

INITIAL RESPONSE OF *SHOREA* WIDLINGS TRANSPLANTED IN GAP AND UNDERSTORY MICROSITES IN A LOWLAND RAIN FOREST

P. A. Palmiotto

School of Forestry and Environmental Studies, Yale University, New Haven, Ct., United States of America

Received December 1991

PALMIOTTO, P.A. 1993. Initial response of *Shorea* wildlings transplanted in gap and understory microsities in a lowland rain forest. Wildlings of six dipterocarp species, *Shorea pinanga*, *S. parvistipulata*, *S. johorensis*, *S. hopeifolia*, *S. parvifolia* and *S. leprosula* were transplanted in gap and understory microsities to assess their survival and growth in a lowland rain forest of West Kalimantan, Indonesia. At the end of the dry season in October 1990, 3½-y-old, bare-rooted wildlings were collected from the understory and transplanted; wildlings that died were replaced in a second planting two weeks later. Mortality within the first few weeks ranged from 40 to 85%. There was no significant difference in wildling survival between the gap and the understory microsities for the first planting. Wildlings in the replacement planting two weeks further into the wet season had less overall mortality and showed significantly higher survival in the gap microsities. Moisture stress, due to the extended dry period beginning before collection and continuing up to the time of wildling transplanting, is proposed as the cause of high mortality. This is supported by a strong positive correlation between species total leaf area per wildling and wildling mortality. High leaf area during times of moisture stress could therefore be a problem for transplanted bare-root wildlings. Greater growth occurred in the gap plots than in the understory plots; however, mean growth was not substantial due to die back and resprouting. These findings suggest that moisture stress can have a significant impact on wildling survival. Wildling collection and planting should therefore take place during wetter periods when soil moisture is high.

Key words: Dipterocarps - drought - Indonesia - moisture stress - mortality - seedlings - survival - *Shorea* - wildlings

PALMIOTTO, P.A. 1993. Gerakbalas pemula anak liar *Shorea* yang di alih ke kawasan kecil terbuka dan bawah naungan di kawasan hutan pamah. Anak liar enam spesies dipterokarp, *Shorea pinanga*, *S. parvistipulata*, *S. johorensis*, *S. hopeifolia*, *S. parvifolia* dan *S. leprosula* telah dialihkan ke kawasan kecil terbuka dan bawah teduhan untuk menilaikan kemandirian dan pertumbuhannya di hutan tanah pamah Kalimantan Barat, Indonesia. Pada penghujung musim kering dalam bulan Oktober 1990, anak liar akar terdedah berusia 3½ tahun telah dikutip dari kawasan bawah naungan dan alihan anak liar yang mati diganti dalam penanaman kedua-dua minggu kemudian. Kematian dalam beberapa minggu pertama adalah antara 40 - 85%. Tidak terdapat perbezaan bererti dalam kemandirian anak liar antara kawasan-kawasan kecil terbuka dan bawah naungan untuk penanaman pertama. Anak liar dalam penanaman penggantian 2 minggu selepas musim hujan bermula mempunyai kadar kematian yang rendah dan menunjukkan kemandirian yang lebih tinggi di kawasan kawasan kecil tersebut. Tegasan lembapan disebabkan oleh musim kering yang berpanjangan bermula dari sebelum kutipan dijalankan dan berterusan sehingga anak benih dialih dianjurkan sebagai sebab kadar kematian yang tinggi. Ini disokong oleh korelasi positif antara jumlah luas daun setiap anak

liar dan kematian anak liar. Luas daun yang besar semasa tegasan lembapan mungkin menjadi masalah kepada anak liar akar terdedah. Pertumbuhan yang besar terjadi dalam plot kawasan terbuka berbanding plot kawasan naungan, namun pertumbuhan purata tidak besar disebabkan oleh mati rosot dan memucuk semula. Hasil kajian ini menunjukkan bahawa tegasan lembapan boleh membawa impak yang besar terhadap kemandirian anak liar. Kutipan dan penanaman anak liar harus dilakukan semasa musim hujan manakala lembapan tanahnya tinggi.

Introduction

In 1989 the Indonesian government modified its timber extraction laws requiring forest concessionaires to replace felled trees with nursery grown seedlings. However, maintaining adequate nursery stocks of Indonesia's dipterocarp timber species may be difficult because of their irregular flowering and seed production (masting) at intervals between two and ten years (Chan & Appanah 1980, Ashton 1982). Dipterocarp seeds germinate rapidly once on the ground and have poor viability after storage (Tang 1971, Sasaki 1980b, Maury-Lechon *et al.* 1981, Tompsett 1987). Storing seed stock collected during mast years is therefore also a problem. To overcome the difficulties associated with utilizing dipterocarp seeds in regeneration efforts, it may be possible to use wildlings of the desired species as a source of planting stock.

