

EFFECTS OF TRENCHING ON GROWTH AND SURVIVAL OF PLANTED *SHOREA PARVIFOLIA* SEEDLINGS UNDER PIONEER STANDS IN A LOGGED-OVER FOREST

M. A. Pinard

Department of Forestry, University of Aberdeen, Aberdeen AB24 5UA, United Kingdom

D. W. Davidson

Department of Biology, University of Utah, Salt Lake City, Utah 84112, United States of America

&

A. Ganing

Rakyat Berjaya Sdn. Bhd., Innoprise Corp., Lahad Datu, Sabah 91108, Malaysia

Received August 1996

PINARD, M. A., DAVIDSON, D. W. & GANING, A. 1998. Effects of trenching on growth and survival of planted *Shorea parvifolia* seedlings under pioneer stands in a logged-over forest. We conducted an experiment to determine the value of trenching in reducing potentially negative effects of root competition on growth of *Shorea parvifolia* seedlings planted in the understory of a 13-y-old logged-over forest. Two hundred 1-y-old nursery-raised seedlings were planted in four sites; two sites were in forests logged by high-lead cable yarding, and two were in forests logged using bulldozers for yarding. The ground was trenched (diameter = 1 m) around half of the seedlings in each site to reduce root competition. At 6 months after planting, no effect of trenching treatment was evident on seedling survival or relative height growth for either type of yarding method. Relative growth rates were positively correlated with canopy openness. Although the canopy in the bulldozer yarding sites was more open (15% open) than that in the cable yarding sites (12% open), relative growth rates were greater in cable yarding than in bulldozer yarding sites. At 12 months after planting, relative height growth was similar for trenched and control seedlings and for the two yarding methods. Survival was independent of trenching treatment and was higher in cable yarding than in bulldozer yarding sites. Soil disturbance associated with bulldozer yarding may negatively affect seedling establishment even 13 y after harvest, indicating the importance of pre-harvest planning in reducing the area traversed by bulldozers. Our results suggest that below-ground competition does not limit growth and survival of dipterocarp seedlings in pioneer tree stands. For both trenched and control seedlings, relative growth rates were lower during drier than wetter periods. We recommend that foresters working in drought-prone regions, such as eastern Sabah, explore methods of increasing seedling drought tolerance before outplanting, perhaps by increasing root:shoot ratios, rather than by attempting to reduce below-ground competition by trenching around seedlings in the field.

Key words: Dipterocarp seedlings - enrichment planting - pioneer stands - root competition - trenching - *Shorea parvifolia* - soil compaction

PINARD, M.A., DAVIDSON, D.W. & GANING, A. 1998. Kesan pemangkasan terhadap pertumbuhan dan kemandirian anak benih *Shorea parvifolia* yang ditanam di bawah dirian perintis di hutan sudah kerja. Kami menjalankan uji kaji untuk menentukan nilai pemangkasan bagi mengurangkan kesan negatif yang berpotensi ke atas pertumbuhan anak benih *Shorea parvifolia* yang ditanam di tingkat bawah hutan sudah kerja berumur 13 tahun. Sebanyak 200 anak benih berumur satu tahun yang dibesarkan di tapak semeian ditanam di empat tapak; dua tapak di hutan yang dibalik menggunakan pemagaran kabel manakala dua lagi ditanam di hutan yang dibalik menggunakan jentolak untuk pemagaran. Tanah dipangkas (diameter=1m) di sebahagian keliling anak benih di setiap tapak untuk mengurangkan persaingan akar. Enam bulan selepas penanaman, tiada kesan rawatan pemangkasan didapati pada kemandirian anak benih atau pertumbuhan ketinggian relatif bagi mana-mana jenis kaedah pemagaran. Kadar pertumbuhan relatif adalah berkaitan secara positif dengan keterbukaan kanopi. Walaupun kanopi dalam tapak yang dipagar menggunakan pemagaran kabel (12 % terbuka), kadar pertumbuhan relatif adalah lebih besar dalam tapak yang dipagar dengan kabel berbanding tapak yang dipagar menggunakan jentolak. Dua belas tahun selepas penanaman, pertumbuhan ketinggian relatif adalah sama bagi anak benih yang dipangkas dan dikawal dengan dua anak benih di tapak yang menggunakan kaedah pemagaran. Kemandirian tidak bergantung kepada rawatan pangkasan dan lebih tinggi dalam tapak pemagaran kabel daripada tapak pemagaran jentolak. Kerosakan tanah yang terdapat di tapak pemagaran jentolak mungkin memberi kesan negatif terhadap penubuhan anak benih walaupun 13 tahun selepas pengusahasilan. Ini menunjukkan betapa pentingnya perancangan prapengusahasilan dalam kawasan yang dilalui oleh jentolak. Keputusan kajian kami mengesyorkan bahawa persaingan di bawah tanah tidak menghadkan pertumbuhan dan kemandirian anak benih dipterokarpa dalam dirian pokok perintis. Bagi anak-anak benih yang dipangkas dan dikawal, kadar pertumbuhan relatif adalah rendah pada musim kering berbanding pada musim hujan. Kami mengesyorkan supaya rimbawan yang bekerja di kawasan yang senang mendapat kemarau, seperti di bahagian timur Sabah, menggunakan kaedah menambahkan anak benih tolerans kemarau sebelum melakukan penanaman luar. Cara yang lebih baik ialah menambahkan nisbah akar: pucuk, berbanding dengan cara mengurangkan persaingan bawah-tanah melalui pemangkasan di sekeliling anak benih di ladang.

