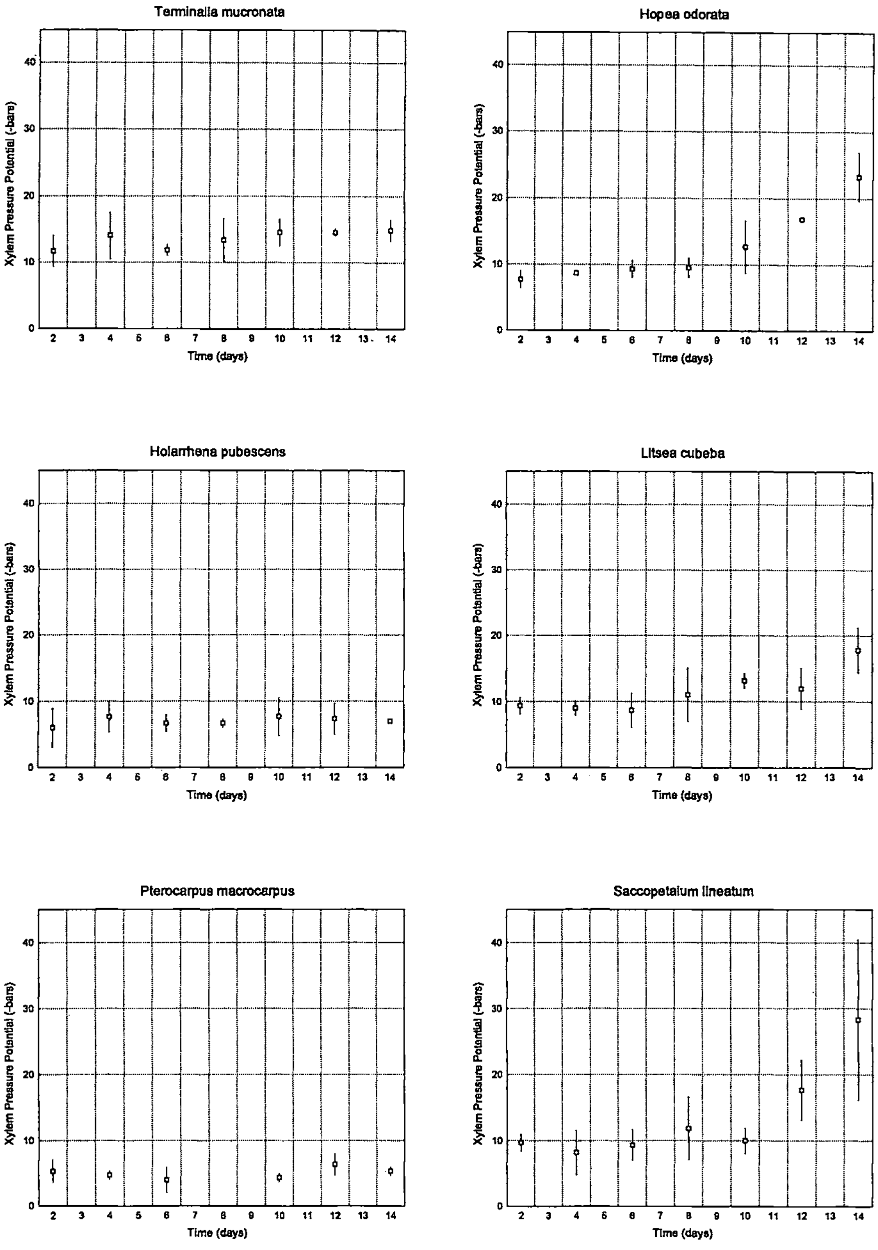


Figure 8. Mean mid-day xylem pressure potential (-bars) of seedlings exposed to drought of varying duration (2-14 days). Vertical bars represent 95% confidence intervals. [The species in the left column (*Terminalia mucronata*, *Holarrhena pubescens*, and *Pterocarpus macrocarpus*) are commonly found in the deciduous forest; the species in the right column (*Hopea odorata*, *Litsea cubeba*, and *Saccopetalum lineatum*) are found in the evergreen forest.]

Table 8. One-factor (Watering Treatment) ANOVA on seedling height (* P<0.1, ** P<0.05, *** P<0.01). In Treatment 1 seedlings were watered once a week; in Treatment 2 seedlings were watered once every 2 weeks; and in Treatment 3 seedlings were watered once every 3 weeks. (See Figure 8 for graph of height means for species in which treament effects were significant.)

Species	df	F	P	Sign.
Terminalia mucronata (D)	27	4.58	0.019	**
Holarrhena pubescens (D)	26	0.40	0.673	ns
Pterocarpus macrocarpus (D/E)	26	3.42	0.048	**
Afzelia xylocarpa (D/E)	24	0.24	0.791	ns
Hopea odorata (E)	24	2.28	0.124	ns
Litsea cubeba (E)	23	0.67	0.523	ns
Saccopetalum lineatum (E)	20	1.28	0.299	ns

DISCUSSION

Soil moisture levels in the lower portion of the soil column were significantly higher in the evergreen forest than in the deciduous forest (Figure 2). There was no difference between forest types in soil moisture content at the sub-surface level (15 cm depth).

