

## Factors limiting the growth of indigenous tree seedlings planted on degraded rainforest soils in Sabah, Malaysia

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### Abstract

During selective logging of tropical rainforest in Malaysia, the topsoil is removed from log landings and skid trails by bulldozers. The exposed subsoil is compacted, nutrient-poor, low in organic matter, drought-prone and hot. Vegetation on log landings and skid trails recovers extremely slowly. Tree seedlings planted on these degraded areas perform much less well than those planted in adjacent manually disturbed areas. An experiment was set up to investigate whether soil factors reduced early tree growth. The treatments used were: digging to reduce soil compaction; fertilizing to replace lost nutrients; mulching to reduce soil temperatures and evaporation rates; replacement of topsoil. Two pioneer tree species (*Macaranga hypoleuca* and *M. gigantea*) and two dipterocarp species (*Dryobalanops lanceolata* and *Shorea leprosula*) were planted in treated plots. Fertilizing of seedlings resulted in a dramatic improvement in height, basal diameter and dry weight increments of all species 6 months after planting. Digging improved seedling growth slightly, but mulching had little effect. This suggests that nutrient deficiency is the most important factor limiting early tree growth on degraded soil. Topsoil replacement resulted in growth as good as that of fertilized seedlings. The topsoil plots also contained 35 times more volunteer plants than any other treatment. Pioneer tree seedlings grew significantly faster than dipterocarp seedlings.

**Keywords:** Degraded soil; Growth limiting factors; Logging; Rainforest

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### 1. Introduction

Concern about the rapid loss of tropical rainforests has led to increasing emphasis on the importance of sustainable long-term management based on both economic and ecological principles (e.g. Gomez-Pompa et al., 1991). One of the principal causes of disturbance to the rainforest in southeast Asia is commercial timber harvesting. In Sabah (Malaysia), forests are generally left to recover without further intervention following

timber extraction (Poore, 1989). The rate of forest regeneration following logging is a function of the severity of disturbance to vegetation and soils. Gaps and debris piles formed by felled trees are similar to the natural gaps found in rainforests, and are often able to follow the same successional pathways to recovery (Whitmore, 1991). The areas traversed repeatedly by bulldozers during logging operations are much more severely damaged. All vegetation and most topsoil is removed (Gillman et al., 1985), and regeneration on such mechanically damaged areas is extremely slow. Even 20 years after logging operations have been com-

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pleted, the vegetation is often sparse with few or no tree species (Malmer and Grip, 1990). Uhl et al. (1982) estimated from growth and yield plots in Venezuela that a mechanically cleared area could take up to 1000 years to regain its original biomass. Selective logging, the main method of timber harvesting in Malaysia, results in a patchwork of fragmented forest with varying degrees of damage to soils and vegetation. The areas most disturbed during timber harvesting are log landings, used to store logs (which can cover areas of up to 0.4 ha), and skid trails made by the bulldozers extracting logs from the forest.

Slow regeneration of forest following logging has three main adverse environmental and economic consequences. Firstly, most erosion occurs on the bare soil of log landings and skid trails (Nussbaum et al., in press) and tends to continue until vegetation or a litter layer are re-established. Secondly, large open areas in the forests in Sabah allow the rapid growth of light-demanding vines or climbing bamboo, which then invade surrounding forest fragments arresting natural recovery (Mead, 1937; Chai, 1975; Tang and Wadley, 1976; Priasukmana, 1991). Thirdly, skid trails and log landings can represent a significant proportion of the total area of logged forest and therefore result in a substantial loss of potentially productive forest. In Malaysia it has been estimated that these areas cover up to 40% of the logged area (e.g. Nicholson, 1979; Kamaruzaman Jusoff, 1991). Two surveys in eastern Sabah estimate the extent of skid trails at somewhere between 15% (M. Pinard, personal communication, 1994) and 30% (Nussbaum, 1995).

Many factors may contribute to arrested succession of these severely disturbed areas. Much of the seed bank in topsoil is removed during logging or by subsequent erosion of the exposed soil (Whitmore, 1991). Seed rain from the surrounding forest tends to be washed off the soil surface or fails to establish because of hostile micro-environmental conditions (Pinard et al., in press) resulting from the removal of litter and vegetation cover. Operations by heavy bulldozers result in severe soil compaction (Van der Weert, 1974; Seubert et al., 1977; Dias and Nortcliff, 1985). The resultant reduced rates of surface water infiltration lead to increased volumes of overland flow and accelerated erosion (Malmer and Grip, 1990; Nussbaum, 1995). The increase in bulk density reduces the water-holding capacity of the compacted soil (Chauvel et al., 1991).