Introduction

Enrichment planting trials in Malaysian forests date from the 1930s (Wyatt-Smith 1995). This type of artificial regeneration involves planting seedlings of preferred species in natural forest to supplement the existing stock of seedlings. Although there are examples of successful line-planting programmes (e.g. Tang & Chew 1980), attempts at artificial regeneration have generally failed (reviewed by Pierront 1995). Common problems include high maintenance costs, improper selection of planting stock, incidental damage to advanced regeneration during planting operations, and poor seedling survivorship (Pierront 1995). However, given that regeneration of commercial species is poor in a large proportion of logged Malaysian forests (Tang 1987), efforts to improve enrichment planting systems continue to be important (e.g. Moura-Costa 1994).

Logged-over forests in Sabah are extremely heterogenous both in space and time. In recently-logged sites, patches of relatively undisturbed residual forest are scattered among skid trails, roads, landslides and felling gaps. As the forest recovers, pioneer trees establish in the post-logging habitats with severe canopy

disturbance, and provide environmental conditions that appear suitable for the establishment of dipterocarps. However, due perhaps to the paucity of dipterocarp propagules, natural regeneration in these stands is often very limited. For these reasons we chose to conduct our experiment on enrichment planting in pioneer tree stands.

Generally, the growth of dipterocarp seedlings in forest understory is limited by light (Turner 1989, Ashton 1995), and opening the canopy directly above seedlings results in increased seedling growth (Adjers *et al.* 1995), though not all species respond equally (Ashton 1995, Ashton *et al.* 1995). Below-ground competition between dipterocarp seedlings and their neighbours may reduce seedling growth rates (Bhatnagar 1959), particularly for seedlings in logged forests dominated by shallowly-rooted early successional vegetation and pioneer trees (Nicholson 1960).

In this study we examined the value of trenching in reducing possible detrimental effects of root competition on growth of seedlings planted in logged-over forest. We conducted the experiments in a 13-y-old logged forest where either a high-lead cable system or bulldozers were used for log extraction. High-lead cable systems retrieve logs with cables radiating out from a central pole that is set on a cleared platform. Logs are lifted only partially off the ground, and residual trees often receive extensive damage (Borhan *et al.* 1987). Bulldozer yarding also results in extensive damage to the residual stand, as well as leaving 20-40% (Chai 1975, Nussbaum *et al.* 1995, Pinard 1995) of the area covered with roads, skid trails and decking sites.

Materials and methods

Study site

The study was conducted in a logged forest in Ulu Segama Forest Reserve in eastern Sabah, Malaysia (9782 km² Class II Commercial Forest, 5° 0' N, 117° 30' E, *c.* 200 m above sea-level). Soils are clay-rich Ultisols, derived from uplifted alluvial, tertiary sediments (Ohta & Effendi 1992). The climate is monsoonal with the wettest period between November and March and one dry period, usually in April, when mean monthly precipitation is about 100 mm. Mean annual rainfall is about 2800 mm; mean daily temperature is about 27 °C (unpubl. Danum Valley Field Centre records, 1986-1992). Four of the twelve months of observation had total monthly rainfall below 100 mm (January 96 mm, February 86 mm, March 66 mm, April 28 mm).