Because thousands of wildlings germinate under individual adult dipterocarp trees and initially survive in large numbers between masting events, a source of wildlings exists for transplanting. Previous work in Malaysia has shown a broad range of survival (33-96%) for transplanted *Shorea* wildlings (Gill 1970, Tang & Wadley 1976). If wildlings can tolerate transplant shock, they could be used to replant cleared or degraded forests that are understocked with dipterocarp timber species. Furthermore, if the microsite preference of planted species is known, appropriate site selection and/or preparation may enhance wildling survival. For example, many studies have demonstrated the importance of canopy openings for the establishment and growth of dipterocarp seedlings (Nicholson 1960, Sasaki & Mori 1981, Raich & Christensen 1989, Ashton & De Zoysa 1989, Ashton 1990, Raich & Khoon 1990). This study was conducted to test the survival and growth of $3\frac{1}{2}$ -year-old wildlings of six dipterocarp species transplanted beneath open gaps and closed canopy forest.

Methods

The study was conducted at the Cabang Panti Research Site, which encompasses 1500 ha of the 90,000 ha Gunung Palung National Park, West Kalimantan, Indonesia ($1^{\circ} 00' - 1^{\circ} 20' \text{ S}$, $109^{\circ} 00' - 110^{\circ} 25' \text{ E}$). The study site has an aseasonal climate with mean annual rainfall of 4500 mm and mean annual daytime temperature of approximately 32° C . Wildlings of dipterocarp species (*Shorea pinanga*, *S. parvistipulata*, *S. johorensis*, *S. hopeifolia*, *S. parvifolia* and *S. leprosula*) that germinated from the 1987 masting event and had been growing in the understory were collected from the lowland dipterocarp forest underlain by weathered sandstone. To compare survival

and growth, wildlings were transplanted in openings of five recently-created natural treefall gaps of varying size and slope angle (150-600 m², 1 - 20°) and under closed canopy forest adjacent to each gap within the lowland sandstone habitat (Table 1). An area within 30 m and with a slope angle similar to each gap plot was chosen as the understory plot. All woody debris and live vegetation less than one meter tall were removed from within and one meter around plots in the gaps and adjacent understory. The experiment consisted of two transplantings which began two weeks after the apparent end of a prolonged dry period. Individuals of each species were collected and transplanted during October 10-14, 1990, in each microsite at each of the five locations (n=480). Wildlings that died within two weeks of the first transplanting were replaced by wildlings collected and planted during October 30-31, 1990 (n=203).

Wildlings of each species were collected from the understory within 15 m of the base of four separate adult *Shorea* trees which had abundant wildling regeneration (>1/m²). Wildlings were not selected if more than 50% of the existing leaf area had been removed by herbivory or if stem growth form was poor (leaning >30° from vertical or resprouted). Fewer than 2% were rejected due to these criteria.

The soil around each wildling was loosened until it could be lifted from the ground with little resistance. Wildlings were stored in the shade with their roots immersed in water for up to 3½ days until planting. Holes were made with a wooden stake to depths dictated by the length of the wildlings' roots. The bare-rooted wildlings were placed with soil.

Eight individuals of each species were planted 0.5 m apart in six adjacent plots in the gap and understory at each location. For each location a different random arrangement of species plots was chosen. The random arrangement of species plots at each location was matched in the gap and understory microsites.

At the time of planting, data collected on each wildling consisted of total height, number of leaves with less than 25% of the existing leaf area removed due to herbivory, total number of leaves and number of secondary roots categorized into four classes (0, 1-4, 5-10, >10 roots per plant). The length from the root tip to root collar and from the root collar to stem tip was measured for the first 16 wildlings of each species planted. Leaf area of a subsample of wildlings (n=24 for *S. hopeifolia*, n=12 for other species) was measured using a LICOR (model 3100) leaf area meter.

After transplanting, the number of leaves per individual were counted at two weeks, four weeks, and thereafter at four-week intervals. Heights were measured after four weeks and then at eight-week intervals. The final analysis summarized in Tables 1-3 and Figures 1-3 includes six months of data (171 days for the first planting, 155 days for the replacement planting).

Relative light intensities in the gap and the forest microsite at each transplanting location were determined using integrating light meters (ILMs). ILMs were constructed of 12 layers of photosensitive paper placed between two layers of cardboard with a 0.5 cm hole punched in the top cardboard (Friend 1961). Three ILMs were placed 40 cm above the ground in the gap and understory at each transplant location and left exposed for three days. Calibration of the ILMs against

Table 1. Characteristics of planting locations for transplanted *Shorea* wildlings at the Cabang Panti research site

Location	Microsite	Area(m ²)	Canopy ht(m)	Orientation(°)	Slope(°)	Light (mol m ⁻² day ⁻¹)	Land form
1	Gap understory	600	40	100	3 1	37.8 1.0	Lowland bench
2	Gap understory	150	40	210	18 14	18.2 0.3	Side slope
3	Gap understory	400	30	330	8.5 11	7.5 0.5	Base of slope
4	Gap understory	300	40	200	6 5.5	5.6 0.5	Lowland bench
5	Gap understory	200	45	180	19 20	2.3 0.1	Side slope

Table 2. Mean and \pm standard deviation of measured characteristics of 3½-y-old *Shorea* wildlings at the Cabang Panti research site

