VIII. DIPTEROCARPS AND MYCORRHIZA
An ecological adaptation and a factor in forest regeneration

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Summary

Each dipterocarp has its own species of fungus, forming an ectomycorrhiza. From literature and experiments (in East Kalimantan and in vitro) ecological consequences are explored. These help explain the clumping of dipterocarp trees in the forest, the lack of hybrids, the poor dispersal, and speciation as dependent on the viability of the root-fungus combination on a particular soil type.

Mycorrhizas are located in the top soil. They are extremely sensitive to increase of soil temperatures as occur after canopy opening, and to soil compaction by machinery and log skidding. This explains the setback of dipterocarp growth after crude logging.

It is suggested that avoidance of soil compaction during logging, quick restoration of soil cover, and the use of fungus-inoculated seedlings for enrichment planting are important consequences for forest management.

Key words: Dipterocarpaceae, ecology, enrichment planting, logging, management, mycorrhiza.

Mycorrhiza

Mycorrhizas are intimate and mutually advantageous symbiotic associations of roots and fungi. They are nearly universal in terrestrial plants, and can be classified into two major groups: endomycorrhiza and ectomycorrhiza. Endomycorrhizas have been observed in some 200 families and more than a thousand genera (see reference 1). Endomycorrhizas are formed with c. 30 morpho-species of 'phycomycetous' fungi, which are ubiquitous in distribution and physiologically unspecialized. The fungus penetrates roots to form characteristic intracellular vesicles and arbuscles. This is the principal difference with the other major type, the ectomycorrhiza, where the fungus does not penetrate living cells but, instead, only surrounds the cells of the root outside the endodermis. Mycelium grows between the cortex cells of the roots and can be seen on longitudinal sections as the 'Hartig net'. Often the epidermis cells show alterations in their structure and may look similar to palisade parenchyma in a leaf. The mycelium of an ectomycorrhiza extends from the roots outward into the soil. Many more facts are given in (2).

Ectomycorrhizas are unknown in monocots. Cooke (3) estimates that about 3% of all plants form ectomycorrhiza, mainly forest trees like

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Betulaceae, Cupressaceae, Dipterocarpaceae (subfam. Dipterocarpoideae), Fagaceae, most species of Myrtaceae, also Pinaceae, Salicaceae. The roots of ectomycorrhizal trees support a wide spectrum of fungal symbionts, probably amounting to more than 5000 species worldwide.

Ectomycorrhizal forests are generally temperate or occur on infertile soils in the tropics, as those described by Janzen (4). In most cases, ectomycorrhizal symbiosis is obligatory. The ectomycobiont is often specific to one or only a few root partner species. The latter have the capacity of forming consortia with a wide range of mycobionts, usually simultaneously, so that individuals occurring side by side may avoid direct mutual competition. The plants appear to take up mycobionts selectively, according to developmental phase, ecological conditions and possibly climatic fluctuations (1). Dipterocarpoideae seem to be a special case among ectomycorrhizal species and have not yet been investigated extensively.

Through the ectomycorrhizal combination several functions are fulfilled, as described in (5). The transfer of carbon compounds from the higher plant to the fungus is one of them. A main function of the fungus seems to be the uptake of nutrients, especially phosphate. Melin & Nilsson (6) showed by means of isotopes that phosphorus, calcium, &c are transported in the fungal hyphae to the mycelium layer around the root, which might be able, because of its close contact, to transfer them fast and efficiently to the root cells. It is, however, not known yet how these processes work. Besides phosphate, an increased absorption of compounds of K, S, Sr, and Zn by mycorrhizal plants has been shown experimentally (7). Some reports also mention increase of N, Na, and other mobile elements, but this may be related to an overall increase of the metabolism of the plant following the increased uptake of P. The response of the plant partner can be enormous, especially on poor soils. Much work has been done with pines by various authors like Mikola (8), Marx (9), and others. Sometimes the beneficial effect of inoculation with ectomycorrhizal fungi can be substituted by application of fertilizer, especially phosphate (9).

Another function of ectomycorrhiza, besides nutrient uptake, may be protection against pathogens. Zak (10) postulated several mechanisms by which ectomycorrhiza may afford protection from disease, to the feeder roots of plants. He suggested that ectomycorrhizal fungi may

a. utilize surplus carbohydrates in the roots, thereby reducing the amounts of nutrients stimulatory to pathogens,

b. provide a physical barrier, in this case the fungal mantle, to penetration by the pathogen,

c. secrete antibiotics inhibiting pathogens,

d. support, around the root, a protective microbial rhizosphere population.