As a consequence of the loss of topsoil and on-going erosion, the exposed soil surface is severely depleted in organic matter and nutrients, most of which occur in the top 15 cm of the soil profile (Acres et al., 1975; Nussbaum, 1995).

In a preliminary study, we found that seedlings planted in undisturbed soil in areas with an open canopy performed significantly better than seedlings planted on skid trails with similar canopy opening (Nussbaum, 1995). Therefore, we decided to investigate the effect of soil factors on seedling establishment on degraded sites. An experiment was established to investigate the importance of soil compaction, loss of nutrients, reduced moisture and high soil temperatures on the early growth of indigenous tree seedlings planted on log landings. Forest soil was also translocated onto the log landing to investigate tree seedling growth under conditions analogous to situations where topsoil is not bladed off the skid trails and log landings. Seedlings of four different tree species were used as test plants: two dipterocarps, slow-growing, shade-tolerant trees which produce valuable timber; and two pioneer trees, fast-growing, light-demanding early successional species which produce less useful timber.

## 2. Materials and methods

### 2.1. Study site

The Ulu Segama Forest Reserve (5°0'N, 117°30'E) is part of the 972 804 ha concession of Yayasan Sabah (the Sabah Foundation) in eastern Sabah, Malaysia. The area is covered by dipterocarp forest (Newbery et al., 1991) and is dedicated to timber production except for 43 800 ha set aside as a conservation area (Danum Valley Conservation Area). The complex geology of eastern Sabah has resulted in the formation of heterogeneous soils dominated by Acrisols, Cambisols and Luvisols (Wright, 1975; Marsh and Greer, 1992). Goh et al. (1993) report that the plant nutrient status of soils is extremely variable. Mean annual rainfall recorded at the nearby Danum Valley Field Centre is approximately 2700 mm (records 1986–1992). The highest rainfall occurs from November to March, with drier periods around April and September; there is, however, considerable monthly and annual variation. Mean daily temperature recorded over 6 years is 26.7°C, with a

mean maximum of 30.9°C and mean minimum of 22.5°C.

## 2.2. Planting material

Seeds of two dipterocarp species (*Dryobalanops lanceolata* Burck. and *Shorea leprosula* Miq.) were collected in September 1992 and germinated immediately in 4 cm × 12 cm polybags filled with forest topsoil. A small quantity of topsoil taken from around the mother trees was added to each pot to ensure mycorrhizal infection of seedling roots. Seedlings were kept in a nursery under two layers of neutral-density shade netting. Light intensity, measured using a light meter attached to a Parkinson leaf chamber (ACA LCA-3, Hoddestorn, UK), was approximately 280  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , equivalent to 25% of full direct radiation. Relative humidity, measured using a continuous chart recorder (Cassella, London), varied between a minimum of 50% at around 14:00 h and 100% at night. Mean monthly maximum and minimum air temperatures were 32 and 22°C, respectively.

Seeds of the two pioneer species (*Macaranga hypoleuca* Muell. Arg. and *Macaranga gigantea* Muell. Arg.) were collected in October 1992 and germinated on sand beds in full sunlight during December. When seedlings were about 2 cm tall, they were transplanted into 4 cm × 12 cm polybags containing forest topsoil. After transplanting, the seedlings were kept in a nursery under a single layer of neutral-density shade netting with a light intensity of approximately 830  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , equivalent to 70% of full direct radiation. The microclimate was approximately the same as for the dipterocarp seedlings. All seedlings were watered twice a day while kept in the nursery.

Ten days prior to planting in April 1993, the shade netting was removed from all seedlings. At the same time 3 or 4 seedlings of each dipterocarp species were selected randomly and the roots examined to verify the presence of mycorrhizal infection, which was confirmed for all seedlings.

## 2.3. Experimental design

The experiment was established using a randomised block design with four blocks. Each block was a log landing spaced between 0.5 km and 1.5 km apart. The area had been logged approximately 1 year previously,

but there was still no vegetation regrowth on any of the log landings. The experiment consisted of seven treatments replicated three times per block, giving a total of 21 treatment plots per log landing. Treatment plots, which were 2 m × 1 m in size and at least 0.5 m apart, were located randomly on the log landings, rejecting any coordinates which were located in erosion gullies. The seven treatments, which were assigned randomly to plots, were: (1) compacted soil; (2) compacted soil with fertilizer; (3) compacted soil with mulch; (4) dug soil; (5) dug soil with fertilizer; (6) dug soil with mulch; (7) replacement of topsoil.