Species	n	Stem	Height(cm)	#Leaves/wildling	Area/leaf (cm ²)	¹ Herbivory	² Leaf area/ wildling(cm ²)	Root shoot ratio
<i>S. parvifolia</i>	111	26.0	(± 5.4)	8.1 (± 2.5)	9.15 (± 4.42), n=104	1.4 (± 1.2)	74	0.64
<i>S. hopeifolia</i>	106	19.4	(± 3.4)	3.3 (± 1.8)	7.82 (± 4.11), n=63	0.9 (± 1.0)	26	1.02
<i>S. parvistipulata</i>	127	29.3	(± 5.8)	6.3 (± 1.8)	34.06 (± 17.35), n=83	1.6 (± 1.3)	215	0.93
<i>S. johorensis</i>	109	28.4	(± 5.6)	6.1 (± 2.0)	19.50 (± 10.55), n=79	1.0 (± 1.0)	119	0.83
<i>S. pinanga</i>	120	50.4	(± 12.0)	7.9 (± 2.7)	39.70 (± 18.51), n=76	1.4 (± 1.3)	314	0.63
<i>S. leprosula</i>	110	24.9	(± 4.4)	5.9 (± 1.7)	12.30 (± 6.58), n=69	1.7 (± 1.3)	73	0.88

¹ number of leaves with < 25% leaf area removed by herbivores.

² leaf area/wildling = (mean #leaves/wildling).

a measurable light source allowed conversion of the number of layers exposed ($\pm \frac{1}{3}$ of a layer) to a relative index of light intensity in $\text{mol m}^2 \text{day}^{-1}$.

Logistic regression and Chi-square test (Fisher's Exact test, two-tailed) were used to determine significant differences in mortality between locations, microsites and species. Analysis of variance was used to determine significant differences in growth and number of leaves between locations and microsites (SAS Institute Inc. 1988).

Results

The initial characteristics of the $3\frac{1}{2}$ -y-old wildlings used in this study are listed in Table 2. Average stem height ranged from 19.4 cm for *S. hopeifolia* to 50.4 cm for *S. pinanga*. The number of leaves ranged from 3.3 per plant for *S. hopeifolia* to 8.1 per plant for *S. leprosula*. Herbivory was low for all wildlings, only 0.9 to 1.7 leaves (17-29% of the total number of leaves) had greater than 25% tissue loss.

First transplanting, survival

Six months after transplanting, survival ranged from 3 to 58% (Table 3). Contrary to what was expected, there was no significant difference in the overall survival between the gap and the forest microsites. There was, however, significant variation in survival among the five locations ($X^2 = 87.15$, $p=0.00001$). Locations 1, 3 and 4 (slope $<11^\circ$) had significantly higher survival than Locations 2 and 5 (slope $>14^\circ$).

Table 3. Survival (%) after six months for transplanted *Shorea* wildlings at the Cabang Panti research site

First planting	Gap		Understory	
<i>S. parvifolia</i> ^{ns}	n=40	50	n=40	50
<i>S. hopeifolia</i> ^{ns}	n=40	45	n=40	58
<i>S. parvistipulata</i> ^{ns}	n=40	28	n=40	28
<i>S. johorensis</i> ^{ns}	n=40	25	n=40	38
<i>S. pinanga</i> ^{ns}	n=40	3	n=40	8
<i>S. leprosula</i> ^{ns}	n=40	43	n=40	45
Replacement planting				
<i>S. parvifolia</i> ^{ns}	n=15	33	n=16	13
<i>S. hopeifolia</i> [*]	n=15	43	n=13	0
<i>S. parvistipulata</i> [*]	n=25	36	n=22	9
<i>S. johorensis</i> [*]	n=17	71	n=12	17
<i>S. pinanga</i> ^{ns}	n=22	9	n=16	6
<i>S. leprosula</i> ^{ns}	n=14	71	n=16	31

% Survival = number alive after 6 months/total planted \times 100.

* significantly greater survival in gap than understory microsite (Chi-square test; $p < 0.05$).

^{ns}not significant.

Additionally, there was significant variation among species ($X^2=50.20$, $p<0.00001$). This was explained by the low survival of *S. pinanga* relative to other species in both microsites across all locations.

Mortality due to transplant shock was high as 63 to 100% of the total mortality over the entire study occurred in the first $2\frac{1}{2}$ weeks. Mortality after $2\frac{1}{2}$ weeks ranged from 40 to 85%. Thereafter, mortality rate declined dramatically (Figures 1a & b). Mortality after $2\frac{1}{2}$ weeks and mortality after six months were significantly correlated with total leaf area per plant in the first planting; from 84 to 98% of the mortality could be explained by leaf area ($R^2=0.94$ & 0.92 after $2\frac{1}{2}$ weeks and $R^2=0.84$ & 0.98 after six months in the gap and understory respectively) (Figures 2a & b). Species with highest total leaf area per plant suffered the highest mortality. No correlation existed between wildling mortality and the root to shoot ratios in either microsite.