The dipterocarp forest in the study sites had been logged in 1978, 13-14 y prior to the study. At two sites, crawler-tractors (D7 bulldozers) were used to extract logs from the forest; at the other two, a high-lead cable system was used for log extraction. Mean volume of timber extracted was 93 m³ ha⁻¹ (unpubl. records, Pacific Hardwoods Sdn. Bhd.). At the time of the study, the forest contained relatively large (1-2 ha) patches of pioneer tree stands dominated by *Macaranga hypoleuca* and *M. gigantea*.

Within each of the four sites, a 0.25-ha plot was established for line-planting with *Shorea parvifolia* seedlings. *Shorea parvifolia*, a light hardwood species that is a common canopy emergent in the area, was used for the study because seedlings were readily available and it has a reputation for relatively fast growth rates in young regenerating stands (Meijer & Wood 1964). *Shorea parvifolia* seedlings require partial shade for establishment (Nicholson 1960). Plots were selected based on accessibility, slopes $< 30^\circ$, and an overstory dominated by pioneer trees. Mean basal areas (trees > 5 cm dbh) in cable and bulldozer yarding sites were 26.8 and 22.2 $\text{m}^2 \text{ha}^{-1}$ respectively. About 82% of the basal area consisted of pioneer tree species.

Planting lines were cut in a 10×5 m grid. Seedlings raised from seed in a nursery were planted with a hoe on 5 August 1991, and the ground was trenched around half of the seedlings (randomly selected) in each plot. All seedlings were alive at the time of planting and trenching. Trenches (radius ≈ 0.5 m, depth ≈ 0.3 m) were cut in circles around each seedling and lined with a layer of veneer (about 1-1.5 mm thick). During the study period, living plants of other species were removed from inside the trench. Seedlings planted in sites that were 'non-trenchable', due to close proximity to a tree > 10 cm dbh, were excluded from the experiment; 23 seedlings were thus excluded. Total planting costs were about U.S. \$400 ha^{-1} , or about twice the cost of line-clearing and planting without trenching.

Initial height of each seedling was measured and canopy openness over each seedling was estimated using a spherical densiometer (Lemmon 1957). To examine the relationship between canopy openness and photon flux density (PFD), measurements were made over seedlings at mid-day (9 October 1991) in one of the four plots using a quantum sensor. A Pearson Correlation test was used to determine if canopy densiometer readings were correlated with measurements of PFD. Seedling height was remeasured at 6 and 12 months after planting. Relative growth rates were calculated as the natural log of the height at time 2 minus the natural log of the height at time 1. Two canopy openness readings were identified as outliers and excluded from analyses (Grubb's test statistic = 3.39, 3.05; $p < 0.05$; Rohlf & Sokal 1981), and a further seedling was excluded due to extremely high initial height (Grubb's test statistic = 4.55, $p < 0.005$).

For statistical comparisons of relative growth rates, we used an analysis of covariance, with trenching treatment and logging method as categorical variables and canopy openness as a covariate. We considered each seedling as a replicate and disregarded potential blocking or plot effects. This approach biases in favour of rejecting the null hypothesis, but any bias is conservative in cases where we fail to reject the null hypothesis. Most of our results were non-significant and this was confirmed by alternative analyses that considered potential block effects and avoided pseudoreplication. Survival comparisons were made using Chi-square tests. We used a Pearson Correlation test to determine whether relative growth rates were correlated with canopy openness. In order to test whether survival was related to canopy openness, we used a *t*-test on arcsine-transformed data to compare canopy openness above dead and live seedlings 6 and 12 months after planting.