In addition, Marx (11) suggested that

e. metabolites produced by symbiotically infected cortical cells of the host may also function as inhibitors to infection and to the spread of pathogens in ectomycorrhizal roots. He showed that over 100 species of ectomycorrhizal fungi were found to produce antibiotics.

Slankis (12) found that some ectomycorrhizas produce auxins, cytokinins, gibberellins and growth-regulating vitamins as well. Allen et al. (13) found cytokinin production by the fungus Bouteloua gracilis. Kondas (14) mentions ectomycorrhizal fungi to produce growth-regulating B-vitamins, besides hormones.

Some reports mention mycorrhizal plants to be more resistant to drought or higher temperatures. Bowen (7) cited as reasons for drought resistance, that the fungal growth into a soil may increase the rate of water movement to the root, especially in sandy soils with low moisture and poor root densities, since hydraulic conductivity of soils may fall by a factor 5-10 between field capacity and wilting point, and in such soils this transport factor may become limiting with regard to the water uptake. Fungal growth into soil may give greater opportunity for 'root'-soil contact, compensating for any separation between roots and soil in times of drought. Probably the most important factor (7) might be that mycorrhiza could increase absorption of ions which are relatively highly mobile in saturated soils but much less so in unsaturated soils. Some ectomycorrhizas can grow at much lower water potential than higher plants suffer (15), and thus make a significant contribution to water uptake by the root in some soils.

Janzen (4) discussed another possible function of mycorrhiza. He claims that an association with phenolic-resistant mycorrhiza might be one of the possible specializations for a tree with phenolic-sensitive root hairs. Plants that shed litter containing large amounts of phenolics and other secondary compounds onto their roots may need mycorrhizal associations to avoid self-intoxication.

Bowen (7) reviews knowledge about the influence of mycorrhiza on nutrient conservation and mentions examples that prove mycorrhiza to compete with other micro-organisms for fresh litter compounds. All these arguments point to mycorrhizas as one of the major factors in the recycling system of the tropical rain forest.

Dipterocarpaceae

This family, which currently yields 25% of the tropical hardwood trade volume (16), is concentrated in west-Malesia. Commercially the wood is known as meranti, keruing, kapur, and bangkirai. In undisturbed primary forest in Borneo and Malaya these trees can form 80% of the upper canopy.

Natural regeneration of dipterocarps in logged-over forest is disappointing, particularly when the logging has been intensive. Artificial regeneration is also problematic since large seed crops are produced at irregular intervals once every 5-13 years, efforts to transplant seedlings often fail, and vegetative propagation is difficult, although Srivastava (17) and Smits (18) obtained good results recently. Ashton (19) who ably summarized previous work in addition to his own, confirms the general absence of dipterocarps in secondary forest in the non-seasonal zone. He attributes their poor colonizing powers to poor dispersal combined with sensitivity to water stress during early stages.

There are many indications indeed that dipterocarps need light shade at least to grow up, until they become light-demanders (20); in my estimate this takes 8-10 years. Plantation trials, too, reveal that seedlings of dipterocarps do not thrive well in the open (21, 22): many become soon chlorotic and die. It was also found (23) that after logging only 13.7% of the original seedling stock survived in primary forest, which is less than the logging can have directly afflicted. Shade is therefore a critical factor for young dipterocarps.

Seeds of dipterocarps are heavy and large and their wings which look adapted to wind dispersal, are of little value in the quiet zone near the equator. This feature may indicate an origin from other regions (24). The dispersal strategy of the dipterocarps is short-distance; seeds fall near the mother tree (19, 25). However, gushes of wind may take up seeds farther which eventually may lead to sporadic outcrossing and spread of genes in a population (24). In general, seeds dispersal is confined to a small area around the mother tree. Dispersal by water can be ruled out; in fact, a method to select viable seeds is to see whether they sink in water. Exceptions may be Vatica wallichii seeds which can float for 22 days, and those of Shorea seminis (Isoptera borneensis) which can float for 60 hours (25). Rivers, even small ones, form important barriers for dipterocarps (24).