Replacement planting, survival

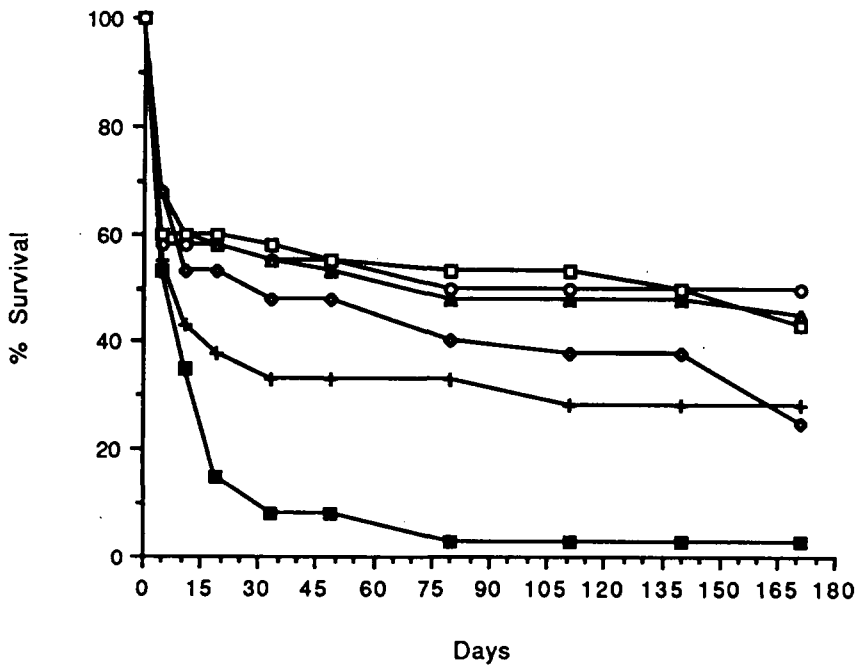
After $5\frac{1}{2}$ months, wildling survival of the replacement planting ranged from 0 to 71% (Table 3). As originally hypothesized, site did have a significant effect on survival ($X^2=16.97$, $p=0.00001$). Wildlings of all species experienced higher survival in gap plots than in understory plots. This difference was significant for *S. hopeifolia*, *S. parvistipulata*, *S. johorensis* ($p<0.05$). Unlike the first planting, significant differences in survival were not detected between locations. Statistical inference of variation in wildling survival for microsite-location combinations was prohibited due to low sample sizes. Species showed a significant variation in survival ($X^2=22.62$, $p=0.0004$). As in the first planting, *S. pinanga* suffered low survival in both gap and understory plots across all locations relative to the other species.

As in the first planting a larger percentage (60-90%) of the total mortality occurred in the first $2\frac{1}{2}$ weeks after planting. However, this mortality, due to transplant shock was low in the gap microsite for *S. parvifolia* (20%), *S. leprosula* (20%), and *S. johorensis* (25%). Mortality after $2\frac{1}{2}$ weeks ranged from 6 to 56% in gap plots and from 50 to 83% in understory plots. Again, as in the first planting the rate of mortality declined after the first $2\frac{1}{2}$ weeks (Figures 1c & d).

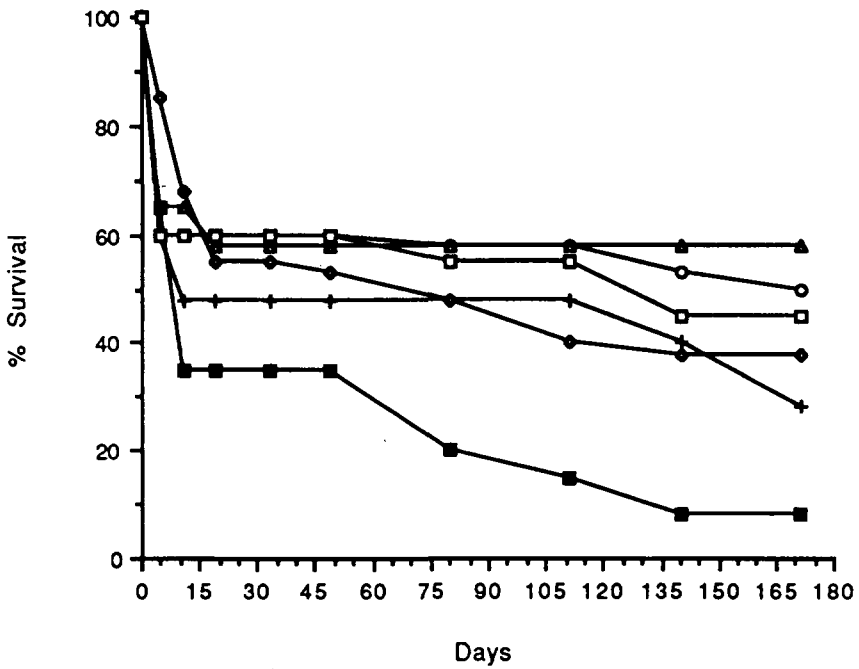
In contrast to the first planting, there was no significant correlation between initial wildling mortality or mortality after six months and leaf area in the replacement planting. As in the first planting, there was no significant correlation between root to shoot ratios and wildling mortality.