Results

At the time of planting, seedling heights were similar for trenched and control seedlings in both the bulldozer yarding sites and the cable yarding sites (trench, mean = 69 cm, sd = 19, n = 95; control, mean = 71, sd = 22, n = 80; $t = 0.64$, $df = 173$, $p = 0.52$). By chance, seedlings planted in the bulldozer yarding sites were taller than those planted in the cable yarding sites (bulldozer, mean = 74 cm, sd = 21, n = 84; cable, mean = 67, sd = 19, n = 91; $t = 2.5$, $df = 173$, $p = 0.01$). Canopy openness was similar for trenched and control seedlings in both bulldozer and cable yarding sites ($p > 0.05$; Table 1). However, openness was greater in bulldozer than in cable yarding sites (bulldozer, mean = 15%, sd = 5; cable, mean = 12, sd = 4; $t = 4.7$, $df = 171$, $p < 0.001$). Photon flux densities ranged from 35 to 238 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (median 85, n = 48) and were positively correlated with canopy openness ($r = 0.70$; Bartlett Chi Square = 31, $df = 1$, $p < 0.001$; Figure 1).

Table 1. Descriptive statistics for *Shorea parvifolia* seedlings planted in two types of logged forest. Mean values (sd) are presented with sample sizes. Relative growth rates were calculated as $\text{LN}(H_{t_2}/H_{t_1})$.

Yarding and trenching treatments	Canopy openness (%)	Relative growth rate 0-6 months	Relative growth rate 6-12 months
Bulldozer			
Control	14 (6), N = 38	0.30 (0.40), N = 35	0.08 (0.43), N = 29
Trenched	15 (4), N = 45	0.29 (0.23), N = 43	0.15 (0.26), N = 36
Cable			
Control	11 (4), N = 41	0.35 (0.23), N = 40	0.17 (0.25), N = 39
Trenched	12 (4), N = 49	0.39 (0.32), N = 48	0.21 (0.22), N = 46

Six months after planting, 96% and 92% of the seedlings were alive in the cable and bulldozer yarding sites respectively. Survival was independent of trenching treatment and yarding method (trenching treatment, $\chi^2 = 1.4$, $df = 1$, $p = 0.24$; yarding method, $\chi^2 = 1.15$, $df = 1$, $p = 0.28$). Canopy openness was greater above dead seedlings (mean = 17%, sd = 5, n = 11) than above live seedlings (mean = 13%, sd = 5, n = 166) six months after planting ($t = 2.2$, $df = 175$, $p = 0.03$). In all sites, the common causes of death were trampling by elephants and crushing by fallen branches. Non-fatal apical shoot damage, both by browsers (10% of seedlings) and by shoot-boring insects (19%), was fairly common during the first six months. A positive correlation between openness and mortality may occur because fallen branches and feeding by elephants both open the canopy and crush seedlings.

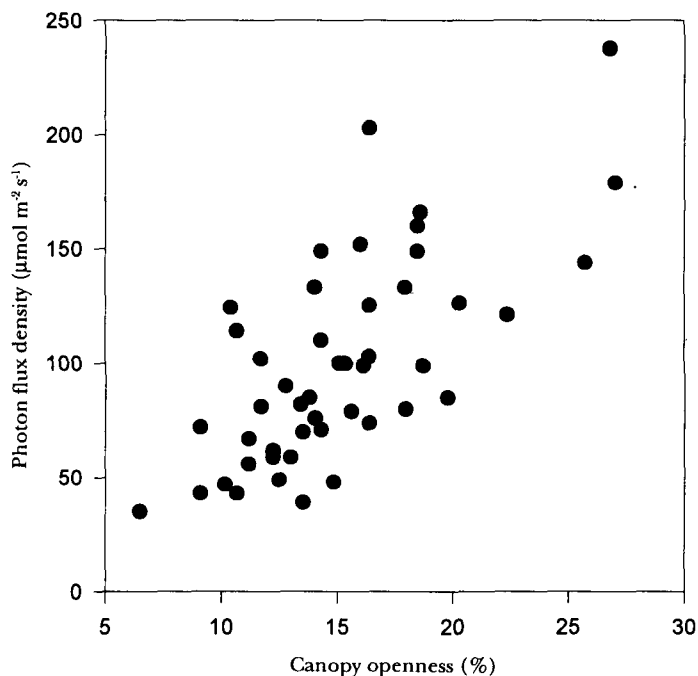


Figure 1. Mid-day photon flux density (light sensor) related to percentage canopy openness measured using a spherical densiometer, measured above seedlings planted in four logged-over sites in Ulu Segama Forest Reserve, Sabah, Malaysia