De Vogel (27), who made a classification of seedling types, confirmed that seeds of primary forest trees mostly have a considerable reserve of food (his types 2, 6, 7 and 11). The Sloanea-type, his 2, and the Heliciopsis-type, his 6, are those with a persistent food reserve, and to these the dipterocarp seedlings belong. De Vogel states that seedlings of those types mostly do not thrive well in exposed places, but have a much better chance to survive under dense cover than other types. This, by the way, confirms Merrill's conclusion (25) that the Philippines during the late Tertiary must have been completely under forest. Obviously this feature of dipterocarp seeds favoured the spread of this young family.

An interesting passage in De Vogel's work (p. 27) reads: "Some big-seeded genera such as Shorea, Hopea, Dipterocarpus, etc. .... show a germination pattern which can even cause the death of the seedlings under adverse circumstances. The fruit is provided with large wing-like projections which represent the persistent sepals that keep the fruit tip pointing more or less oblique to above. On germination, the hypocotyl and root emerge from this tip and have to turn a relatively large semi-circle to reach the soil. In this process they are often hampered by the wing-like projections. For a prolonged period the root is then free in the air, and a dry spell will result in the loss of the majority of a germinating seedcrop. Apparently a germination like this can only have developed under constant everwet conditions." See De Vogel's figures 66a, 67a, 71a, 72a, and plate 9.

The gregarious flowering of dipterocarps is well known. Once in about 5-13 years after a more or less pronounced dry period, they produce a large seed crop that results in a dense layer of seedlings under the mother tree (28, 29, 30). This strategy has been interpreted by Janzen (4) as a mechanism to escape from seed predators. When dipterocarp trees grow up and approach adulthood, they produce some big branches which extend quite far horizontally (30), and show conspicuous crown reiteration. Thus the spreading of the crown at the time that flowers and fruits appear for the first time may result in a better light supply for the tree's own seedlings underneath.

Flowering does not necessarily start at ages of 40 or more, as is often stated. In virgin forest this is approximately the time needed by the dominating tree species to reach their customary height, and therefore the time of first flowering. A plantation trial with Shorea leprosula showed that the trees at an age of 15 years all flowered after a drought period and produced a dense carpet of seedlings under their crowns (20). There are reports of flowering at even younger ages, but no viable seeds were produced then (32, 17).

From all these aspects of dipterocarp ecology, one important conclusion can be drawn: dipterocarps belong to the primary forest formation, and they are completely adapted to the micro-climatic conditions in undisturbed forest. In this paper we will show that the mycorrhiza of dipterocarps are another adaptation to the shaded, humid conditions under a closed forest cover, and offer a neat explanation of many features of dipterocarp ecology.

The role of the symbiosis

The ideas and views now to be set forth evolved from experiments on vegetative propagation in vitro and in vivo of Shorea cf. obtusa. Work was begun at the ITCI (Weyerhaeuser) concession NW. of Balikpapan in East Kalimantan, and continued in the Horticulture Department of the Agricultural University Wageningen, the laboratory of the Dorschkamp at Wageningen, supervised by Mr. P. Evers, and at the Institut de Botanique, Strasbourg, France, as far as the in vitro experiments were concerned. Experiments in vivo (stem and leaf cuttings) were conducted in the greenhouse of the Silvicultural Department of the Agricultural University Wageningen. The results were combined with facts from literature and observations made in logged-over forest in Indonesia.

The seedlings of Shorea cf. obtusa that were used in our experiments germinated normally and produced several healthy-looking leaves. Subsequent leaves, however, became more and more yellowish except for some small zones along the main nerves. Growth retarded until no more new leaves were produced. Because it was thought that lack of mycorrhiza accounted for the standstill, fertilizer with extra phosphate was added to the soil but this did not help. Neither was there any difference between plants under different light intensities. Soil with mycorrhizal roots of Fagus sylvatica and Quercus robur was added, but to no avail. Some soil with ectomycorrhizal roots of some dipterocarps from close near the place where the seeds were collected was also added, and some ectomycorrhizal roots of Pinus sylvestris, but this resulted only in the death of many seedlings due to transplanting. Some rooted cuttings that were transplanted in soil mixed with the mycorrhizal roots of the mother tree, however, did produce mycorrhiza and started growing normally without deficiencies. Average height difference between cuttings with and without mycorrhiza was 40 cm, 8 months after inoculation. A seedling of Dipterocarpus grandiflorus, brought to Holland with some soil, grew very well and proved to have abundant mycorrhiza. But inoculation with roots of this plant did not result in any change in the growth of Shorea cf. obtusa seedlings.