In the compacted soil treatments the only disturbance to the log landing soil was the planting holes. For “dug” treatments the soil in the whole plot was turned over and broken up with a spade to a depth of 30 cm, 2 or 3 weeks before the seedlings were planted. In fertilised treatments each seedling received 100 g of rock phosphate, placed in the planting hole, and 40 g of granular fertilizer (12:12:17 N:P:K + micro-nutrients) placed in a ring about 10 cm from the seedling just below the soil surface to prevent loss through surface erosion. For mulched treatments, pieces of bark, which had been stripped from felled trees a year earlier, were used to cover the surface of the plot. For topsoil treatments, the soil was removed from the plot to a depth of 30 cm and replaced with soil taken from the top 0–30 cm in the adjacent undisturbed forest.

## 2.4. Planting

Seedlings were planted after three consecutive rainy days to minimise transplant water-stress. Four planting holes, approximately 20 cm × 20 cm × 20 cm, were dug per treatment plot, 50 cm apart and at least 25 cm from the plot edge. The seedlings were planted with minimum disturbance to the rootball. One seedling of each of the four species was planted in each treatment plot. After all the seedlings were planted, a 1-m-high fence was built around each group of 21 treatment plots to reduce browsing by deer.

## 2.5. Soil analysis

Soil samples were taken at the time of planting from each of the three compacted, three dug and three forest soil plots in each block. For bulk density and moisture content measurements, samples of known volume were

taken from 0–20 cm deep and results were calculated after oven-drying at 105°C to constant weight. Samples for chemical analysis were taken from 0–30 cm deep, as this was the depth to which soil was dug for the dug treatments, and all the samples from each treatment were bulked. The composite samples were air-dried and ground to 2 mm prior to analysing for organic carbon, total nitrogen, total phosphorus, available phosphorus (Bray) and pH using the methods described by Anderson and Ingram (1989).

## 2.6. Seedling assessments and data analysis

Seedling height and basal diameter were measured immediately after planting (Table 1) and again after 6 months, when crown diameter (diameter of all leaves and branches of the seedling) was also measured. Figures for basal diameter and crown diameter were calculated as the means of two measurements per seedling.

Two seedlings from each plot, one dipterocarp (*S. leprosula*) and one pioneer tree (*M. gigantea*) were harvested after 6 months. The other two seedlings were left in order to allow longer-term assessments of performance to be carried out. The above-ground portion

of the seedlings were cut off and the roots were then carefully excavated in order to harvest as much as possible of the fine root system. The extent and depth of the rooting systems were measured. Seedlings were oven-dried to constant weight at 70°C and the dry weight of the leaves, stem, large roots (> 2 mm) and fine roots (< 2 mm) were recorded.

In addition to harvesting the planted seedlings, all the volunteer plants in the plots more than 5 cm tall were also harvested and identified to family level.

The growth data for the seedlings were log-transformed prior to analysis because the data were skewed. Analysis of variance was carried out on log-transformed data for the six log landing soil treatments. A second analysis was made to compare the results from the forest soil treatment.

## 3. Results

### 3.1. Soil properties

Concentrations of organic-C and total-N at the soil surface on the log landings were less than half those in

Table 1

Initial mean height and basal diameter measurements (mm) for seedlings in each soil treatment. Means are not significantly different ( $n = 12$ )

Treatment	<i>Dryobalanops lanceolata</i>		<i>Shorea leprosula</i>		<i>Macaranga gigantea</i>		<i>Macaranga hypoleuca</i>	
	Height	Basal diameter	Height	Basal diameter	Height	Basal diameter	Height	Basal diameter
Compacted	405	3.6	311	3.1	122	2.5	94	2.1
Compacted + fertilizer	450	4.0	320	3.2	110	2.4	84	2.0
Compacted + mulch	467	4.2	332	3.2	105	2.4	90	2.1
Dug	432	4.0	346	3.5	99	2.4	91	2.1
Dug + fertilizer	410	3.9	307	3.2	102	2.4	83	2.2
Dug + mulch	397	4.0	298	3.3	110	2.9	81	2.1
Forest soil	425	4.1	343	3.5	108	2.6	92	2.1

Table 2

Average chemical properties of soils at the beginning of the experiment, prior to fertilizer addition

	Organic C (%)	Total N (%)	Total P (mg kg <sup>-1</sup> )	Soluble P (mg kg <sup>-1</sup> )	pH (H <sub>2</sub> O)
Compacted soil	1.27	0.07	123.2	1.01	5.0
Dug soil	1.47	0.09	123.4	0.98	5.0
Forest soil	2.70	0.23	177.8	2.27	4.7