Relative growth rates of seedlings during the first 6 months ranged from -0.18 to 2.30 (Table 1). Relative height growth was greater in cable yarding sites than in bulldozer yarding sites (Table 1; $F = 17.9$, $df = 1161$, $p < 0.001$). No effect of trenching treatment was evident ($F = 0.01$, $df = 1161$, $p = 0.92$) nor was an interaction between yarding method and trenching treatment evident ($F = 0.09$, $df = 1161$, $p = 0.77$). Relative growth rates at 6 months were weakly correlated with initial canopy openness for seedlings planted both in the (more shaded) cable yarding sites ($r = 0.59$, Bartlett Chi square = 37, $df = 1$, $p < 0.001$; Figure 2) and in the (more open) bulldozer yarding sites ($r = 0.46$, Bartlett Chi square = 18, $df = 1$, $p < 0.001$; Figure 2).

At 12 months, 92% and 77% of the seedlings were alive in the cable and bulldozer yarding sites respectively. Between 6 and 12 months after planting, survival was independent of trenching treatment ($\chi^2 = 0.4$, $df = 1$, $p = 0.53$). However, seedling survival was higher in the cable yarding site than in the bulldozer yarding site ($\chi^2 = 8.4$, $df = 1$, $p = 0.004$). Canopy openness (measured at the start of the experiment) above dead seedlings did not differ from that above live seedlings ($t = 1.4$, $df = 175$, $p = 0.16$).

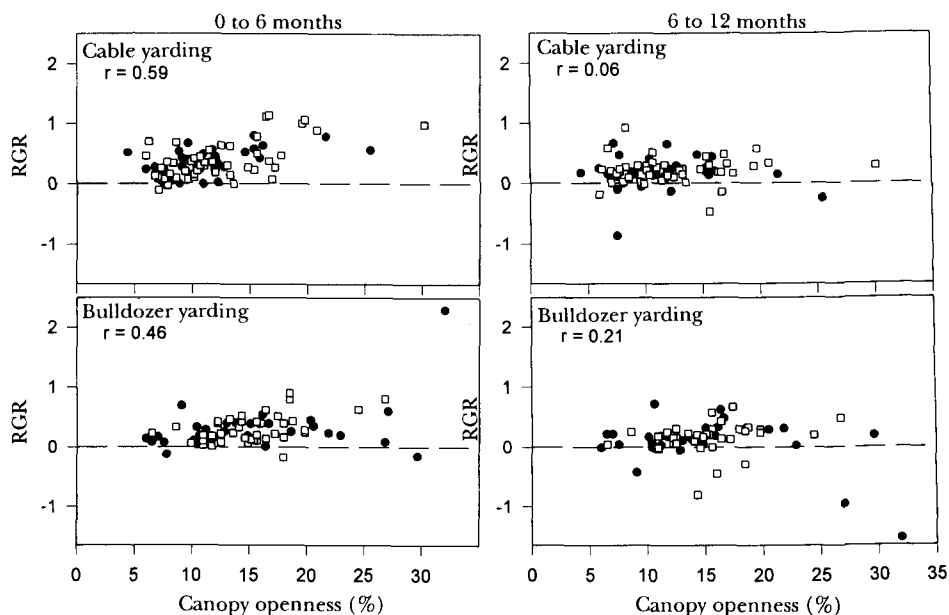


Figure 2. Relative growth rates related to percentage canopy openness of seedlings planted in logged-over forest. Closed circles represent controls, open squares represent trenched seedlings. For both the bulldozer and cable yarding sites, the two variables were weakly positively correlated during the first six months after planting but not during the second six months.

Between 6 and 12 months, relative growth rates were similar for trenched and control seedlings ($F = 1.47$, $df = 1145$, $p = 0.23$) and for seedlings in cable and bulldozer yarding sites ($F = 1.31$, $df = 1145$, $p = 0.25$; Table 1); no interaction between trenching treatment and yarding method was evident ($F = 0.13$, $df = 1$, 145 , $p = 0.72$). Relative height growth was not correlated with initial canopy openness ($p > 0.05$; Figure 2) for either cable or bulldozer yarding sites. However, had we repeated canopy openness measurements at 6 months, we might have increased the probability of finding an effect of openness during the second 6 months. Drier conditions prevailed during the second 6-month measurement interval, and perhaps for this reason, relative height growth during this period was less than that between zero and 6 months (bulldozer yarding, paired $t = 2.6$, $df = 64$, $p = 0.01$; cable yarding, paired $t = 4.6$, $df = 84$, $p < 0.001$).