Growth rates

Relative mean height growth was minimal in the first six months ranging from - 5.2% for *S. pinanga* to + 15.6% (4.2 cm) for *S. leprosula*. There was no significant difference in relative mean growth between the first and replacement plantings. Though there was a trend for higher growth in the gap microsites, only *S. leprosula* showed significant relative growth increases in the gap microsites when compared to growth in the understory microsites (ANOVA, $p<0.0001$). Several individuals of all



(a)



(b)

Figure 1. Survival (%) for each *Shorea* species at each sampling interval up to six months. -○- *Shorea parvifolia*, -+- *Shorea parvistipulata*, -●- *Shorea johorensis*, -Δ- *Shorea hopeifolia*, -□- *Shorea leprosula*, -■- *Shorea pinanga*. a) gap, 1st planting ; b) understory, 1st planting

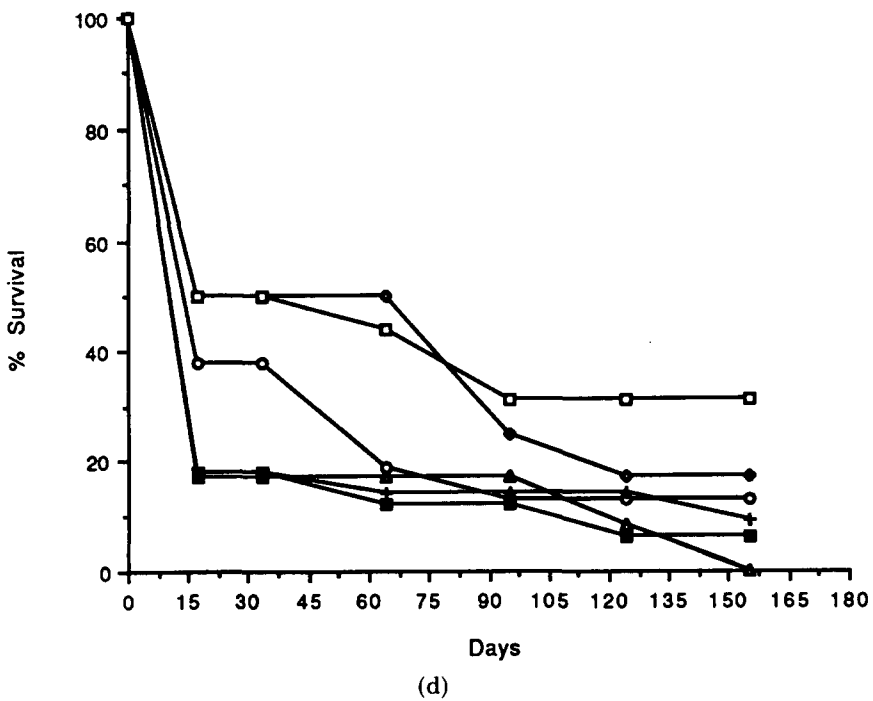
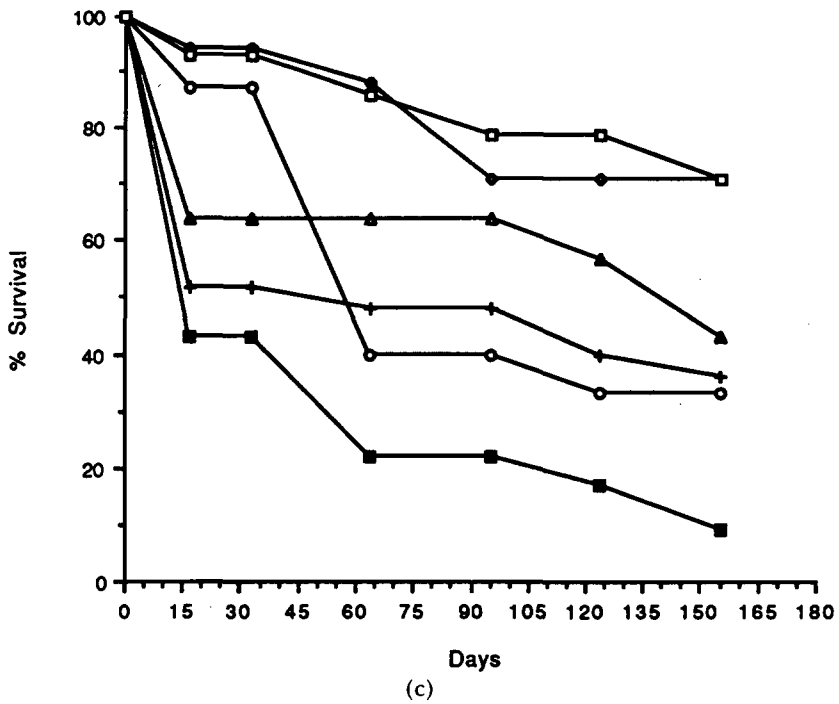
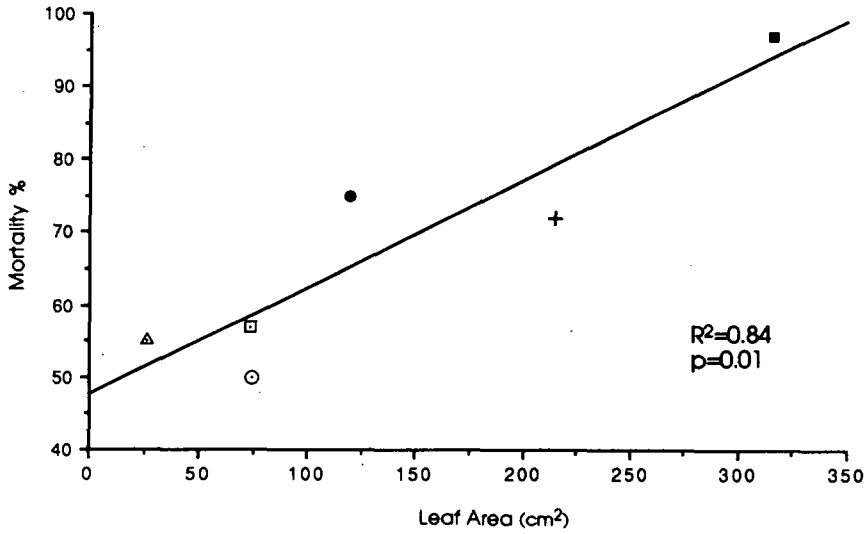
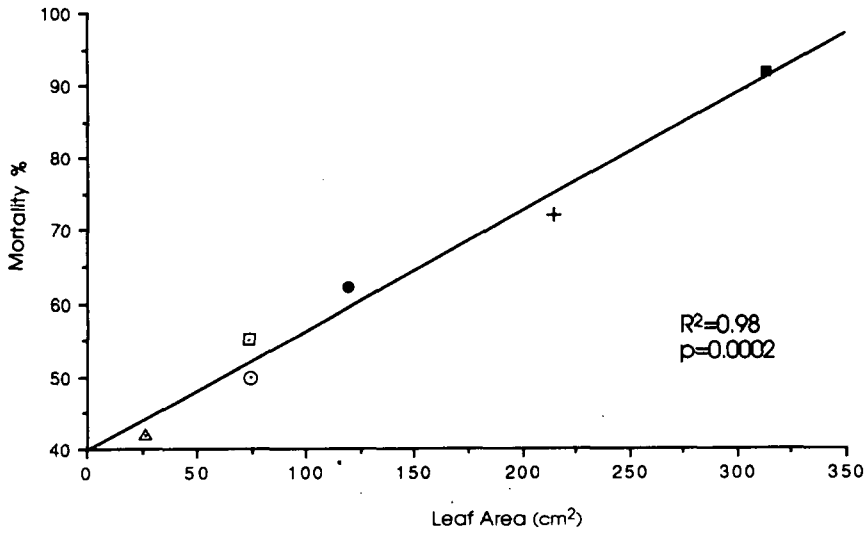