Table 3

Bulk density and moisture content of soils. Each figure is the mean of 12 samples, three from each of the four blocks

	Bulk density ( $\text{g cm}^{-3}$ )		Moisture content (%)
	0 months	6 months	
Compacted soil	1.44	1.34	19.7
Dug soil	0.73	1.00	26.3
Forest soil	0.52	0.89	28.8
LSD ( $p=0.05$ )	0.15		4.90

the forest topsoil (Table 2). This reflects the rapid decrease in C and N concentrations down the undisturbed soil profile and the removal of most forest topsoil by the logging operations. The difference in total phosphorus between the forest and log landing soils is less marked as a consequence of a more even distribution of total-P concentrations down the soil profile. Available P, even in the forest soil, was almost at the limits of detection and was extremely low in the log landing soil.

The bulk density of the compacted log landing soil was around  $1.4 \text{ g cm}^{-3}$  (Table 3), compared with approximately  $0.9 \text{ g cm}^{-3}$  for undisturbed forest topsoil in the surrounding area (Nussbaum et al., in press). Treatments involving digging compacted areas or translocating forest soil initially reduced the bulk densities by about half. After 6 months the bulk densities of soils in these treatments increased to approximately  $1 \text{ g cm}^{-3}$ .

Table 4

Analysis of variance (ANOVA) for the effect of soil treatments on the growth of two dipterocarps (*Dryobalanops lanceolata* and *Shorea leprosula*) and two pioneer trees (*Macaranga gigantea* and *Macaranga hypoleuca*). *F* ratios are shown for the results presented in Figs. 1 and 2. The analysis excluded the forest soil treatment, which was analysed separately

	Relative height increment	Relative basal diameter increment	Crown diameter	Leaf dry weight	Stem dry weight	Large root dry weight	Fine root dry weight	Total dry weight
Pioneer or dipterocarp	333.9 ***	116.3 ***	14.6 ***	109.0 ***	ns	12.3 ***	49.3 ***	48.8 ***
Fertilizer	36.9 ***	130.9 ***	64.5 ***	117.9 ***	135.5 ***	149.5 ***	84.4 ***	147.8 ***
Digging	5.12 *	ns	3.90 *	ns	4.72 *	4.32 *	ns	4.05 *
Mulch	ns	ns	ns	ns	ns	ns	ns	ns
Block	ns	3.40 *	5.07 **	6.48 ***	3.35 *	4.70 **	3.11 *	5.56 **

\*  $p < 0.05$ ; \*\*  $p < 0.02$ ; \*\*\*  $p < 0.001$ ; ns = not significant.

The moisture contents of the forest soil and dug soil treatments (Table 3) were similar (28.8% and 26.3%, respectively) and significantly higher than that of the compacted soil (19.7%). Assessments were made after three rainy days and approximate to in situ field capacity.

### 3.2. Seedling growth

Results of the analysis of variance for tree growth are summarised in Table 4. Tree type (dipterocarp or pioneer) accounted for a major component of the variance of all growth parameters measured. Of the soil treatments, fertilizer had the largest effect, but there was a comparable magnitude of response in forest soil treatments, which were not significantly different from fertilizer treatments. Table 4 also shows significant block effects for some parameters, probably because of differences in herbivory, aspect, microclimate and light intensity, but their contribution to variance was relatively small. Interactions between block and main effects were not significant. Details of species responses are illustrated in Figs. 1 and 2.

Fertilizer application was the most important factor influencing seedling growth for all four species planted. The relative height increment of fertilized dipterocarp seedlings was two to three times greater than in similar unfertilized treatments, while the pioneer tree height increments were up to four times greater (Fig. 1). Relative basal diameter increment and crown diameter