Over the full 12-month period, the patterns established over the first 6 months were still evident. Relative growth rates were greater in cable than in bulldozer yarding sites ($F = 16.4$, $df = 1145$, $p < 0.001$). As with the two 6-month periods of observation, no trenching treatment effect was evident ($F = 0.64$, $df = 1145$, $p = 0.42$), nor was there an interaction between yarding method and trenching treatment ($F = 0.08$, $df = 1145$, $p = 0.78$). Relative growth rates were only weakly

correlated with canopy openness ($r = 0.26$, $p = 0.04$). Seedling survival was independent of trenching treatment and yarding method.

Discussion

Root competition did not appear to limit establishment of *S. parvifolia* seedlings in the pioneer tree stands where we worked. Over the first year after planting, no increase in growth or survival was recorded for seedlings receiving a trenching treatment to reduce root competition. It is unlikely that our negative results are due to either confinement of seedling root growth to trenched areas or failure to effectively reduce below-ground competition; the trenched area was relatively large (0.8 m^2) and the slit for the trench was cut deeply enough to sever most superficial roots (to 0.3 m depth).

Experimental studies of the relative importance of above- and below-ground competition for woody plants have produced variable results (reviewed by Wilson 1988), suggesting that the relative importance of root and light competition may vary depending on site conditions and species (see, e.g. Putz & Canham 1992, Davidson 1993).

Our results support the common assertion that light is an important limiting factor for dipterocarp seedlings (Turner 1989, Ashton 1995); height growth and canopy openness were positively correlated during the first 6 months, and PFD values (ranging from 35 to $238 \mu\text{mol m}^{-2} \text{ s}^{-1}$) recorded in the 13-y logged forest were below the level at which *S. parvifolia* reaches light saturation ($> 300 - 400 \mu\text{mol m}^{-2} \text{ s}^{-1}$, Mori *et al.* 1990; $310 - 350 \mu\text{mol m}^{-2} \text{ s}^{-1}$, Barker *et al.* 1997). The absence of a correlation between seedling height growth and canopy openness during the second 6-month period supports our conclusion that some other factor limited growth during this period.

Growth and survival may be limited more by soil moisture than by nutrients in dipterocarp forests of Sabah (Turner *et al.* 1993). In our study, rates of relative height growth were lower during the drier (February - July) than the wetter (August - January) season. Trenching around seedlings may have reduced the root mass of neighbouring plants within the trenched area, but all seedlings experienced reduced growth rates during the drier season. Dipterocarp seedlings, including relatively light-demanding species such as *S. parvifolia*, tend to make a proportionally greater investment in shoot rather than root growth in shaded understory conditions (Palmiotto 1993, Ashton 1995) and it has been speculated that resulting low root:shoot ratios may make such seedlings especially prone to desiccation (Ashton 1995), although allocation patterns within the shoot may also be important (Palmiotto 1993). Soil compaction, typical of bulldozer yarding sites, might exacerbate moisture stress, since compacted soils typically have lower water infiltration rates (Greacen & Sands 1980). This relationship between compaction and reduced soil water availability may explain, in part, the observation of higher mortality in the bulldozer yarding sites than in the cable yarding sites during the dry season.

Six months after planting, we recorded greater height growth for seedlings planted in cable yarding as compared to bulldozer yarding sites. This difference in height growth does not appear to be related to light, since the cable yarding sites were more shaded and the analysis of covariance removed any variation attributable to canopy openness. Nor can the difference be attributed to below-ground competition, because the trenching treatment was ineffective at enhancing growth rates, and the basal area was higher in the cable yarding (mean = 27 m²) than in the bulldozer yarding sites (mean = 22 m²). Both of these observations suggest that the direction of the difference would have been reversed. Bulldozer damage to soil structure during logging may be responsible for the differential growth (Nussbaum 1995).