After several trials it was found that the pigmented roots of dipterocarps can best be stained with the second method of Phillips & Hayman (33), when roots are kept in a 10% H_2O_2 solution for 40 minutes. Riess & Rambelli (34) found that fixation of root tips was done best in glutaraldehyde with pH 7.2. They used 7.2 ml of glutaraldehyde (25% solution), 15.0 ml of phosphate buffer (pH 7.2), and 37.8 ml of distilled water, together 60 ml. After staining the roots, the seedlings of Shorea cf. obtusa turned out to be non-mycorrhizal, as already could be expected from the appearance of their roots.

Even more important was the conclusion that no pathogen caused the stunted growth of the seedlings. The fact that inoculation could only be effected with roots of the mother tree may indicate that specific fungi are needed, or that temperature or other circumstances had prohibited infection with the seedlings. Since D. grandiflorus and some other Shorea species which do have ectomycorrhizal roots thrive well in the same environment, it may be expected that environmental conditions were right. We therefore assume that different dipterocarps have different fungal symbionts, as usual with ectomycorrhizal plants (1). This is in agreement with investigations on dipterocarp mycorrhizas so far. A wide variation of fungal symbionts has been found (see 35, 36, 37, 38).

During the in vitro experiments, the reaction of axial explants of Shorea cf. obtusa was found to be similar to that of the cuttings without mycorrhiza in the vegetative propagation trials. Almost no new shoots developed from the buds, and when they did, the few yellowish leaves dropped very soon. When vitamins were added to the medium, including vitamin B, the deficiency disappeared, and newly produced leaves looked healthy and persisted (39). This made us think of dipterocarp mycorrhiza being responsible for the production of a growth-regulating vitamin B, as has been found for other ectomycorrhizal associations (14). Half the number of seedlings was then treated with a vitamin B solution (10^{-4}) sprayed on the leaves once a week for 6 weeks. The seedlings reacted very well, starting to produce new leaves which were dark green like the first ones produced after germination. Stem elongation seemed to be hampered, however. Probably more substances are necessary to regain normal growth, and vitamin B seems to be one of them.

Considering the above facts, we concluded that probably most Dipterocarpoideae are obligately mycorrhizal and that they take up their fungal partners selectively.

Malloch et al. (1) think it difficult for ectomycorrhizal plants to extend their area, possibly due to the need of combined seed and fungus-dispersal, and dipterocarps seem to illustrate this. When seeds have been produced at their long intervals, the right combination of spores — often four types per species of fungus — must land at less than 1 mm from each other near the seedling in the right stage, under the right temperature and humidity, if they are to germinate, fuse, and start mycelium growth. Even while many spores are produced, airborne infection of dipterocarp seedlings seems a highly improbable event, especially at greater distances from the mother tree.

This might explain why dipterocarps often occur in clumps (23), with their seedlings nearby: the specific mycorrhiza is already there. Besides, it has recently been established (35) that in some plant species a mother individual is connected to its seedlings by means of hyphae and that substances are transported from the mother tree to its seedlings through them.

Other features of Dipterocarpaceae can be explained on this basis, too. The morphological characters of dipterocarps are very constant across the whole island of Borneo; Ashton (23) attributes this homogeneity to a selection against hybrids. The highly specific relationship between dipterocarps and fungi might well be one factor in this selection (although there is some genetic variation between trees in relation to distance: 38). Long evolution under stable conditions, which allowed the ecosystem to differentiate into smaller ecological units or niches (23), would also involve symbiosis as an important factor in dipterocarp speciation, resulting in rather isolated communities.

According to the Founder Principle, new species, and also new symbiotic associations, evolve under different local selection pressures in isolated populations. The inability of subsoil mycelium to cross even the smallest rivers enhances the isolation of populations. Ashton (39) has suggested a relation between the differences in species composition and phosphorus levels on the one hand, and the mycorrhizal status of dipterocarps on the other. We assume that the fungus of a mother dipterocarp tree is well-adapted to the conditions on its site. Seedlings outside its range have to find another fungus and during development face heavy selection pressure. But when by accident a seedling would contract a better-adapted fungus, it would grow more vigorously, become more competitive, and so would be its seedlings. Thus in the long run, this new combination of dipterocarp and fungus will replace the former one, until a still more successful combination comes up: the latter might be called an ecological mutation. During the long existence of the dipterocarp forests, all trees may be expected to have eventually developed viable symbioses with fungi. This, too, seems to have been an important factor in the clumping of dipterocarps and in their speciation mechanism described by Ashton (23).