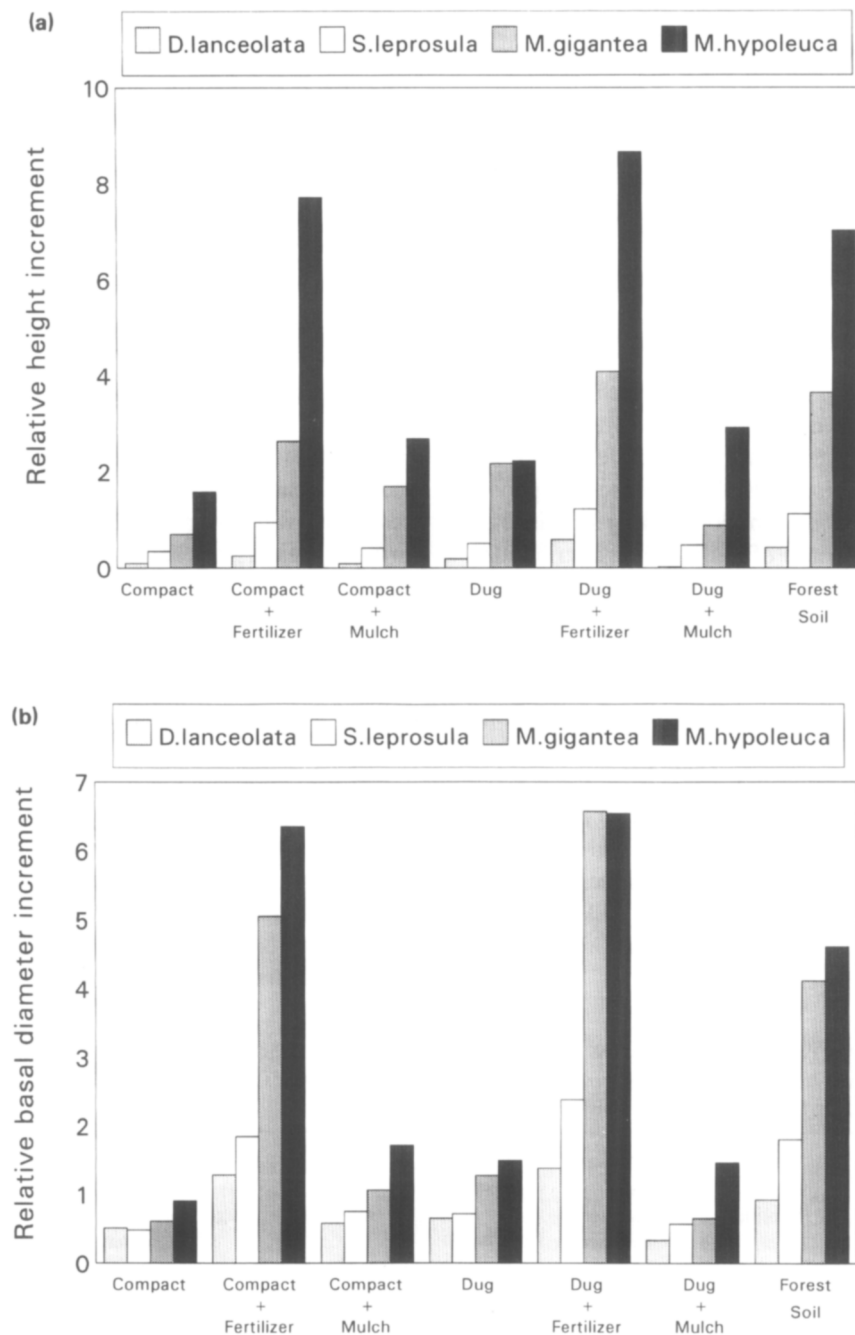
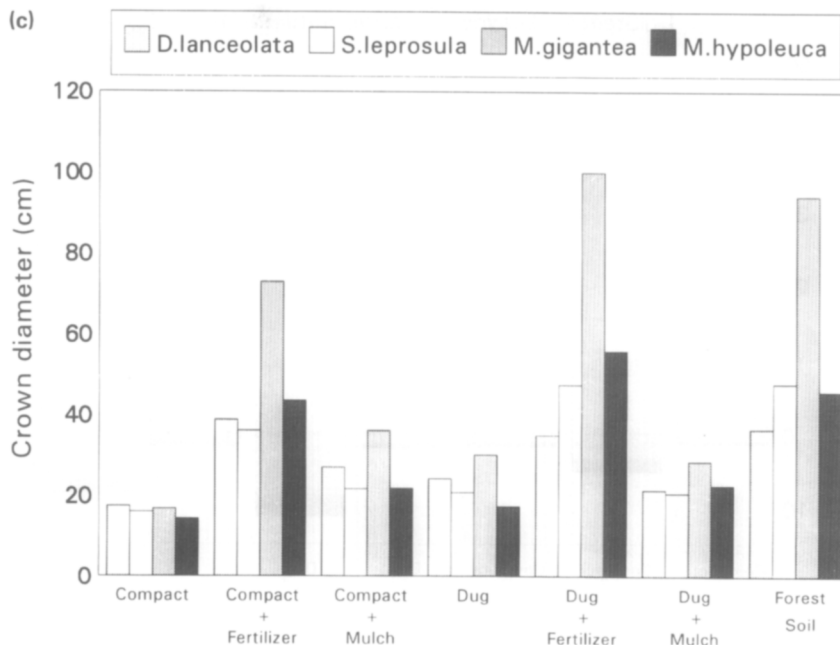