Our results support the general conclusion that, for dipterocarp seedlings growing in pioneer tree stands, the primary factor limiting growth may change as environmental conditions change throughout the year, or possibly between years. For *S. parvifolia* seedlings, competition for light may be more important than competition for water or nutrients during the wet season. However, during the dry season, competition for water may be more important than competition for light. Effects of competition with the overstory may increase as the seedlings increase in size.

Even in eastern Sabah, where droughts are common (Woods 1989), we see no advantage to installing trenches around seedlings planted in pioneer stands. A more cost-effective treatment to increase the growth and survival of outplanted seedlings might be to increase the drought tolerance of seedlings prior to outplanting (see also Sasaki & Mori 1981). One way to achieve this would be to provide conditions that foster the development of higher root:shoot ratios (Kramer & Kozlowski 1979, Claussen 1996). Providing seedlings with more light (Ashton 1995) or less fertiliser (Lyr & Hoffman 1967 or Klepper 1991 in Gerhardt & Fredriksson 1995) during development may effectively shift these ratios.

Acknowledgements

We thank Yayasan Sabah (Forestry Upstream Division), Danum Valley Management Committee, State Internal Affairs & Research Office of the Sabah Chief Minister's Department, and the Economic Planning Unit of the Prime Minister's Department for permission to conduct research in Danum Valley. Rakyat Berjaya Sdn. Bhd. provided seedlings and labour to plant the seedlings. The project was supported by the U.S. Department of State's Man and the Biosphere Program (#173-000567), and by the National Science Foundation (DEB 9123668). PFD data were provided by M. G. Barker. The manuscript benefitted by comments from M. G. Barker, F. E. Putz and two anonymous referees. This is project number 77 of the Danum Valley Rainforest and Training Programme.

References

- ADJERS, G., HADENGGANAN, S., KUUSIPALO, J., NURYANTO, K. & VESA, L. 1995. Enrichment planting of dipterocarps in logged-over secondary forests: effect of width, direction and maintenance method of planting line on selected *Shorea* species. *Forest Ecology and Management* 73 : 259 - 270.
- ASHTON, P.M.E. 1995. Seedling growth of co-occurring *Shorea* species in the simulated light environments of a rain forest. *Forest Ecology and Management* 72 : 1 - 12.
- ASHTON, P. M. E., GUNATILLEKE, C. V. S. & GUNATILLEKE, I. A. U. N. 1995. Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. *Journal of Tropical Ecology* 11: 263 - 279.
- BHATNAGAR, H. P. 1959. The effect of root competition on the growth of sal natural regeneration. *Indian Forester* 85 (7): 408 - 414.
- BARKER, M. G., PRESS, M.C. & BROWN, N. D. 1997. Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments : a basis for niche partitioning? *Oecologia* 112 : 453 - 463.
- BORHAN, M., JOHARI, B. & QUAH, E. S. 1987. Studies on logging damage due to different methods and intensities of harvesting in a hill dipterocarp forest of Peninsular Malaysia. *Malaysian Forester* 50 : 135 - 147.
- CHAI, D. N. 1975. Enrichment planting in Sabah. *Malaysian Forester* 38: 271- 277.
- CLAUSSEN, J. W. 1996. Acclimation abilities of three tropical rainforest seedlings to an increase in light intensity. *Forest Ecology and Management* 80 : 245 - 255.
- DAVIDSON, D. 1993. The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68: 23 - 35.
- GERHARDT, K. & FREDRIKSSON, D. 1995. Biomass allocation by broad-leaf mahogany seedlings, *Swietenia macrophylla* (King), in abandoned pasture and secondary dry forest in Guanacaste, Costa Rica. *Biotropica* 27: 174 - 182.
- GREACEN, E. L. & SANDS, R. 1980. Compaction of forest soils. A review. *Australian Journal of Soil Resources* 18 : 163 - 189.
- KRAMER, P. J. & KOZLOWSKI, T.T. 1979. *Physiology of Woody Plants*. Academic Press, New York, United States of America. 811 pp.
- LEMMON, P. E. 1957. A new instrument for measuring forest overstory density. *Journal of Forestry* 55 : 667 - 669.
- MEIJER, W. & WOOD, G. H. S. 1964. *Dipterocarps of Sabah (North Borneo)*. Sabah Forest Record No. 5. Forest Department, Sandakan, Sabah, Malaysia. 344 pp.
- MORI, T., NAKASHIZUKA, T., SUMIZONO, T. & YAP, S. K. 1990. Growth and photosynthetic responses to temperature in several Malaysian tree species. *Journal of Tropical Forest Science* 3 : 44 - 57.
- MOURA-COSTA, P. 1994. Large scale enrichment planting with dipterocarps, methods and preliminary results. Pp. 72 - 77 in Suzuki, K., Sakurai, S. & Ishii, K. (Eds.) *Proceedings of the Yogyakarta Workshop, BIO-REFOR/IUFRO/SPDC: Bio-reforestation in Asia-Pacific Region*. 20-23 September 1993, Indonesia.
- NICHOLSON, D. I. 1960. Light requirements of seedlings of five species of Dipterocarpaceae. *Malaysian Forester* 23: 344 - 356.
- NUSSBAUM, R. 1995. The effect of selective logging on rainforest soil and the implications for recovery. Ph.D. dissertation, University of Exeter, Exeter, United Kingdom.
- NUSSBAUM, R., ANDERSON, J. & SPENCER, T. 1995. The effects of selective logging of tropical rainforest on soil characteristics and growth of planted dipterocarp seedlings in Sabah, Malaysia. Pp. 105-115 in Primack, R. & Lovejoy, T. (Eds.) *Ecology, Conservation, and Management of Southeast Asian Forests*. Yale University Press, New Haven, Connecticut, United States of America.
- OHTA, S. & EFFENDI, S. 1992. Ultisols of "lowland dipterocarp forest" in East Kalimantan, Indonesia. II. Status of carbon, nitrogen, and phosphorus. *Soil Science and Plant Nutrition* 38 : 207- 216.
- PALMIOTTO, P. A. 1993. Initial response of *Shorea* wildings transplanted in gap and understory microsites in a lowland rain forest. *Journal of Tropical Forest Science* 5 : 403- 415.