Figure 1. (cont.) Survival (%) for each *Shorea* species at each sampling interval up to six months. -o- *Shorea parvifolia*, -+- *Shorea parvistipulata*, -●- *Shorea johorensis*, -Δ- *Shorea hopeifolia*, -□- *Shorea leprosula*, -■- *Shorea pinanga* c) gap, replacement planting; d) understory, replacement planting



(a)



(b)

Figure 2. Mortality (%) versus mean total leaf area per wildling of *Shorea* species after 5½ to 6 months. -o- *Shorea parvifolia*, +- *Shorea parvistipulata*, -●- *Shorea johorensis*, -Δ- *Shorea hopeifolia*, -□- *Shorea leprosula*, -■- *Shorea pinanga*. a) gap, 1st planting ; b) understory, 1st planting

species actually had negative height growth because of dieback from planting shock and resprouting after initial leaf loss.

After the initial 2-3 weeks, when the majority of the leaf loss for all species occurred, there was a slow but steady increase in the number of leaves per species (Figure 3). Six months later, however, no species had attained the mean number of leaves recorded when first transplanted. There was no significant differences in the regrowth of the number of leaves between microsites in each planting.

Discussion

High initial mortality suggests that transplanting had a strong negative affect on wildling survival. Sixty-three to 100% of the total mortality after six months occurred in the first 2½ weeks for most combinations of species, plantings and microsites. This high initial mortality and variation in mortality and growth may be related to rainfall