Fig. 1. Mean growth of seedlings of four tree species (*Dryobalanops lanceolata*, *Shorea leprosula*, *Macaranga gigantea*, and *Macaranga hypoleuca*) 6 months after planting in each of seven soil treatments ( $n=12$ ). (a) Relative height increment; (b) relative basal diameter increment; (c) crown diameter.

were similarly increased by fertilizer addition. These results were even more clearly reflected by the dry weights of the harvested seedlings. The mean dry

weight of the *Macaranga gigantea* and the *Shorea leprosula* seedlings in compacted soil without fertilizer were 4.18 g and 3.67 g, respectively (Fig. 2). After the



addition of fertilizer the mean dry weight of the *M. gigantea* seedlings was 36 times greater, while that of the *S. leprosula* seedlings was eight times greater than the weight of unfertilized seedlings.

The effects of reduced soil compaction on seedling growth were less pronounced. There was a significant 1.5–2-fold improvement in height and crown diameter growth of seedlings in dug treatments, but basal diameter increments were not significantly improved. The two species harvested, *S. leprosula* and *M. gigantea*, both had significantly greater mean dry weights in dug than in compacted soil, with increases of three and nine times, respectively. Of the separate plant components, only stem and large (> 2 mm) root dry weights were significantly improved by digging.

Mulching slightly improved growth of seedlings in compacted soil but tended to reduce seedling growth in dug soil. The dry weights of the mulched seedlings on compacted soil were as much as three or four times greater than those without mulch, but this difference was not significant.

The performance of seedlings planted in forest topsoil was very similar to that of seedlings planted in fertilised log landing subsoil. In general, the growth of seedlings in the dug with fertilizer treatment was somewhat better than that of the seedlings in topsoil, but not significantly so.

Large differences in the performance of the tree types and species were observed. The relative height and basal diameter increment and the crown diameter of the two pioneer tree seedlings were up to seven or eight times greater than those of the two dipterocarp seedlings. Of the two dipterocarps, *D. lanceolata* grew more slowly than *S. leprosula*. Between the two pioneer tree seedlings, *M. hypoleuca* had the most rapid height and basal diameter growth, but the crown diameter of *M. gigantea* was almost twice that of *M. hypoleuca*.

The dry weights of the pioneer tree species harvested (*M. gigantea*) were also greater than those of the dipterocarp species (*S. leprosula*). For the seedlings grown in compacted soil this difference was slight, as the mean seedling weight for both species was less than 5 g. However, in the dug treatment the dry weight of *M. gigantea* was three times that of *S. leprosula*, while seedlings of *M. gigantea* from the dug plus fertilizer treatment had a mean dry weight of 250 g, more than five times greater than the 47 g mean dry weight of the *S. leprosula* seedlings. The root mass of *M. gigantea* was about five times greater than that of *S. leprosula* (Fig. 2), with the greatest responses for both species in the dug plus fertilizer treatment. *M. gigantea* also showed the greatest extent of root development, with fine roots within 20 mm of the soil surface extending up to 0.8 m from the plant, well beyond the margins of