To understand other features of dipterocarp forests, especially their reactions on logging, we first take a closer look at the reproduction cycle of the Dipterocarpaceae, and describe the combined life cycle of fungus and tree in the undisturbed forest. After the seed has fallen, it starts germinating and a root penetrates the soil. Melin & Nilsson (6) described the infection process as follows. Exudates of the young root are diffused into the soil and activate the fungus — that we presume to be available as the seed falls close to the mother tree — to start mycelium growth towards the root. The fungus then surrounds the root and infects young lateral rootlets as they develop. They infect the layer of cortex cells and form the dense layer which is characteristic of ectomycorrhiza. These laterals are thickened, remain short, and have no root hairs. The seedling, sapling, pole, grows very slowly until the canopy overhead is opened. This results in vigorous growth and an increased supply of carbohydrates for the fungus which stimulates it to higher activity; this again is beneficial to the plant. The young dipterocarp tree grows up in slender habit, until it starts spreading its branches and produces its first crop of seeds.

Temperature must play a role in this, and fungi are known to be highly sensitive to this factor. Harley (40) mentions that temperature — as related to the intensity of light reaching the ground — thus influences the kind of fungus that can infect the roots, related both to the carbohydrates supplied by the plant and the soil temperature. Marx et al. (41) found that the vigour of different fungi varies with the temperature. Meyer (42) mentions that ectomycorrhizal plants appear to take up fungal associates selectively, according to developmental phase, ecological conditions, and possibly fluctuations of climate.

The influence of logging on mycorrhiza

We will now try to relate the effects of logging to the sensitivity of the fungal population in the top soil to alterations in temperature and density. The felling of trees and skidding of logs brings well-known major disturbances to the virgin forest. The influence which these might have on mycorrhizas — and, along with this, on the movements of nutrients — seems to have been little explored as a subject of concern.

Of the physical changes caused by logging, the first, most obvious one is the increase of light that reaches the soil. Although there are also increases when an old tree falls down and opens the canopy, this cannot be compared with the degree of opening during logging, especially when it is done intensively in high timber stands. Figure 1 shows diagrammatically what happens if a senescent tree falls down. At point I the trees below it are little damaged and will fill the gap very soon. Saplings and poles below a dipterocarp tree of the same species can be expected to do this, hence species composition will remain very much the same in here. Neither is the micro-climate seriously disturbed in this place. At point II, however, the crown of the fallen tree has crushed many trees where it fell. The increased light that reaches the soil stimulates the germination of seeds belonging to the secondary forest formation, which are already dormant in the soil (23). Seedlings very quickly cover the soil with vegetation and stabilize its temperature. Under the layer of secondary species, dipterocarp seeds can invade from around. As a result of logging, the canopy is removed over more than 50% of the area (personal observation, confirmed by aerial photographs), and the soil below is exposed to direct sunlight. Such increase in light intensity affects almost 100% of the area in logged-over forest. The increased radiation reaching the soil results in a higher soil temperature, particularly in the top 30 cm. Harley (40) mentioned that most ectomycorrhizas have their temperature optimum between 18 and 27°C. This is also stated by Marx & Krupa (43), who indicate that growth of most mycorrhizas stops below 5° and above