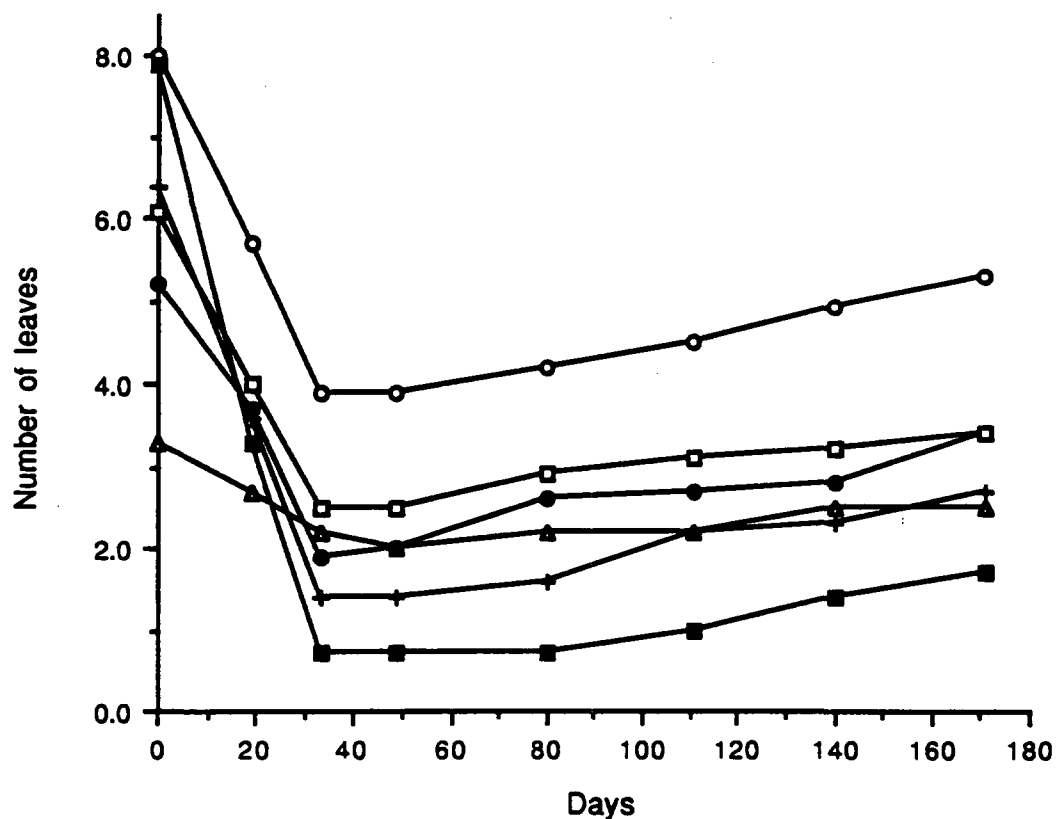


Figure 3. Mean number of leaves of each *Shorea* species at each sampling interval up to six months in both plantings and microsites combined. - ○ - *Shorea parvifolia*, - + - *Shorea parvistipulata*, - ● - *Shorea johorensis*, - △ - *Shorea hopeifolia*, - □ - *Shorea leprosula*, - ■ - *Shorea pinanga*

patterns preceding the plantings, the physical characteristics of each planting location, and certain species characteristics.

The dry months preceding the first planting could have created moisture stress in wildlings which have roots growing in the surface horizons. Much of the rain during the dry months fell in single large storms with several dry days in between. Moisture stress conditions diminished by the time of the replacement planting because twice as much rain fell (475 mm) in the month preceding the replacement planting as in the month preceding the first planting (274 mm). Although measurements of evapotranspiration were not made, it is probable that during the dry months evapotranspiration exceeded precipitation over short periods of several days. This is supported by observations of wilted wildling leaves in forest gaps and the understory during these periods.

In the first planting the lack of significant difference of survival between microsites and the high variation of survival between locations suggest that spatial variability, unrelated to gap versus understory differences, existed in soil moisture during and immediately following the dry period. Wildling survival was higher on gradual sloping microsite locations than on steeper sloping locations. Gradual sloping locations, because of their slower runoff and slower ground water flow, may retain more water during dry periods. These locations could recharge faster with the onset of rain prior to, and during planting, than steeper locations. Wildling susceptibility to desiccation when soils are relatively dry could be an important factor causing high mortality. The relationship between short term drought events and survival of both *in situ* and transplanted wildlings requires further study.

Wildlings in the gap plot at Location 1 also suffered high mortality (81 %) which may again be attributed to desiccation caused by high radiation intensities because of the gap's larger size (600m²) and east-west orientation. The highest relative light index, 37.8 mol m² day⁻¹, was measured at this site (Table 1). Even though the site had gradual slope, the large gap size could have caused higher surface temperatures and excessive soil drying.

The smaller variation in survival between locations in the replacement planting may have been due to more uniform soil moisture conditions that resulted from month-long daily wetting of all sites prior to transplanting. At the time of the replacement planting, wildlings collected from the forest were probably no longer in a moisture stressed condition and soil moisture at the planting sites was probably at or above field capacity. This may have been particularly true for the gap sites where moisture levels would have been higher because of less overstory transpiration loss. Because moisture would not have been limiting under those circumstances, wildlings in the gap plots would have been able to utilize increased sunlight to overcome transplant shock. Such an explanation is the most plausible for the observed differences of growth and survival between the initial and replacement plantings and between gap and understory microsites for the replacement planting.

Leaf area was the crucial determinant of drought survival in the first planting shown by the high correlation of wildling mortality with the total leaf area of each species (Figures 2a & b). *Shorea pinanga* and *S. parvistipulata*, with the highest leaf

area per wildling, had consistently higher mortality than the other species, especially during the first planting when soil moisture was low. The importance of the small leaf area for drought resistance is further supported by a comparison of the survival of *S. pinanga* and *S. parvifolia*, which possess the same root to shoot ratio (0.63 and 0.64). *Shorea parvifolia*, with a lower leaf area per plant, had higher survival at all sites (Tables 2 & 3). Root to shoot ratios may in part explain mortality differences as seen when comparing *S. pinanga* and *S. leprosula*. *Shorea pinanga* with a large leaf area (314 cm^2) and a small root to shoot ratio (0.63) had the poorest survival, and *S. leprosula* with a small leaf area (73 cm^2) and a large root to shoot ratio (0.88) had the highest survival. Although the root to shoot ratios may explain performance differences between these two species, no significant correlation exists for this relationship among all species ($R^2 = 0.13$ – 0.47 , $p = 0.47$ – 0.134). Interestingly, leaf area was not significantly correlated with mortality during the second planting which occurred only $2\frac{1}{2}$ weeks after the first planting ($R^2 = 0.41$, $p = 0.174$ & $R^2 = 0.42$, $p = 0.167$). If moisture was limiting during the first planting the strong relationship between leaf area and mortality during the first planting could reflect the general linear relationship between leaf area and transpiration water loss (Pereira & Kozlowski 1977, Sasaki 1980a, Salisbury & Ross 1985).