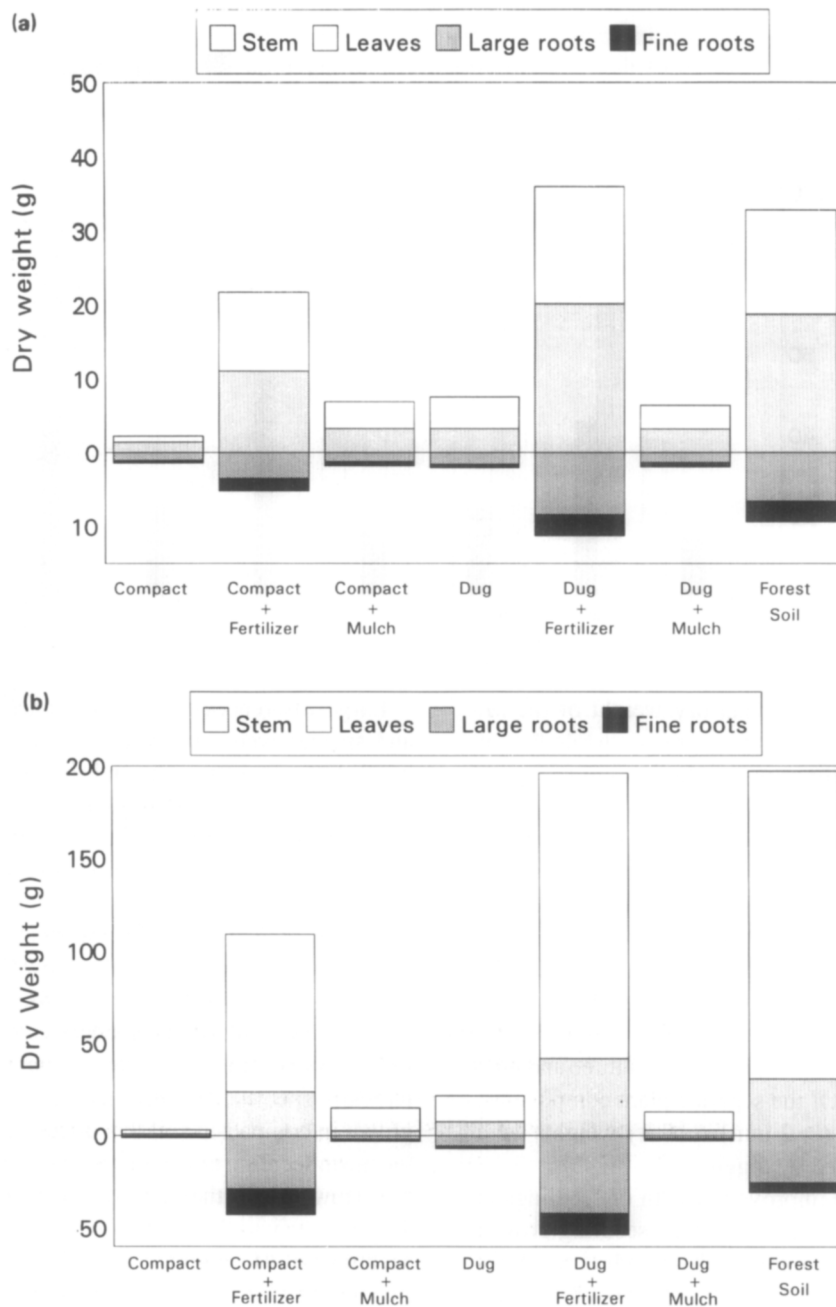


Fig. 2. Dry weights of 6-month-old seedlings of (a) *Shorea leprosula* and (b) *Macaranga gigantea* showing leaf and shoot dry weight above the 0 line and large ( $> 2$  mm) and fine ( $< 2$  mm) root dry weights below the line. Note that the scale for *M. gigantea* is four times that of *S. leprosula*; ( $n = 12$ ).

the treatment plot. *S. leprosula* showed less extensive root development, which did not extend beyond the treatment plot after 6 months.

### 3.3. Volunteer plants

The number of volunteer plants growing in the forest topsoil plots was much greater than for any other treat-



Table 5

Numbers of volunteer plants greater than 5 cm tall harvested from the 2 m × 1 m experimental plots for each soil treatment after 6 months. Each figure is a sum for all 12 plots with the same treatment, three from each block

Treatment	<i>Macaranga</i> spp.	<i>Neolamarkia</i> <i>cambada</i>	Other pioneer trees	<i>Hopea</i> <i>oderata</i>	Grasses and sedges	Ferns	Vines	Herbs	Total pioneer trees	Total seedlings
Compacted										0
Compacted + fertilizer				2	2	1		9		14
Compacted + mulch	1		1			1	1	8	1	12
Dug	1							2	1	3
Dug + fertilizer				1	13	3		8		25
Dug + mulch			1	4	1			2	1	8
Forest soil	35	48	14	5	35	119	41	74	97	371

ment (Table 5). The average number of volunteer plants > 5 cm tall per square metre of log landing soil over all treatments was 0.44, while for the forest soil plots it was 15.4 plants m<sup>-2</sup>, a factor of 35 times greater. In the forest soil plots approximately 27% of the volunteers were tree seedlings while 63% were other species, mainly grasses, sedges, ferns, vines and herbs. In the landing soil plots the ratio was lower, with only 17% of the volunteers being tree seedlings, and even fewer (4%) pioneer tree seedlings. There was some variation between non-forest soil treatments, with a greater number of seedlings found in the dug, fertilised and mulched treatment plots than in untreated compacted soil, but the total numbers of plants were too low for analysis.