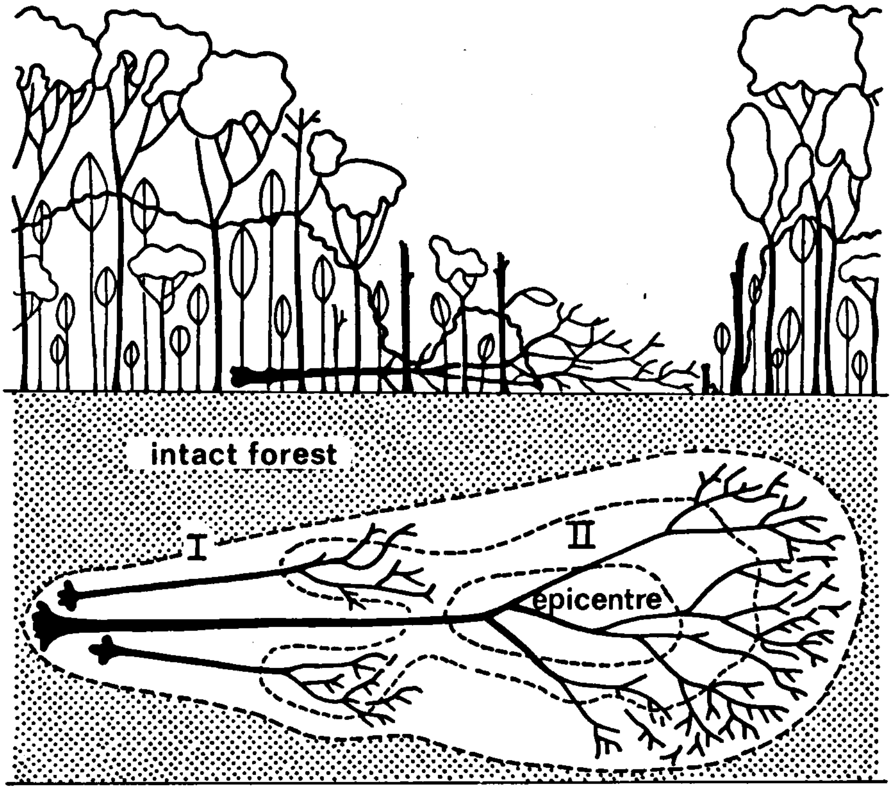

Fig. 1. Senescent tree fallen down. Drawn after a figure in a paper by Oldeman, Rev. Ecol. Appl. 28 (1974).

35°C. Limonard (pers. comm.) mentioned that temperatures approaching 50° are lethal to almost all mycorrhizas.

Under dense cover, as in the intact tropical rain forest, the temperature of the top soil is an almost constant 27°C, buffered by the vegetation overhead. This is about the same temperature as the average one of the air in the understorey (45, and personal observation). Schulz (45) and also Sanchez (46, p. 123) mention that when a forest is cleared, the soil temperatures increase by 7-11°C because of the higher solar radiation. This accelerates decomposition of organic matter, and in some cases adversely affects soil structure (47). Since organic matter content of the soil influences fungal activity (48), a double effect on the mycorrhizas will make itself felt, directly through heat and indirectly through decrease of humus. Big changes will thus occur, and they are likely to last a long time even when a secondary forest has covered these formerly exposed places. Dwivedi & Dwivedi (49) found that ecological activity of fungi in secondary forest was lower than in older forest soils.

It thus becomes clear why dipterocarps are so extremely scarce in secondary forest. Given the low migration speed of plants and fungi, it will take a long time before the original species composition has been restored. Summarizing: a higher top soil temperature induced by opening of the canopy has a negative effect on the growth of ectomycorrhiza, or may even cause their death (50). At least, the temperature can be expected to influence the composition of the fungal population in the soil, and probably warmth-adapted fungi will take advantage of the higher soil temperatures, and decomposition of organic matter by bacteria will be accelerated. Living conditions for dipterocarps are thus seriously affected.

In areas with less intensive logging, where disturbance does not exceed by 10 times the number of trees that fall as a result of natural senescence, the forest is expected to recover, starting from undisturbed patches. In such a way the original species composition is gradually built up again. This was indeed found for an area 40 years after logging when only a few stems were removed (50). If logging is done intensively, much of the disturbance is expected to be irreparable or will last for centuries.

Ashton (20) explains the death of many trees which were isolated by felling operations as a result of water stress. However, I have seen big Shorea leptoclados trees in exposed places with sufficient water supply that were still slowly dying. Halting growth of dipterocarp forest after logging and low survival of seedlings may not be the result alone of wounds — by which pathogens may enter causing rot and leading to poor quality of the wood later — and logging damage: death of the mycorrhizal fungi may be another major cause of this.