Studies with other *Shorea* species suggest accelerated height growth of bare-rooted seedlings cannot be expected until at least ten months after transplanting (Sasaki 1980a). The slow, steady increase in the mean number of leaves for each species in this study suggests that surviving wildlings were initially allocating their resources more to the development of leaf area and likely root biomass than to increasing height.

High mortality of the $3\frac{1}{2}$ y-old wildlings transplanted in this study concur with the results of earlier studies suggesting that bare-rooted planting should always coincide with the wet season and that water loss by transpiration is a serious problem in transplants, especially when leaf areas are high relative to plant size (Gill 1970, Sasaki 1980a). Sasaki (1980a) suggests that reducing the number of leaves at the time of transplanting, thereby reducing the potential transpiration loss, increases a wildling's chance of survival. It is apparent, even in aseasonal tropical rain forests, that periodic drought events may have a significant effect on forest regeneration. This may be especially important when regenerating areas where human disturbance has substantially changed microsite conditions. Research on the response of planted species to varying soil moisture conditions is needed to confidently match species with appropriate microsites in disturbed areas. Further, research focusing on ways to mitigate transplant shock, such as the effect of reducing leaf area per plant, is needed.

Acknowledgments

I would like to thank the Center for Research and Development in Biology at the Indonesian Institute of Sciences (LIPI) and the Subdirector of Nature Conservation under the Ministry of Forestry for permission to carry out this study in Indonesia.

Special thanks are directed to the late T. Hainald at LIPI for all his advice and efficient assistance in obtaining the necessary letters and permits. I also acknowledge the support of the Tropical Resources Institute, Yale University, School of Forestry and Environmental Studies, the Conservation, Food and Health Foundation Inc. and M. Leighton. My thanks are due to M. Kusneti and Utahi for their support in the field, and to C. Webb whose dipterocarp seedling key was invaluable. Finally, I sincerely thank K. Vogt, M. Ashton, D.R. Peart and D. Zarin for critical comments.

References

- ASHTON, P. M. S. & DE ZOYSA, N.D. 1989. Performance of *Shorea trapezifolia* (Thw.) Ashton seedlings growing in different light regimes. *Journal of Tropical Forest Science* 1(4): 356-364.
- ASHTON, P.M.S. 1990. Seedling Response of Shorea Species Across Moisture and Light Regimes in a Sri Lanka Rain Forest. Ph. D. dissertation. Yale University, New Haven, CT.
- ASHTON, P.S. 1982. Dipterocarpaceae. *Flora Malesiana* ser. 1, *Spermatophyta* 9: 251-552.
- CHAN, H. T. & APPANAH, A. 1980. Reproductive biology of some Malaysian Dipterocarps. I. Flowering biology. *Malaysian Forester* 43: 132-143.
- FRIEND, D.T.C. 1961. A simple method of measuring integrated light values in the field. *Ecology* 42(3):577-580.
- GILL, L.S. 1970. Enrichment planting - its future in hill forest silviculture. *Malaysian Forester* 23(2):135-143.
- MAURY-LECHON, G., HASSAN, A. M. & BRAVO, D.R. 1981. Seed storage of *Shorea parvifolia* and *Dipterocarpus humeratus*. *Malaysian Forester* 44(2&3): 267-280.
- NICHOLSON, D.I. 1960. Light requirements of five species of Dipterocarpaceae. *Malaysian Forester* 23: 344-356.
- PEREIRA, J. S. & KOZLOWSKI, T.T. 1977. Influence of light intensity, temperature and leaf area on stomatal aperture and water potential of woody plants. *Canadian Journal of Forest Research* 7: 145-153.
- RAICH, J. W. & KHOON, G. W. 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *Journal of Tropical Ecology* 6(2): 203-217.
- RAICH, J. W. & CHRISTENSEN, N. L. 1989. Malaysian dipterocarp forest: tree seedling and sapling species composition and patterns of small-scale disturbance. *National Geographic Research* 5: 348-363.
- SALISBURY, F. B. & ROSS, R. W. 1985. *Plant Physiology*. 3rd edition. Wadsworth Publishing Co., Belmont. 540 pp.
- SAS Institute Inc. 1988. *SAS/STAT™ SAS Users Guide*. Release 6.03 Edition. Cary, N. C: SAS Institute Inc. 1028 pp.
- SASAKI, S. 1980a. Growth and storage of bare root planting stock of dipterocarps with particular reference to *Shorea talura*. *Malaysian Forester* 43(2): 144-160.
- SASAKI, S. 1980b. Storage and germination of dipterocarp seeds. *Malaysian Forester* 43(3): 290-308.
- SASAKI, S. & MORI, T. 1981. Growth responses of dipterocarp seedlings to light. *Malaysian Forester* 44: 319-345.
- TANG, H. T. 1971. Preliminary tests on the storage and collection of some *Shorea* seeds. *Malaysian Forester* 34: 84-98.
- TANG, H. T. & WADLEY H. 1976. *Report on the survival and development survey of areas reforested by line-planting in Selangor*. Research Pamphlet No. 67. Forest Research Institute, Kepong, Peninsular Malaysia.
- TOMPSETT, P. B. 1987. Desiccation and storage studies on *Dipterocarpus* seeds. *Annals of Applied Biology* 110: 371-379.