#### 4. Discussion

The performance of seedlings of all four tree species was dramatically improved by the addition of fertilizer. Sundralingam (1983) and Bruzon (1982) both reported that fertilizer increased the growth of dipterocarp seedlings grown in forest topsoil or potting mixture in pots. Other studies, such as those of Turner et al. (1993) and Ang et al. (1992), did not show any significant improvement in growth of dipterocarps after fertilizer application. There are several possible explanations for this. Firstly, when seedlings are grown in shaded conditions, as in the study of Turner et al. (1993), light rather than nutrients may be the primary factor limiting growth, so that seedlings are unable to respond to increased nutrient availability. Secondly, the rates of fertilizer application in the studies of both

Turner et al. (100 mg each of N, P and K per plant) and Ang et al. (1.44 g organic N, 0.5 g P and 1.3 g K per plant) were considerably lower than our rates of 4.8 g, 2.1 g and 4.7 g of N, P and K, respectively, per plant. It is possible that these low rates of additions did not exceed losses due to leaching, denitrification and immobilisation, and hence available nutrients did not meet plant requirements. Finally, all of these studies were on different species of dipterocarp seedling. It is likely that there is considerable variation in the physiology of different dipterocarps (M. Barker, personal communication, 1994) which may explain differences in their responses.

Our observation that pioneer tree seedlings responded more strongly to fertilizer than the dipterocarps is also supported by Turner (1991). This may reflect the more rapid growth habits of pioneer trees, which allows them to respond more quickly to available nutrients (Chapin et al., 1986). Another factor selecting for growth response to fertilizer may be the smaller size of pioneer tree seeds, which do not provide any store of nutrients for the emerging seedling, unlike the larger dipterocarp seeds (P. Grubb, personal communication, 1994).

Soil compaction did not appear as a major factor limiting early seedling growth. This is probably because, during early growth, the structural roots of the seedlings were largely confined to the looser soil in the planting hole. As seedlings get larger and their root systems expand beyond the planting hole, soil compaction is more likely to become a constraint to growth, as occurs in plantation forestry (Whitmore, 1991). Soil compaction also inhibits the process of re-establishment of natural regeneration (Pinard et al., in press).

Mulching of compacted soil resulted in only a slight improvement in seedling growth suggesting that, in the absence of additional nutrients, neither low soil moisture nor high soil temperatures were major limitations to seedling growth. In the dug soil, mulching resulted in reduced seedling growth. This was probably the result of waterlogging of the soils, which was apparent from the extensive gleying, typical of the anaerobic conditions of waterlogged soils, which was observed when harvesting seedlings after 6 months.

The results of our study have shown that these two species of dipterocarp seedlings, when provided with adequate nutrients, grew well in full sunlight. Dipterocarps have tended to be classified as intolerant of full sunlight during establishment. However, there is growing evidence that seedlings of many species of dipterocarp are able to survive and grow in high light conditions (e.g. Wan Razali Wan Mohamed and Ang, 1991; Ang et al., 1992). Physiological studies on dipterocarp seedlings suggest that there are significant differences between species in rates of photosynthesis and transpiration under shade and in the open (Ang et al., 1992; M. Barker, personal communication, 1994), hence tolerance of high light intensities may be species-specific.

This study was not set up to investigate the importance of the soil seed bank versus seed rain as a source of seeds for natural regeneration. However, the harvesting of volunteer plants after 6 months yielded interesting results. On the log landing soil plots the number of plants was extremely low, while in the forest soil plots large numbers of volunteer plants appeared. This suggests that the soil seed bank in the forest topsoil was a much more important source of seeds than incoming seed rain, particularly for pioneer tree seedlings. The appearance of many pioneer tree species in the forest topsoil plots suggests that topsoil replacement as a means of rehabilitation has the advantage of simultaneously improving the soil and providing natural regeneration. Alternatively, logging practices can be modified to minimise the disturbance and loss of topsoil. A potential disadvantage of this treatment was the large number of weed species, such as grasses, sedges, ferns, annual herbs, vines and creepers, which would compete with the pioneer tree seedlings.

In conclusion, we have shown that nutrient availability is a major factor limiting the establishment of tree seedlings on degraded soils. Seedlings of pioneer trees

showed the largest response to fertilizer, but the two species of dipterocarp also showed good growth in full sunlight when fertilised. The results from this study are already being used as the basis of a rehabilitation programme for degraded areas in Sabah, part of a larger replanting project in logged-over forest (Pinso and Moura Costa, 1993).

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