- PIERONT, K. 1995. Enrichment planting in tropical forests: a review. M.S. thesis paper, School of Forestry and Natural Resource Conservation, University of Florida, Gainesville, Florida, United States of America.
- PINARD, M. 1995. Carbon retention by reduced-impact logging. Ph.D. dissertation, Department of Botany, University of Florida, Gainesville, Florida, United States of America.
- PUTZ, F. E. & CANHAM, C. D. 1992. Mechanisms of arrested succession in shrublands: root and shoot competition between shrub and tree seedlings. *Forest Ecology and Management* 49: 267- 275.
- ROHLF, F. J. & SOKAL, R.R. 1981. *Statistical Tables*. 2nd edition. W. H. Freeman and Company, New York, New York, United States of America : 213 - 214.
- SASAKI, S. & MORI, T. 1981. Growth responses to dipterocarp seedlings to light. *Malaysian Forester* 44: 319 - 345.
- TANG, H. T. 1987. Problems and strategies for regenerating dipterocarp forests in Malaysia. Pp. 23 - 41 in Mergen, F. & Vincent, J.R. (Eds.) *Natural Management of Tropical Moist Forests*. Yale University, School of Forestry and Environmental Studies, New Haven, Connecticut, United States of America.
- TANG, H. T. & CHEW, T. K. 1980. Preliminary results of two six-year-old under-planting trials at Tapah Hills Forest Reserve, Perak. *Malaysian Forester* 43 : 193 - 221.
- TURNER, I. M. 1989. A shading experiment of some tropical rain forest tree seedlings. *Journal of Tropical Forest Science* 1: 383 - 389.
- TURNER, I. M., BROWN, N. D. & NEWTON, A. C. . 1993. The effect of fertilizer application on dipterocarp seedling growth and mycorrhizal infection. *Forest Ecology and Management* 57: 329 - 337.
- WYATT-SMITH, J. 1995. Enrichment planting. Chapter 6 in *Manual of Malayan Silviculture for Inland Forest*. Volume I. 2nd edition. Malayan Forest Records No. 23, Forest Research Institute Malaysia, Kepong, Malaysia.
- WILSON, J. B. 1988. Shoot competition and root competition. *Journal of Applied Ecology* 25 : 279 - 296.
- WOODS, P. 1989. Effects of logging, drought, and fire on structure and composition of tropical forest in Sabah, Malaysia. *Biotropica* 2 1: 290 - 298.