Soil compaction is of special intensity on the skidroads below the caterpillar tracks. When a bulldozer has passed the same skidroad several times, the soil gets seriously compacted. Effects of bulldozer clearing on bulk densities of the soil are shown in the diagram (fig. 2). Bowen (7) mentions that when a soil was compacted from bulk density 1.2 g/cm^3 to 1.6 g/cm^3, mycelial growth was reduced by 90% and this is expected to reduce nutrient uptake by mycorrhiza considerably. Root growth almost stopped when bulk density increased from 1.50 to 1.65 g/cm^3 (46). Dwivedi & Dwivedi (49) showed that fungal activity in a Shorea robusta forest is mainly confined to the upper 15 cm. Griffin (48)

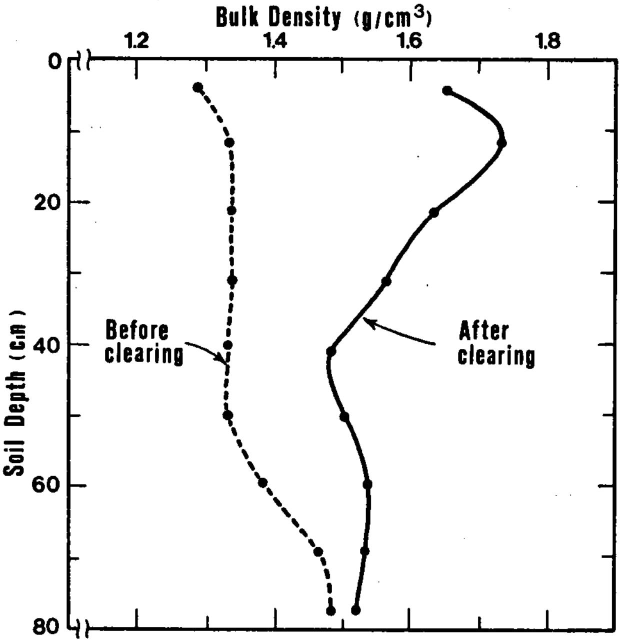

Fig. 2. Effect of bulldozed clearing on bulk density. Copied from Sanchez (ref. 46), original source Van der Weert (1974).

proved that the number of fungal propagules within a soil sample is positively correlated with organic matter content and so is highest in the surface horizon and lowest in the B horizon. When we combine these facts and look again at the diagram, we see that the heaviest soil compaction is found in the upper 20 cm, just where the fungal activity is highest. Moreover, this compaction is of such a degree that growth of roots as well as of mycelium is hampered. Germinating seeds of the primary forest formation run a high risk of desiccation, since canopy opening also results in lower air humidity. Their roots grow badly in the compacted parts, their exudates will be less efficiently diffused and there will be less response by the fungus.

Conclusion

Dipterocarps, as we have seen, are in all aspects primary forest species and should be treated accordingly. If we agree with the theory presented in this paper about the role of mycorrhiza in the ecology of dipterocarps, the problems about enrichment planting are clarified, and dipterocarp silviculture assumes hopeful perspectives.

Starting from the proven importance of ectomycorrhiza for the regeneration of dipterocarps, we can develop a system that complies with their needs. First, it will be necessary to maintain or restore the original microclimate near the soil. Second, methods must be developed to inoculate dipterocarp seedlings with the right fungi, enabling them to grow independently of the mother tree. As soon as the trees become light-demanding, the canopy could be opened cautiously. This system has in fact already been tried with seedlings of Shorea leprosula and proved to be successful. It is difficult to see why such promising results (20) have never led to large-scale application, unless from a lack of understanding of the ecological mechanism that made them possible. Smits (21) has described a system based on the silvicultural conditions mentioned before. In this system, Anthocephalus chinensis is used to provide feeble shade for the dipterocarp seedlings. This system has the advantage of giving a quick return of investment, thanks to the wood produced by the Anthocephalus, and the homogeneous growth of the dipterocarps. Diameters will be very much the same among one generation, and the young trees be free of heartrot. Moreover, with each harvest, the concentration of valuable meranti timber per hectare will be higher.

If a method can be developed to make available planting stocks of dipterocarps which have been inoculated with the proper fungus, the TPI-system (i.e., the Indonesian silvicultural cutting system) will have better prospects. Its basis, however, should always be the fact that young dipterocarps need shade.

Finally, the complex and (as far as we know at present) unique ecology of the Dipterocarpaceae, points to one more argument to conserve these forests. The wholesale destruction of these ecosystems as practised at present, amounts to a crime to the entire world and its population. The first thing to do therefore should be the establishment of nature reserves where under absolute protection the survival of these marvelous ecosystems can be assured.

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