Survival of seedlings outplanted to gaps in both forest types was lower in the evergreen forest for all study species (Table 1). Nonetheless, seedlings of species from both forest types survived and grew in both forest types (with the exception of the *Litsea cubeba* which did poorly in both forest types). Over 40% of the seedlings of *Hopea odorata*, a common evergreen forest emergent, that were planted in the deciduous forest plots survived and grew. For the deciduous species *Terminalia mucronata* and *Holarrhena pubescens*, survival of the seedlings planted in the evergreen forest was 70% and 90%, respectively. Yet, in the deciduous forest *Hopea odorata* is found only in riparian areas and in the evergreen forest *Terminalia mucronata* and *Holarrhena pubescens* are unknown.

Seedling survival was not independent of initial growth metrics and showed a forest-type response. Seedlings from the evergreen forest had a higher probability of surviving through the final measurement if they had more leaves. Seedlings from the deciduous forest had a higher probability of surviving if they were shorter.

The results from growth measurements of the outplanted seedlings showed that the deciduous forest species, *Terminalia mucronata* and *Holarrhena pubescens*, grew better in the evergreen forest sites than in the deciduous forest sites. The only growth response of an evergreen forest species to forest type was for root collar diameter in *Hopea odorata* and was higher in the evergreen forest. Leaf flush and increased root collar diameter and height growth for the deciduous forest species corresponded with the onset of the rainy season. The same pattern occurred for *Hopea odorata* but was less pronounced.

Rank tests and linear regression analyses demonstrated little to no correlation between seedling survival or growth and soil moisture content. The shade-house experiment in which treatments of varying watering frequency are applied to seedlings experimentally corroborated these results. The only exception in both sets of data was the high correlation between final height in *Terminalia mucronata* and soil moisture content in the cold and early dry season measurements (November 1994 and January 1995). The increased performance of *Terminalia mucronata* under conditions of higher soil moisture may explain the occurrence of patches in the mixed deciduous forest dominated almost exclusively by *Terminalia mucronata*. A period of several wetter-than-average years may have given saplings of *Terminalia mucronata* an increased competitive advantage in height growth allowing the seedlings to outgrow and eventually exclude seedlings of competing species.

The shade-house experiments similarly showed that conditions of varying water availability did not consistently affect seedling growth, although length of drought had a clear effect on xylem pressure potential for species of the evergreen forest. Xylem pressure potential for seedlings of the deciduous forest species showed no reaction to short-term droughts; however, further tests with longer drought periods may provide better results. A comparison of elapsed time between rainfall events during the dry season and species-specific reaction to varying lengths of drought may offer some useful insights into the dynamics of seedling populations through the dry season.

An ancillary result of the variable watering regime was the growth response of the *Litsea cubeba*. In the field transplant experiment *Litsea cubeba* experienced high mortality and correspondingly poor growth (Figs. 3–6). In contrast, the seedlings used in the shade house experiments had high survival and height growth rates across all watering treatments (Fig. 9). This clear distinction in survival and growth performance suggests that the light environment may play a role for *Litsea cubeba*. In the evergreen forest *Litsea cubeba* is typically found in the canopy below the crowns of the dominant species. If the species is shade-tolerant then the light environment of the gaps in the field transplant experiment may have heightened seedling mortality, while the light environment of the shade house may have provided more appropriate conditions for growth and survival.

The pattern that emerges from the data is that higher survival and occasionally higher growth occurs for all species, from both the deciduous and evergreen forest, when growing under evergreen forest conditions. It is important to note that fire and mammalian herbivory were excluded from the experiments and that only the seedling stage was investigated. The effects of fires on the vegetation is largely unknown and is limited by the difficulty of implementing prescribed burn experiments within the wildlife sanctuary. Herbivory in the evergreen forest appears to be taxon-specific (P.J. BAKER, *unpublished data*). Differential grazing pressure may limit establishment in the evergreen forest of taxa specific to the deciduous forest and vice versa. Competition from grasses may limit the availability of below-ground growing space necessary for germination and establishment (OLIVER & LARSON, 1996), particularly in the deciduous forests. Studies of the germination stage may generate an entirely different suite of questions regarding the species-specific adaptations to environmental conditions found in different forest types (GRUBB, 1977).

CONCLUSION

The patterns of seedling survival and growth demonstrated in this study do not correspond with the distribution patterns of forest type at HKK. If species-specific patterns of survival and growth were responsible for differentiation of forest types, a given species would be expected to perform best in the forest type in which it is found. This was not the case. Seedlings of species from both the evergreen and deciduous forests had higher rates of survival in the evergreen forest. Seedlings of deciduous forest species typically grew best in the evergreen forest sites. Seedlings of evergreen forest species had an equivocal growth response to forest type. These results suggest either that 1) community-level patterns in vegetation are determined at different life-history stages than seedling establishment (i.e., germination or dispersal), or 2) factors excluded from the study such as fire and mammalian herbivory may be responsible for the vegetation patterns at HKK.

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APPENDIX

Voucher Specimens:

Hopea odorata: HKK (tree # 1918, 2224, 4816); PJBaker 9504, 9505, 9506.
Litsea cubeba: HKK 625, 962; PJBaker 9510, 9511, 9512.
Terminalia mucronata: PJBaker 9519, 9520, 9521.
Holarrhena pubescens: PJBaker 9507, 9508, 9509.
Afzelia xylocarpa: HKK 76, 77; PJBaker 9501, 9502, 9503.
Saccopetalum lineatum: HKK 32, 109, 171; PJBaker 9516, 9517, 9518.
Pterocarpus macrocarpus: HKK (tree # 109589), PJBaker 9513, 9514, 9515.